A DESCRIPTIVE AND QUANTITATIVE COMPARISON OF THE COMMUNICATION OF GREY SEALS, *Halichoerus grypus*, AT THREE SITES IN THE NORTH ATLANTIC OCEAN

JOHN WARREN LAWSON

A Descriptive and Quantitative Comparison of the Communication of Grey Seals, *Halichoerus grypus*, at Three Sites in the North Atlantic Ocean

by

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Abstract

Detailed, comparative studies of pinnipeds are rare, particularly between breeding and non-breeding groups of phocids. During 1988 and 1989 I observed two breeding colonies of the land-breeding grey seal, *Halichoerus grypus*, at North Rona, Scotland (59° 08' N; 5° 49' W), and Sable Island, Nova Scotia (43° 55' N; 59° 48' W). I also observed a non-breeding aggregation during the summers of 1986 to 1988 on the island of Miquelon (45° 45' N; 56° 14' W). At these sites, from distances as little as one metre, I videotaped sequences of behavioural interaction that occurred between seals of all age classes and both sexes. During frame-by-frame analyses of the video records I quantified 34 measures (one of which included 33 behavioural acts in an ethogram) for each behavioural act within the sequences.

Although behaviour types in the ethogram were robust, and clearly discernible by a näive observer, grey seal behaviour was individually variable. Except for the male Open Mouth Display, coefficients of variation for a number of measures (e.g., duration and inter-seal distance) were large, and behavioural acts were often used in a variety of contexts. Most behaviour types were of short duration (< 5 sec) and were performed in close proximity to other interactants (< 1 m). Except during play, copulation or unusually aggressive interactions, grey seals avoided physical contact and normally oriented their bodies and heads in a parallel or head-on configuration to emphasise the mouth, eyes and enlarged snout.

While sex, age and reproductive stage affected patterns of communication, topographic and meteorological features of the local habitats had little effect. Though many aspects of interactive behaviour were similar at all three locales, significant differences included: 1) differences in the form, frequency and inter-seal distance of behaviour categories among the colonies (which may be explained by the differing social structure of seals on Miquelon and Sable Island), 2) male-male interactions were briefer than male-female or female-female, 3) play occurred almost exclusively in the non-breeding group and had many behaviour types in common with aggressive interactions and 4) a male behaviour common at breeding sites, Open Mouth Display, was not seen at Miquelon.

Markov analyses established that grey seal communication was structurally variable, but that succeeding acts (intra-individual) or responses (inter-individual) were predictable on the basis of immediately antecedent acts (first-order), but primarily during interactions between males at all sites (and male-female bouts at North Rona).

These data establish significant behavioural differences between breeding and non-breeding grey seals, and support a prediction of game theory that suggests animals engaged in agonistic interactions minimise the quantity of information they transmit about their intentions, and react less predictably to the signals of cohorts. Differences in communication between breeding and non-breeding grey seals were greater than those between the breeding sites on opposite sides of the Atlantic Ocean. These dissimilarities were small relative to the marked individual variability in behaviour at all sites.

"No pleasure is fully delightsome without communication" - Montaigne

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Chapter One: Introduction

One of the primary objectives of this investigation was to establish a comprehensive, quantitative ethogram for grey seals (*Halichoerus grypus*) engaged in social interactions at both breeding and non-breeding sites. This study endeavours to redress one of Miller's (1991) criticisms of pinniped ethology:

> *"To date, our understanding of display diversity, repertoire structure and the relationship of display to function is meagre, and reflects the fact that only a few species have been studied in detail - mainly just for prominent acoustic displays used during the breeding season ..."* (page 159)

To assess the influence sex, age, reproductive phase and habitat have on the communication of this species, this study provides comparisons of social interactions at three sites using quantified behavioural characteristics, measures of physical features of the nearby environments and Markov sequence analyses.

The results of this study are compared with those of published accounts for other pinnipeds to assess signal function, and the relative extent to which social context and habitat govern the communication of this species.

Communication Defined

Communication can be defined as a process in which an animal influences the behaviour of another by means of signals or displays during an interaction (Immelmann and Beer, 1989). This enables an animal to exchange information during a social encounter that may alter the behaviour of the receiver(s) to benefit the sender, receiver or both (e.g., Dawkins and Krebs, 1978; Smith, 1977).

With mammals this process is often subtle and may not be apparent to the untrained observer. According to Miller (1991):

> *"Communication is complex and variable in long-lived and adaptable species and it is shaped by learning, differing individual histories, variable social and ecological*

> *circumstances and inter-individual bonds. It is also often extremely subtle in social species which continuously monitor and respond to movement, activity levels, distances, postures, sounds, smells and appearance."* (p. 128)

In general, mammalian social signals are composed of behavioural and/or morphological constituents such as appendage and body postures or orientations, facial expressions, vocalisations and pheromones (e.g., Geist, 1971; Moynihan, 1970; Smith, 1969; Tembrock, 1968).

Pinniped Communication

Pinniped (seals, sea lions, fur seals and walrus) social signals, like those of other mammals, are numerous and typically complex in form (e.g., Miller, 1991; Sullivan, 1981). Signal configurations of pinnipeds are typically different from those of terrestrial mammals, primarily because seals are morphologically adapted to an amphibious existence (e.g., King, 1983; Ridgway and Harrison, 1981; Riedman, 1990): the limbs and tail are reduced and streamlined (Bigg, 1981; Vaughn, 1975) the pelage is short and non-erectile (Ling, 1977) and they have vestigial, or no, external pinnae (King, 1983). Nonetheless, they have evolved means to send signals using foreflippers (English, 1977; Sullivan, 1981; 1982), anterior body characteristics such as neck manes (Gentry, 1981; Stirling, 1971) and pharyngeal pouches (Mohr, 1966; Schevill, Watkins, and Ray, 1966), or encephalised structures such as tusks (Miller, 1975a; 1975c), inflatable hoods (Cox, 1981; Le Boeuf, 1972; Mohr, 1966; Peterson; 1968; Sandegren, 1976a) and nasal pouches (Berland, 1958; Mohr, 1966).

These diverse social signals are essential since most pinnipeds are gregarious during the breeding season and engage in social interactions that serve to maintain contact among mothers and young, or among cohorts (Allen, 1985; Anderson *et al.*, 1975; Bartholomew, 1952; Cameron, 1967; Cline *et al.*, 1971; Kaufman *et al.*, 1975; Le Boeuf, 1972; Miller, 1975b; Miller and Boness, 1979; Poulter, 1968; Ronald and Healey, 1981; Siniff *et al.*, 1979; Sullivan, 1982; Watkins and Wartzok, 1985; Winn and Schneider, 1977).

In some species, these interactions also serve to maintain dominance hierarchies (Godsell, 1990; Hewer, 1960a; Le Boeuf, 1974; McCann, 1981; Sullivan, 1981) and/or territories (Cox, 1981; Hewer, 1957; Le Boeuf, 1972; McCann, 1980; Miller, 1975b; Sandegren, 1976a; Stirling, 1971).

Miller (1991) stated that, "Ritualised display behaviour and accompanying morphological specialisations abound in pinnipeds." (p. 131) Despite this, there have been comparatively few thorough, quantitative studies of pinniped communication (Boness and James, 1979; Miller and Boness, 1979; Sullivan, 1981; 1982); most have been predominantly qualitative descriptions of acoustic or visual signals (e.g., Anderson *et al.*, 1975; Bartholomew, 1953; Boness *et al.*, 1982; Cameron, 1967; 1969; Chwedenczuk and Frysz, 1983; Cleator *et al.*, 1989; Gentry, 1970; Hewer and Backhouse, 1960b; Le Boeuf, 1972; Le Boeuf and Petrinovich, 1974b; Möhl, Ronald, and Terhune, 1975; Rasa, 1971; Sandegren, 1976a; Siniff *et al.*, 1979; Venables and Venables, 1955; Wilson, 1974b).

Further, most research on this topic has been undertaken with otariid (eared) seals (e.g., Gentry, 1970; Harestad and Fisher, 1975; Miller, 1975b; Peterson and Bartholomew, 1969; Sandegren, 1975; 1976b; Schusterman, 1977; 1978; Stirling, 1972). This is not unexpected since most groups of otariids are easier to approach and observe for longer periods than odobenids (walrus; Schevill *et al.*, 1966) and most phocids (earless seals; Miller, 1991).

Otariids customarily spend significant portions of each year ashore (Boness, 1991; King, 1983; Riedman, 1990). Moreover, the sexes of adult otariids are distinctive as they display marked sexual dimorphism (Costa *et al.*, 1988; Gentry, 1981; King, 1983; Vaz-Ferrira, 1981). In contrast, phocids spend much of each year at sea (Jouventin and Cornet, 1980; Riedman, 1990), often breed in areas difficult for ethologists to access, such as drifting pack ice or Antarctic fast ice (Bowen *et al.*, 1985; Cline *et al.*, 1971; Cornet and Jouventin, 1980; Hammill, 1987; Kaufman *et al.*, 1975; Kovacs, 1987a; Ronald and

Dougan, 1982) and most manifest sexual dimorphism that is less pronounced (King, 1983).

Despite these generalizations, using grey seals as subjects with which to study phocid communication is an appropriate choice for a study in the Atlantic Ocean. This species engages in frequent social communication during aggressive, copulatory (Anderson *et al.*, 1975; Boness, 1984; Boness and James, 1979), filial (Boness *et al.*, 1982) or playful interactions (Wilson, 1974b). Unlike harbour (*Phoca vitulina* sp.: Fogden, 1971; Ronald and Dougan, 1982; Smith, 1968; Terhune *et al.*, 1979), harp (*Phoca groenlandica*: Merdsoy *et al.*, 1978; Ronald and Dougan, 1982; Ronald and Healey, 1981) and Weddell seals (*Leptonychotes weddelli*: Cline *et al.*, 1971; Jouventin and Cornet, 1980; Kaufman *et al.*, 1975; Le Boeuf, 1986), grey seals conduct all aspects of their reproductive behaviour, including inter-male conflict, courtship, copulation, birth and nursing, on land. In addition, the sexes of grey seals are readily distinguished by reason of their dimorphism (Bonner, 1981; Davies, 1949; King, 1983).

Even though grey seals do not appear to maintain as exceptionally structured a social system as those of elephant seals (*Mirounga* sp.: e.g., Le Boeuf, 1972) or many otariids (Boness and James, 1979), they do have a more organized system than most other phocids and communicate with each other frequently during their time ashore.

Male grey seals display and fight amongst themselves to forestall others' access to nearby females (Anderson *et al.*, 1975; Boness, 1984; Boness and James, 1979). One reason postulated to explain why male grey seals do not father as many pups as a dominant bull elephant seal is that the former do not have a prominent and easily localised signal with which to advertise superior rank or territorial possession (Boness and James, 1979; Le Boeuf, 1972). Perhaps to ameliorate this apparent limitation, male grey seals have evolved high levels of sexual activity to mate with as many cows as possible (Anderson *et al.*, 1975). Also, smaller males are forced to make forays into the breeding group from peripheral positions. Thus there are probably more social interactions among male grey seals than male elephant seals. Further, until they enter oestrous, grey seal cows raising pups within the populous breeding groups aggressively reject male advances, and defend their pups against both male and female approaches (Burton *et al.*, 1975). Therefore the sexes interact frequently throughout the breeding season. They interact at short range since they are not adapted for prolonged bouts of locomotion on land (Anderson *et al.*, 1975; Boness, 1979; 1984; Boness *et al.*, 1982; Wilson, 1974b) and do not have the aforementioned "prominent and easily localised signal".

During times of the year when they are not breeding, grey seals become more gregarious and gather to form tightly packed haul-out groups. While not quantitatively investigated before this study, grey seals have been observed to interact frequently in both aggressive and playful manners during these periods (Wilson, 1974b).

Like elephant seals, grey seals have been the subject of a number of physiological investigations (e.g., Anderson and Fedak, 1987; Bowen *et al.*, 1992; Fedak and Anderson, 1982; Godsell, 1990; McDermid and Bonner, 1975; Øritsland *et al.*, 1985; Ridgway *et al.*, 1975; Ronald *et al.*, 1984; Worthy and Lavigne, 1987; and see a review by Wartzok, 1991). Despite this, relatively few quantitative studies of grey seal behaviour have been undertaken and, as for virtually all pinnipeds, a complete, quantitative ethogram for this species does not exist. There are general and anecdotal descriptions of interactive behaviour during the reproductive period (Anderson *et al.*, 1975; Boness, 1979; Boness *et al.*, 1982; Boness and James, 1979; Cameron, 1967; 1969; Godsell, 1990; Hewer, 1960a). Grey seal play, observed most frequently in non-breeding aggregations, has been mentioned briefly, yet it occurs frequently at Miquelon, and sites in Britain (Davies, 1949; Fogden, 1971; Lockley, 1966; Wilson, 1974b).

Site and Seasonal Comparisons

There are few published comparisons of grey seal behavioural repertoires at different study sites (Anderson and Harwood, 1985; Boness, 1984), although this species lives on both sides of the Northern Atlantic ocean. This study redresses this deficiency in our knowledge of grey seal ethology with videotape records of the behaviour of three disparate aggregations. It was thus possible to construct a comprehensive ethogram from records of behavioural interactions of this species in breeding and non-breeding contexts in the East and West Atlantic Ocean. This ethogram is distinctive in its detail, accompanying quantitative constituents and includes both breeding and non-breeding behavioural components.

Video recording techniques have been used to quantify behaviour in birds (Slater and Ollason, 1972; 1973), wolves (McLeod, 1987), whales (Chase, 1989; D'Vincent, Nilson, and Sharpe, 1989) and pinnipeds (Renouf and Lawson, 1986a; 1987). Hazlett and Bussert (1965) stipulated that there must be many observations and long interactive sequences to be statistically certain that a particular behaviour type has signal properties. Videotape analyses are an exemplary means to achieve both these goals, and I have been able to observe and videotape grey seals from positions of proximity at all study sites for prolonged periods.

While the behaviour of grey seals probably differs during breeding and non-breeding periods are probable, few researchers have examined communication in more than one portion of a seal specie's annual cycle (Miller, 1975c; Miller and Boness, 1983; for studies of captive pinnipeds, see Chwedenczuk and Frysz, 1983; Gailey-Phipps, 1984; Gehnrich, 1984). Virtually all research has been restricted to the breeding period when this species comes ashore to give birth and mate (Anderson *et al.*, 1975; King, 1983; Ridgway and Harrison, 1981).

It is reasonable to expect grey seal behaviour to change over the course of a year since behavioural changes have been noted in an anecdotal manner for other pinnipeds. Perhaps in response to increased titres of testosterone during the breeding season, it is known that many male pinnipeds become increasingly aggressive towards each other (Sandegren, 1970; Wartzok, 1991) and vocalise more frequently at this time (bearded

(*Erignathus barbatus*; Burns, 1981; Stirling *et al.*, 1983), harp (Terhune and Ronald, 1986), ringed (*Phoca hispida*; Stirling *et al.*, 1983) and spotted (*Phoca largha*; Beier and Wartzok, 1979) seals and walrus (*Odobenus rosmarus*; Ray and Watkins, 1975)]. Some female pinnipeds also become more aggressive towards cohorts after their pups are born (Christenson and Le Boeuf, 1977).

Northern elephant seal, *M. angustirostris*, behaviour undergoes substantial alteration outside the breeding season; they exhibit reduced thigmotaxis (Sandegren, 1976a) and agonistic behaviour, and segregate themselves to a greater degree by sex and age (Riedman, 1990). The autonomous and interactive behaviour of Steller sea lions (*Eumetopias jubatus*) changes during non-pupping periods (Harestad and Fisher, 1975), as does that of walrus during their northward migration (Miller, 1975c). Godsell (1988) noted differences in harbour seal herd segregation according to members' sex, age and reproductive condition.

This thesis provides the first quantitative and comparative study involving both breeding and non-breeding grey seal groups. While the individuals observed at Miquelon and Sable Island may not be the same, a number of the seals that come to Miquelon outside the breeding season are members of the Sable Island stock, and some of these individuals, identified by brand markings, return to Sable Island to breed during the winter (B. Beck, pers. comm.). The grey seals in the North Rona group are completely isolated from the west Atlantic colonies.

Topographic Influences

A second objective of this study involves examining the degree of behavioural difference between sites as a function of group structure or geographic dissimilarity, rather than time of year. From limited data from investigations with pinnipeds, observed during the same stage in their annual cycle, the behaviour of the same species at different sites was dissimilar. Christensen and Le Boeuf (1977) studied female

Northern elephant seals at several breeding beaches. They reported inter-site differences in the incidence of aggressive behaviour. Researchers reported evidence of intersite differences in activity levels of breeding grey seal groups in the British Isles (Davies, 1949; Wilson, 1974b; and see Cameron, 1970) for a cursory comparison of diurnal activity in colonies in Nova Scotia and Britain}. In a more detailed study, Boness (1984) compared time budgets of breeding grey seals at Sable Island and the Monach Isles and found significant differences in the quantity of time spent ashore, time spent in locomotory and aggressive behaviour, and sexual interactions.

In several studies, topography has been implicated as a factor influencing behaviour. Hewer (1960a) postulated that breeding site topography affected the territorial strategy adopted by male grey seals, and Anderson and Harwood (1985) subsequently found evidence of increased polygyny in colonies where narrow gullies restricted access to breeding areas. Kovacs (1987b) also reported that topography governed females' diurnal time budgets (such as time with pups or time spent checking pups). As a means to assess this potential factor, the breeding sites I compare in this thesis have appreciably different topography. Stirling (1975) asserted that "this species offers the greatest opportunity for study of the effects of different breeding habits on social behaviour" (p. 209).

Climatic Influences

Another factor that might generate site differences in grey seal behaviour is variation in local weather patterns such as wind strength. While Renouf and Lawson (1986b; 1987) found no significant meteorological effects on harbour seal play or vigilance, El Niño (a major climatic disturbance) has been demonstrated to cause changes in the behaviour patterns of California sea lions (*Zalophus californianus*; Ono *et al.*, 1987). Again, the three sites utilised in this investigation facilitate examination of climatic impact on behaviour as they not only have dissimilar local climates, but longitudinal observations for sufficient periods allow an observer to record behavioural changes which short term climatic events may elicit at the local level.

Sex Differences

Sex differences in the behavioural repertoires of pinnipeds have been documented in the literature. At a fundamental level, females do not engage in the same types of combative interactions as their male counterparts in breeding groups of Galapagos fur seals (*Arctocephalus galapagoensis*), walrus, ringed seals, bearded seals, weddell seals and elephant seals (Carrick *et al.*, 1962a; Cleator *et al.*, 1989; Kaufman *et al.*, 1975; Le Boeuf and Petrinovich, 1974b; Le Boeuf and Reiter, 1988; Miller, 1975a; Sandegren, 1976a; Smith, 1987; Stirling *et al.*, 1983; Trillmich, 1984). Nor do they engage in terrestrial boundary displays common to most male otariids (e.g., Gentry, 1970; Miller and Boness, 1979). While not explicitly studied, it is probable that grey seal bulls, who copulate on land and have to search for receptive females, do not perform underwater displays like those of male phocids such as walrus (Stirling *et al.*, 1983; 1987), weddell (Thomas and Kuechle, 1982) or spotted seals (Gailey-Phipps, 1984).

Although grey seals participate in altercations of lesser intensity than those of many other pinnipeds (Miller, 1991), several behavioural differences relating to sex have been documented. Males seek and engage in combat with each other, whereas females normally fight in response to the approach of other individuals (Anderson and Fedak, 1987). While other studies (Boness and James, 1979; Miller and Boness, 1979) have established sex-related differences in activity budgets and behaviour in a descriptive fashion, a detailed comparison of the signal repertoires of male and female grey seals could enable ethologists to answer specific questions regarding the nature and potential bases for these differences. For instance, are females' behavioural repertoires dissimilar to males' because of dissimilar selection based on functional needs, or simply due to sex-related variations in temporal and physical characteristics among suites of behaviour types common to both sexes? In addition, the influence of body size or secondary sexual characteristics on communication needs to be addressed. In the context of this work, interacting male grey seals might be expected to exaggerate the use of their prominent snouts to a greater extent than females (Miller and Boness, 1979). During breeding seasons, where the risk of physical damage during an aggressive encounter is greater, or the energetic cost of prolonged combat with a competitor is high, signals may be transmitted over distances to obviate the need for physical combat (but see Smith, 1977; 1986b). Comparisons of signal repertoires of breeding and non-breeding grey seals could yield information about the relationships between the displays and their functions in both contexts.

Age Comparisons

Quantitative comparisons of structural and temporal variation in the behaviour of different age classes is another poorly-studied aspect of pinniped ethology. Age-related differences have been described as part of studies of aggressive (Davis and Renouf, 1986; Harestad and Fisher, 1975; Sullivan, 1981; 1982), copulatory (Godsell, 1990), vigilance (Renouf and Lawson, 1986b; Terhune, 1985), play (Rasa, 1971; Renouf and Lawson, 1986a; Wilson, 1974b) and suckling (Boness *et al.*, in press) behaviour. In particular, studies of how signal repertoires vary according to age have never been conducted with grey seals. Doing so permits a preliminary evaluation of behavioural ontogeny in this species, and to a lesser extent, development of signal stereotypy (using coefficients of variation; Miller, 1991; Slater, 1978).

Quantified behavioural measures provide the means to describe and compare grey seals' behaviour at different sites, and for different sexes and age classes. Further, although it has been an approach rarely used during studies of pinnipeds, by establishing communication matrices for behavioural acts and responses to them (e.g., Sullivan, 1981; 1982; Wiepkema, 1961), an ethologist can calculate Markov sequential dependencies (Fagen and Young, 1978; Slater, 1973).[1]

Sequence Analyses

In behavioural systems as seemingly flexible as that of seals, it is likely that the chances of one behaviour following another are probabilistic rather than deterministic. That is, while there may be a high probability that one particular behaviour will follow another during an interaction, these sequences are not so rigid as to preclude individual variation, thus revealing imperfect predictability.

Since there has been no research with pinnipeds comparable to that with other mammals, it is difficult to foresee the level of predictability of grey seals' behavioural sequences. There are certainly many incidences of stereotyped, rigidly programmed behavioural patterns in other mammals and birds. For example, the strut display of the male Sage grouse, *Centrocercus urophasianus*, is extremely predictable in the arrangement of its component behaviour patterns (Wiley, 1973). This is also the case for the dewlap display of the male anolis lizard, *Anolis aeneus* (Stamps and Barlow, 1973). Even social signals as elaborate as the songs of the humpback whale, *Megaptera novaeangliae*, are repetitive and individually stereotyped (Payne and McVay, 1971; Tavolga, 1983). The same has been established for the acoustic underwater phonations of walrus (Stirling *et al.*, 1987) and bearded seals (Cleator *et al.*, 1989; Stirling *et al.*, 1983).

However, a more detailed examination of pinniped behaviour would likely reveal greater individual or site variation in behaviour patterns. A study by Bonner (1968) of Antarctic fur seal bulls (*Arctocephalus gazella*) showed that there was significant

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[1] In Markov theory, a sequence in which one can predict the identity of the second behavioural act in a sequence on the basis of the previous act only is termed a first-order interaction. Sequences in which there are no statistical dependencies between succeeding acts are termed zero-order.

individual variation in behaviour during interactive sequences. This thesis evaluated variation in sequence predictability of the behaviour of grey seals, and how this variation was influenced by contextual factors such as sex, sequence type or locale.

Besides determining the general predictability of interaction sequences, and hence the degree of grey seal behavioural plasticity, one can review behavioural plasticity by considering the conflicting approaches of so-called "classical" and "modern" ethology.

Classical ethology considers communication as a mutual co-evolution of signals for minimum ambiguity and maximal informativeness (Marler, 1961; Maynard-Smith, 1982; Maynard-Smith and Price, 1973; Smith, 1977). Recent work, with a game theory ("modern") perspective, has suggested instead that communication serves a role in a selfish, manipulative process {the "manipulative communicator" (Dawkins, 1976; Dawkins and Krebs, 1978); but see Hamilton (1970)}. In the former view, we might predict that the sequential dependencies and the degree of signal stereotypy are greater in groups of breeding grey seals, where communication ambiguity should be reduced to minimize conflict (Maynard-Smith, 1982; Miller, 1991), and encode <u>more</u> information (Zahavi, 1980). Alternately, if stereotyped behaviour conveys <u>less</u> information about the performer's internal state and future actions (Morris, 1957), we would predict grey seals behaving as "manipulators" would again exhibit greater sequential dependencies in breeding situations. Thus information estimates are important attributes to consider when evaluating whether a communication system is cooperative or manipulative. In fact, observations have shown that intention is transmitted in many competitive encounters (Moynihan, 1982).

Seals in non-breeding aggregations might exhibit lower sequential dependencies where interactions are less intense (and potentially less likely to result in injury) than during the breeding season. Sequential flexibility can be further augmented if non-breeding seals complement their behavioural repertoires with types uncommon during breeding interactions (e.g., climbing), or by employing combative behaviour types in non-aggressive manners (e.g., play biting).

Summary

The strength of this study was not simply its quantitative nature, but that demonstrated the merit of applying a consistent, comparative method to several populations (see Gentry, 1975c). By applying uniform observational and analytic techniques to data from all sites, this study eliminated the effects that differences in these approaches normally have when comparing discrete animal populations using data from several published studies. This work established a comprehensive taxonomy of grey seal behaviour that served to document this species' behavioural diversity, organisation and possible functions (Klopfer and Hatch, 1968; Wilson, 1975). The resulting ethogram also provided the means to compare quantitatively grey seal communication at several study sites, and to establish this species' behaviour within the context of that of other pinnipeds, and vertebrates generally (e.g., Moynihan, 1970; Peters, 1980). The quantitative nature of this study also facilitated sequential analyses as a means to distinguish sites, and tested the "manipulative communicator" prediction of game theory.

Chapter Two: Materials and Methods

Study Sites

Data for this thesis were gathered during observations of grey seal groups at three different sites in the Northern Atlantic ocean. The seals at Miquelon were a non-breeding aggregation, whereas the groups at North Rona and Sable Island were breeding colonies.

Miquelon

During the summers of 1987 and 1988 (mid May to late July), I studied a herd of 130 to 150 grey seals that returns each year to a sheltered, sandy tidal lagoon, the Grand Barachois, on Miquelon. Miquelon is an island located approximately 19 km southeast of Newfoundland, Canada at 45° 45′ N; 56° 14′ W (indicated in Figure 1). The herd normally hauled-out at specific places (**A** and **B** in Figure 2), as the sand became exposed during ebb tide, either on the periphery of a three km^2 sand flat, or on a sand bar at the edge of a narrow channel to the sea.

The substrata where the group hauled-out were firm, virtually-level, sand except where they sloped into the tidal channels at an average angle of less than 20° from horizontal. At high tide, the sites were covered by shallow water normally less than 0.5 m deep.

The weather was usually cool (mean temperature 13°C) with frequent periods of fog and rain. The prevailing wind was from the South and blew across the exposed sand flats into the rear of the haul-out group.

I established elevated observation blinds (Figures 2 and 5B) 15 m from the edge of the channel at both locations, as measured at ebb tide, and further up the shore behind the seal herd. I entered one of the blinds at high tide before the start of the seals' assembly on the beach to ensure minimal disruption. In all but a few cases I left the blind after the group had departed as a result of external disturbance or the returning tide. The grey seals quickly habituated to the blinds and the nearest seals in the group normally settled within 10 m of it.

During spring and summer the grey seal herd at Miquelon was a non-breeding blend of both sexes and all ages, although adults predominated.

North Rona

From September 19 to November 19, 1988, I observed breeding grey seals on a small island, North Rona, located 74 km off the Northwest coast of Scotland (59° 08' N5°; 49' W; indicated in Figure 1). The island is a rocky outcrop with an area of three km^2. More than 9,000 grey seals return each Fall to its flattened Northern peninsula (Anderson *et al.*, 1975; Twiss, 1991). The breeding season on North Rona extends from late September to late November during which time these seals return to the island to bear their pups and mate.

The terrain at this site was grass or mud slopes, varying from flat to 40 degrees from horizontal, among tracts of bare rock. For the seals, access to this area from the sea was restricted to a few large gullies that led up from the shore. I installed my observation blind at two sites, for consecutive periods, on the tip of the Northern end of the island (Figures 3 and 5A). The blind was positioned such that I viewed activity near several large rain pools in a gully for the first 33 days (A in Figure 3). For the final portion of the study period, I moved the blind to a new locale (B in Figure 3) to watch the seals on a grass slope near the edge of the gully.

My entry into the blind was concealed by a rock ridge, enabling me to use the blind with minimal disturbance to nearby seals. For example, a female gave birth, and nursed her pup[2] for several weeks, within one m of the blind, and on several occasions fighting males jostled against the walls of the blind.

The weather was usually mild with occasional rain squalls and a mean day-time air temperature of 8°C. The prevailing winds were from the South or West (from the landward side of the study area).

Sable Island

From January 11 to January 18, 1989, I observed three subgroups within a herd of approximately 25,000 breeding grey seals on Sable island, located 188 km ESE of Halifax, Nova Scotia, Canada (43° 55′ N; 59° 48′ W; Figure 1). Sable Island is a narrow crescent-shaped sand bar 40 km long with a mid-region width of 1.5 km (Boness, 1979). There is an irregular ridge of sand dunes, consolidated by marram grass (*Ammophila breviligulata*), running along its longitudinal axis.

The grey seal breeding season on Sable Island extends from approximately mid-December to early February. During this period the climate is relatively cool with a mean day-time air temperature of -1°C (Boness, 1979), moderate to strong winds blowing across the island, and occasional snow flurries.

Seals are found on many of the beaches, in gullies among the dunes and upon some of the central dunes. I chose to conduct observations at three sites that represented the predominant topographies used by the seals on the island. Initially, I recorded seals' activities in a 20 m wide sandy valley between two large interior dunes (**A** in Figure 4). The second locale was directly in front of a large dune that had a flat beach more than 280 m wide between it and the sea (**B** in Figure 4). Finally, I spent several days videotaping seals at a location that had a 60 m, sloped (less than 15 degrees from horizontal) beach leading to a dune breached by a wide gully (**C** in Figure 4). In each

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[2] This pup was a constant nuisance since she pulled up the pegs holding the blind's support ropes every day !

place I established myself in a position several metres up the face of a nearby sand dune to obtain better recordings of interactions and inter-seal distance estimates.

Logistical limitations precluded use of an observation blind on Sable Island, but the seals appeared to be relatively inured to human presence and normally ignored me. Mothers nursed their pups within one m of my position, and I frequently had to pluck my equipment out of harm's way as fighting males backed past me.

Equipment

Observation Blinds

I utilised the same type of observation blinds at both Miquelon and North Rona. The blind was a rectangular canvas tent 1.5 m in height supported on a tubular, aluminum frame (2 cm diameter) with a one m^2 floor area (Figure 5A). Three removable, transparent vinyl windows were situated on the front and two sides of the blind to allow observation regardless of the exact location of the seals relative to the blind. Black plastic curtains obscured the windows not in use during observation to eliminate the possibility of the seals being disturbed by my silhouette against an uncovered, backlit window. Entries and exits were effected through a zippered opening at the rear.

At Miquelon the twice-daily tidal influxes necessitated that the blind be installed upon an elevated one m^2 platform supported by four angle-iron (5 cm wide) legs. Each leg was tipped with an automobile tire rim and the four rims were buried in the sand for increased stability (Figure 5B).

At North Rona I did not need the platform, but instead used four nylon guy ropes to brace the blind against strong winds and obstreperous males.

During observations at all three study sites, which exceeded 435 hrs (Miquelon: more than 260 hrs, North Rona: 147 hrs and Sable Island: 28 hrs), I was equipped with a pair of Bushnell 8 × 40 binoculars and a Pentax LX 35 mm camera with both Pentax 75-150 mm *f* 4.0 zoom, and Vivitar 400/800 mm *f* 5.6 telephoto, lenses. The still photographs, with their higher resolution, complemented the video recordings I was able to make with two models of portable video recording systems described below.

Video Recording Apparatus

Records of behavioural interactions were made on VHS format video tape. Data for the Miquelon group were taped using a JVC low light colour video camera (model GX N4UT) with either an 8.5-51 mm (*f* 1.2) 6:1 zoom video lens or, by using an LA-C7L(U) bayonet adapter, Pentax 75-150 mm (*f* 4.0) zoom or 400 mm (*f* 5.6) telephoto lenses. The camera had 270 lines•mm^{-1} horizontal and 300 lines•mm^{-1} vertical resolution and its built in microphone had an average audio sensitivity of -68.8 dB over a frequency range of 20 to 20,000 Hz.

Data from the camera were recorded by an accompanying portable JVC videocassette recorder (model BR-1600U) onto T-120 videotapes at standard speed (33.4 mm/s). The videocassette recorder had an audio sensitivity of -45 dB over a frequency range of 70 to 10,000 Hz. This video system was powered by a 12-volt battery (Canadian Tire Motomaster RV/Marine Deep Cycle, model 10-2799-4).

Video data for the North Rona and Sable Island study areas were recorded using a GE portable, colour camcorder (model 9-9806) with a 9-51 mm (*f* 1.2) 6:1 power zoom lens. The camera had 525 lines•mm^{-1} horizontal and 525 lines•mm^{-1} vertical resolution, and its built-in microphone had an average audio sensitivity of -70 dB over its frequency range of 20 to 20,000 Hz.

Like the JVC unit, the camcorder was powered by a 12-volt deep cycle battery and recordings were made onto T-120 videotapes at standard speed (33.4 mm/s).

Data Extraction

Sampling Methods

I recorded primarily dyadic interactions, which are the most common type documented in grey seals (Anderson *et al.*, 1975). For the purposes of this thesis, an interaction was defined as a sequence of behavioural acts performed by two seals and apparently directed towards each other as indicated by their attention and body orientation towards each other, and reactions to each others' behaviour.

As an observer, I was limited to recording signals transmitted in one of three sensory modalities: visual, acoustic or tactile. I could not determine if chemical signals were being exchanged between two seals.

At each locale I recorded only those interactions performed by clearly-visible individuals (Anderson *et al.*, 1975; Twiss, 1991). The maximum distance at which I could record interactions and still resolve anatomical features was 30 metres. The video records included interactions involving all age classes and both sexes.

In addition to these sequential records, I also recorded hourly five-minute total record (Altmann, 1974) video samples of a subgroup of seals chosen at random, using a sampling method like that described for Miquelon (see below), from the larger group within my field of view. I later calculated the mean number of observed visual scans performed by each individual within the sample group per minute. A scan was counted when an individual opened its eyes and looked about, or more frequently, lifted its head to look about. These scores provided a quantitative measure of vigilance level.

I maintained a regular account of time, weather (including an estimate of wind strength and direction, and presence of precipitation), tide state, and descriptions, timing and consequences of disruptive disturbances during all observations. These data were recorded onto the audio track of the video tapes by speaking into the cameras' microphones.

In addition to these standardised measures for each site, I augmented my sampling methods at Miquelon to account for the different haul-out group structure of this site. At this site there were interactions across a variety of age and sex classes, whereas most interacting seals were adults at the breeding colonies. Younger animals were excluded from the breeding areas through harassment and pursuit. At Miquelon different age classes exhibited an irregular distribution within the haul-out group. Adult males aggregated at the centre of the group (Figure 6), while female and younger seals gathered at the peripheral ends. To sample equally all sex and age classes I recorded interactions from zones within the group chosen at random.

I divided the area on which the group rested into a six-celled grid by using either distant landmarks, or markings on the exposed sand, as references (Figure 7). The total width of the grid was continuously adjusted so that its left and right edges corresponded to the positions of seals hauled-out on the left and right ends of the group. The grid cells were usually larger than the area I defined as the Focal Area (see page 25) since the group formed rapidly and spread along the periphery of the sand flat. Next, I assigned a number from one to six to each cell according to the scheme illustrated in Figure 7. Which cell to observe was determined by a roll of a six-sided die or from a table of random numbers. Interactions within that cell were then recorded.

I alternated cells at approximately five minute intervals, or when all of the seals within the cell I was observing had stopped interacting. By using this sampling technique I eliminated problems associated with *ad lib* sampling, such as over-sampling the most active seals or a predominant age class (Altmann, 1974; Martin and Bateson, 1986; Slater, 1978). I was able to recognize a few individuals during each haul-out using markings and scars, however the majority were indistinguishable. Therefore it was not possible to quantify the extent to which an individual was observed more than once.

At North Rona and Sable Island the study groups were composed mainly of mother/pup pairs and adult males. Seals were more dispersed and interactions normally occurred less frequently than at Miquelon. As a result of these factors, I videotaped all clearly-visible interactions as they occurred. I rarely had to resort to sample selection; usually when I observed interactions at the water's edge.

I coded a total of 239 interactions (or bouts) from all three sites for which I was able to derive data for measured variables (see page 24). These produced 8642 lines of data, each of which represented a single behavioural act in an interactive sequence. In addition, I coded 85 partial bouts which provided additional data on total duration, sequence sex and sequence type values. These partial bouts resulted from poor video records caused by adverse weather conditions, disruption of the interaction by an external event or excessive distance between myself and the interacting seals (e.g., Miquelon: 61 complete bouts plus an additional three partial sequences; North Rona: 98 complete bouts plus two additional partial sequences; Sable Island: 80 complete bouts plus 80 additional partial sequences). Thus, while the observation time at the sites was unequal, the number of interaction sequences analysed during this study were similar.

Videotape Playback and Data Entry

Thirty percent of the video tapes were viewed during playback on a video editing suite comprised of a Panasonic video cassette recorder (model AG-6300), a Panasonic editing controller (model NV-A500) and two Panasonic Colour Video Monitors (model CT-110 MCA; 28 cm diagonal diameter).

I viewed the remaining 70% of the videotapes on either a JVC digital four head videocassette player (model HR-D63OU) and Sony Trinitron Colour Monitor (model 25XBRII; 63.5 cm diagonal diameter), or a Sharp four-head videocassette player (model VC A600) and Hitachi Colour Video Monitor (model CT1365; 33 cm diagonal diameter).

All three systems provided the essential capability to play the videotapes at slow speed (one frame per second), or paused, without picture distortion. The videocassette recorders and monitors provided horizontal and vertical resolution of at least 300 lines•mm^{-1}.

During playback, the videotape was advanced at normal speed until an interaction between two seals commenced. I transcribed data from an interaction only if it met the following criteria:

1) The recording of the interaction included both the apparent onset and conclusion of the interaction.
2) The interactants were clearly visible for virtually the entire duration of the recording. If one member was obscured for more than 15 seconds, the interaction was not used as a data source.
3) At least four of the five defined corporal variables were discernible for both participants at all times (given criterion 2). These variables were eye, mouth, vibrissae, nares and tail status.

The interaction was initially viewed at normal speed to determine its total duration, describe local topography and catalogue all seals within 10 m of the interactants. A bout was presumed complete when the participants moved more than 10 m apart, when either of the participants began an interaction with a third (and did not return to the second within 60 seconds), or more than 60 seconds elapsed with no discernible interaction. The tape was then rewound to the beginning of the bout, and playback was resumed by advancing the videotape frame-by-frame or at a reduced rate.

Durations of, and among, behavioural categories were determined with the aid of either a Herwin stop watch or the electronic counters on the video editing suite. Time values of less than one second were rounded to the nearest second.

Intervals of less than one second between an act and response to it were classified as "instantaneous" (see variable 29, page 30). When the behavioural acts were performed at the same time, they were classified as "simultaneous".

I followed guide-lines formulated by Slater (1978) to delimit categories of behaviour. To be defined as a "discrete" category, the behaviour act's components (body posture and motion) must have occurred together with a high degree of similarity with previous occurrences of that act (homogeneity).

The behaviour categories had also to be repeatedly recognizable. I defined, and coded, behavioural types such that each was seen to occur as independently of any other type as practically possible. That is, there had to be clearly-observable changes during a seal's behaviour for there to be two independent behaviour types tallied. These changes were expressed in one of two ways; either the seal returned to a prior state, or it began performing another behaviour. These could be illustrated as:

Prior State → Behaviour "A" → Prior State
OR
Prior State → Behaviour "A" → Behaviour "B"

Although the behavioural categories I defined were as close to mutually exclusive as practical, there was unavoidable overlap of some features since it can always be argued that behavioural units lie on a continuum and share some features with others (Andrew, 1972; Fentress, 1973; Golani, 1973). By careful definition, behaviour "B", above would share none, or few, features with "A".

Testing The Reliability of The Ethogram's Behaviour Categories Using a Naïve Observer

To evaluate the reliability of the behaviour categories in the ethogram used in this study, an associate with no previous experience with seal behaviour scored an extended interactive bout, which contained many different behaviour types and which I had coded previously. The observer had a copy of the ethogram and coded the bout using the same techniques as described herein.

When comparing the observer-coded sequence with my own, I examined total behaviour category counts, and their order in the transcribed sequence. This was achieved by using a chi-square statistic to test differences between the numbers of behaviour types coded by me and those coded by the naïve observer for the bout.

I also compared the sequence transcriptions to determine if there were discrepancies in the types of behaviour coded by myself and the naïve observer using the Kappa (κ) coefficient (Hollenbeck, 1978). The Kappa coefficient is a superior measure of inter-observer reliability than an Index of Concordance because it accounts for the effects of chance agreements between categories coded by observers.

Quantified Variables

I transcribed values measured for the following variables for each behavioural act within a sequence:

1) **Date** - the number of days since January 1st of that year (1 to 365) - not the Julian date (Wilimovsky, 1990).

2) **Study Site** - the study site at which the behaviour occurred (Miquelon, North Rona or Sable Island).

3) **Time** - the local time of day during the interaction, in 24-hour format.

4) **Time Relative to High Tide** - the number of hours the interaction occurred before or after peak flood tide (placed within whole-hour intervals). Exact times for local high tides were determined by consulting relevant tide tables for each site:
   - Miquelon - Service Hydrographique et Océanographic de la Marine, France, 1987 and 1988.
   - North Rona - Admiralty Tide Tables, Great Britain, Vol. 1, 1988.
   - Sable Island - Canadian Hydrographic Services, 1989.

5) **Weather** - a categorical description of local meteorological conditions (clear/sunny, overcast, raining, snowing or foggy).

6) **Horizontal Visibility** - the average horizontal visibility (m) around the interactants resulting from meteorological conditions and/or physical obstructions. This was estimated by determining what the furthest visible object was relative to the interacting seals using known positions of local objects, and accounting for obstructing terrain (for instance, the walls of a narrow gully at North Rona).

7) **Wind Velocity** - a categorical estimate of the wind velocity (no wind, light, moderate or strong).

8) **Wind Direction** - the direction from which the wind originated (North, Northeast, East, Southeast, South, Southwest, West or Northwest).

9) **Substratum Type** - a categorical description of the substratum upon which the seals were interacting (sand, grass, cobble, or water less than 1 m deep).

10) **Substratum Slope** - the slope of the substratum upon which the seals were interacting (zero to 15 degrees, greater than 15 degrees or irregular) was measured with a plumb bob and hand-held compass at the outset of each season at each site.

11) **Position Within The Group** - the relative position of the interactants; either within the group (left front, left rear, centre front, centre rear, right front or right rear) or further than 10 m from the margin of the group.

12) **Focal Area** - the total number of seals within a 10 m radius of the interactants; this included the interacting individuals. These counts were also subdivided into total number of seals of specific age classes {adults, subadults (two to four years old) and weaner/yearlings}, sexes (Focal Male, Focal Female) and, where relevant, the total number of mother/pup pairs.[3] I assessed the accuracy of Focal Area estimates at

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[3] Grey seal sex was readily distinguished even in moulted pups on the basis of fur colouration and skull morphology. Similarly, external physical characteristics such as size,

North Rona and Sable Island by comparing mean Focal Area values from the videotapes ($n = 324$) with values derived from aerial photographs of groups near the observation sites ($n = 16$) taken at the same time. The photographs were 20.3 cm × 25.4 cm frames on Ektachrome continuous strip, large-format colour film, and when viewed on a light table, permitted unequivocal identification of age class and dispersion. Natural and man-made landmarks provided scale referents. There was no significant difference between mean Focal Area values estimated from videotapes and photographs ($F = 1.4$, $df = 1, 339$, $p = .28$).

13) **Vigilance** - the vigilance level of seals in the Focal Area near the interactants. This was calculated as the mean number of visual scans performed per seal per minute from a five to 10 minute sample of clearly-visible individuals.

14) **Interaction Distance** - an estimate of the minimum distance (cm) between the interacting seals' bodies. This estimate was based on both the known size of morphological features (body or head length) and subsequent measurements of adjacent substratum features. Distance was registered at the onset of each act.

15) **Precedent Type** - a general classification of the seal performing the behaviour act (adult, subadult, mother, pup, or weaner/yearling). During data coding a seal alternated between being designated a "precedent" or "successor" as the interaction proceeded and each seal performed a behavioural act following the behavioural act performed by the other interactant. For example, on one line in the data, seal A performed a behavioural act (and was designated the precedent) after which seal B performed a behaviour act (and was classed the successor). On the next line Seal B would be designated as a precedent, its behavioural act (from the previous line)

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colouration, scarring, skull morphology and (for males) presence of neck rugous neck folds made age class estimation relatively easy for an experienced observer.

coded as a precedent's behavioural act. Seal A would then become the successor and its next behavioural act would become the successor's behaviour type. For example:

1) precedent: seal A precedent 's behaviour: W successor: seal B successor's behaviour: X
2) precedent: seal B precedent 's behaviour: X successor: seal A successor's behaviour: Y
3) precedent: seal A precedent 's behaviour: Y successor: seal B successor's behaviour: Z

The following variables, defined as measures of "precedent's" behaviour and posture were also measured for the "successor" at the same instant.

16) **Precedent Sex** - the sex of the precedent (male, female or unknown).

17) **Precedent's Behaviour Type** - the behaviour type performed by the precedent, which could have been one of the following categories (the three-letter code accompanying each type is used in place of the whole name in the text, tables and figures). In the rare instance when a seal performed more than one behaviour type at the same time, the case was noted as such in the multiact variable (see 32 below; for detailed descriptions see Chapter Three). I have provided the reader with a detachable reference card listing these behaviour types and their abbreviations in Appendix A. I did not use a "no behaviour act" type.

In this thesis the words "act", "type" and "category" are used interchangeably when indicating individual behavioural acts performed by a seal. Similarly, the terms "bout", "interaction" or "sequence" were used to denote a series of behavioural acts performed by two interacting seals.

- Open mouth display (OMD)
- Extend foreflipper (EFF)
- Foreflipper scratch successor (FSR)
- Foreflipper slap water (FSW)
- Head swing (HSW)
- Nose-to-nose (NTN)
- Sniff (SNI)
- Stare (STA)
- Bite (BIT)
- Head thrust (HTH)
- Foreflipper wave (FFW)
- Foreflipper scratch substratum (FSS)
- Foreflipper slap body (FSB)
- Extend head (HEX)
- Poke with nose (PON)
- Glance (GLA)
- Look away (LAW)
- Climb (CLI)

- Clasp (CLA)
- Chase (CHA)
- Depart or turn away (DPA)
- Yawn (YAW)
- Raise head vertically (RHV)
- Roll on side (ROS)
- Body scratch or rub (BSR)
- Avert face (AVF)
- Approach or turn towards (APT)
- Roll away (ROA)
- Rush away (RAW)
- Neck and head shake (NHS)
- Eyes closed (ECL)
- Nurse (NUR)
- Penile thrust (PT)

(n = 33 categories)

18) **Interaction Duration** - the precedent's behavioural act duration (seconds).

19) **Precedent's Vocalisations** - the type of vocalisation emitted by the precedent during the behavioural act:

- open-mouthed whoo - a monotonal howl with the mouth slightly open.
- growl - a guttural growl, with the mouth open.
- snort - a short-duration expulsion of breath through the nares.
- silent - no audible vocalisation.
- pup cry - a high-pitched bleat performed by pups alone.
- warble - a vocalisation unique to Sable Island in which the male performed a low-pitched vibrato trill. It was very difficult to locate the individual performing this type of vocalisation (Boness and James, 1979).
- unknown - I was unable, due to wind noise or distance, to determine if the precedent vocalised.

20) **Precedent's Vibrissae Position** - the position of the precedent's vibrissae (protracted, retracted or unknown) at the outset of the behavioural act.

21) **Precedent's Nares Status** - the state of the precedent's nares (open, closed or unknown) at the outset of the behavioural act.

22) **Precedent's Eye Status** - the state of the precedent's eyes (open, closed or unknown) at the outset of the behavioural act.

23) **Precedent's Mouth Status** - the state of the precedent's mouth (open, closed or unknown) at the outset of the behavioural act.

24) **Precedent's Tail Position** - the position of the precedent's tail (up, down or unknown) at the outset of the behavioural act.

25) **Precedent's Height** - the height of the precedent's head relative to the successor's (higher, same, lower or unknown) at the outset of the behavioural act.

26) **Body Orientation** - the relative orientation of the interacting seals' bodies at the outset of the behavioural act. This was determined by comparing the orientations of two imaginary lines extending from the two seals' shoulders to the bases of their hind flippers (Figure 8A). The options were (see Figure 9):

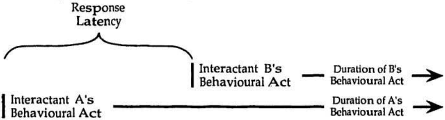
- parallel, same direction
- facing towards, from directly ahead
- facing towards, from directly behind
- facing towards, from obliquely behind
- facing away, perpendicular
- unknown
- parallel, opposing direction
- facing towards, perpendicular
- facing towards, from obliquely ahead
- facing away, from posterior
- facing away, from anterior

This category's first and subsequent values were relative to the position of the seal performing the first act.

27) **Head Orientation** - the relative orientation of the interactants' heads at the outset of the behavioural act. This was determined by comparing the relative orientations of two imaginary lines extending from the seals' noses to the bases of their skulls (Figure 8B). The options were the same as those for Body Orientation (Figure 10). This category's first and subsequent values were relative to the position of the seal performing the first act.

28) **Response Latency** - the latency (seconds) between the onset of the precedent's behavioural act and onset of the successor's response.

29) **Simultaneity** - this variable recorded whether or not the successor's behavioural act occurred at the same time as the precedent's behavioural act (simultaneous, not simultaneous or unknown). While a successor's behavioural act could be coded as "simultaneous" if it were performed at the same time as the precedent's, it could also have a response latency value greater than "0" if the successor began its behavioural act at some time subsequent to the start of the precedent's. The following diagram illustrates this point:



30) **Wind Approach** - the position of the precedent relative to the successor and the prevailing wind (upwind, crosswind, downwind or unknown).

31) **Total Duration** - the total duration (seconds) of the interaction.

32) **MultiAct** - the number of behavioural categories performed during a behavioural act (single category, more than one category or unknown). In rare cases where a seal performed more than one defined behavioural category at the same time, the behavioural act was given a special code number, in addition to the notation in this variable (Figure 11).

33) **Sequence Type** - a categorisation of the content of an interaction sequence:

- aggressive - at least one of the two seals behaved aggressively towards the other with behaviour types such as bites, head thrusts, fore flipper waves or chases.
- mother/pup interaction - a mother/pup pair engaged in nursing, play or investigative behaviour.

- play - the seals engaged in behaviour such as climbing, chasing and mock biting which was either of unusual exuberance, caused no physical injury or served no discernible benefit (Fagen, 1981; Renouf and Lawson, 1986a). This did not include play by mother/pup pairs.
- copulatory - the male performed penile thrusting which was usually followed by intromission (although this was not required to code for this sequence type).

34) **Weighted Behavioural Act Frequency** - the frequency of behavioural acts per sampled seal per sample minute. Since the frequency of interaction may be influenced by the number of seals nearby the interacting pair, a weighted frequency value was derived for each act in an interaction using the following formula:

$$\text{Weighted frequency} = \frac{1 \,/\, \text{Number of seals in Focal Area}}{\text{Total duration of interaction (sec)} \times 60}$$

This measure is a comprehensive estimate of behavioural frequency within the Focal Area since I transcribed *all* interactions that occurred inside this area.

I also derived a weighted behavioural act frequency per sampled seal of each age class per sample minute. When determining which age class performed a particular behaviour type most often, I could not use total behavioural act counts since age classes were not equally represented in the samples. Instead of dividing the value "1" by the total number of seals within the Focal Area, I used the number of seals of the same age class as the precedent, within the Focal Area, as the denominator. By using a weighted frequency, I avoided confusing behaviour performed rarely by a particular age class with behaviour performed by rarely-recorded age classes.

Methods for Quantitative Analyses

The numeric data sets derived from written transcriptions of the videotapes were entered into the StatView and SuperANOVA statistical programmes (Abacus Concepts, 1989; 1992) on a Macintosh II computer for manipulation and analyses. These data were also exported to Panorama II (ProVUE Development Corporation, 1991) for cross tabulation. These programmes generated contingency tables and probability matrices used in sequential dependency (Chalmers and Locke-Hayden, 1981; Colgan and Smith, 1978; Gottman and Roy, 1990; Stevenson and Poole, 1982). Discriminant, cluster and log-linear analyses were conducted using the SPSSx statistical package (Norusis, 1985) on a Digital VAX mainframe computer.

During Chi-square tests where the degrees of freedom exceeded 100 (the maximum in tables of chi-square values such as those in Rohlf and Sokal (1969), or samples were small, I used several methods to calculate minimum chi-square quantiles or correct the Chi-square estimates (Appendix B).

ANOVA Analyses

When comparing the mean values of a variable from three or more groups, the SuperANOVA programme's ANOVA procedure provides both overall F and individual between-group Scheffé S statistic values. The following is a sample of the output from the SuperANOVA programme's ANOVA test comparing the mean values of a variable for three groups:

Group	Mean	Count	Sceffé's S	Overall F = 67.0 *
Miquelon	184.206	846	22.7 *	Miquelon vs North Rona
North Rona	130.150	499	65.2 *	Miquelon vs Sable Island
Sable Island	107.338	942	4.2 *	North Rona vs Sable Island
	Total df = 2286			* values significant at $p \leq .05$

In the Results sections I quote the overall F value when two groups are compared. The significance of differences among three or more groups is evaluated on the basis of individual between-group Scheffé S values. These S values are accompanied by the degrees of freedom for the numerator and denominator.

Homogeneity of variance was tested during each ANOVA using a *post hoc* procedure called Bartlett's test of sphericity. If group variances were unequal, then a modified ANOVA, Welch's, was used instead.

The primary problems with the F ratio are that its size is directly related to that of the sample (Keppel and Saufley, 1980; Maxwell and Delaney, 1990), and, more importantly, nothing can be said about the magnitude of a treatment effect.[4]

While as yet rarely cited in the animal behaviour literature (Keppel, 1982; Keppel and Saufley, 1980), the omega squared index ($\hat{\omega}^2_\Lambda$) provides an invaluable estimate of the magnitude of treatment effects; its value represents the percentage of the total variance accounted for by the experimental treatments. If both the F value and the omega squared index are large, then the difference between the treatment conditions is statistically significant (a significant F value), and this difference represents a sizable effect (a large omega squared value; Hays, 1988). The method for calculating the omega squared index is described in Appendix C.

I calculated omega squared indices for ANOVAs which yielded significant F values. While Keppel and Saufley reported that typical index values for published datasets ranged from .05 to .35, I chose .60 as the minimum omega squared value above which I reported an F value *and* the "treatment" effect as significant. That is, at least 60 % of the variance was accounted for by experimental "treatments". This relatively conservative level assured that the effects of my subjective choice of grouping categories (such as behaviour types or interaction type) in this study would be controlled for.

Since many measures in this thesis exhibited non-normal distributions, which reduce the reliability of a standard ANOVA, I also tested the differences among values using a Kruskal-Wallis ANOVA. However, since neither of these non-parametric tests have

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[4] In the context of this thesis, the categories within the independent variables are "treatments". A comparison of dependent variable values of subjects assigned to groups on the basis of an independent variable is an "experiment".

means to partition variance, I cite the ANOVA and omega squared indices in the text. In only three instances did the parametric and non-parametric methods disagree, and in these cases I cite the non-parametric statistic. Also, in instances where the number of measures in any one group fell below five, I tested for unequal means non-parametrically using a Kruskal-Wallis ANOVA. These results are reported in the text.

In statistical manipulations a type I error rate of at least $\alpha = .05$ was adopted as the criterion for rejecting the null hypothesis (Sokal and Rohlf, 1976). I employed three significant decimal places during calculations and report one in the Results sections.

Catalogue Completeness Estimation

I estimated the completeness of my behavioural catalogue by utilizing Fagen's (1978) procedure for examining the adequacy of sample coverage. Sample coverage, represented by the quantity θ, is the probability that in a new, independent sample of behaviour, a randomly chosen act will be the same as a type already represented in an initial sample. That is, θ measures the ability to predict the composition of a species' behaviour on the basis of information derived from behavioural samples. A distribution-free estimate of the average value of θ ($\hat{\theta}_g$) is given by:

$$\hat{\theta}_g = 1 - \frac{N_1}{I}$$

where N_1 is the number of behavioural acts represented exactly once in the sample and I is the total number of acts recorded in the sample. Note that $\hat{\theta}_g$ is an average θ for all samples of I acts from the animal's repertoire, rather than a strict estimate of θ itself. An $\hat{\theta}_g$ value greater than .9 indicates acceptable sample coverage. Note, as well, that this method places no emphasis on rare behavioural events.

Coefficients of Variation

According to Slater (1978) and others (e.g., Miller, 1991; Stamps and Barlow, 1973; Wiley, 1973) coefficients of variation of a physical parameter (CV; the standard deviation of a measured parameter expressed as a percentage of its mean) provide a useful guide to stereotypy. In this study CVs also provided an additional measure with which to compare behaviour types among sites.

Discriminant Analyses

As objective means to examine relationships between behavioural categories I used both discriminant and cluster analyses. Discriminant analyses (procedure DISCRIMINANT in SPSSx) were used to determine which variables (such as inter-seal distance, act duration and eye position) best differentiated behavioural categories.

While one of the assumptions in a discriminant analysis is that all expected covariance matrices of the sampled groups are equal, researchers using Monte Carlo simulations and empirical studies have demonstrated that discriminant analyses are robust even when no real precautions, beyond careful sampling technique, are taken (Pimental and Frey, 1978).

Initially I examined pooled, within-groups correlation matrices for any correlations between measured variables greater than 0.5. I rejected the member of a correlated pair which produced the lesser standardised discriminant function coefficient. In addition, since discriminant analysis only compares groups which have values for *all* variables used in the comparison, there is normally a reduction in the number of cases used in any evaluation. As a by-product of this reduction, I removed groups for which only one case contained the prerequisite data for all criterion variables. The discriminant analysis was then re-calculated without the highly intercorrelated variables and with more than one case per group. In assessing results from the final analyses, I only extracted canonical discriminant functions with eigenvalues greater than 1.0. Within these selected functions, only variables possessing a conservative, minimal loading of 0.6 were used to interpret the orthogonal aspect(s) of the data set (Kerlinger, 1974). These were then used during subsequent agglomerative clustering of behaviour types into assemblages for visual inspection using complete linkage (Everitt, 1980; Kaufman, 1989; Norusis, 1985; Wishart, 1978).

Discriminant analyses also provided an approach to determine which variables could best differentiate the study sites. Again, the resultant significant variables provided a quantitative rationale for creation of agglomerative clusters of the sites.

Trend Analyses Using the Page's L Test

Since I had collected data from a complete breeding season at North Rona, I was able to search for seasonal trends in selected variables by employing the conservative, nonparametric Page's L test (Page, 1963; Senter, 1969; Sokal and Rohlf, 1976). Each value within a variable was assigned a rank relative to the others within that variable, and compared with an *a priori* prediction about the direction of the trend in the magnitude of the expected ranks. Identical values were given the same average rank values using procedures detailed in Page (1963). If the calculated Page's L_{variable} value exceeded a formulated L_{critical} threshold, a significant trend in these ranked values was indicated. Since the standard table of critical values for L does not include those necessary to assess single row data, I calculated the critical value for each test using the formula:

$$L_{\text{critical}} = \frac{r\,(k^3 - k)}{12} \left\{ \frac{z_{\text{critical}}}{\sqrt{r\,(k-1)}} + \frac{3\,(k+1)}{k-1} \right\}$$

where r equals the number of rows, k the number of columns and z_{critical} the minimum z value necessary to reach the desired one-tailed rejection level (for $p \leq .05$ $z_{\text{critical}} = 1.65$, and for $p < .01$, $z_{\text{critical}} = 2.33$; Senter, 1969). Computed L_{critical} values are listed in Appendix D.

Despite its robustness, Page's L is subject to decreased reliability when more than 20% of the ranks are tied (Page, 1963). Effects of ties were countered by the standard method of choosing an $\alpha = .01$ level of acceptance. This occurred in only one variable, and an alternate $\alpha = .01$ L_{critical} value was calculated.

Sequential Dependencies

1) Sample Size Considerations

Simulation studies of behavioural sequence analyses, using a first-order Markov model, indicated that acceptable sample size is repertoire-dependent (Fagen and Young, 1978). When using standard techniques for transition analyses, there must be a minimum number of behavioural records to ensure optimum reliability. This minimum number for optimum reliability is a function of how many different types of behaviour the animal is expected to perform. Assuming R is repertoire size, Fagen and Young found that $5R^2$ records were a theoretical minimum sample size sufficient to ensure statistical reliability.

My data from the study sites do not achieve this theoretical minimum value. Calculated minimum ($5R^2$) sample size values for Miquelon, North Rona and Sable Island are 3645, 5445 and 4205 acts, respectively. Actual sample sizes were 1437 ($2.0R^2$), 4229 ($3.9R^2$) and 1799 ($2.0R^2$). I did not pool any of the behaviour categories to increase row or column totals since I had no basis on which to measure the functional relatedness between behaviour types as far as the seals were concerned.

Since this is the first time a comprehensive catalogue of grey seal behaviour has been created, and Markovian analyses were a preliminary effort to detect sequential dependencies subsequently used to compare sites, I employed these datasets with Colgan and Young's (1978) perspective in mind:

> *"In practice, one should not be too conservative about sample size whenever the analysis is of an exploratory nature to detect structure and is not intended for drawing hard and fast conclusions"* (p. 173).

Conclusions regarding sequential dependencies are made with caution, particularly with results from Miquelon and Sable Island.

2) Sequential Analyses Using Markov Models

Markov models were used to test for significant transitions between acts performed by two seals (inter-individual), and by successive acts performed by the same seal (intra-individual).

The first step in using Markov models in sequential analyses is to determine which model best describes the transition probabilities in the data (Fagen and Young, 1978). That is, does the *identity* of the preceding behavioural act decide the probability that a particular succeeding behavioural act will occur ? If there is a significant relationship, *how many* preceding acts, of particular types, influence the probability that a particular succeeding behavioural act will occur ?

Due to the nature of my data, I searched for significant sequential dependencies using log-linear modeling, rather than the chi-square method.[5] A potentially powerful and flexible approach (Feick and Novak, 1985; Gottman and Roy, 1990), log-linear modeling offers a technique to explain matrix values in terms of a hierarchical, linear interaction among the variables from which the matrix is derived. The probability of an observation in the ij^{th} cell in a contingency table is assumed to be the product of equal marginal probabilities (Bishop, Fienberg, and Holland, 1975).

The HILOGLINEAR hierarchical, log-linear modeling procedure of the SPSSx package was used to derive adjusted likelihood ratio chi-square goodness-of-fit test statistics (denoted as G). These provided the means to assess inter- and intra-individual

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[5] If expected values are less than one, and more than 20% of expected values are less than five, as was the case for my data, a chi-square test is contra-indicated (Everitt, 1979; Siegel and Castellan, 1988). A second concern to address in matrix analysis is the presence of structural zeros. These are combinations of variables (in this case behavioural acts and responses to them) that are not expected to occur in the sequences. For instance, one would not expect the "penile thrust" behaviour category to follow a "nurse" by a pup, since mothers could not perform this response. Although it has minimum sample size considerations, log-linear analysis is more robust than chi-square when modified to counter the effects of structural zeros (Everitt, 1979).

sequential dependencies (Bishop *et al.*, 1975; Everitt, 1979; Gokhale and Kullback, 1978; Gottman and Roy, 1990).

I adjusted the log-linear analyses in accordance with the presence of structural zeros that I had determined were present in the matrices (see subsection 3). This was accomplished by assigning zero weights to those cells with structural zeros in matrices processed by the HILOGLINEAR procedure. The degrees of freedom were then adjusted according to the following paradigm: $df = N_1 - N_2 - N_3$ where N_1 = number of cells in table, N_2 = number of parameters in the model that require estimating and N_3 = number of *a priori* empty cells (structural zeros; Bishop *et al.*, 1975; Everitt, 1979). Note that the adjusted degrees of freedom may be an underestimate of the true degrees of freedom and is therefore more conservative (SPSS Inc., 1988).

A non-significant G value would indicate that the Markov model of effect for the interactions was zero order (independence model). That is, for interactive sequences, there were no relationships between the identity of preceding and succeeding behavioural acts. A significant G value would indicate that there was at least a first-order Markov relationship between the acts performed by the precedent and the successor's responses to them; the probability of a certain act occurring is determined by the identity of the act immediately preceding it (act A ⇒ **act B**).

If at least a first-order Markov relationship was indicated, I then tested for a second-order relationship by applying the HILOGLINEAR procedure to transition matrices with a third dimension (the variable "interactant's behavioural act B"). In these cases, a significant G value indicates that the probability of a particular behavioural act occurring was determined by the identities of two preceding acts (act A ⇒ act B ⇒ **act C**).

Significant G values, indicating the presence of significant sequential dependencies in the matrix as a whole, were appraised in greater detail by calculating an adjusted (standardised) residual value for each cell (using formulae from Bishop *et al.*, 1975) with variables forming the table normally distributed with mean=0 and SD=1. These standardised residuals revealed which cells contributed significantly to the overall G, and were especially useful when structural zeros had been removed (Haberman, 1973).

I calculated residual values to expose transitions that occurred at greater frequencies than expected (Bishop *et al.*, 1975). To calculate an adjusted residual, Y, for each cell I used the formula:

$$Y = \frac{(x_{ij} - m_{ij})}{\sqrt{(m_{ij})}}$$

where x_{ij} were the observed, and m_{ij} were the expected, cell frequencies.

If $|Y| > \sqrt{(\chi^2) / R^2}$, where χ^2 was the calculated minimum significant chi-square value for the df of the matrix, then the transition (act $i \rightarrow$ act j) occurred at a frequency which differed significantly, at $p \leq .05$, from chance. If $Y > 0$, and the transition was significant, act i was said to have directed j. If $Y < 0$, and the transition was significant, act i was said to have inhibited act j.[6]

I concurred with Baylis' (1975) arguments that an important aspect of transition analysis, where the sexes of the participants are known, should involve subdivision of the matrices into male and female sections to properly execute analysis of courtship sequences. I therefore further subdivided my data into groups for analysis on the basis of the sex of the interactants (male-male, female-female and male-female sequences) at the two breeding sites, as well as for the non-breeding group at Miquelon. That is, I performed log-linear transition analyses with precedent sex as a third variable (dimension).

3) Intra-individual Sequential Dependencies

Several complications arise when tests of intra-individual behaviour sequences are made using a matrix incorporating homogeneous transitions (those between identical act types), a practice common in earlier studies such as those by Wiepkema (1961). If any act

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[6] There are no restrictions regarding minimum m_{ij} values, but if $m_{ij} \ll 1$, caution is advised in interpretation of calculated results (Fagen and Young, 1978).

can follow any other, and if acts occur in repetitious bouts, then transitions between identical acts (located on the descending diagonal in a transition matrix) will be more probable than those between different acts, thereby overshadowing off-diagonal transitions. Lemon and Chatfield (1971) felt that most animal behaviour occurs in bouts.

Secondly, while criteria for choosing when the first performance of a particular act type ends and the second begins can be reasonably objective, these criteria will not be the same as those for homogeneous transitions of other behaviour types.[7] As the number of every transition contributes to the grand total, the differences between the criteria used for each behaviour type may have an undesirable effect on all expected values throughout the matrix.

Except when trying to demonstrate that behavioural acts by an individual occur in bouts, inclusion of the descending diagonal "renders statistical tests meaningless" (Lemon and Chatfield, 1971). The effects of the aforementioned problems can be limited by eliminating homogeneous transitions (A → A, B → B, ...) by assigning these cells a zero weighting during analyses (Fagen and Young, 1978; Lemon and Chatfield, 1971; Slater and Ollason, 1972). Expected values in these reduced contingency tables were modified automatically by the HILOGLINEAR procedure so row and columns totals for resultant expected values still equaled those of the observed (Colgan and Smith, 1978; Haberman, 1974).

4) Stationarity Considerations

Markov chain analysis techniques assume that estimates of transition probabilities remain constant throughout the predictive period (a condition of stationarity; e.g., Collins, 1975). It is unlikely that the condition of stationarity can ever be satisfied for

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[7] Since the criteria used to define each behaviour type are unique, it is also likely that the features used to categorise the onset and termination of each behaviour type are dissimilar.

data from behavioural interactions (Dingle, 1972), but there are methods to examine the influence of this variable.

Lemon and Chatfield (1971) tested for stationarity in their data by comparing probabilities between two halves of an observation session; they split the data set into a three-way table with the third dimension being the half-session identity. Unlike Lemon and Chatfield's analysis of bird song, grey seal bouts were not long enough to permit me to subdivide them into halves and still produce significant results.

However, I had data for the entire breeding season at North Rona and used this to test for longitudinal variation in sequential predictability (rather than sequential stationarity *per se*) by subdividing the North Rona season into two halves and using the halve identities as a third dimension in the HILOGLINEAR procedure, as *per* Lemon and Chatfield (1971).

Chapter Three: The Ethogram

Few quantitative descriptions of behaviour exist in the pinniped literature, and of these, few have sufficient detail to permit seasonal, site or species comparisons. Although the grey seal resides in locations on both sides of the Northern Atlantic ocean, there are few published comparisons of grey seal behavioural repertoires at different locales (Anderson and Harwood, 1985; Boness, 1984). The detail and accuracy of the video recordings of terrestrial interactions obtained during this study permitted the construction of a comprehensive, quantitative ethogram which included both breeding and non-breeding behavioural components at different sites.

Following the methods and recommendations of a number of authors (Altmann, 1967; Anderson, 1978; Boness and James, 1979; Drummond, 1981; Fentress, 1973; Gailey-Phipps, 1984; Golani, 1976; Harestad and Fisher, 1975; Lewontin *et al.*, 1984; Miller, 1975a; 1986; 1988; 1991; Miller and Boness, 1979; Renouf and Lawson, 1986a; Slater, 1978; Smith, 1977; Stirling, 1970; Sullivan, 1979; 1982), I compiled a catalogue of behavioural types which were distinctive and predominantly independent in form.

Testing Behaviour Categories Using a Naïve Observer

I tested these behaviour categories by having a naïve observer code a sample of my videotapes using the ethogram as the sole guide.

There were no significant differences between the number of behavioural acts which I and the naïve observer coded in the sequence ($\chi^2 = 2.9$, df = 108, $p = .27$). The Kappa coefficient was .84 (df = 229), indicating a high concordance between the categories that we both coded, and a robust and predictive ethogram.

The only behaviour types which seemed to cause the naïve observer difficulty were Look Away and Glance (only eight percent of all acts coded). When I reviewed the bout with the observer, I was able to point out the subtle way in which one of the interactants could Glance at the other while apparently (to the naïve observer) doing nothing. Had the naïve observer been coding the bouts for eye status as well, these errors may have been reduced or eliminated. Similarly, a seal could appear to the observer as if it was Looking Away when in fact it had simply Averted its Face, and was still watching the successor.

Sample Coverage and Catalogue Completeness

Utilizing Fagen's (1978) procedure for estimating sample coverage, I obtained values of $\hat{\theta}g$ for Miquelon ($N_1 = 3$, $I = 1657$), North Rona ($N_1 = 0$, $I = 4926$) and Sable Island ($N_1 = 1$, $I = 2059$) of 0.998, 1.0 and 0.999, respectively.

These substantial completeness estimates indicate that I can assume, with reasonable confidence, that sample coverage at all three sites was representative and the resulting ethogram is a comprehensive catalogue of these seals' repertoires during the periods sampled.

The Ethogram

Each behaviour type subsection begins with a physical description of the behaviour type, followed by inter-site comparisons of measures such as duration, inter-seal distance and behavioural act frequency. The three-letter abbreviation listed in each behaviour type heading is used in place of the full name in subsequent text and tables. The reader is encouraged to keep the enclosed reference card (Appendix A) at hand.

Tables 1 and 2 provide summaries of the characteristic features of each behaviour type discussed in detail in the subsections below. In measures for which there were no significant differences among the study sites, or the pattern of results were the same at all sites, I cite aggregated values only (e.g., if the seals' eyes were more likely to be open than closed during a particular behaviour type at all three locales, I report that the eyes were more likely to be open in the tables). Where there were significant differences among the sites within a categorical variable, I note all possible occurrences. For continuous variables I cite overall mean values and discuss site differences in the text.

This study revealed that there were site and sex differences in repertoire size (see table on page 116), and these are noted when discussing relevant behaviour types.

Open Mouth Display (OMD)

Description: A male slowly extended its head and neck (less rapidly than an HTH), usually towards the successor (Figure 12A). It then opened its mouth wide enough to display the contrasting, pink buccal cavity, and performed a barely audible exhalation. The nares were closed during the exhalation phase. After the male closed its mouth, it inhaled through the nares. An OMD was never observed at Miquelon.

Anatomical Characteristics: The eyes were more likely to be open (81.2%) during this behaviour type ($\chi^2 = 95.1$, df = 539, $p \leq .05$; Table 1). The vibrissae were most likely to be protracted (99.5%; $\chi^2 = 390.3$, df = 552, $p \leq .05$) and the tail was rarely elevated (91.6%; $\chi^2 = 353.5$, df = 509, $p \leq .05$). The nares were always open.

At North Rona an OMD was more likely to occur with the performer's head higher than the successor's (69.3%) than at the same height or lower ($\chi^2 = 37.2$, df = 391, $p \leq .05$). At Sable Island, on the other hand, the two interactants' heads were most likely to be at the same height during an OMD ($\chi^2 = 6.8$, df = 155, $p \leq .05$). Further, both the body ($\chi^2 = 139.8$, df = 566, $p \leq .05$) and head ($\chi^2 = 178.7$, df = 565, $p \leq .05$) were more likely to be oriented directly facing each other (81.3% and 85.4%, respectively) during performance of this behaviour category.

Duration: The mean duration of this behaviour type was 2.8 seconds (SD = 0.7). The mean duration was not sufficiently different for OMDs recorded at Sable Island and

North Rona (Table 3; $F = 10.4$, $df = 1, 565$, $p \leq .05$; but $\hat{\omega}^2 = .18$). The coefficients of variation (CV) were also similar at the two breeding sites (Table 4), and the lowest of all behaviour types.

Inter-seal Distance: The mean distance between interactants when one performed an OMD was 307.7 cm (SD = 107.9). The mean distance between interacting seals for this behaviour type was larger at North Rona than Sable Island ($F = 13.0$, $df = 1, 565$, $p \leq .05$; $\hat{\omega}^2 = .68$; Table 5), although the CV was also larger (Table 6).

Sex and Age Differences: This behaviour category was performed exclusively by adult males at the two breeding sites. Further, a male was more likely to direct an OMD towards another adult male (77.5%) , than towards a female ($\chi^2 = 37.3$, $df = 565$, $p \leq .05$). Similarly, the frequency of OMDs was greater during interactions between males than during male-female interactions at both North Rona ($F = 36.9$, $df = 1, 406$, $p \leq .05$; $\hat{\omega}^2 = .60$) and Sable island ($F = 25.7$, $df = 1, 157$, $p \leq .05$; $\hat{\omega}^2 = .64$).

Behavioural Frequency: This behaviour type was performed at a greater frequency at Sable Island than North Rona ($F = 22.2$, $df = 1, 565$, $p \leq .05$; $\hat{\omega}^2 = .7$; Table 7 and Figure 15).

Context: The greatest frequency of OMD occurred during aggressive interactions at North Rona ($F = 34.6$, $df = 1, 40$, $p \leq .05$; $\hat{\omega}^2 = .87$). OMDs occurred only during aggressive interactions at Sable Island.

Head Thrust (HTH)

Description: The precedent extended its head and neck quickly towards the successor with a piston-like movement, then retracted it (Figure 12B). The precedent's motion was directed along the longitudinal axis of its neck.

Anatomical Characteristics: The mouth (99.3%; $\chi^2 = 436.1$, $df = 450$, $p \leq .05$) and eyes (99.3%; $\chi^2 = 429.1$, $df = 439$, $p \leq .05$) were virtually always open, and the vibrissae extended (99.8%; $\chi^2 = 423.0$, $df = 425$, $p \leq .05$; Table 1). The tail was rarely elevated

(15.4%; $\chi^2 = 164.7$, df = 342, $p \leq .05$) and the nares were virtually always closed (98.7%%; $\chi^2 = 74.0$, df = 77, $p \leq .05$).

At Miquelon ($\chi^2 = 43.8$, df = 135, $p \leq .05$) and North Rona ($\chi^2 = 63.5$, df = 264, $p \leq .05$) an HTH was more likely to occur with the performer's head at the same height than higher or lower. At Sable Island, on the other hand, the performer's head was more likely to be lower than either higher or the same height ($\chi^2 = 23.3$, df = 46, $p \leq .05$).

Both the body (95.5%; $\chi^2 = 283.3$, df = 444, $p \leq .05$) and head (97.2%; $\chi^2 = 647.1$, df = 444, $p \leq .05$) were more likely to be facing each other directly during an HTH.

Vocal Accompaniment: HTHs were usually performed silently (83.7%; $\chi^2 = 164.7$, df = 134, $p \leq .05$) at Miquelon and Sable Island (55.1%; $\chi^2 = 66.6$, df = 44, $p \leq .05$), but with an open mouth whoo at North Rona (61.0%; $\chi^2 = 298.9$, df = 262, $p \leq .05$; generally when performed by females).

Duration: The mean duration of this behaviour type was 1.3 seconds (SD = 1.2; Table 3). Note that the CVs for HTHs were relatively small (Table 4). The mean duration of HTHs was not sufficiently different (F = 3.2, df = 2, 453, $p \leq .05$; but $\hat{\omega}^2 = .21$) among the sites.

Inter-seal Distance: The mean distance between interactants when one performed an HTH was 19.0 cm (SD = 37.5). The mean distance between interacting seals for this behaviour type was not sufficiently different between any two sites (F = 7.7, df = 2, 453, $p \leq .05$; but $\hat{\omega}^2 = .22$; Table 5). The CVs for HTH did not differ among the sites (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by females at North Rona (83.9%; $\chi^2 = 124.5$, df = 246, $p \leq .05$) and Sable Island (65.3%; $\chi^2 = 4.6$, df = 49, $p \leq .05$), and males at Miquelon (67.4%; $\chi^2 = 26.3$, df = 128, $p \leq .05$). Females performed HTHs with greater frequency when interacting with other females than with males, or between males, at North Rona (F = 27.8, df = 2, 266, $p \leq .05$, $\hat{\omega}^2 = .68$). There were no significant differences in the frequencies of this behaviour type on the basis of interactants' sex at either North Rona ($F = 0.7$, $df = 2, 85$, $p = .34$) or Miquelon ($F = 2.9$, $df = 2, 62$, $p = .18$).

This behaviour category was performed exclusively by adults at North Rona (of which 62.5% were mothers; $\chi^2 = 442.5$, $df = 265$, $p \leq .05$) and Sable Island (of which 65.3% were mothers; $\chi^2 = 85.0$, $df = 47$, $p \leq .05$), and subadults at Miquelon (63.0%; $\chi^2 = 216.9$, $df = 135$, $p \leq .05$).

Behavioural Frequency: There were no significant differences between the frequency of HTHs at any site ($F = 1.2$, $df = 2, 452$, $p = .28$; Table 7 and Figure 15).

Context: HTHs occurred more frequently during aggressive interactions than any other sequence types at Miquelon ($F = 18.3$, $df = 1, 137$, $p \leq .05$, $\hat{\omega}^2 = .61$), North Rona ($F = 25.4$, $df = 3, 266$, $p \leq .05$, $\hat{\omega}^2 = .78$) and Sable Island ($F = 9.8$, $df = 3, 48$, $p \leq .05$, $\hat{\omega}^2 = .64$).

Extend Foreflipper (EFF)

Description: The seal extended a foreflipper until it projected approximately 90 degrees from its body's longitudinal axis, and held it in that posture for a few seconds (Figure 12C). The seal rolled over so as to lie on its side opposite to the extended foreflipper, but to a lesser degree than the behaviour type, ROS (see below).

Anatomical Characteristics: The eyes (98.7%; $\chi^2 = 429.1$, $df = 148$, $p \leq .05$) and mouth (70.8%; $\chi^2 = 142.1$, $df = 142$, $p \leq .05$) were more likely to be open during this behaviour type (Table 1). The vibrissae were more likely to be protracted (96.1%; $\chi^2 = 423.0$, $df = 125$, $p \leq .05$) and the tail was not normally elevated (86.5%; $\chi^2 = 164.7$, $df = 124$, $p \leq .05$). The nares were usually closed (89.7%; $\chi^2 = 18.2$, $df = 27$, $p \leq .05$).

At Miquelon (61.5%; $\chi^2 = 12.5$, $df = 35$, $p \leq .05$), North Rona (60.0%; $\chi^2 = 8.1$, $df = 95$, $p \leq .05$) and Sable Island (66.6%; $\chi^2 = 10.5$, $df = 18$, $p \leq .05$) the performer's head was more likely to be lower than that of the seal at which the behaviour was apparently directed.

At all sites, the interactants' bodies (34.2%; $\chi^2 = 35.2$, df = 149, $p \leq .05$) and heads (30.5%; $\chi^2 = 23.7$, df = 148, $p \leq .05$) were most likely to be oriented parallel and facing the same direction during performance of this behaviour type.

Vocal Accompaniment: EFFs were more likely to be performed silently at Miquelon (63.2%; $\chi^2 = 11.1$, df = 35, $p \leq .05$) and North Rona (47.8%; $\chi^2 = 61.8$, df = 94, $p \leq .05$). At Sable Island an extended foreflipper was as likely to be accompanied by an open mouth whoo as no vocalisation ($\chi^2 = 0.8$, df = 18, $p = .36$).

Duration: The mean duration was 5.1 sec (SD = 8.1). The durations of EFFs were not sufficiently different at any site (F = 3.9, df = 2, 156, $p \leq .05$; but $\hat{\omega}^2 = .09$; Table 3). The CV was lower at Miquelon than either breeding site (Table 4).

Inter-seal Distance: The mean distance between interactants when one extended its foreflipper was 19.4 cm (SD = 30.5). There were no significant differences among the mean distance values at any of the sites (Table 5), although again the CV was greater at Sable Island than at Miquelon and North Rona (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by females at North Rona (88.5%; $\chi^2 = 57.0$, df = 94, $p \leq .05$) and Sable Island (71.4%; $\chi^2 = 3.9$, df = 19, $p \leq .05$). There was no significant difference between the sexes at Miquelon (62%; $\chi^2 = 1.7$, df = 35, $p = .25$). EFF occurred more frequently when females interacted with other females than when females interacted with males or males interacted with males, at North Rona (F = 84.4, df = 2, 78, $p \leq .05$; $\hat{\omega}^2 = .8$). There were no significant differences at Miquelon (F = 1.4, df = 2, 33, $p = .18$) or Sable Island (F = 4.5, df = 2, 20, $p \leq .05$; but $\hat{\omega}^2 = .16$).

This behaviour category was performed predominantly by adults at North Rona (of which 70.4% were mothers; $\chi^2 = 127.2$, df = 94, $p \leq .05$), Sable Island (of which 71.4% were mothers; $\chi^2 = 3.9$, df = 19, $p \leq .05$), and Miquelon (68.4%; $\chi^2 = 45.2$, df = 35, $p \leq .05$).

Behavioural Frequency: The weighted frequency of EFFs was greater at Miquelon than either North Rona or Sable Island (Table 7 and Figure 15).

Context: EFF occurred with the greatest frequency during aggressive interactions at Miquelon (F = 18.1, df = 1, 37, $p \leq .05$; $\hat{\omega}^2 = .60$) and North Rona (F = 56.9, df = 3, 97, $p \leq .05$; $\hat{\omega}^2 = .64$). There were no significant differences among frequencies of EFFs on the basis of interaction type at Sable Island (F = 0.9, df = 3, 28, $p = .31$).

Foreflipper Wave (FFW)

Description: The seal waved a foreflipper, which it had extended perpendicular to the longitudinal axis of its body, within an arc perpendicular to the ground with the wrist and digits held rigid (Figure 12D). The seal had rolled slightly onto the side opposite the waving foreflipper, comparable to an EFF, but to a lesser extent than a ROS (see below).

Anatomical Characteristics: The eyes (100%) and mouth (90.3%; $\chi^2 = 99.8$, df = 152, $p \leq .05$) were more likely to be open during this behaviour type (Table 1). The vibrissae were more likely to be protracted (97.2%; $\chi^2 = 129.4$, df = 143, $p \leq .05$) whereas the tail was not usually elevated (84.0%; $\chi^2 = 57.8$, df = 123, $p \leq .05$) and the nares were rarely open (12.5%; $\chi^2 = 22.5$, df = 38, $p \leq .05$).

The performer's head was more likely to be lower than that of the seal at which the FFW was directed (Miquelon: (70.1%; $\chi^2 = 16.6$, df = 36, $p \leq .05$; North Rona: 36.0%; $\chi^2 = 4.8$, df = 93, $p \leq .05$; and Sable Island: 34.0%; $\chi^2 = 13.5$, df = 23, $p \leq .05$). Interacting seals were as likely to be facing each other head-on (23.0%) or perpendicular (24.2%) to one another during an FFW ($\chi^2 = 19.7$, df = 155, $p \leq .05$). The interactants' heads (24.6%; $\chi^2 = 55.4$, df = 155, $p \leq .05$) were more likely to be oriented in a head-on direction during performance of an FFW.

Vocal Accompaniment: Open mouth whoos were the most common vocal accompaniment to FFWs at Miquelon (61.1%; $\chi^2 = 51.2$, df = 36, $p \leq .05$), North Rona (47.7%; $\chi^2 = 61.1$, df = 93, $p \leq .05$) and Sable Island (78.6%; $\chi^2 = 77.2$, df = 23, $p \leq .05$).

Duration: The duration of this behaviour type was 4.2 seconds (SD = 6.0). There were no significant differences between the mean duration values at any site (Table 3), and the CVs were similar (Table 4).

Interseal Distance: The mean distance between interactants when one performed a FFW was 33.7 cm (SD = 81.1). The mean distance between interacting seals for this behaviour type was not significantly different among the sites (Table 5), although the CV was much smaller at Sable Island (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by females at North Rona (81.2%; $\chi^2 = 34.4$, df = 94, $p \leq .05$) and Sable Island (75.9%; $\chi^2 = 7.8$, df = 27, $p \leq .05$), but by either sex at Miquelon ($\chi^2 = .9$, df = 37, $p = .37$). There were no significant differences between the frequencies of FFWs depending on the sexes of the interactants at Miquelon (F = 0.4, df = 2, 38, $p = .4$) or North Rona (F = 0.2, df = 2, 95, $p = .45$). At Sable Island, however, a greater frequency of foreflipper waving occurred when a male was interacting with another than during female-female or male-female bouts (F = 84.4, df = 2, 28, $p \leq .05$; $\hat{\omega}^2 = .82$).

This behaviour category was performed exclusively by adults at Miquelon and predominantly by mothers at North Rona (60.4%; $\chi^2 = 98.0$, df = 93, $p \leq .05$) and Sable Island (63.0%; $\chi^2 = 43.5$, df = 27, $p \leq .05$).

Behavioural Frequency: There were no significant differences among the frequencies of FFWs at any site (Table 7 and Figure 15).

Context: Foreflipper waving was more frequent during aggressive interactions at Miquelon (F = 19.1, df = 1, 38; $\hat{\omega}^2 = .60$), but there were no significant differences in these measures at North Rona (F = 2.8, df = 3, 95, $p = .26$) or Sable Island (F = 1.0, df = 3, 28, $p = .19$).

Foreflipper Scratch Successor (FSR)

Description: The seal scratched the body of a nearby seal using the nails of an outstretched foreflipper which was being swung in a plane perpendicular to the ground with the wrist and digits held rigid, and perpendicular to the longitudinal axis of the body (Figure 13A). The seal performing the FSR leaned slightly towards the successor.

Anatomical Characteristics: The seals' eyes (94.1%; $\chi^2 = 105.9$, df = 136, $p \leq .05$) and mouths (62.9%; $\chi^2 = 8.9$, df = 139, $p \leq .05$) were more likely to be open during this behaviour type (Table 1). Their vibrissae were more likely to be protracted (90.7%; $\chi^2 = 71.7$, df = 139, $p \leq .05$) but their tails were not normally elevated (92.4%; $\chi^2 = 94.0$, df = 139, $p \leq .05$). The nares were usually closed (94.7%; $\chi^2 = 30.4$, df = 37, $p \leq .05$)

The performer's head was more likely to be lower than that of the seal at which the FSR was directed (Miquelon: $\chi^2 = 9.6$, df = 27, $p \leq .05$; North Rona: $\chi^2 = 4.4$, df = 66, $p \leq .05$). At Sable Island, the interactants' heads were more likely to be at the same height during an FSR ($\chi^2 = 49.3$, df = 39, $p \leq .05$)

During performance of this behaviour category, interacting seals were more likely to be facing each other perpendicularly (25.2%; $\chi^2 = 21.6$, df = 132, $p \leq .05$). Interactants' heads (36.2%; $\chi^2 = 37.8$, df = 132, $p \leq .05$) were more likely to be oriented parallel to each other in the same direction.

Vocal Accompaniment: When subdivided by site, FSRs were more likely to be performed silently at Miquelon (72.4%; $\chi^2 = 64.9$, df = 27, $p \leq .05$) and North Rona (60.3%; $\chi^2 = 86.4$, df = 66, $p \leq .05$), but with an open mouth whoo at Sable Island (66.7%; $\chi^2 = 70.2$, df = 40, $p \leq .05$).

Duration: The duration of an FSR was 7.1 seconds (SD = 8.4). There were no significant differences among durations of FSRs at any site (Table 3) and the CVs were similar (Table 4).

Interseal Distance: The mean distance between interactants when one began to perform a FSR was 3.7 cm (SD = 7.6). The mean distance between interacting seals for this behaviour type was significantly greater at Sable Island than North Rona (Table 5), although the CV was smaller at Sable Island (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by females at North Rona (96.7%; $\chi^2 = 52.3$, df $= 67$, $p \leq .05$) and Sable Island (85.7%; $\chi^2 = 21.4$, df $= 40$, $p \leq .05$), and males at Miquelon (73.3%; $\chi^2 = 5.6$, df $= 28$, $p \leq .05$). Subdividing interactions on the basis of the sexes of both interactants, I found that there were no significant differences among interactive pairs of different sex on the basis of the frequency with which they performed FSRs at Miquelon (F = 0.4, df = 2, 28, $p = .24$), North Rona (F = 6.1, df = 2, 37, $p \leq .05$; but $\hat{\omega}^2 = .12$) or Sable Island (F = 47.7, df = 2, 34, $p \leq .05$; but $\hat{\omega}^2 = .51$).

This behaviour category was performed predominantly by mothers at North Rona ($\chi^2 = 139.2$, df $= 66$, $p \leq .05$) and Sable Island ($\chi^2 = 113.4$, df $= 40$, $p \leq .05$), and subadults at Miquelon ($\chi^2 = 17.2$, df $= 27$, $p \leq .05$).

Behavioural Frequency: The frequency of FSRs at Miquelon was greater than Sable Island (Table 7 and Figure 15).

Context: The greatest frequency of FSR occurred during aggressive interactions at Miquelon (F = 21.4, df = 1, 29, $p \leq .05$; $\hat{\omega}^2 = .71$) and North Rona (F = 14.8, df = 3, 68, $p \leq .05$; $\hat{\omega}^2 = .69$). The differences between categories at Sable Island were not sufficient (F = 5.9, df = 3, 41, $p \leq .05$; but $\hat{\omega}^2 = .18$).

Foreflipper Scratch Substratum (FSS)

Description: The seal scratched the substratum near its side with the nails of an outstretched foreflipper which was swept back and forth parallel to the body with the wrist and digits held rigid (a similar configuration to that adopted during an FSR). On sand or grass substrata, this behaviour frequently caused small quantities of sand or grass, to be tossed backwards into the air. This behaviour type was not observed at Miquelon.

Anatomical Characteristics: The eyes and mouth were always open during this behaviour type (Table 1). The vibrissae were protracted, but the tail was not elevated.

A performer's head was more likely to be lower than that of the seal at which the FSS was directed (North Rona: 80.0%; $\chi^2 = 4.4$, df = 2, $p \leq .05$; Sable Island: 62.5%; $\chi^2 = 6.9$, df = 5, $p \leq .05$).

Both the performer's body (38.5%; $\chi^2 = 11.7$, df = 8, $p \leq .05$) and head (30.8%; $\chi^2 = 6.2$, df = 9, $p \leq .05$) were most likely to be oriented parallel and facing the same direction as the successor during performance of this behaviour type.

Vocal Accompaniment: This behaviour type was most likely to be accompanied by an open-mouthed whoo vocalisation (75.0%; $\chi^2 = 29.4$, df = 10, $p \leq .05$). When subdivided by site, an FSS was more likely to be performed silently at North Rona (50.0%; $\chi^2 = 4.6$, df = 2, $p \leq .05$) but always with an open mouth whoo at Sable Island.

Duration: The duration of this behaviour type was 4.7 seconds (SD = 7.4),. The durations were not different for FSSs recorded at Sable Island and North Rona (Table 3). The CV for Sable Island was much greater than that for North Rona, however (Table 4).

Inter-seal Distance: The mean distance between interactants when one performed an FSS was 84.4 cm (SD = 261.9). The distances between interacting seals at North Rona and Sable Island were not significantly different (Kruskal-WallisH = 71, df = 1, 12, $p = .11$; Table 5), although the CV was larger at Sable Island (Table 6).

Sex and Age Characteristics: This behaviour type was performed solely by females at North Rona and Sable Island (and not recorded at all at Miquelon). Subdividing interactions on the basis of the sexes of both interactants, I found that females performed FSSs only when interacting with males in aggressive interactions.

This behaviour category was performed predominantly by adults at North Rona ($\chi^2 = 5.0$, df = 3, $p \leq .05$) and exclusively by mothers at Sable Island.

Behavioural Frequency: There were no significant differences between the frequency of FSSs at the two breeding sites (Table 7 and Figure 15).

Context: All FSS behaviour occurred during aggressive interactions at North Rona and Sable Island.

Foreflipper Slap Water (FSW)

Description: The seal struck the surface of the water, in which it lay partially on its side, with the palmar surface of a stiffly extended foreflipper held perpendicular to the body (in much the same configuration as an FFW). This behaviour was only seen at North Rona.

Anatomical Characteristics: The eyes (77.3%; $\chi^2 = 6.5$, df = 21, $p \leq .05$) and mouth (100%) were more likely to be open during this behaviour type (Table 1). The vibrissae were always protracted and the tail was rarely elevated (21.0%; $\chi^2 = 6.4$, df = 18, $p \leq .05$). The nares were always closed.

The performer's head was most likely to be at the same height as that of the seal at which the FSW was directed (67.9%; $\chi^2 = 15.0$, df = 25, $p \leq .05$).

The seals usually lay parallel to each other in the same direction (50.0%; $\chi^2 = 113.6$, df = 15, $p \leq .05$) as the interactant slapped the water. The seals' heads, however, were more likely to be oriented directly facing each other (57.1%; $\chi^2 = 152.3$, df = 16, $p \leq .05$).

Vocal Accompaniment: A FSW was more likely to be accompanied by an open-mouthed whoo (60.0%) than a growl (36.0%; $\chi^2 = 33.8$, df = 23, $p \leq .05$).

Duration: The mean duration of this behaviour type was 1.9 seconds (SD = 1.1; Table 3). The CV was relatively low compared to other behaviour types (Table 4).

Interseal Distance: The mean distance between interactants when one performed an FSW was 46.1 cm (SD = 32.6; Table 5). The CV was among the lowest (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by females (78.6%; $\chi^2 = 9.1$, df = 27, $p \leq .05$). Subdividing interactions on the basis of the sexes of both interactants, I found that this behaviour type was performed by females more often when interacting with other females than with males ($\chi^2 = 155.0$, df = 27, $p \leq .05$).

This behaviour category was performed exclusively by adults at North Rona.

Context: FSW behaviour always occurred during aggressive interactions.

Foreflipper Slap Body (FSB)

Description: The seal slapped its flank using the palmar surface of a foreflipper. The seal typically struck itself a number of times in quick succession. This behaviour category was seen only at North Rona.

Anatomical Characteristics: The seal's eyes (100%) and mouth (94.7%; $\chi^2 = 15.2$, df = 19, $p \leq .05$) were more likely to be open during this behaviour type (Table 1). The vibrissae were always protracted and the tail rarely elevated (86.7%; $\chi^2 = 8.1$, df = 19, $p \leq .05$). The nares where as likely to be closed (66.6%) as open ($\chi^2 = 3.0$, df = 2, $p = .08$).

A performer's head was more likely to be either higher (50.0%), or the same height (40.5%), than lower than that of the seal at which an FSB was directed ($\chi^2 = 3.5$, df = 17, $p \leq .05$).

Seals' bodies were most likely to be oriented facing directly towards each other during performance of this behaviour type (30.0%; $\chi^2 = 8.9$, df = 16, $p \leq .05$). Their heads were either facing directly towards (25.0%) or facing towards from obliquely ahead or behind (20.0%; $\chi^2 = 11.7$, df = 17, $p \leq .05$).

Vocal Accompaniment: This behaviour type was more likely to be accompanied by an open-mouthed whoo (50.0%) than a growl (38.9%; $\chi^2 = 15.3$, df = 17, $p \leq .05$).

Duration: The mean duration of this behaviour type was 3.8 seconds (SD = 3.1; Table 3).

Inter-seal Distance: The mean distance between interactants when one performed this behaviour category was 51.2 cm (SD = 51.1; Table 5). The distance CV was relatively low (Table 6).

Sex and Age Characteristics: This behaviour category was performed exclusively by mothers, and was performed as frequently during bouts when mothers interacted with others as with males ($F = 0.1$, $df = 2, 19$, $p = .31$).

Context: This behaviour category occurred equally frequently during aggressive and copulatory bouts ($F = 0.6$, $df = 2, 19$, $p = .22$).

Head Swing (HSW)

Description: The performer swung its neck rapidly through at least a 45 degree arc in a coronal plane parallel to the substratum (Figure 13B). The interacting seals were normally in close proximity, and the HSW passed the precedent's snout close to the successor's.

Anatomical Characteristics: The eyes (99.1%; $\chi^2 = 306.1$, $df = 340$, $p \leq .05$) and mouth (97.5%; $\chi^2 = 292.8$, $df = 340$, $p \leq .05$) were almost always open during this behaviour type (Table 1). The vibrissae were normally protracted (99.4%; $\chi^2 = 309.9$, $df = 318$, $p \leq .05$) while the tail was not usually elevated (93.7%; $\chi^2 = 184.7$, $df = 287$, $p \leq .05$). The precedent's nares were always closed.

The performer's head was more likely to be at the same height as that of the seal at which the HSW was directed at Miquelon (81.3%; $\chi^2 = 200.2$, $df = 190$, $p \leq .05$), North Rona (54.7%; $\chi^2 = 23.6$, $df = 103$, $p \leq .05$) and Sable Island (48.3%; $\chi^2 = 6.9$, $df = 26$, $p \leq .05$).

The seals' bodies were more likely to be either face-to-face or with one member facing the other from obliquely ahead than in any other direction during this behaviour category (37.2%; $\chi^2 = 482.5$, $df = 320$). The seals' heads were more likely to be oriented directly face-to-face (74.4%; $\chi^2 = 511.0$, $df = 319$, $p \leq .05$).

Vocal Accompaniment: When subdivided by site, HSWs were more likely to be performed silently at Miquelon (96.4%; $\chi^2 = 882.8$, df = 191, $p \le .05$), but with open mouth whoos at North Rona (51.5%; $\chi^2 = 63.7$, df = 103, $p \le .05$) and Sable Island (66.7%; $\chi^2 = 53.1$, df = 26, $p \le .05$).

Duration: The mean duration of this behaviour type, the second briefest of all types, was 1.5 seconds (SD = 1.5). The duration was greater for HSWs recorded at North Rona than at Miquelon (Table 3). The CV at Sable Island was much smaller than that of Miquelon or North Rona (Table 4).

Inter-seal Distance: The mean distance between interactants when one performed a HSW was 16.3 cm (SD = 28.5). The distance between interacting seals for this behaviour type was greater at North Rona and Sable Island than Miquelon (Table 5). The CV was smallest at Sable Island and largest at Miquelon (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by females at North Rona (76.4%; $\chi^2 = 29.6$, df = 105, $p \le .05$) and males at Miquelon (94.7%; $\chi^2 = 91.3$, df = 192, $p \le .05$). Either sex was as likely to perform a HSW at Sable Island ($\chi^2 = 1.7$, df = 280, $p = .19$). Subdividing interactions on the basis of the sexes of interactants, I found no significant differences between bouts in the frequency of this behaviour type at Miquelon (F = 0.0, df = 2, 37, $p = .91$), North Rona (F = 21.3, df = 2, 103, $p \le .05$; but $\hat{\omega}^2 = .2$) or Sable Island (F = 1.9, df = 2, 28, $p = .38$).

This behaviour category was performed principally by subadults at Miquelon (90.2%; $\chi^2 = 593.7$, df = 192), mothers at North Rona (67.0%; $\chi^2 = 146.2$, df = 105) and adults at Sable Island (69.0%; $\chi^2 = 43.5$, df = 28).

Behavioural Frequency: The frequency of HSWs was greater at the two breeding sites than at Miquelon (Table 7 and Figure 15).

Context: Finally, the greatest frequency of HSWs occurred during aggressive interactions at Miquelon (F = 32.1, df = 1, 192, $p \le .05$; $\hat{\omega}^2 = .64$), North Rona (F = 23.3, df = 2, 105, $p \le .05$; $\hat{\omega}^2 = .73$) and Sable Island (F = 29.0, df = 2, 28, $p \le .05$; $\hat{\omega}^2 = .83$).

Extend Head (HEX)

Description: The seal slowly extended its head and neck towards the successor in a manner resembling a slow head thrust. The head was usually held in the extended position, rather than rapidly retracted as during a head thrust.

Anatomical Characteristics: The eyes (95.6%; $\chi^2 = 284.6$, df = 341, $p \leq .05$), mouth (87.7%; $\chi^2 = 194.6$, df = 341, $p \leq .05$) and nares (77.4%; $\chi^2 = 28.0$, df = 92, $p \leq .05$) were more likely to be open during this behaviour type (although this was primarily the case when the head extension was performed by a female threatening a nearby male; Table 1). The vibrissae were more likely to be protracted (99.4%; $\chi^2 = 309.9$, df = 319, $p \leq .05$) and the tail was not normally elevated (93.8% down; $\chi^2 = 184.7$, df = 288, $p \leq .05$).

At Miquelon (40.0%; $\chi^2 = 16.4$, df = 48, $p \leq .05$) and Sable Island (44.4%; $\chi^2 = 5.0$, df = 88, $p \leq .05$) the precedents' heads were more likely to be lower than the successor's during a HEX. At North Rona a HEX more likely to occur with the precedent's head at the same height as the successor's (58.7%; $\chi^2 = 64.3$, df = 206, $p \leq .05$).

The interactants' bodies (29.3%; $\chi^2 = 144.2$, df = 341, $p \leq .05$) and heads (42.2%; $\chi^2 = 401.9$, df = 340, $p \leq .05$) were more likely to be facing each other from directly ahead during performance of a HEX.

Vocal Accompaniment: When subdivided by site, this behaviour category was more likely to be performed silently at Miquelon (56.8%; $\chi^2 = 51.1$, df = 48, $p \leq .05$) and with an open mouth whoo at Sable Island (49.4%; $\chi^2 = 67.2$, df = 87, $p \leq .05$). At North Rona a HEX was as likely to be accompanied by an open mouth whoo (39.3%) as by silence (41.3% $\chi^2 = 1.3$, df = 205, $p = .75$).

Duration: The mean duration of this behaviour type was 3.8 seconds (SD = 4.0). The mean duration of HEXs recorded at Sable Island was greater than at North Rona (Table 3). The CV at Sable Island was much larger than that at Miquelon (Table 4).

Inter-seal Distance: The mean distance between interactants when one performed a HEX was 37.4 cm (SD = 69.2). There were no significant differences between the mean inter-seal distances for this behaviour type at any site (Table 5), although the CVs for North Rona and Sable Island were much larger than Miquelon's (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by females at North Rona (61.1%; $\chi^2 = 10.0$, df = 202, $p \leq .05$) and males at Miquelon (77.6%; $\chi^2 = 14.9$, df = 48, $p \leq .05$). There was no significant difference between the numbers of HEXs performed by males or females at Sable Island ($\chi^2 = 0.7$, df = 89, $p = .61$). Subdividing interactions on the basis of the sexes of both interactants, I found that there were no sufficient differences between bout types at Miquelon (F = 1.3, df = 2, 47, $p = .12$), North Rona (F = 5.9, df = 2, 198 $p \leq .05$; but $\hat{\omega}^2 = .11$) or Sable Island (F = 7.1, df = 2, 89 $p \leq .05$; but $\hat{\omega}^2 = .31$).

This behaviour category was performed predominantly by adults at North Rona (54.3%; $\chi^2 = 153.2$, df = 205, $p \leq .05$), Sable Island (52.2%; $\chi^2 = 58.4$, df = 89, $p \leq .05$) and Miquelon (62.0%; $\chi^2 = 55.1$, df = 49, $p \leq .05$).

Behavioural Frequency: The frequency of HEX was greater at Miquelon than either breeding site (Table 7 and Figure 15).

Context: There were no significant differences between sequence types on the basis of behaviour frequency of HEX at Miquelon (F = 1.3, df = 1, 49, $p = .25$), North Rona (F = 3.3, df = 1, 105 $p \leq .05$; but $\hat{\omega}^2 = .11$) or Sable Island (F = 2.4, df = 1, 89, $p = .2$[illegible]).

Nose-to-Nose (NTN)

Description: The precedent and successor touched muzzles, with their vibrissae protracted (Figure 13C). Normally, both partners inhaled and exhaled noticeably several times during the contact.

Anatomical Characteristics: The seal's eyes (98.3%; $\chi^2 = 111.1$, df = 56, $p \leq .05$) and nares (93.0%; $\chi^2 = 45.6$, df = 56, $p \leq .05$) were more likely to be open during this behaviour type and the mouth closed (77.8%; $\chi^2 = 36.1$, df = 116, $p \leq .05$; Table 1). The vibrissae were protracted in all cases and the tail was rarely elevated (8.7%; $\chi^2 = 77.5$, df = 113, $p \leq .05$).

The performer's head was more likely to be the same height as that of the seal at which the NTN was directed at Miquelon (61.5%; $\chi^2 = 4.7$, df = 11, $p \leq .05$) and North Rona (73.6%; $\chi^2 = 77.3$, df = 104, $p \leq .05$). At Sable Island, on the other hand, there was no significant difference between relative head heights ($\chi^2 = 1.6$, df = 3, $p = .45$).

During performance of this behaviour category the two interacting seals were usually lying parallel to each other, facing the same direction, (26.6%; $\chi^2 = 38.0$, df = 116, $p \leq .05$). Their heads were more likely to be oriented face-to-face during a NTN (84.7%; $\chi^2 = 768.3$, df = 119, $p \leq .05$).

Vocal Accompaniment: When subdivided by site, NTNs were more likely to be performed silently at Miquelon (100%) and North Rona (80.9%; $\chi^2 = 312.4$, df = 101, $p \leq .05$), but with either an open mouth whoo (during aggressive interactions) or silently at Sable Island.

Duration: The mean duration of NTNs was 4.2 seconds (SD = 4.5). The mean duration of this behaviour type was greater at Sable Island than Miquelon or North Rona (Table 3). CVs for the two breeding sites were similar and much larger than that for Miquelon (Table 4).

Inter-seal Distance: The distance between interactants when one began to perform an NTN was 3.1 cm (SD = 8.7). The mean distances between interacting seals for this behaviour type were not significantly different between any site (Table 5), although the CV was smaller at Sable Island (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by males at Miquelon (84.6%; $\chi^2 = 6.2$, df = 12, $p \leq .05$), females at North Rona (75.3%; $\chi^2 = 18.7$, df = 72, $p \leq .05$) and either sex at Sable Island ($\chi^2 = 1.0$, df = 3, $p = .32$). Subdividing interactions on the basis of the sexes of both interactants, I found that males performed NTNs more frequently when interacting with other males than with females or than when females engaged in NTN together, at North Rona ($F = 88.8$, df = 2, 39; $\hat{\omega}^2 = .71$). There were no significant differences at Miquelon (Kruskal-Wallis $H = 9.1.0$, df = 1, 12, $p = .22$) or Sable Island (Kruskal-Wallis $H = 4.0$, df = 2, 3 $p = .16$).

This behaviour category was performed primarily by mothers at North Rona (41.5%; $\chi^2 = 30.7$, df = 103, $p \leq .05$) and Sable Island (60.0%; $\chi^2 = 5.0$, df = 3, $p \leq .05$). There were no significant differences between the number of NTNs performed by adults or subadults at Miquelon ($\chi^2 = 2.9$, df = 11, $p = .23$).

Behavioural Frequency: There were no significant differences among the frequencies of NTNs at any site (Table 7 and Figure 15).

Context: There were insufficient differences between sequence types on the basis of behaviour frequency of NTN at Miquelon (Kruskal-Wallis $H = 7.4$, df = 1, 12, $p = .9$), North Rona ($F = 20.9$, df = 2, 105, $p \leq .05$; but $\hat{\omega}^2 = .46$) or Sable Island (Kruskal-Wallis $H = 0.1$, df = 2, 4, $p = .09$).

Poke With Nose (PON)

Description: The precedent pushed the tip of its snout against the body of the successor. It was frequently performed by pups against their mothers' sides as an apparent instigation action prior to nursing.

Anatomical Characteristics: The seal's eyes were usually open (93.3%; $\chi^2 = 78.9$, df = 104, $p \leq .05$) and its mouth closed (88.0%; $\chi^2 = 50.3$, df = 91, $p \leq .05$; Table 1). The vibrissae were normally protracted (99.0%; $\chi^2 = 98.0$, df = 15, $p \leq .05$) and the tail was not elevated (14.3%; $\chi^2 = 46.4$, df = 90, $p \leq .05$). The nares were always open.

At North Rona, the precedent's head was most likely to be lower than that of the seal at which the PON was directed (48.3%; $\chi^2 = 9.2$, df = 89, $p \leq .05$). At Miquelon all precedents' heads were higher when they performed a PON. Finally, there was no significant difference in relative head heights at Sable Island ($\chi^2 = 1.4$, df = 14, $p \leq .05$).

The interactants' bodies were more likely to be either facing perpendicularly towards (20.2%), or parallel in the same direction (22.9%) during the performance of this behaviour type ($\chi^2 = 36.4$, df = 101, $p \leq .05$). As the seal poked the successor it was more likely to do so with its head facing towards the successor's obliquely from behind (23.0%; $\chi^2 = 14.9$, df = 101, $p \leq .05$).

Vocal Accompaniment: This behaviour type was usually performed silently at Miquelon (100%), North Rona (96.6%; $\chi^2 = 419.7$, df = 87, $p \leq .05$) and Sable Island (86.7%; $\chi^2 = 52.9$, df = 14, $p \leq .05$).

Duration: The mean duration of this behaviour type was 7.1 seconds (SD = 7.2). The durations for this behaviour type were not significantly different at any site (Table 3), although the CV at Miquelon was smaller than those of the breeding sites (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a PON was 2.5 cm (SD = 5.9). The mean distance between interacting seals for this behaviour type was greater at Sable Island than North Rona and Miquelon (Table 5), and the CV was much smaller (Table 6).

Sex and Age Characteristics: This behaviour type was performed solely by males at Miquelon and Sable Island, but primarily females at North Rona (82.1%; $\chi^2 = 16.0$, df = 38, $p \leq .05$). Subdividing interactions on the basis of the sexes of both interactants, I found no significant differences at any site. This category was performed by adults or subadults at Miquelon ($\chi^2 = 1.5$, df = 2, $p = .6$) and pups at North Rona (57%; $\chi^2 = 78.5$, df = 89, $p \leq .05$) and Sable Island (100%).

Behavioural Frequency: There were no significant differences between the weighted frequency of PONs at any site (Table 7 and Figure 15).

Context: Most PONs occurred during mother/pup interactions at breeding sites and play at Miquelon.

Sniff (SNI)

Description: The precedent inhaled and exhaled several times and typically with the tip of its snout in close proximity to, or directed towards, the successor.

Anatomical Characteristics: The eyes were normally open (94.4%; $\chi^2 = 14.2$, df = 17, $p \leq .05$) and the mouth was always closed during this behaviour type (Table 1). The vibrissae were always protracted and the tail rarely elevated (5.9%; $\chi^2 = 13.2$, df = 16, $p \leq .05$).

There were no significant differences between the relative heights of the performers' heads during SNIs at Miquelon (one case), North Rona ($\chi^2 = 2.7$, df = 13, $p = .1$) and Sable Island ($\chi^2 = 0.0$, df = 1, $p = 1$).

The interactants' bodies were more likely to be oriented parallel in the same direction (27.8%) or facing towards from obliquely ahead during a SNI (22.2%; $\chi^2 = 18.7$, df = 9, $p \leq .05$). There were no significant differences between the frequencies of relative head orientation categories ($\chi^2 = 13.1$, df = 9, $p = .21$).

Vocal Accompaniment: This behaviour type was never heard to be accompanied by a vocalisation.

Duration: The mean duration of this behaviour type was 4.0 seconds (SD = 4.8). The mean durations for this behaviour type were not significantly different at any site (Table 3). The CV at North Rona was much larger than at the other sites (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a SNI was 28.9 cm (SD = 62.7). The distances between interacting seals for this behaviour type were not significantly different between any two sites (Table 5), although the CV for North Rona was much higher than Sable Island (Table 6).

Sex and Age Characteristics: This category was performed predominantly by females at North Rona (80.0%; $\chi^2 = 5.4$, df = 14, $p \leq .05$) and males at Sable Island (two cases), and Miquelon (one case). Subdividing interactions on the basis of the sexes of both interactants, I found that SNIs were performed by females more frequently when interacting with females than with males at North Rona (Kruskal-Wallis H = 6.4.0, df = 2, 13, $p = .04$). There were no differences at Miquelon (n=1) or Sable Island (n=1).

This behaviour category was performed predominantly by mothers at North Rona ($\chi^2 = 26.7$, df = 13, $p \leq .05$) and adults at Sable Island (two cases) and Miquelon (one case).

Behavioural Frequency: There were no significant differences between the frequency of SNIs at any site (Table 7 and Figure 15).

Context: Further, there were no significant differences among the frequencies of SNIs subdivided by sequence type at any site.

Glance (GLA)

Description: The precedent looked briefly in the direction of the successor for one second or less. The precedent's eyes were oriented towards the successor, usually by a turn of the precedent's head. A Glance could also be as subtle as only shifting its eyes to look sidelong at the successor while maintaining its relative head orientation.

Anatomical Characteristics: The mouth (66.2%; $\chi^2 = 36.2$, df = 352, $p \leq .05$) and nares (77.8%; $\chi^2 = 23.6$, df = 35, $p \leq .05$) were more likely to be closed during this behaviour type (Table 1). The vibrissae were usually protracted (60.6%; $\chi^2 = 11.0$, df = 245, $p \leq .05$) and the tail was not normally elevated (94.2%; $\chi^2 = 255.4$, df = 326, $p \leq .05$).

The precedent's head was more likely to be the same height as that of the successor at North Rona (49.4%; $\chi^2 = 33.0$, df = 231, $p \leq .05$). A GLA was as likely to occur with the precedent's head at any height relative to the successor's at Miquelon ($\chi^2 = 1.4$, df = 55, $p = .5$) and Sable Island ($\chi^2 = 1.6$, df = 57, $p = .7$).

The seals' bodies were most likely to be facing each other from directly ahead (18.6%) or parallel to each other and oriented in the same direction (18.6%; $\chi^2 = 140.5$, df = 348, $p \leq .05$). Interactants' heads (22.0%; $\chi^2 = 321.3$, df = 348, $p \leq .05$) were more likely to be facing each other from directly ahead.

Vocal Accompaniment: A GLA was performed silently at Miquelon (94.6%; $\chi^2 = 245.2$, df = 55, $p \leq .05$), North Rona (73%; $\chi^2 = 478.5$, df = 237, $p \leq .05$) and Sable Island (96%; $\chi^2 = 256.5$, df = 58, $p \leq .05$).

Duration: The duration of this behaviour type was, by definition, one sec, and thus its mean durations were not significantly different between sites.

Inter-seal Distance: The mean distance between interactants when a seal glanced at another was 51.5 cm (SD = 89.1). The distance between interacting seals for this behaviour type was greater at Sable Island than Miquelon or North Rona (Table 5), although the CV was also larger (Table 6).

Sex and Age Characteristics: This behaviour type was performed more often by females at North Rona (57.1%; $\chi^2 = 4.6$, df = 223, $p \leq .05$) and by males at Miquelon (76.8%; $\chi^2 = 16.1$, df = 55, $p \leq .05$) and Sable Island (66.1%; $\chi^2 = 6.1$, df = 58, $p \leq .05$). Subdividing bouts on the basis of the sexes of both interactants, I found no sufficient differences between the frequencies of GLA during any bout type at Miquelon (F = 0.4, df = 2, 52; $p = .26$), North Rona (F = 20.8, df = 2, 210, $p \leq .05$; but $\hat{\omega}^2 = .14$) or Sable Island (F = 3.9, df = 1, 57; but $\hat{\omega}^2 = .25$).

This behaviour category was performed more often by adults at Miquelon (75.0%; $\chi^2 = 90.7$, df = 55, $p \leq .05$), North Rona (55.6%; $\chi^2 = 190.9$, df = 238, $p \leq .05$) and Sable Island (67.8%; $\chi^2 = 84.2$, df = 58, $p \leq .05$).

Behavioural Frequency: The mean frequency of GLAs at Miquelon was greater than that at North Rona and Sable Island (Table 7 and Figure 15).

Context: A GLA was performed as frequently during any sequence type at Miquelon (F = 5.2, df = 1, 56, $p \leq .05$; but $\hat{\omega}^2 = .31$), North Rona (F = 4.7, df = 3, 240, $p \leq .05$; but $\hat{\omega}^2 = .09$) and Sable Island (F = 2.4, df = 3, 58, $p = .16$).

Stare (STA)

Description: The precedent looked at the successor for several seconds or more. The precedent 's eyes were oriented towards the successor, usually by a turn of the precedent's head.

Anatomical Characteristics: The mouth was usually closed (56.3%; $\chi^2 = 17.5$, df = 1137, $p \leq .05$) during this behaviour type, although it was more likely to be open when the precedent and successor were within a short distance of one another (Table 1). The vibrissae were more likely to be protracted (57.0%; $\chi^2 = 16.5$, df = 840, $p \leq .05$) and the tail was not normally elevated (92.5%; $\chi^2 = 768.1$, df = 1062, $p \leq .05$). The nares were usually closed (77.0%; $\chi^2 = 95.6$, df = 147, $p \leq .05$).

The precedent's head was most likely to be at the same height as the successor's at North Rona (40.4%; $\chi^2 = 21.8$, df = 606, $p \leq .05$) and Sable Island (41.1%; $\chi^2 = 9.2$, df = 339, $p \leq .05$). Relative head heights were not significantly different at Miquelon ($\chi^2 = 1.4$, df = 184, $p = .5$).

During a STA, the precedent's body was more often oriented towards the successor's (towards perpendicular 16.6%, from obliquely ahead 15.0% and parallel in the same direction 17.2%; $\chi^2 = 231.0$, df = 1153, $p \leq .05$). Interactants' heads were more likely to be oriented facing directly towards each other (20.5%; $\chi^2 = 141.9$, df = 1163, $p \leq .05$).

Vocal Accompaniment: A STA was more likely to be performed silently at Miquelon (83.8%; $\chi^2 = 561.6$, df = 184, $p \leq .05$), North Rona (60.8%; $\chi^2 = 869.7$, df = 632, $p \leq .05$) and Sable Island (87.8%; $\chi^2 = 1224.0$, df = 338, $p \leq .05$).

Duration: The mean duration of this behaviour type was 5.7 seconds (SD = 6.7). STA durations were greater at Sable Island than at North Rona (Table 3). The CVs were similar (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a STA was 110.7 cm (SD = 190.5,). The mean distance between interacting seals for this behaviour type was greater at North Rona and Sable Island (which were themselves not significantly different) than at Miquelon (Table 5). The CVs were also relatively large compared with those of other behaviour types (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by females at North Rona (65.9%; $\chi^2 = 60.2$, df = 689, $p \leq .05$), and by males at Miquelon (77.3%; $\chi^2 = 52.4$, df = 175, $p \leq .05$) and Sable Island (75.5%; $\chi^2 = 87.3$, df = 334, $p \leq .05$). Subdividing interactions on the basis of the sexes of both interactants, I found that STAs were performed more frequently during male-male bouts at North Rona (F = 15.9, df = 2, 576; $\hat{\omega}^2 = .63$) and Sable Island (F = 27.9, df = 2, 334; $\hat{\omega}^2 = .72$). There were no significant differences between bout types at Miquelon (F = 2.2, df = 2, 166, $p = .2$).

This behaviour category was performed mainly by adults (47.2%) and mothers at North Rona (45.9%; $\chi^2 = 746.7$, df = 634, $p \leq .05$) and adults at Miquelon (62.4%; $\chi^2 = 208.6$, df = 183, $p \leq .05$) and Sable Island (75.4%; $\chi^2 = 653.3$, df = 339, $p \leq .05$).

Behavioural Frequency: There were no significant differences between the frequencies of STAs at any site (Table 7 and Figure 15).

Context: The greatest frequency of STA occurred during aggressive interactions at Miquelon (F = 22.3, df = 1, 185, $p \leq .05$; $\hat{\omega}^2 = .7$). Staring was as frequent during aggressive, mother/pup or copulatory bouts at North Rona (F = 6.9, df = 3, 635, $p \leq .05$; but $\hat{\omega}^2 = .19$) and Sable Island (F = 1.0, df = 2, 340, $p = .67$).

Look Away (LAW)

Description: The precedent looked away from the successor by turning its head in the coronal plane, often to watch a third seal.

Anatomical Characteristics: The mouth (79.2%; $\chi^2 = 272.3$, df = 800, $p \leq .05$) was more likely to be open during this behaviour type (Table 1). The vibrissae were usually retracted (66.0%; $\chi^2 = 60.8$, df = 593, $p \leq .05$) and the tail rarely elevated (95.3%; $\chi^2 = 628.8$, df = 765, $p \leq .05$). The nares were as likely to be open as closed ($\chi^2 = 0.1$, df = 74, $p = .9$).

There was no one height at which the performer's head was more likely to be than any other during a LAW at Miquelon ($\chi^2 = 3.1$, df = 119, $p = .2$), North Rona ($\chi^2 = 2.1$, df = 469, $p = .3$) and Sable Island ($\chi^2 = 0.8$, df = 223, $p = .52$).

The interactants' bodies were more likely to be oriented parallel, facing the same direction, during a LAW (28.0%; $\chi^2 = 119.1$, df = 819, $p \leq .05$). Their heads were usually facing perpendicularly away (21.4%; $\chi^2 = 89.2$, df = 817, $p \leq .05$)

Vocal Accompaniment: When a precedent looked away it was more likely to do so silently at Miquelon (100%), North Rona (81.9%; $\chi^2 = 1455.6$, df = 479, $p \leq .05$) and Sable Island (95.9%; $\chi^2 = 984.7$, df = 223, $p \leq .05$).

Duration: The mean duration of this behaviour type was 10.8 seconds (SD = 54.8). The duration was greater for LAWs recorded at Sable Island than at North Rona (Table 3). The CVs were much larger at the two breeding sites than at Miquelon (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a LAW was 64.2 cm (SD = 161.3). The distance between interacting seals for this behaviour type was greater at Sable Island than Miquelon and North Rona (which were themselves not significantly different; Table 5). The CV was largest at North Rona (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by males at Miquelon (82.0%; $\chi^2 = 45.4$, df = 110, $p \leq .05$), and by females at North Rona (76.9%; $\chi^2 = 123.6$, df = 428, $p \leq .05$). The difference was not significant at Sable Island ($\chi^2 = 0.4$, df = 221, $p = .16$). Subdividing interactions on the basis of the sexes of both interactants, I found that LAWs were performed most frequently during male-male bouts at North Rona (F = 15.9, df = 2, 358, $p \leq .05$; $\hat{\omega}^2 = .62$) and Sable Island (F = 28.9, df = 2, 209, $p \leq .05$; $\hat{\omega}^2 = .72$). There were not sufficient differences at Miquelon (F = 1.1, df = 2, 100, $p \leq .05$; $\hat{\omega}^2 = .11$).

This behaviour category was performed mainly by mothers at North Rona (59.3%; $\chi^2 = 146.7$, df = 480, $p \leq .05$), adults (50%) and mothers (48.7%) at Sable Island ($\chi^2 = 319.2$, df = 222, $p \leq .05$), and subadults at Miquelon (50.4%; $\chi^2 = 15.9$, df = 119, $p \leq .05$).

Behavioural Frequency: There were no significant differences between the frequency of LAWs at any site (Table 7 and Figure 15).

Context: The greatest frequency of LAW occurred during aggressive interactions at Miquelon (F = 23.0, df = 2, 120, $p \leq .05$; $\hat{\omega}^2 = .82$) and Sable Island (F = 15.2, df = 2, 224, $p \leq .05$; $\hat{\omega}^2 = .67$), and aggressive or mother/pup interactions at North Rona (F = 25.9, df = 3, 481, $p \leq .05$; $\hat{\omega}^2 = .8$)

Bite (BIT)

Description: The precedent extended its head and bit the successor. This was in the form of either a brief nip, or a BIT of greater duration with some twisting of the performer's neck and head. Bites rarely resulted in significant injury.

Anatomical Characteristics: The seal's eyes (88.2%; $\chi^2 = 177.0$, df = 303, $p \leq .05$) were more likely to be open during this behaviour type (Table 1). The vibrissae were more likely to be protracted (97.6%; $\chi^2 = 188.4$, df = 207, $p \leq .05$) and the tail was not normally elevated (88.4%; $\chi^2 = 168.3$, df = 254, $p \leq .05$). The nares were normally closed (89.5%; $\chi^2 = 35.5$, df = 56, $p \leq .05$).

At Sable Island, a BIT was most likely to occur with the precedent's head lower than the successor's (46.1%; $\chi^2 = 5.5$, df = 75, $p \leq .05$). At Miquelon ($\chi^2 = 2.9$, df = 100, $p = .4$) and North Rona ($\chi^2 = 4.1$, df = 141, $p = .32$) there were no significant differences.

The seals' bodies were usually parallel to each other, facing the same direction, during a BIT (26.8%; $\chi^2 = 100.6$, df = 311, $p \leq .05$), while the precedents' heads were more likely to be oriented facing perpendicularly towards the successors' (77.8%; $\chi^2 = 41.4$, df = 312, $p \leq .05$).

Vocal Accompaniment: A BIT was more likely to be performed silently at Miquelon (99.0%; $\chi^2 = 493.1$, df = 100, $p \leq .05$), North Rona (73.8%; $\chi^2 = 296.2$, df = 125, $p \leq .05$) and Sable Island (83.1%; $\chi^2 = 206.4$, df = 64, $p \leq .05$).

Duration: The mean duration of this behaviour type was 3.0 seconds (SD = 3.7). The mean duration was greater for BITs recorded at Miquelon than at North Rona or Sable Island (Table 3). The CV was largest at North Rona (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a BIT was 5.3 cm (SD = 17.0). There were no significant differences among the mean inter-seal distances for this behaviour type at any site (Table 5) and the CVs indicated high variability in this measure (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by males at Miquelon (72.8%; $\chi^2 = 19.2$, df = 91, $p \leq .05$) and Sable Island (75.0%; $\chi^2 = 19.0$, df = 75, $p \leq .05$), but either sex at North Rona (53.3%; $\chi^2 = 0.6$, df = 138, $p \leq .05$). Subdividing interactions on the basis of the sexes of both interactants, BITs were not performed more frequently during any one sequence type at Miquelon (F = 2.9, df = 2, 85, $p = .3$), North Rona (F = 0.8, df = 2, 135, $p = .62$) or Sable Island (F = 7.8, df = 2, 75, $p \leq .05$; but $\hat{\omega}^2 = .08$).

This behaviour category was performed exclusively by adults at North Rona (78.5%; $\chi^2 = 59.6$, df = 142, $p \leq .05$) and Sable Island (78.2%; $\chi^2 = 116.4$, df = 75, $p \leq .05$) and subadults at Miquelon (63.4%; $\chi^2 = 118.7$, df = 99, $p \leq .05$).

Behavioural Frequency: There were no significant differences between the weighted frequency of BITs at any site (Table 7 and Figure 15).

Context: The greatest frequency of biting occurred during aggressive interactions at Miquelon (F = 57.1, df = 1, 100, $p \leq .05$; $\hat{\omega}^2 = .75$) and North Rona (F = 12.1, df = 3, 143, $p \leq .05$; $\hat{\omega}^2 = .7$). BITs were as frequent during aggressive as copulatory bouts at Sable Island (F = 2.6, df = 3, 75, $p = .23$).

Climb (CLI)

Description: Using foreflippers to pull itself up, the precedent climbed onto the hind flippers or body of the successor.

Anatomical Characteristics: The precedent's eyes (99.6%; $\chi^2 = 219.0$, df = 222, $p \leq .05$) and mouth (65.6%; $\chi^2 = 20.9$, df = 214, $p \leq .05$) were more likely to be open during a CLI (Table 2). The vibrissae were usually protracted (89.4%; $\chi^2 = 104.7$, df = 168, $p \leq .05$) and the tail was rarely elevated (5.3%; $\chi^2 = 164.3$, df = 205, $p \leq .05$). The nares were as likely to be open as closed ($\chi^2 = 2.6$, df = 13, $p = .1$).

The precedent's head was more likely to be higher than that of the successor at the start of a CLI at Miquelon (96.2%; $\chi^2 = 184.7$, df = 103, $p \leq .05$), North Rona (87.9%; $\chi^2 = 86.4$, df = 63, $p \leq .05$) and Sable Island (90.9%; $\chi^2 = 82.0$, df = 74, $p \leq .05$).

The interactant's body was more likely to be oriented perpendicularly towards the successor as it began a CLI (32.6%; $\chi^2 = 127.0$, df = 213, $p \leq .05$). On the other hand, the seals' heads were more likely to be facing perpendicularly away from each other (40.2%; $\chi^2 = 224.7$, df = 214, $p \leq .05$).

Vocal Accompaniment: A CLI was usually performed without an accompanying vocalisation at Miquelon (100% silent), North Rona (98.4%; $\chi^2 = 303.3$, df = 64, $p \leq .05$) or Sable Island (96.3%; $\chi^2 = 241.6$, df = 52, $p \leq .05$).

Duration: The mean duration of this behaviour type was 8.1 seconds (SD = 9.8). The duration was greater for CLIs recorded at Sable Island than at Miquelon (Table 3). The CV at North Rona was larger than the other sites (Table 4).

Inter-seal Distance: The mean distance between interactants when the precedent began to perform a CLI was 2.3 cm (SD = 6.3). There were no significant differences between the mean inter-seal distances at the start of a CLI at any study site (Table 5), and the CVs were relatively large at all sites (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by males at Miquelon (79.2%; $\chi^2 = 24.0$, df = 76, $p \leq .05$), North Rona (79.7%; $\chi^2 = 22.6$, df = 63, $p \leq .05$) and Sable Island (78.2%; $\chi^2 = 17.5$, df = 54, $p \leq .05$). Subdividing interactions on the basis of the sexes of both interactants, I found no significant differences between the behaviour frequency of any bout types at Miquelon (F = 0.5, df = 2, 54, $p = .41$), North Rona (F = 1.1, df = 2, 50, $p = .36$) or Sable Island (F = 0.4, df = 2, 54, $p = .42$).

This behaviour category was performed exclusively by adults at North Rona (78.5%; $\chi^2 = 138.9$, df = 62, $p \leq .05$) and Sable Island (78.2%; $\chi^2 = 116.4$, df = 54, $p \leq .05$), and by subadults at Miquelon (84.6%; $\chi^2 = 271.2$, df = 99, $p \leq .05$).

Behavioural Frequency: There were no significant differences between the frequency of climbing at any site (Table 7 and Figure 15).

Context: The greatest frequency of climbing occurred during aggressive interactions at North Rona (F = 22.8, df = 2, 64, $p \leq .05$; $\hat{\omega}^2 = .66$). The differences between the frequency of CLI during aggressive or play sequences were not significant at Miquelon or Sable Island (F = 2.9, df = 3, 54, $p = .15$).

Clasp (CLA)

Description: The precedent pulled itself laterally against the successor, and clasped the successor with the claws and palmar surfaces of one or both foreflippers (Figure 13D). Clasping always preceded, and accompanied, the prolonged intromission of copulation, and was performed exclusively by males at all three study sites (including Miquelon, although these were subadult males at play).

Anatomical Characteristics: The seal's eyes (88.6%; $\chi^2 = 67.9$, df = 113, $p \leq .05$) were more likely to be open during this behaviour type and the tail was not normally elevated (2.8%; $\chi^2 = 96.3$, df = 107, $p \leq .05$; Table 2). There were no significant differences in the position of the vibrissae ($\chi^2 = 2.4$, df = 70, $p = .1$), mouth ($\chi^2 = 2.6$, df = 108, $p = .1$) or nares ($\chi^2 = .2$, df = 17, $p = .6$).

The precedent's head was more likely to be higher than that of the successor at North Rona (61.3%; $\chi^2 = 26.5$, df = 72, $p \leq .05$) and Sable Island (77.5%; $\chi^2 = 35.1$, df = 38, $p \leq .05$). There were no significant differences at Miquelon (too few cases).

Seals' bodies (91.5%; $\chi^2 = 871.4$, df = 110, $p \leq .05$) and heads (69.5%; $\chi^2 = 464.0$, df = 111, $p \leq .05$) were most likely to be oriented parallel to each other while facing the same direction during performance of this behaviour category.

Vocal Accompaniment: A CLA was predominantly performed silently at Miquelon (100% silent), North Rona (98.7%; $\chi^2 = 363.1$, df = 74, $p \leq .05$) and Sable Island (100%).

Duration: The mean duration of this behaviour type was 49.5 seconds (SD = 220.0; the second largest overall). There were no significant differences between the mean durations of CLA at any site (Table 3), although the CVs at the two breeding sites were much larger than that at Miquelon (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a CLA was 0.5 cm (SD = 3.1). The distance between interacting seals for this behaviour type was not significantly different between the three sites (Table 5), although the CVs were much greater at the North Rona and Sable Island (Table 6).

Sex and Age Characteristics: Subdividing interactions on the basis of interactant sex, I found that CLAs were performed exclusively by males when interacting with females at North Rona and Sable Island. There were no adult bouts at Miquelon and too few subadult bouts to analyze. This behaviour category was performed exclusively by adults at North Rona and Sable Island, but subadults at Miquelon.

Behavioural Frequency: There were no significant differences between the frequency of CLAs at any site (Table 7 and Figure 15).

Context: The greatest frequency of CLAs occurred during aggressive interactions at North Rona ($F = 19.4$, $df = 1, 74$, $p \leq .05$; $\hat{\omega}^2 = .67$) and Sable Island ($F = 90.1$, $df = 1, 39$, $p \leq .05$; $\hat{\omega}^2 = .82$), but always during play at Miquelon.

Approach or Turn Towards (APT)

Description: The precedent either moved, or turned its body, towards the successor thereby reducing the distance between them.

Anatomical Characteristics: The seal's eyes (98.8%; $\chi^2 = 630.4$, $df = 661$, $p \leq .05$) were more likely to be open during this behaviour type (Table 1). The vibrissae were usually protracted (62.6%; $\chi^2 = 28.4$, $df = 448$, $p \leq .05$) and the tail was not normally elevated (14.6%; $\chi^2 = 289.0$, $df = 575$, $p \leq .05$). The mouth was as likely to be open as closed ($\chi^2 = 0.6$, $df = 648$, $p \leq .05$), but the nares were usually closed (67.0%; $\chi^2 = 10.6$, $df = 90$, $p \leq .05$).

At Miquelon the precedent's head was most likely to be higher than the successor's (51.2%; $\chi^2 = 14.7$, $df = 86$, $p \leq .05$), whereas at North Rona this behaviour type was more likely to occur with the precedent's head at the same height as the successor's (46.8%; $\chi^2 = 35.2$, $df = 375$, $p \leq .05$). There was no significant difference at Sable Island ($\chi^2 = 3.7$, $df = 195$, $p \leq .05$).

During an APT most seals were likely to do so with their bodies (82.5%; $\chi^2 = 70.1$, $df = 661$, $p \leq .05$) and heads (62.5%; $\chi^2 = 297.3$, $df = 661$, $p \leq .05$) oriented directly towards each other from directly or obliquely ahead.

Vocal Accompaniment: An APT was usually performed silently at Miquelon (89.7%; $\chi^2 = 333.7$, $df = 85$, $p \leq .05$), North Rona (71.0%; $\chi^2 = 799.5$, $df = 382$, $p \leq .05$) and Sable Island (86.2%; $\chi^2 = 682.8$, $df = 194$, $p \leq .05$).

Duration: The mean duration of this behaviour type was 3.2 seconds (SD = 3.3). The duration was greater for APTs recorded at Sable Island than at either Miquelon or North Rona (Table 3), and the CV was also lowest at Sable Island (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform an APT was 144.3 cm (SD = 280.6). The distance between interacting seals for this behaviour type was greater at North Rona and Sable Island (themselves not significantly different) than Miquelon (Table 5). The CV was greatest at North Rona (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by males at Miquelon (83.0%; $\chi^2 = 38.2$, df = 87, $p \leq .05$) and Sable Island (78.8%; $\chi^2 = 62.9$, df = 188, $p \leq .05$). The differences between the sexes was not significant at North Rona ($\chi^2 = 0.6$, df = 339, $p = .49$). Subdividing interactions on the basis of the sexes of both interactants, I found that there were no sufficient differences at Miquelon (F = 0.4, df = 2, 85, $p = .31$), North Rona (F = 10.2, df = 2, 313, $p \leq .05$; but $\hat{\omega}^2 = .2$) or Sable Island (F = 4.8, df = 2, 185, $p \leq .05$; but $\hat{\omega}^2 = .13$).

This behaviour category was performed predominantly by adults at Miquelon (64.8%; $\chi^2 = 110.3$, df = 86, $p \leq .05$), North Rona (51.4%; $\chi^2 = 237.7$, df = 381, $p \leq .05$) and Sable Island (77.2%; $\chi^2 = 402.2$, df = 194, $p \leq .05$).

Behavioural Frequency: There were no significant differences between the frequency of APT at any site (Table 7 and Figure 15).

Context: The greatest frequency of APT occurred during aggressive interactions at Miquelon (F = 12.3, df = 1, 87, $p \leq .05$; $\hat{\omega}^2 = .6$), North Rona (F = 27.1, df = 3, 384, $p \leq .05$; $\hat{\omega}^2 = .68$) and Sable Island (F = 27.8, df = 3, 196, $p \leq .05$; $\hat{\omega}^2 = .8$).

Chase (CHA)

Description: The precedent chased the successor at a rapid pace.

Anatomical Characteristics: The eyes (100%) and mouth (77.1%; $\chi^2 = 14.1$, df = 47, $p \leq .05$) were more likely to be open during a CHA (Table 2). The vibrissae were more likely to be protracted (72.7%; $\chi^2 = 4.5$, df = 21, $p \leq .05$) and the tail was not usually elevated (27.8%; $\chi^2 = 7.1$, df = 35, $p \leq .05$). The nares were as likely to be open (50%) as closed ($\chi^2 = 2.0$, df = 1, $p = .2$).

The precedent's head was most likely to be at the same height as that of the successor at North Rona (60.0%; $\chi^2 = 6.4$, df = 19, $p \leq .05$). The differences were not significant at Miquelon ($\chi^2 = 0.4$, df = 4, $p = .8$) or Sable Island ($\chi^2 = 2.4$, df = 22, $p = .3$).

Both the body (60.9%; $\chi^2 = 53.5$, df = 41, $p \leq .05$) and head (60.9%; $\chi^2 = 53.5$, df = 40, $p \leq .05$) were usually oriented facing toward the successor from behind during performance of this behaviour category.

Vocal Accompaniment: When subdivided by site, CHAs were most likely to be performed silently at Miquelon (100%), North Rona (82.7%; $\chi^2 = 17.7$, df = 18, $p \leq .05$) and Sable Island (100%).

Duration: The mean duration of this behaviour type was 6.5 seconds (SD = 10.3). The duration was greater for CHAs recorded at Miquelon than both North Rona and Sable Island (Table 3). The CV was also larger at Miquelon (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a CHA was 251.1 cm (SD = 329.3; the second largest). The mean distances between interacting seals for this behaviour type were not significantly different between study sites (Table 5), although the CV at Sable Island was smaller than the other sites (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by males at North Rona (75.0%; $\chi^2 = 5.0$, df = 19, $p \leq .05$) and Sable Island (100%), but by either sex at Miquelon ($\chi^2 = 0.0$, df = 3, $p = 1$). Subdividing interactions on the basis of the sexes of both interactants, I found no significant differences at Miquelon (Kruskal-Wallis H = 3.6, df = 1, 2, $p = .17$), North Rona (Kruskal-Wallis H = 31.0, df = 1, 19, $p = .9$) or Sable Island (F = 0.03, df = 2, 54, $p = .57$).

This behaviour category was performed principally by adults at North Rona (80.0%; $\chi^2 = 45.0$, df = 19, $p \leq .05$) and Sable Island (100%), but by subadults at Miquelon (80.0%; $\chi^2 = 11.2$, df = 4, $p \leq .05$).

Behavioural Frequency: CHAs were performed with greater frequency at Sable Island than at North Rona or Miquelon, and the latter two frequencies were not significantly different (Table 7 and Figure 15).

Context: There were no sufficient differences between sequence types on the basis of the frequency of chasing at Miquelon (Kruskal-Wallis H = 3.6, df = 1, 3, $p = .16$), North Rona (F = 0.7, df = 1, 19, $p = .48$) or Sable Island (all aggressive).

Roll Away (ROA)

Description: The precedent rolled away, around the longitudinal axis of its body, from the successor (Figure 14A).

Anatomical Characteristics: The precedent's eyes were more likely to be open (74.6%; $\chi^2 = 15.2$, df = 693, $p \leq .05$) and the vibrissae retracted (71.4%; $\chi^2 = 9.0$, df = 477, $p \leq .05$) during this behaviour type (Table 2). The mouth was usually closed (76.7%; $\chi^2 = 17.1$, df = 675, $p \leq .05$), the tail always depressed and the nares always closed.

At North Rona, the precedent's head was more likely to be at the same height as that of the successor (54.5%; $\chi^2 = 4.5$, df = 20, $p \leq .05$). At Sable Island, on the other hand, the precedent's head was more likely to be either lower or the same height during a ROA than higher (47.1%; $\chi^2 = 7.1$, df = 32, $p \leq .05$). The precedent's head was more likely to be lower at Miquelon (71.4%; $\chi^2 = 4.6$, df = 6, $p \leq .05$).

Interactants' bodies (30.6%; $\chi^2 = 15.2$, df = 55, $p \leq .05$) and heads (30.6%; $\chi^2 = 15.2$, df = 54, $p \leq .05$) were most likely to be oriented parallel, facing the same direction.

Vocal Accompaniment: When subdivided by site, this behaviour type was more likely to be performed silently at Miquelon (100%), North Rona (68.2%; $\chi^2 = 42.0$, df = 20, $p \leq .05$) and Sable Island (100%).

Duration: The mean duration of this behaviour type was 4.0 seconds (SD = 2.8). The mean duration was not significantly different among the three sites (Table 3), although the CV at North Rona was much larger than at Miquelon or Sable Island (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a ROA was 198.8 cm (SD = 300.4). The distance between interacting seals for this behaviour type was larger at Sable Island than Miquelon or North Rona (Table 5). The CV was largest at North Rona (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by females at North Rona (71.4%; $\chi^2 = 5.8$, df = 20, $p \leq .05$) and males at Sable Island (94.1%; $\chi^2 = 26.5$, df = 33, $p \leq .05$). The difference was not significant at Miquelon ($\chi^2 = 3.6$, df = 3, $p = .06$). Subdividing interactions on the basis of the sexes of both interactants, I found that ROAs were not performed any more frequently during any bout type at Miquelon (Kruskal-Wallis H = 4.1, df = 1, 4, $p = .13$), North Rona (F = 5.1, df = 2, 19, $p \leq .05$; but $\hat{\omega}^2 = .3$) or Sable Island (F = 1.3, df = 2, 33, $p = .67$).

This behaviour category was more likely to be performed by adults or mothers at North Rona (65% and 33%; $\chi^2 = 26.7$, df = 21, $p \leq .05$), by adults at Sable Island (97.1%; $\chi^2 = 126.2$, df = 33, $p \leq .05$), and by subadults at Miquelon (71.4%; $\chi^2 = 11.6$, df = 6, $p \leq .05$).

Behavioural Frequency: There were no significant differences between the frequency of ROAs at any site (Table 7 and Figure 15).

Context: The greatest frequency of ROA occurred during aggressive interactions at Miquelon (Kruskal-Wallis H = 8.6, df = 1, 6, $p \leq .05$) and North Rona (F = 11.8, df = 2, 21, $p \leq .05$; $\hat{\omega}^2 = .71$). A ROA was as frequent during an aggressive as a copulatory bout at Sable Island (F = 0.3, df = 3, 31, $p = .73$).

Depart or Turn Away (DPA)

Description: The precedent either crawled or turned its body away from the successor, thereby increasing the distance between them.

Anatomical Characteristics: The precedent's eyes (74.6%; $\chi^2 = 15.2$, df = 693, $p \leq .05$) were more likely to be open during this behaviour type (Table 2). The vibrissae were usually protracted (57.9%; $\chi^2 = 12.1$, df = 477, $p \leq .05$) and the tail was not normally elevated (20.3%; $\chi^2 = 79.7$, df = 609, $p \leq .05$). The mouth was as likely to be open as closed ($\chi^2 = 3.1$, df = 675, $p \leq .05$), but the nares were normally closed (70.9%; $\chi^2 = 13.8$, df = 78, $p \leq .05$).

At North Rona a DPA more likely to occur with the precedent's head at the same height as the successor's (41.0%; $\chi^2 = 13.5$, df = 353, $p \leq .05$). On the other hand, the interactant's head was more likely to be lower at Miquelon (47.9%; $\chi^2 = 13.3$, df = 138, $p \leq .05$) and Sable Island (47.2%; $\chi^2 = 16.8$, df = 193, $p \leq .05$).

Both the body (25.9%; $\chi^2 = 93.0$, df = 694, $p \leq .05$) and head (24.6%; $\chi^2 = 21.3$, df = 694, $p \leq .05$) were more likely to be oriented parallel, facing the same direction, at the beginning of this behaviour category.

Vocal Accompaniment: This behaviour category was more likely to be performed silently at Miquelon (97.1%; $\chi^2 = 637.8$, df = 136, $p \leq .05$), North Rona (69.6%; $\chi^2 = 720.9$, df = 364, $p \leq .05$) and Sable Island (84.4%; $\chi^2 = 633.7$, df = 190, $p \leq .05$).

Duration: The mean duration of this behaviour type was 3.9 seconds (SD = 4.8). The duration was greater for DPAs recorded at Sable Island than at Miquelon or North Rona (Table 3). The CV was also smallest at Sable Island (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a DPA was 79.7 cm (SD = 243.1). The mean distance between interacting seals for this behaviour type was greater at North Rona and Sable Island (themselves not significantly different) than Miquelon (Table 5), although the CV at North Rona was almost twice as large as at Sable Island (Table 6).

Sex and Age Characteristics: This behaviour was performed predominantly by males at Sable Island (70.2%; $\chi^2 = 31.1$, df = 190, $p \leq .05$) and Miquelon (81.9%; $\chi^2 = 51.7$, df = 149, $p \leq .05$). Either sex was as likely to perform a DPA at North Rona ($\chi^2 = 1.0$, df = 322,

$p = .3$). Subdividing interactions on the basis of the sexes of both interactants, I found that there were no sufficient differences between bout types at Miquelon (F = 1.7, df = 2, 108, $p = .3$), North Rona (F = 11.0, df = 2, 299, $p \leq .05$; but $\hat{\omega}^2 = .14$) or Sable Island (F = 3.7, df = 1, 184, $p \leq .05$; but $\hat{\omega}^2 = .2$).

This behaviour category was performed predominantly by adults at North Rona (50.0%; $\chi^2 = 207.0$, df = 365, $p \leq .05$) and Sable Island (71.8%; $\chi^2 = 326.9$, df = 192, $p \leq .05$), and subadults at Miquelon (59.3%; $\chi^2 = 135.0$, df = 138, $p \leq .05$).

Behavioural Frequency: There were no significant differences between the frequency of DPAs at any site (Table 7 and Figure 15).

Context: The greatest frequency of this behaviour type occurred during aggressive interactions at Miquelon (F = 21.7, df = 1, 139, $p \leq .05$; $\hat{\omega}^2 = .8$), North Rona (F = 14.4, df = 3, 367, $p \leq .05$; $\hat{\omega}^2 = .65$) and Sable Island (F = 12.1, df = 2, 194, $p \leq .05$; $\hat{\omega}^2 = .73$).

Rush Away (RAW)

Description: The precedent moved away rapidly from the successor, usually in the context of an adult male chasing another. This behaviour type is the converse of the chase category.

Anatomical Characteristics: The eyes (100%) were always open, and the mouth (65.7%; $\chi^2 = 6.9$, df = 69, $p \leq .05$) was more likely to be closed (Table 2). The vibrissae were as likely to be protracted as retracted ($\chi^2 = 0.5$, df = 33, $p = .5$), the tail as likely to be elevated as depressed ($\chi^2 = 0.2$, df = 68, $p = .5$), and the nares as likely to be open as closed ($\chi^2 = 0.0$, df = 1, $p = 1.0$).

The precedent's head was more likely to be either higher (37.5%), or the same height (47.5%), than lower than that of the seal from which the precedent was rushing away at North Rona ($\chi^2 = 6.7$, df = 2, $p \leq .05$). Relative head heights during this behaviour type were not significantly different at Miquelon ($\chi^2 = 3.0$, df = 2, $p = 37$) or Sable Island ($\chi^2 = 3.8$, df = 2, $p = .25$)

A precedent's body (39.5%; $\chi^2 = 73.4$, df = 68, $p \leq .05$) and head (39.5%; $\chi^2 = 73.4$, df = 68, $p \leq .05$) were usually facing obliquely away from the successor's as it began to RAW.

Vocal Accompaniment: RAWs were usually performed silently at Miquelon (100%), North Rona (72.5%; $\chi^2 = 89.8$, df = 74, $p \leq .05$) and Sable Island (100%).

Duration: The mean duration of this behaviour type was 4.1 seconds (SD = 3.7). The duration values for RAWs were not significantly different between any two sites (Table 3), although the CV at Sable Island was larger (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a RAW was 219.5 cm (SD = 298.4). The mean distances between interacting seals were not significantly different at any two sites (Table 5), although the CV was much smaller at Sable Island (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by males at North Rona (95.0%; $\chi^2 = 30.6$, df = 39, $p \leq .05$) and Sable Island (93.3%; $\chi^2 = 22.5$, df = 29, $p \leq .05$), and by either sex at Miquelon ($\chi^2 = 0.0$, df = 5, $p = .4$). Subdividing interactions on the basis of the sexes of both interactants, I found that there were no significant differences between bouts on the basis of the frequencies of RAWs at Miquelon (F = 13.2, df = 1, 5, $p \leq .05$; but $\hat{\omega}^2 = .2$), North Rona (F = 0.1, df = 2, 39, $p = .64$) or Sable Island (F = 0.1, df = 2, 29, $p = .61$).

This behaviour category was performed predominantly by adults at North Rona (97.5%; $\chi^2 = 145.4$, df = 39, $p \leq .05$) and Sable Island (96.7%; $\chi^2 = 110.2$, df = 29, $p \leq .05$), and by subadults at Miquelon (66.7%; $\chi^2 = 8.2$, df = 6, $p \leq .05$).

Behavioural Frequency: There were no significant differences between the frequency of RAWs at any site (Table 7 and Figure 15).

Context: The differences between the frequency of RAW subdivided by interaction type were not significant at Miquelon (Kruskal-Wallis H = 7.1 df = 1, 5, $p = .06$), North Rona (F = 0.8, df = 4, 39, $p = .3$) or Sable Island (all aggressive).

Yawn (YAW)

Description: The seal lifted its chin in the sagittal plane and opened its mouth wide to yawn (without any detectable accompanying vocalisation). This was frequently followed by a neck and head shake (NHS). I did not observe this behaviour type at Sable Island.

Anatomical Characteristics: The precedent's eyes were as likely to be open as closed at the start of this behaviour type ($\chi^2 = 1.0$, df = 15, $p \leq .05$; Table 2). The vibrissae were usually protracted (87.5%; $\chi^2 = 9.0$, df = 15, $p \leq .05$) whereas the tail was never elevated. The nares were as likely to be open as closed ($\chi^2 = 0.7$, df = 5, $p = .41$).

At North Rona a YAW always occurred with the performer's head higher than the successor's. Relative head heights during this behaviour type were not significantly different at Miquelon ($\chi^2 = 1.7$, df = 6, $p = .4$)

The seals' bodies (37.5%; $\chi^2 = 13.4$, df = 10, $p \leq .05$) and heads (37.5%; $\chi^2 = 13.4$, df = 10, $p \leq .05$) were more likely to be oriented parallel, facing the same direction, during a YAW.

Duration: The mean duration of this behaviour type was 1.9 sec (SD = .7). The durations were not significantly different between Miquelon and North Rona (Table 3). The CVs were similar (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a YAW was 28.8 cm (SD = 30.5). The distance between interacting seals for this behaviour type was not significantly different between Miquelon and North Rona (Table 5), although the CV was larger at North Rona (Table 6).

Sex and Age Characteristics: This behaviour category was performed exclusively by males at Miquelon and females at North Rona. There were no significant differences in the frequency of YAWs, subdivided by the sex of both interacting seals, at either Miquelon (Kruskal-Wallis H = 3.1, df = 1, 6, $p = .21$) and North Rona (all female-female).

This behaviour category was performed primarily by adults at Miquelon (87.5%; $\chi^2 = 22.6$, df = 7, $p \leq .05$) and by mothers (not including lone adult females) at North Rona (87.5%; $\chi^2 = 22.6$, df = 7, $p \leq .05$).

Behavioural Frequency: There were no significant differences between the frequencies of YAWs at these two sites (Table 7 and Figure 15).

Context: There were no significant differences between the frequencies of YAW during any interaction type at Miquelon (Kruskal-Wallis H = 4.2, df = 1, 7, $p = .10$) and North Rona (Kruskal-Wallis H = 6.0, df = 2, 7, $p = .053$).

Neck and Head Shake (NHS)

Description: The precedent extended its head and neck out and up in the sagittal plane, then rolled its head from side to side in a 20 to 40 degree arc about the longitudinal axis of the neck (Figure 14B). The neck skin and fat twisted at a slower rate than the skeletal/muscle core. I never observed this behaviour type on Sable Island.

Anatomical Characteristics: The eyes and mouth were always closed (Table 2). The tail was not elevated and the vibrissae were as likely to be protracted as not ($\chi^2 = 1.0$, df = 3, $p \leq .05$). The nares were as likely to be open as closed ($\chi^2 = 3.0$, df = 2, $p = .08$).

At both Miquelon and North Rona the precedents' heads were always higher than those of the successor.

There were no significant differences in the frequencies of relative body ($\chi^2 = 6.5$, df = 1, $p = .8$) or head ($\chi^2 = 16.5$, df = 1, $p = .4$) orientation during this act.

Vocal Accompaniment: None.

Duration: The mean duration of this behaviour type was 2.0 sec (SD = 2). The durations were not significantly different for NHSs recorded at the two sites (Table 3). The CV (calculable at North Rona only) was the lowest of all behaviour types (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a NHS was 61.3 cm (SD = 30.6). The distance between interacting seals for this behaviour type was again not significantly different between Miquelon and North Rona (Table 5). The CV at North Rona was the lowest of all behaviour types (Table 6).

Sex and Age Characteristics: This behaviour category was performed by a female at Miquelon and either males or females at North Rona ($\chi^2 = 0.3$, df = 2, $p \leq .05$). Also, NHSs were performed by an adult at Miquelon and an adult (not including mothers) or mother at North Rona (66.7%; $\chi^2 = 0.3$, df = 3, $p = .56$).

Behavioural Frequency: There were no significant differences between the frequency of NHS' at any site (Table 7 and Figure 15).

Context: All NHS events occurred during aggressive interactions.

Raise Head Vertically (RHV)

Description: The precedent raised its head and neck from the substratum and held it vertically. The precedent's chest and neck were normally oriented towards the successor (Figure 14C).

Anatomical Characteristics: The eyes (100%) and mouth (94.1%; $\chi^2 = 159.8$, df = 204, $p \leq .05$) were almost always open during this behaviour type, as were the vibrissae protracted (98.4%; $\chi^2 = 175.2$, df = 3, $p \leq .05$; Table 2). The tail was never elevated and nares were as likely to be closed as open ($\chi^2 = 1.4$, df = 34, $p = .24$).

The precedent's head was more likely to be higher than that of the successor at Miquelon (67.8%; $\chi^2 = 46.5$, df = 79, $p \leq .05$), North Rona (50.6%; $\chi^2 = 46.7$, df = 79, $p \leq .05$) and Sable Island (65.8%; $\chi^2 = 19.5$, df = 39, $p \leq .05$).

Both the body (41.1%; $\chi^2 = 225.3$, df = 202, $p \leq .05$) and head (54.1%; $\chi^2 = 450.9$, df = 202, $p \leq .05$) were more likely to be oriented facing directly towards each other during performance of this behaviour category.

Vocal Accompaniment: This behaviour category was more likely to be performed silently at Miquelon (61.2%; $\chi^2 = 121.2$, df = 85, $p \leq .05$), North Rona (72.4%; $\chi^2 = 169.8$, df = 78, $p \leq .05$) and Sable Island (54.1%; $\chi^2 = 37.2$, df = 39, $p \leq .05$).

Duration: The mean duration of this behaviour category was 2.6 seconds (SD = 2.7). The duration was greater for RHVs recorded at Miquelon than at North Rona and Sable Island (Table 3). The CVs were similar (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a RHV was 11.5 cm (SD = 13.8). The distance between interacting seals during this behaviour type were not significantly different between the study sites (Table 5), and the CVs were similar (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by males at Miquelon (76.7%; $\chi^2 = 24.6$, df = 85, $p \leq .05$), North Rona (77.2%; $\chi^2 = 23.4$, df = 78, $p \leq .05$) and Sable Island (90.2%; $\chi^2 = 26.6$, df = 40, $p \leq .05$). Subdividing interactions on the basis of the sexes of both interactants, there were no significant differences at Miquelon (F = 0.2, df = 2, 85, $p = .4$), North Rona (F = 6.7, df = 2, 78, $p \leq .05$; but $\hat{\omega}^2 = .08$) or Sable Island (F = 0.1, df = 1, 40, $p = .31$)

This behaviour category was performed predominantly by adults at Miquelon (66.7%; $\chi^2 = 118.4$, df = 85, $p \leq .05$), North Rona (80.2%; $\chi^2 = 183.7$, df = 79, $p \leq .05$) and Sable Island (92.7%; $\chi^2 = 135.4$, df = 39, $p \leq .05$).

Behavioural Frequency: There were no significant differences between the frequency of RHVs at any site (Table 7 and Figure 15).

Context: There were no significant differences between sequence types on the basis of the frequency of RHV at Miquelon (F = 3.9, df = 1, 86, $p = .36$), North Rona (F = 14.1, df = 2, 80, $p \leq .05$; $\hat{\omega}^2 = .14$) or Sable Island (F = 0.4, df = 2, 40, $p = .48$).

Eyes Closed (ECL)

Description: The seal adopted what appeared to be a relaxed demeanor, often with its chin or cheek resting on the substratum, with its eyes closed. The performer may have been trying to sleep, but this did not always result in termination of the interaction.

Anatomical Characteristics: The mouth was always closed during performance of this behaviour type (Table 2). The vibrissae were usually retracted (99.2%; $\chi^2 = 221.1$, df = 228, $p \leq .05$) and the tail was not elevated. The nares were usually closed (85.7%; $\chi^2 = 14.3$, df = 27, $p \leq .05$).

The precedent's head was most likely to be the same height as that of the successor at both North Rona (52.7%; $\chi^2 = 26.8$, df = 79, $p \leq .05$) and at Sable Island (70.1%; $\chi^2 = 40.9$, df = 39, $p \leq .05$). The precedent's head was most likely to be the lower than that of the successor at Miquelon (50.0%; $\chi^2 = 4.2$, df = 85, $p \leq .05$)

The body (28.3%; $\chi^2 = 93.3$, df = 202, $p \leq .05$) and head (32.7%; $\chi^2 = 143.3$, df = 202, $p \leq .05$) were more likely to be oriented to face parallel in the same direction.

Vocal Accompaniment: None.

Duration: The mean duration of this behaviour type was 27.0 seconds (SD = 139.0). The mean durations of this behaviour type were not significantly different among the three sites (Table 3). The CV was much greater at North Rona (the largest for any behaviour type) than Miquelon or Sable Island (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform an ECL was 166.6 cm (SD = 489.4). The mean distances between interacting seals for this behaviour type were not significantly different among the study sites (Table 5), although the CV was largest at North Rona (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by males at Miquelon (88.2%; $\chi^2 = 19.9$, df = 33, $p \leq .05$) and Sable Island (78.8%; $\chi^2 = 21.9$, df = 65, $p \leq .05$), but either sex at North Rona ($\chi^2 = 1.7$, df = 145, $p \leq .05$). Subdividing interactions on the basis of the sexes of both interactants, there were no sufficient differences between bouts on the basis of the frequency of ECL at Miquelon (F = 0.1, df = 1, 33, $p = .2$), North Rona (F = 10.2, df = 2, 123, $p \leq .05$; $\hat{\omega}^2 = .12$) or Sable Island (F = 4.6, df = 2, 60, $p \leq .05$; but $\hat{\omega}^2 = .1$).

This behaviour category was performed predominantly by adults at Miquelon (97.1%; $\chi^2 = 126.2$, df = 33, $p \leq .05$), North Rona (72.5%; $\chi^2 = 64.7$, df = 148, $p \leq .05$) and Sable Island (77.6%; $\chi^2 = 139.0$, df = 65, $p \leq .05$).

Behavioural Frequency: The frequency of ECL at Miquelon was greater than that at North Rona (Table 7 and Figure 15).

Context: There were no significant differences between the frequencies of ECL, subdivided by sequence type, at Miquelon (F = 0.8, df = 1, 33. $p = .2$), North Rona (F = 3.4, df = 2, 149, $p = .13$) and Sable Island (F = 0.5, df = 1, 65, $p = .41$).

Roll on Side (ROS)

Description: The precedent rolled along its longitudinal axis to lie on one side.

Anatomical Characteristics: The eyes (92.3%; $\chi^2 = 74.5$, df = 103, $p \leq .05$) were more likely to be open during this behaviour type (Table 2). The vibrissae were usually protracted (62.4%; $\chi^2 = 5.2$, df = 84, $p \leq .05$) and the tail was not normally elevated (97.9%; $\chi^2 = 85.2$, df = 92, $p \leq .05$). The mouth was as likely to be open as closed ($\chi^2 = 0.4$, df = 98, $p \leq .05$), but the nares were always closed.

During a ROS the performer's head was most likely to be lower than that of the successor at Miquelon (66.7%; $\chi^2 = 9.0$, df = 17, $p \leq .05$) and Sable Island (53.8%; $\chi^2 = 4.9$, df = 25, $p \leq .05$). At North Rona there was no significant difference between the frequency of the categories of relative head height (42.9%; $\chi^2 = 4.2$, df = 2, $p = .3$).

The interacting seals' bodies were more likely to be either parallel (20.6%), facing the same direction, or the precedent facing perpendicularly towards the successor (16.8%; usually during a nursing bout) at the start of a ROS ($\chi^2 = 47.8$, df = 98, $p \leq .05$). The seals' heads were more likely to be parallel to each other, facing in the same directions (18.7%; $\chi^2 = 14.2$, df = 99, $p \leq .05$).

Vocal Accompaniment: This behaviour type was usually performed silently at Miquelon (94.1%; $\chi^2 = 73.4$, df = 17, $p \leq .05$) and North Rona (54.8%; $\chi^2 = 65.0$, df = 61, $p \leq .05$) and Sable Island (80.8%; $\chi^2 = 76.9$, df = 25, $p \leq .05$).

Duration: The mean duration of this behaviour type was 2.9 sec (SD = 4.0). The duration was greater for ROSs recorded at North Rona and Sable Island than at Miquelon (Table 3), although their CVs were also larger (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a ROS was 40.9 cm (SD = 139.9). The distance between interacting seals for this behaviour type were not different between the study sites (Table 5), although the CV at Sable Island was three times larger than at Miquelon (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by females at North Rona (91.9%; $\chi^2 = 43.6$, df = 61, $p \leq .05$), but either sex at Sable Island ($\chi^2 = 0.6$, df = 25, $p = .45$) and Miquelon ($\chi^2 = 1.0$, df = 15, $p = .21$). Subdividing bouts on the basis of the sexes of both interactants, there were no significant differences between bouts in the frequencies of ROS at Miquelon (F = 0.1, df = 2, 15, $p = .3$), North Rona (F = 5.7, df = 2, 42, $p \leq .05$; but $\hat{\omega}^2 = .21$) or Sable Island (F = 0.2, df = 2, 21, $p = .37$).

This behaviour category was performed predominantly by mothers at North Rona (77.8%; $\chi^2 = 131.4$, df = 60, $p \leq .05$) and subadults at Miquelon (66.7%; $\chi^2 = 24.5$, df = 17, $p \leq .05$). Adults and mothers were equally likely to roll on their sides at Sable Island ($\chi^2 = 0.0$, df = 62).

Behavioural Frequency: There were no significant differences between the frequency of ROSs at any site (Table 7 and Figure 15).

Context: The greatest frequency of ROS occurred during aggressive interactions at Miquelon (F = 10.0, df = 2, 17, $p \leq .05$; $\hat{\omega}^2 = .82$). It was as likely to occur during any bout type at North Rona (F = 1.5, df = 2, 62, $p = .34$) and Sable Island (F = 4.0, df = 1, 25, $p = .11$).

Nurse (NUR)

Description: The pup suckled its mother by grasping one of her nipples in its mouth (sucking noises often accompanied this action). I only observed this behaviour type at the breeding sites.

Anatomical Characteristics: Pups' eyes (80.9%; $\chi^2 = 8.1$, df = 2, $p \leq .05$) were more likely to be closed during nursing (Table 2). The pups' tails were always down and their vibrissae were more likely to be protracted (95.0%; $\chi^2 = 16.2$, df = 2, $p \leq .05$). I could not determine nares position.

The pup's head was more likely to be higher than that of its mother as it nursed at North Rona (57.1%; $\chi^2 = 5.4$, df = 19, $p \leq .05$) and Sable Island (100%; $\chi^2 = 4.0$, df = 3, $p \leq .05$).

Both the pups' bodies (72.0%; $\chi^2 = 68.0$, df = 24, $p \leq .05$) and heads (76.0%; $\chi^2 = 68.0$, df = 23, $p \leq .05$) were usually oriented to face perpendicularly towards their mothers at the beginning of a NUR.

Duration: The mean duration of this behaviour type was 143.5 seconds (SD = 217.4), a value which was greater than many other behaviour types (Tables 1 and 2). The mean duration was greater for NURs recorded at Sable Island than at North Rona (Table 3).

Inter-seal Distance: The mean distance between interactants when a pup began to perform a NUR was 8.8 cm (SD = 10.1). The mean distances between pups and their mothers at the start of this behaviour type were not different between North Rona and Sable Island (Table 5), and the CVs for this measure were similar (Table 6).

Behavioural Frequency: The frequency of NURs at North Rona was greater than at Sable Island (Table 7 and Figure 15), and thus the total amount of time pups spent nursing at North Rona was greater as well.

Body Scratch or Rub (BSR)

Description: The precedent scratched itself with the nails of a foreflipper, or rubbed a part of its body (usually the pelvis or neck) on the substratum, in a rhythmic motion.

Anatomical Characteristics: The precedent's eyes were as likely to be open as closed ($\chi^2 = 0.0$, df = 15, $p = 1$) and its mouth was always closed (Table 2). The vibrissae were as likely to be protracted as not ($\chi^2 = 0.1$, df = 14, $p = .8$) and the tail was not elevated. I could not determine if the nares were open in any case.

The differences in proportions of relative head heights at North Rona ($\chi^2 = 0.0$, df = 9, $p = 1$) and Sable Island ($\chi^2 = 3.1$, df = 3, $p = .32$) were not significant. The precedent's head was lower than the successor's in the single case of this behaviour type recorded at Miquelon.

There were no significant differences in the frequencies of relative body ($\chi^2 = 16.5$, df = 9, $p = .2$) or head ($\chi^2 = 9.0$, df = 9, $p = .31$) orientation at the beginning of this behaviour category.

Vocal Accompaniment: A BSR was always performed silently.

Duration: The mean duration of this behaviour type was 4.4 sec (SD = 12). The mean duration was not significantly different between BSRs recorded at any site (Table 3). The CV was highest at North Rona (Table 4).

Inter-seal Distance: The mean distance between interactants when a seal began to perform a BSR was 106.5 cm (SD = 293.4). The distance between interacting seals for this behaviour type was greater at North Rona than Sable Island (Table 5), although the CV was much larger at North Rona than Sable Island or Miquelon (Table 6).

Sex and Age Characteristics: This behaviour category was as likely to be performed by males as females at North Rona ($\chi^2 = 0.8$, df = 10, $p = .37$) and Sable Island ($\chi^2 = 1$, df = 3, $p = .32$), and by a male at Miquelon (one case). Subdividing bouts on the basis of the sexes of both interactants, there were no significant differences between bouts in the frequencies of BSRs at North Rona (Kruskal-Wallis H = 4.5, df = 2, 8, p = .21) or Sable Island (Kruskal-Wallis H = 2.7, df = 2, 1, p = .26).

This behaviour category was performed predominantly by mothers at North Rona (63.6%; χ^2 = 13.1, df = 10, $p \leq .05$) and Sable Island (75.0%; χ^2 = 7.6, df = 3, $p \leq .05$), and by an adult at Miquelon (one case).

Behavioural Frequency: There were no significant differences between the frequency of BSRs at any site (Table 7 and Figure 15).

Context: There were no significant differences between the frequencies of BSRs during any interaction types at North Rona (Kruskal-Wallis H = 7.9, df = 1, 10, p = .07) and Sable Island (Kruskal-Wallis H = 4.1, df = 1, 5, p = .32); except that BSR was never seen during play.

Penile Thrust (PT)

Description: The precedent, always an adult male, rhythmically thrust his hips in an attempt to insert his penis into the vagina of the female successor. The male normally clasped the female with a foreflipper while lying on his side with his belly against the female's back (similar to a clasp). This behaviour type was never observed at Miquelon.

Anatomical Characteristics: The male's eyes (73.8%; χ^2 = 15.0, df = 59, $p \leq .05$) were more likely to be open during penile thrusting (Table 2). His vibrissae were usually protracted (83.3%; χ^2 = 16.0, df = 35, $p \leq .05$) and his tail was rarely elevated (5.8%; χ^2 = 40.7, df = 51, $p \leq .05$). The male's mouth was usually closed (72.9%; χ^2 = 12.4, df = 59, $p \leq .05$), but the nares could be either open or closed (χ^2 = 1.8, df = 4, p = .18).

At North Rona (63.0%; χ^2 = 18.3, df = 44, $p \leq .05$) and Sable Island (47.4%; χ^2 = 9.2, df = 17, $p \leq .05$), males' heads were more likely to be higher than females' during PT.

During a PT, the interactants' bodies were always oriented parallel, facing the same direction, and their heads were also normally seen in this attitude (68.5%; χ^2 = 169.6, df = 60, $p \leq .05$).

Vocal Accompaniment: A PT was more likely to be performed silently at North Rona (97.8%; $\chi^2 = 174.2$, df = 45, $p \leq .05$) and Sable Island (100%).

Duration: The mean duration of this behaviour type was 18.4 seconds (SD = 24.3). The mean durations for PTs recorded at the two breeding sites were not significantly different (Table 3), although the CV was much larger at Sable Island (Table 4).

Inter-seal Distance: The mean distance between interacting seals at the commencement of this behaviour type was always zero cm.

Behavioural Frequency: The frequency of PTs at North Rona was greater than that at Sable Island (Table 7 and Figure 15).

Avert Face (AVF)

Description: The precedent turned and rigidly held its head at least 45° from the successor's in the coronal plane (Figure 14D). Unlike the LAW behaviour type, the precedent watched the successor in a sidelong manner and its posture was maintained more rigidly.

Anatomical Characteristics: The eyes (97.8%; $\chi^2 = 381.8$, df = 416, $p \leq .05$) and mouth (73.1%; $\chi^2 = 84.1$, df = 394, $p \leq .05$) were more likely to be open. (Table 2) The vibrissae were usually protracted (91.1%; $\chi^2 = 213.0$, df = 314, $p \leq .05$) and the tail was rarely elevated (11.5%; $\chi^2 = 225.3$, df = 380, $p \leq .05$). The nares were as likely to be open as closed ($\chi^2 = 3.0$, df = 26, $p = .08$).

An AVF performed at Miquelon was more likely to occur with the precedent's head lower than the successor's (44.7%; $\chi^2 = 5.9$, df = 101, $p \leq .05$). At North Rona (53.6%; $\chi^2 = 49.3$, df = 226, $p \leq .05$) and Sable Island (41.5%; $\chi^2 = 18.4$, df = 78, $p \leq .05$) the interactants' heads was more likely to be at the same height.

During an AVF, the interactants' bodies were most likely to be facing directly towards each other (34.7%; $\chi^2 = 283.1$, df = 411, $p \leq .05$). Their heads, on the other hand, were usually held parallel to each other, facing the same direction (66.8%; $\chi^2 = 99.6$, df = 409, $p \leq .05$).

Vocal Accompaniment: AVFs were more likely to be performed silently at Miquelon (92.7%; $\chi^2 = 399.7$, df = 101, $p \leq .05$), North Rona (73.2%; $\chi^2 = 515.7$, df = 232, $p \leq .05$) and Sable Island (87.5%; $\chi^2 = 289.0$, df = 79, $p \leq .05$).

Duration: The mean duration of this behaviour type was 3.4 sec (SD = 4.6). The mean durations for AVFs recorded at each site were not significantly different (Table 3). The CV much larger at Miquelon than Sable Island (Table 4).

Inter-seal Distance: The inter-seal distance at the start of an AVF was 31.8 cm (SD = 109.1). This distance was greater at North Rona than Miquelon (Table 5), and the CV was larger (Table 6).

Sex and Age Characteristics: This behaviour category was performed predominantly by males at Miquelon (87.9%; $\chi^2 = 56.8$, df = 98, $p \leq .05$), North Rona (64.9%; $\chi^2 = 20.7$, df = 230, $p \leq .05$) and Sable Island (84.8%; $\chi^2 = 38.3$, df = 79, $p \leq .05$). Subdividing bouts on the basis of the sexes of both interactants, there were no significant differences between bouts in the frequencies of AVFs at Miquelon (F = 0.3, df = 2, 93, $p = .87$), North Rona (F = 22.4, df = 2, 230, $p \leq .05$; but $\hat{\omega}^2 = .4$) or Sable Island (F = 0.4, df = 2, 78, $p = .8$).

This behaviour category was performed predominantly by adults at Miquelon (58.3%; $\chi^2 = 94.2$, df = 102, $p \leq .05$), North Rona (71.9%; $\chi^2 = 395.9$, df = 233, $p \leq .05$) and Sable Island (86.3%; $\chi^2 = 219.4$, df = 78, $p \leq .05$).

Behavioural Frequency: There were no significant differences between the frequencies of AVF at any site (Table 7 and Figure 15).

Context: The greatest frequency of AVF occurred during aggressive interactions at Miquelon (F = 6.0, df = 1, 102, $p \leq .05$; $\hat{\omega}^2 = .63$) and North Rona (F = 6.3, df = 3, 234, $p \leq .05$; $\hat{\omega}^2 = .68$). An AVF was as likely to occur during aggressive, mother/pup or copulatory bouts at Sable Island (F = 1.2, df = 2, 79, $p = .7$).

Behaviour Category Clustering

One practical utility of cluster analysis is in discovering any systematic organization within an assemblage of related items. In an effort to discover if there were natural groupings of the 33 grey seal behaviour types, I first ascertained which variables (see page 24) best differentiated the behaviour types, but in such a way that any interactions among the variables would be accounted for (see Altmann, 1965; Lefebvre and Joly, 1982; Maurus and Pruscha, 1973; McQuitty, 1987; van Hooff, 1970).

The following dendrograms group behaviour types into clusters on the basis of their relatedness based on these variables (Everitt, 1980; Kaufman, 1989).

Clustering of Miquelon Behaviour Types

An initial analysis revealed that the variables Focal Area and Focal Male were highly correlated (0.97); I removed the latter from subsequent analyses.

Six variables failed the minimum tolerance test for inclusion (at $p \leq .05$) in subsequent analysis (direction of approach relative to wind, sequence sexes, precedent class, multiact and whether the behaviour type was simultaneous). I excluded the variable precedent nares position due to its preponderance of unknown values.

I also excluded the behavioural types sniff, clasp, chase, neck and head shake, and body scratch or rub from subsequent analyses since each had only one case with values for all variables. The resultant 22 behaviour types accounted for 848 cases (Table 16)

Of the 23 orthogonal functions resulting from the final discriminant analysis, only two had eigenvalues greater than 1.0 and accounted for 79.1% of the cumulative variance (Table 16).

Within these functions, only precedent eye position (function 1: 0.9) and precedent mouth position (function 2: 0.8) had standardised canonical function coefficients which were acceptably large enough to be used as a means to discriminate among behaviour types at Miquelon. Agglomerative clustering of behaviour types at Miquelon, using these two variables, produced the complete-linkage dendrogram in Figure 16.

Clustering of North Rona Behaviour Types

The variables Focal Area and Focal Male (0.97), precedent type and sex (0.8), successor type and sex (0.8) and precedent height and successor height (0.7) were highly correlated; I removed Focal Male, precedent and successor sex, and successor height from the subsequent analysis.

Seven variables failed the minimum tolerance test for inclusion (at $p \leq .05$) in subsequent analysis (number of mother/pup pairs in the Focal Area, successor reaction, direction of approach relative to wind, sequence sexes, precedent class, multiact and whether the behaviour type was simultaneous). I excluded the variable precedent nares position due to its preponderance of unknown values.

I also excluded the behavioural types sniff and yawn from subsequent analyses since each had only one case with values in all defining variables. The resultant 31 behaviour types accounted for 2624 cases (Table 17)

Of the 19 orthogonal functions resulting from the final discriminant analysis, only two had eigenvalues greater than 1.0 and accounted for 68.6% of the cumulative variance (Table 17).

Within these functions, only precedent eye position (function 1: 0.9) and precedent mouth position (function 2: 0.7) had standardised canonical function coefficients which were acceptably large enough to be used as a means to discriminate among behaviour types at North Rona. Agglomerative clustering of behaviour types at North Rona, using these two variables, produced the complete-linkage dendrogram in Figure 17.

Clustering of Sable Island Behaviour Types

Initial analysis revealed that the variables Focal Area and Focal Male (0.8), precedent type and precedent sex (0.9), successor type and successor sex (0.9), and precedent height and successor height (0.66741) were highly correlated; I removed Focal Male, precedent sex, successor sex and precedent height from the subsequent analysis.

Six variables failed the minimum tolerance test for inclusion (at $p \leq .05$) in subsequent analysis (number of mother/pup pairs in the Focal Area, direction of approach relative to wind, sequence sexes, precedent class, multiact and whether the behaviour type was simultaneous). I excluded the variable precedent nares position due to its preponderance of unknown values.

I also excluded the behavioural types poke with nose and sniff from subsequent analyses since each had only one case with values in all defining variables. The resultant 27 behaviour types accounted for 1138 cases (Table 18)

There were 21 orthogonal functions resulting from the final discriminant analysis, and like the results from Miquelon and North Rona, only two had eigenvalues greater than 1.0 (Table 18). These accounted for 64.7% of the cumulative variance.

Within these two functions, only precedent eye position (function 1: 0.9) and precedent mouth position (function 2: 0.7) had standardised canonical function coefficients which were acceptably large enough to be used as a means to discriminate among behaviour types at Sable Island. Behaviour types from Sable Island were agglomeratively clustered, using these two variables, to produce the complete-linkage dendrogram in Figure 18.

Discussion

Ethogram Categories and Sample Completeness

John Krebs (1980) asserted: "... there is no such thing as a pristine, unbiased observation". (p. 409). With this admonition in mind, I delineated behavioural types in this study that were not only distinctive and predominantly independent of each other in form (e.g., Altmann, 1967; Anderson, 1978; Boness and James, 1979; Drummond, 1981; Fentress, 1973; Gailey-Phipps, 1984; Golani, 1976; Harestad and Fisher, 1975; Lewontin *et al.*, 1984; Miller, 1975a; 1986; 1988; 1991; Miller and Boness, 1979; Renouf and Lawson, 1986a; Slater, 1978; Smith, 1977; Stirling, 1970; Sullivan, 1979; 1982), but most importantly, were readily discernible by other observers.

The detail and accuracy inherent in video recording techniques not only facilitated the construction of a comprehensive ethogram, but provided a means to authenticate the category list with the help of a näive observer. This observer, with no prior experience in animal behaviour research, coded an extended interactive bout with no assistance other than the descriptive ethogram. The large Kappa coefficient indicated an excellent concordance between the behaviour types that I and the observer had coded, and we both recorded similar total numbers of behavioural acts. Thus the structure of this ethogram was of sufficient precision to ensure inter-observer reliability, yet descriptive enough to accommodate the individual variability inherent in grey seal communication.

Discrepancies between our coded records stemmed from the näive observer simply coding categories, rather than accompanying physical attributes such as eye or body position (which were recorded during the bouts I coded). Behavioural acts such as GLA were more easily discerned when the observer noted head *and* eye position - the seal may not always have made an obvious movement of its head when it glanced at a cohort. Similarly, a LAW and AVF could appear superficially the same, and yet notation of the direction in which the seal's eyes were directed, as well as the relative head and body orientation and sequence type context, clearly distinguished these behaviour types.

Catalogue completeness estimates indicated the datasets in this study provided excellent sample coverage with which to build a comprehensive catalogue of terrestrial behaviour. During the relatively limited time that I observed grey seals interacting in water, I saw no behaviour patterns that did not have counterparts in a terrestrial context (see also Lockley, 1966). Nonetheless, future research on this species should investigate aquatic behaviour as well. Pinniped terrestrial vocal activity does not seem to be constrained by a switch to an aquatic medium,[8] and the weightlessness and three dimensional space provided by water could permit performance of behavioural acts not feasible on land (such as the rolling (Venables and Venables, 1959; Wilson, 1974b or torpedoing (Renouf and Lawson, 1986a) behaviour types of harbour seals).

The Grey Seal Repertoire

More than a decade ago, Miller and Boness (1979) stated:

> *"... signaling adaptations mark the appearance of many mammals" and "these include simple modifications in piloerection, colour, pattern and ornamentation ... but aquatic life of pinnipeds sets limits to their 'social morphology'"* (p. 140).

This study contradicts this statement as it became evident that grey seals have a labile and broad behavioural repertoire. The behavioural types I observed were diverse and regularly modified in subtle manners by performers depending on contextual factors such as site, interaction type or the age or sex of their partners.

In Smith's (1977) model of communication the information contained in animal signals is fixed, and flexibility in the communication process results from recipients integrating and responding to both signal information and context (Miller, 1991). Other

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[8] Schusterman (1991) stated that many pinniped vocalisations have similar acoustic properties when performed underwater with the mouth closed.

ethologists also believe that an upper limit to animal repertoire size probably exists, with communicatory richness attained primarily through the use of context (Hinde, 1985; Moynihan, 1970; Smith, 1981).

The size of the grey seals repertoire is larger than a number of other species (but less than that of the Steller sea lion; Table 8), but well within the upper limit of 50 to 80 signal types envisaged by Moynihan (1970) or Smith (1977). After examining the relatively limited number of ethograms in the published literature, I concur with Smith's (1977) supposition that interspecific comparisons of repertoire size are hampered by differences in observer effort, and structural and functional definitions of behavioural categories. An extreme example of this is Golani's (1973) work with the Golden Jackel (*Canis aureus*). With analyses of exceptional detail, Golani reported that this species' repertoire comprised 2,000 "system events" which were slight differences in body position and relative orientation. Despite this detail, Golani did not demonstrate that subtle differences in posture and context conveyed distinct information (in terms of the receiver's response), and therefore whether these "system events" were distinct behavioural categories from the Jackals' perspective.

The relatively broad repertoire of the grey seal was likely able to convey a rich spectrum of information when combined with both the individual variability during performance of each behaviour type (e.g., Tables 4, 6, 7, 9 and 10; see also Schusterman, 1978; Shipley *et al.*, 1981) and the variety of contexts in which the seals performed each behaviour type. For instance, a BIT was always responded to as an exceptionally agonistic signal during aggressive interactions between adult males at the breeding sites. On the other hand, this behaviour type was often an invitation to play when performed gently, or with exaggeration during locomotor-rotational movements (e.g., Wilson, 1974b) by one subadult towards another at Miquelon.

As another example, female grey seals on North Rona often demonstrated marked variation in responses to the OMDs of approaching males. A female was less likely to react with vigorous aggressiveness to this behaviour type when the male performing it was familiar to her. On the other hand, the same behaviour performed by an unfamiliar male always elicited extremely vigorous agonistic responses.

Comparing the grey seal repertoire in this study with those from the few other pinniped species for which there have been descriptions of behaviour (Table 8) must be cautious since there were apparent differences in the emphasis researchers placed on creating comprehensive behavioural inventories. Sullivan (1982) described only eight behaviour categories used by harbour seals during terrestrial interactions at haul-out ledges. This was not a complete description of this species' behavioural repertoire since a subsequent, similar study of harbour seals at a haul-out site described more behaviour types than Sullivan had noted (Renouf and Lawson, 1986a). Studies of grey seals in Europe (Anderson and Harwood, 1985; Twiss, 1991) described at least 17 behavioural types, but even in Twiss' investigation, a number of these (e.g., "fight"; p. 40) were too broadly-defined to be considered as components of a comprehensive ethogram. In a study of non-breeding Steller sea lions, Harestad and Fisher (1975) created a reasonably comprehensive catalogue of their behaviour. When combined with other behaviour types reported during the breeding season (Gentry, 1970; Sandegren, 1975; 1976b), this species' repertoire size would be similar to that of the grey seals'.

Classifying vocal displays as distinct behaviour categories, the weddell and bearded seals (Cleator *et al.*, 1989; Thomas and Kuechle, 1982) could be considered to have the largest pinniped repertoires. Should ethologists undertake in-depth study of the communicative behaviour of other pinnipeds, the grey seal repertoire will probably not appear comparatively broad. In particular, social interactions of thigmotactic species such as elephant seals may contain a wider array of subtle behaviour types than currently reported in the literature (e.g., Bartholomew, 1952; Carrick *et al.*, 1962a; Le Boeuf, 1972; Le Boeuf and Petrinovich, 1974b; McCann, 1981; Sandegren, 1976a).

Major Characteristics of Behavioural Acts

In the following sections I summarize physical and temporal features generally characteristic of each grey seal behavioural category, and discuss those sites which depart from these norms. I discuss the behaviour categories as their configuration and potential functions compare with those of other pinnipeds, and where applicable, other animals.

Miller (1991) surmised that behavioural plasticity and individuality, in conjunction with complex and dynamic sources of contextual information that encompass social interactions in pinnipeds, would yield variation in form, usage, and consequences of signaling. Also, Pimental and Frey (1978) criticized single variable measures of behavioural variation. In light of these considerations, behaviour patterns were described and compared using 14 measures. These reveal the degree of behavioural variation and the extent of contextual influences on grey seal behaviour.

1) Eyes Condition

Animal species attend to diverse sources of information during social interactions, many of which are transmitted using visual signals. As a result, they usually keep their eyes open as they communicate. Grey seals should have observed their opponents closely if they wished to receive visual information concerning cohort gender, size, movement and behaviour, especially as any kind of behaviour can be socially informative (Smith, 1977). Circumstantially, it was apparent that grey seals were also monitoring the movements of other individuals, particularly during the breeding season. For instance, a female who moved a small distance at Sable Island aroused the interests of males within a wide area.

That grey seals were sending visual signals was clear from their physical adaptations. Like those of elephant (Le Boeuf, 1972) and hooded seals (Berland, 1958; Mohr, 1966), the enlarged snouts of male grey seals certainly evolved as structures to enhance visual signals (Miller and Boness, 1979; see discussion of head orientation below). Further, many grey seal behaviour types incorporated highly-visible body, head or foreflipper movements.

Except for the relatively sedate behaviour types YAW, NHS, ECL, NUR and BSR, grey seals at all sites customarily kept their eyes open when communicating with others (Tables 1 and 2). The five behaviour types performed with closed eyes were usually done so in contexts where the risk of attack from the cohort was low [9] or, in the case of mothers and pups, non-existent. In these cases there was probably reduced need to attend to the actions of the successor.

Eye condition was not a graded signal modality since grey seals' eyes were either fully open or closed. Eye state could not convey continuously-variable intrinsic information such as degree of arousal. Of course, eye features such as pupil dilation or the amount of the white schlera exposed could provide graded information.

2) Mouth Condition

Grey seals' mouths were open during performance of most behaviour types (Tables 1 and 2), particularly during agonistic or vigorously playful communication. The grey seals kept their mouths closed during only ten (30%) behaviour types: NTN, PON, SNI, GLA, ROA, RAW, NHS, ECL, BSR and PT. These were less likely to be performed during agonistic interactions (except for RAW during which the performer was oriented away from and fleeing the cohort, and NHS) and were less liable to be followed by aggressive behavioural acts.

Despite the frequency with which grey seal behavioural acts were performed with open mouths, they did not always vocalise (and see section 8 below). More than one third of all grey seal behaviour types were silent (OMD, HTH, EFF, FSR, FSS, HEX, STA,

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[9] NHSs occurred during points within aggressive interactions when the pace was slower, and the successor was never observed to attack the performer after an NHS.

LAW, BIT, CLI, CHA, RHV and AVF), even though the seals' mouths were open. In those behaviour types which were begun with either an open mouth whoo or no vocal accompaniment, the latter were more likely to be performed by males. That is, male grey seals commonly used their mouths as a visual display structure whereas females integrated both vocal and visual information.

Since grey seals lack external pinnae or piloerectable hair, the mouth is probably an important signaling instrument. Although he excluded grey seals from consideration[10], I concur with Sullivan's (1982) judgment that open-mouth threats are the most common form of phocid aggression. In addition to grey seals, an open mouth is also an important component of threat displays in harbour (Sullivan, 1982), Hawaiian monk (Kenyon and Rice, 1959), elephant (Sandegren, 1976a) and fur seals (Gentry, 1975c) and sea lions (Sandegren, 1975; 1976b).

Open-mouth threats are common in other animal species. For example, open mouths were used as aggressive threat signals in hippopotamus (*Hippopotamus amphibius*; Walther, 1977a), and were common features of primate agonistic and playful interactions (Eisenberg, 1978; Gautier and Gautier, 1977; Gouzoules *et al.*, 1984; Klopfer, 1977; Marler, 1965).

Grey seals commonly had their mouths open during behavioral acts performed as part of non-agonistic communication, especially during playful interactions at Miquelon where play biting and head swings were frequent actions. This is in accordance with the recurrent observation that playful behaviour often incorporates elements used within other contexts (e.g., aggressive or copulatory; Bekoff, 1974; Fagen, 1974; Grier, 1984; Smith, 1984; Wilson, 1974b).

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[10] Open mouth threats have been previously documented for grey seals in Europe (Anderson, 1978; Anderson *et al.*, 1975) and on Sable Island (Miller and Boness, 1979).

3) Vibrissae Position

With the exception of the behaviour types LAW, ROA and ECL, grey seals customarily kept their vibrissae protracted when interacting with others (Tables 1 and 2). Although I was unable to achieve sufficient resolution and contrast on videotape recordings to describe mid-range vibrissae positions during many behavioural acts, they did exist. Thus, unlike eyes and nares, vibrissae position had the potential to be continuously variable.

Grey seals may have retracted their sensitive vibrissae as they rolled away from an opponent to prevent them from contacting the substrate. In tonic communication, vibrissae may have performed a role by continuously transmitting information regarding the performer's level of arousal (Schleidt, 1973). That is, when a grey seal was highly aroused, such as during a male-male fight, it seemed to protract its vibrissae to a greater degree than a mother would be when closing her eyes as her pup nursed. If this holds true for all behaviour types, then grey seals performing LAW, ROA and ECL may have been less aroused than they were during other behavioural acts. Alternately, in cases of vibrissal contact, such as a NTN between mothers and pups, vibrissae presumably provided tactile information. The vibrissae were also commonly protracted when this behavioural act was performed by other pinnipeds in this context (e.g., Eliason, 1986; Fay, 1982; Fogden, 1971; Kovacs, 1987a; Kovaks, 1987b; Lawson and Renouf, 1987; Miller, 1975a; Tedman and Bryden, 1979; Trillmich, 1981).

4) Nares Position

Grey seals' nares were clearly open at the onset of only three (11%) behaviour categories: OMD, NTN and SNI (Tables 1 and 2). During the performance of a NTN or SNI, the open nares presumably allowed the performer to obtain olfactory information about its partner. These two behaviour types typically occurred during investigatory or reunion contacts between mothers and their pups. The nares were opened during the initial exhalation phase of an OMD, in conjunction with the opening of the mouth, perhaps as a means to further exaggerate the display.

These inferences were tempered by two factors, however. When on land, grey seals' typical respiration pattern dictated that their nares were closed for a greater proportion of time than they were open. A grey seal kept its nares closed, except when it opened them briefly to exhale and inhale relatively rapidly, then held its breath again for an extended period before the next respiration cycle, even during interactive sequences. Therefore, at any one instant I was more likely to record the nares as being closed.

In addition, in a large percentage of the behavioural acts I recorded, I was unable to clearly ascertain the position of the nares. In part this was due to their small size, and the fact that the seal's faces were frequently oriented towards each other, rather than towards me.

5) Tail Position

It was clear that a grey seal's tail was not used as a signaling device like that of the African lion (*Panthera leo*; Schaller, 1972), whose elevated tail is used as an indication of arousal prior to attack. The relatively small tails of grey seals were rarely elevated while they were ashore at any of the sites I studied (Tables 1 and 2). Grey seals were likely to elevate their tails only when they were executing a RAW. However, the elevated tail was more likely a component of the locomotion process, than a form of communicatory signal, since I did see some seals moving more slowly and with elevated tails.

6) Head Height

Relative performer head height was highly variable among, and often within, behaviour categories (Tables 1 and 2). Relative head height was statistically unequivocal in only 33% (11 of 33) of the behaviour types. There were no consistent patterns among the sites as performers' heads were not consistently higher than the successors', for instance, at both breeding sites.

While many behaviour types were performed at any height relative to the successor, at the onset of a CLI, CLA, NHS, RHV or PT performers' heads were consistently higher. The performer of an RHV did so in an active attempt to get its head higher than the successor's, in much the same manner that bull elephant seals do during territorial disputes (Le Boeuf, 1972; Le Boeuf, 1974). As in aggressive interactions, this may have tended to make the performer appear larger and more threatening (Miller and Boness, 1979). The males' heads were usually higher than the females' at the start of a PT because the males often laid their chins on female's shoulder as the bulls pulled the females closer.

During the performance of an FSW were performers' heads consistently at the same height. This was simply a result of both interactants being in water, and usually lying in the same orientation and water depth. They were also at the same height during HSWs and CHAs. In the former, the two seals often performed HSW at the same time as if they were "mirroring" each other - particularly at Miquelon (see diagonal values for HSW in Tables 19 and 20).

Performers' heads were consistently lower during an FSS at both North Rona and Sable Island. This behaviour type was performed by females as one type of aggressive threat in response to male approaches, and the females' heads were often stretched out low and parallel to the males' while they vocalized {like the low open-mouth threat described earlier by Anderson *et al.* (1975)}.

7) Relative Orientation

Head and body postures provide important information during animal communication (Halliday and Slater, 1983; Hinde and Rowell, 1962; Schloeth, 1961a; Wilson, 1972), even for grey seals whose physical adaptations to an aquatic lifestyle may restrict their "social morphology" (Miller and Boness, 1979). While an examination of interactions across mammalian groups has revealed that many postures regarded as distinctive are instead gradations along a continuum {see Ewer (1968) for a comprehensive review}, there are nonetheless particular orientations which are more common.

Fritz Walther (1984) claimed that:

> "*... the signals with the widest interspecific distribution and the greatest reliability in interspecific communication are those which are linked to the sender's orientation relative to the recipient.*" (p. 378)

All pinnipeds adopt similar head and body orientations during intraspecific communication. Like elephant (Cox, 1981; Le Boeuf, 1972; 1974b; McCann, 1981; Sandegren, 1976a), crabeater (Siniff *et al.*, 1979) and harbour seals (Sullivan, 1982; Wilson, 1978), and Steller sea lions (Sandegren, 1975; 1976b), the most common body and head orientations adopted by grey seals at all three sites were either parallel to each other, facing the same direction, or facing each other head-on {Tables 1 and 2; see also Boness (1979); Boness and James (1979)}. During behavioural acts which were performed with little vigour or in non-agonistic contexts (e.g., PON, STA, NHS and BSR) seals were liable to assume other orientations. This suggests that orientation is an important component of grey seal communication, and aspects of their physical morphology augment this.

Male grey seals have enlarged snouts which apparently function to augment aerial displays; other species change the size/shape of their snouts over the year (e.g. elephant and hooded seals; Le Boeuf, 1972; Le Boeuf and Briggs, 1977; Mohr, 1966). The snout has been sexually selected as a display organ and male grey seals "display the snout prominently in numerous short-range agonistic encounters during breeding" (Miller and Boness, 1979). Since male grey seals frequently moved about the breeding areas, they perhaps needed to communicate their status more quickly than the relatively stationary territorial otariids who are familiar with their neighbours (Miller and Boness, 1979).

As a means to enhance the display function of their enlarged snouts, Miller and Boness (1979) stated that grey seals' "close-up threats" were usually oblique. This was true for some of the behaviour types in this study (e.g., EFF, FSR, FSS and AVF), but not all (Tables 1 and 2). Further, the "lateral T-position" so commonly adopted by dominant ungulates (broadside in front of a subordinate; Walther, 1984) was rarely seen during grey seal interactions. Instead many threatening behavioural acts were performed with the seals' heads oriented towards the successors' from directly ahead (e.g., OMD, HTH, FFW, FSW, HSW and HEX). In these contexts the head-on orientation was less likely to emphasize the snout, but rather the brightly-coloured mouth lining so often displayed during close-range communication (see discussion of mouth condition above).

The influence of body and head orientation on behaviour can be seen in how they related to inter-seal distance. The two breeding sites were more similar to each other than Miquelon in the distances at which they interacted when in various body and head orientations. Breeding grey seals normally performed behavioural acts at the greatest distance when one interactant's body or head faced the other's from directly behind (usually during chases; Figures 9 and 10; Tables 10 and 11; body: North Rona: $F = 67.5$, $df = 9, 4925$, $p \leq .05$; $\hat{\omega}^2 = .61$. Sable Island: $F = 79.6$, $df = 9, 2058$, $p \leq .05$; $\hat{\omega}^2 = .72$; head: North Rona: $F = 54.9$, $df = 9, 4925$, $p \leq .05$; $\hat{\omega}^2 = .61$; Sable Island: $F = 62.3$, $df = 9, 2058$, $p \leq .05$; $\hat{\omega}^2 = .68$). The smallest interseal distance usually occurred when the interactants' bodies and heads were oriented parallel or parallel-opposite to each other. The parallel position was often assumed during bouts in which males attempted to copulate with females, while the parallel-opposite orientation was commonly adopted by females either rejecting males' advances or preparing to nurse their pups. That is, these postures occurred frequently in contexts in which at least one partner attempted to engage or prolong physical contact.

At Miquelon, there were no significant differences between the distances seals assumed at any relative body or head position (body: F = 3.0, df = 9, 1656, p = .18; head: F = 1.5, df = 9, 1656, p = .39). Thus at breeding sites relative orientation had a strong relationship with inter-seal distance, whereas body and head positioning did not seem as crucial in this regard in a non-breeding context. This implies that relative body and head orientation of grey seals interacting at the breeding groups contained semantic information.

Nonetheless, unlike the ritualized postures of timber wolves (McLeod, 1987; Moran *et al.*, 1981) or fighting male rats (Barnett, 1981), the comparably limited number of orientations used by grey seals was seldom predictive of subsequent behaviour in any context or any site (since so many behavioural acts shared the same orientations). While orientation contributed to the high degree of form constancy (Immelmann and Beer, 1989) of grey seal behaviour, and seemed linked to inter-seal distance at breeding sites, it probably served as a standardized display characteristic.

8) Vocalisations

Grey seals usually did not vocalize during interactions: two thirds of behaviour types (22/33) were performed silently (Tables 1 and 2), regardless of locale. Exceptions to this were those behavioural acts performed at close range by females, or subordinate[11] males, during aggressive interactions (such as HTH, EFF, FFW, FSR, FSS, FSW, FSB, HSW and HEX).

Compound visual and acoustic signals may evolve in colonial species as adaptations to high ambient noise levels (Miller, 1991). Since grey seal vocalizations were somewhat directional and performed when interactants were in close quarters, extraneous noise was unlikely to prevent seals from discerning which individual was signaling them.

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[11] In this context, subordinate could refer to subadult or, during agonistic interactions at breeding sites, males conceding dominance to another by moving away.

Instead, loud open mouth whoos and growls probably emphasized visual aspects of the behaviour type (e.g. foreflipper waving). In addition, the vocalizations could have served as a graded measure of the performer's degree of arousal or intent to attack (or perhaps body size; e.g. Radwan and Schneider, 1988).

Females often directed open mouth whoos at the males with whom they were copulating. This may have served the same purpose as the complaint/incitation vocalizations of female elephant seals. They ensured that only dominant males copulated with them by alerting all males within a wide area that they were being mated (Anderson *et al.*, 1975; Cox and Le Boeuf, 1977). Anderson *et al.* (1975) suggested that female grey seals challenged approaching males to ensure that they were "aggressive and secure" enough to overcome the female's belligerence and successfully copulate.

Adult male grey seals at the breeding sites did not employ long-distance vocalizations such as the "trumpeted roar" (Miller, 1991; Peterson and Bartholomew, 1969; Sandegren, 1970; 1976b; Stirling, 1972) or "bark" of territorial Otariids (Peterson and Bartholomew, 1969; Schusterman, 1978), nor did they utilize elaborate vocal challenges like elephant seals (Sandegren, 1976a; Shipley *et al.*, 1981). In most instances, when they did vocalize, adult male grey seals were more likely to growl or snort at their opponents, much like harbour seals (Lawson, 1983; Sullivan, 1982; Wilson, 1978). Rarely, and only at the breeding sites, adult males performed a distinctive warbling call which could be heard over distances of several km, yet was extremely difficult to localise (it has also been termed a "yodel"; Boness and James, 1979; Schneider, 1974). When males emitted this call they were usually performing an ECL, and apparently dominant enough to do so with little risk of being attacked by nearby males. Like the call of a territorial male bird in a forest, the warble vocalization may have notified other seals in the area that there was a male present, without actually revealing his exact location. Considerably less energy would have been expended than had the warbling bulls actively searched out interlopers.

Only at close range, usually in agonistic contexts, and often for socially subordinate seals, did vocal accompaniment assume a prominent role in communication. Visual signals were of relatively greater importance to grey seals since they were responsive to movements of cohorts, and vocal activity increased at night (Chwedenczuk and Frysz, 1983) without a matching increase in interactive activities.

9) Behavioural Act Duration

Behavioural acts performed by grey seals were of short duration in many instances, with most normally lasting less than five seconds (Tables 1 and 2). However, act duration was exceedingly variable (Table 3), with coefficients of variation for categories reaching almost 100 percent (Table 4).

Although less than half of all behaviour types (14/33) were significantly different in duration when compared among the study sites, those that were different frequently lasted longer when performed at Sable Island (Table 3). While these included behaviour types used in aggressive contexts, such as EFF and HSW, seals at Sable Island also took longer to perform behavioural acts which resulted in distance changes (NTN, APT, DPA and ROS) or vigilance (STA and LAW). Perhaps factors such as the more mobile males and less organised spatial arrangement of the Sable Island group (Boness, 1979) resulted in more interactions between seals unfamiliar with each other. This may have effected behavioural changes, such as prolonging performances of potentially threatening acts, in accordance with the "dear enemy" [12] effect documented in other species (e.g., Gentry, 1975c; Jarman, 1991; Simpson, 1973; Wilson, 1972).

At Miquelon, the behaviour types BIT, RHV and CHA were of greater duration than those performed at either breeding site (Table 3). Acts such as these, which would

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[12] In species in which males establish territories, they often interact for shorter durations and less intensely with neighboring, familiar males in bordering territories.

normally be brief and serious[13] in aggressive contexts, were often prolonged and gentler in play. For example, playing seals would prolong a bite for up to 20 seconds at Miquelon. As shown previously for grey seals (Wilson, 1974b), Northern elephant seals (Rasa, 1971; Schusterman, 1968) and polecats (Poole, 1967), these motor patterns were otherwise very similar in structural configuration in both contexts. The slower "pace" of these behaviour types within playful contexts may have served a metacommunicative function in assuring the recipient that the acts were intended as playful (e.g., Bateson, 1956; Bekoff, 1972; Smith, 1984).

It was apparent that a continuum existed between those briefer acts performed during aggressive interactions (e.g., HTH, FFW, HSW and GLA), and those performed during longer mother/pup (NUR) or copulatory bouts (CLA and PT; Tables 3 and 12 and Chapter Five). Since behaviour types of shorter duration were characteristic of aggressive interactions in harbour seals as well (Sullivan, 1982), seals may have limited the duration of physical contact with aggressive cohorts to minimize the risk of injury and energy expenditure. Perhaps for similar reasons, aggressive bouts lasted less than other types (see Chapter Five).

Few published works have quantified act duration for any seal species. Therefore, it is difficult to place grey seal behaviour duration within the context of studies which have been restricted to examination of vocal behaviour (e.g., Cleator *et al.*, 1989; Kaufman *et al.*, 1975; Möhl *et al.*, 1975; Peterson and Bartholomew, 1969; Ray and Watkins, 1975; Stirling and Siniff, 1979; Thomas and Kuechle, 1982). Sullivan (1982) reported that most harbour seal behaviour *bouts* lasted less than eight seconds, and that acts within these bouts were curt. Similarly, highly aggressive behaviour types, such as "tusk striking" by walrus (Miller, 1975c) or "head striking" by male elephant seals (Le Boeuf, 1972; Le Boeuf, 1974) were certainly as brief.

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[13] Bites were considered in this context because they were more likely to injure the successor, as indicated by blood from a fresh wound, or the vigorous, aggressive response by the successor.

Conversely, most grey seal behaviour types were briefer than rearing, chest pushing or mounting behaviour performed by male elephant seals, which often lasted for several minutes (Le Boeuf, 1972; 1974), like Otariid "boundary displays" (Gentry, 1975c).

The behaviour types with the least variable act duration were OMD, YAW and NHS (Table 4). The OMD conceivably qualifies as a Modal Action Pattern (MAP; Barlow, 1968; 1977; Finley *et al.*, 1983; Immelmann and Beer, 1989). It was a recognizable spatiotemporal pattern of movement that could be characterized quantitatively, could not be further subdivided into independently occurring MAPs and was widely distributed in similar form throughout the grey seal population. This behaviour type was particularly consistent in measures of act duration, body and head orientation, interactant sex and age, context and other physical attributes (Table 1, and see descriptive section on page 45). Krushinskaya (1983) reasoned that signaling behaviour would tend to be stereotyped and predictable, which are distinctive features of MAPs, during breeding activities and inter-male competition. These were the only contexts in which the OMD was performed.

10) Inter-seal Distance

Condor (1949) distinguished among contact and distance species depending on whether they maintained a minimum threshold distance between themselves and cohorts. Sullivan (1982) characterized harbour seals as a distance species, whereas many land-breeding pinnipeds would be considered thigmotactic contact species (e.g., Bartholomew, 1953; Bonner, 1968; Gentry, 1970; Le Boeuf and Briggs, 1977; McCann, 1980; Miller, 1976; Sandegren, 1976a; Stirling, 1971; Stirling, 1972; Vaz-Ferrira, 1981). Grey seals performed behavioural acts at a variety of inter-seal distances, and could be classified as either a contact or distance species depending on their breeding status (see Chapter Five for inter-seal distance comparisons among sites). Like harbour seals, they did not tolerate physical contact except between mothers and pups, playmates or copulating pairs. Yet, at the non-breeding site these seals often settled into a densely-packed group with individuals interacting at average inter-seal distances of only 19.4 cm apart (Table 5; and see Chapter Five for a discussion of sex differences in inter-seal distances). The situation changed during the breeding season when grey seals were more likely to interact at either long or very short range.

Grey seals were usually less than one m apart when they performed a behavioural act ($\bar{x}$ = 84.4 cm; Tables 1 and 2), although this measure was exceedingly variable (Table 5) with coefficients of variation generally greater than those for duration (Table 6). As an example, males were as far as 30 m apart when they oriented towards each other and exchanged OMDs, yet also performed this behaviour type when they climbed on top of cows.

The range of inter-seal distances was more variable at the breeding sites. At these sites there were more contact (PT, CLA, NUR, NTN, CLI and BIT) and "distant" behaviour types (OMD, RAW and CHA) performed than at Miquelon. This reflected the preponderance of both long-range threat displays, and short-range behaviour types during fights, copulation and mother/pup interactions. Further, like act duration, when inter-seal distance was significantly different among the three sites, behavior types at breeding sites were performed at greater ranges than their counterparts at Miquelon (HSW, STA, and DPA; Table 5). In these cases, the greater group dispersion at breeding sites could account for these differences. Greater dispersion of breeding males likely accounts for the fact that OMDs were performed at greater distances at North Rona than Sable Island.

While results from this study could not be compared to those of other pinnipeds at the level of individual behaviour types, grey seals interacted at greater inter-seal distances than many other land-breeding seal species, and were most similar to harbour seals in this respect (Davis and Renouf, 1986; Sullivan, 1982; Thompson, 1989). Large variation in inter-seal distance for each behaviour type, at all three sites, minimized statistical differences among behaviour types in this measure. Only the OMD was more likely to be performed when the interactants were further apart.

11) Precedent's Sex

In an earlier study of grey seals at Sable Island, Boness (1979) stated that "... the behavioural repertoire of females during the mating period is limited" (p. 29). Similarly, Harestad and Fisher (1975) reported that male Steller sea lions exhibited a greater behavioural repertoire than females (or yearlings). This thesis corroborated these findings at Sable Island and Miquelon, but repertoire size was not different between the sexes at North Rona:

Number of Behaviour Types Performed by Each Sex			
	Miquelon	North Rona	Sable Island
Males' Repertoire	26	29	27
Females' Repertoire	22	29	22
Total Repertoire	27	33	29

At these three sites, repertoire size was not necessarily governed by breeding status, but perhaps instead by group density. Higher group density at Sable Island and Miquelon, combined with males' greater propensity to interact with other seals (Chapter Five and Table 14), may have resulted in use of a broader array of behaviour types by males.

Sixty percent of grey seal behaviour types were as likely to be performed by either sex (20/33; Tables 1 and 2). Of those more likely to be performed by one sex, there were clear patterns. At all sites, the preponderance of behavioural acts involving display or contact with foreflippers were performed by females; males were much less likely to perform an EFF, FSS, FSW or FSB than females (Table 1). There are two possible reasons that females were more inclined to use their foreflippers (thus momentarily reducing their mobility) than males, particularly at the breeding sites. Females were less likely to be attacked than males and therefore had less need to be prepared to move away. Also, females with pups were reluctant to move away from them, or were more likely to interpose themselves between threatening individuals and their pups (Boness *et al.*, 1982) than flee.

Like many other male pinnipeds (e.g., Anderson and Harwood, 1985; Beier and Wartzok, 1979; Boness, 1984; Cox, 1981; Gentry, 1970; Jouventin and Cornet, 1980; Kaufman *et al.*, 1975; Le Boeuf, 1986; McCann, 1980; McCann, 1981; Sandegren, 1976a; Siniff *et al.*, 1979), male grey seals were more likely to perform behavioural acts associated with copulatory (CLI, CLA, PT) or agonistic interactions (OMD, APT, CHA, RHV, DPA and AVF). Unlike territorial breeding males, grey seal bulls were often more mobile within the breeding groups (particularly at Sable Island), and thus more likely to be the sex performing behavioural acts which resulted in distance changes (APT, CHA or DPA). This was also true at the non-breeding colony, but the males performing acts resulting in distance changes were predominantly playing subadults.

12) Precedent's Age

As expected of the oldest age class (e.g., Bekoff, 1972; Burghardt, 1977; Smith, 1985), adult seals had the largest repertoire (31 behaviour types), and were seen to perform virtually all behaviour types (Tables 1 and 2). They were the exclusive performers of two behaviour types, OMD and PT, but did not perform NUR (performed by pups) or FSB (performed by mothers). Harestad and Fisher (1975) reported that older Steller sea lions (males in particular) conserved energy by performing relatively more non-contact behavioural acts. This may have been true for breeding adult male grey seals since they performed a greater proportion of behavioural acts (e.g., OMD and STA) at some distance than did non-breeding males or subadults. However, the greater proportion of acts performed at some distance was a minimal difference since adult seals' repertoires had a predominant contact component at all sites.

Mothers had very similar repertoires (29 behaviour types) to other adults, but did not perform OMDs or PTs (Tables 1 and 2). Perhaps due to mothers' frequent interactions with their nearby pups (Davies, 1949), coupled with their reluctance to move away from them when another seal approached, mothers were more likely to perform behaviour types characteristically executed at close-range. For example, mothers frequently performed FSB, HSW, NTN, SNI, LAW, ROS and BSR, but were unlikely to DPA or RAW as these would take them away from their pups.

Subadults' repertoires (24 behaviour types) were almost 30 percent smaller than adults' and, in this study, included many relatively vigorous behaviour types performed during play. In fact, most interactions recorded between subadults were playful. Like harbour (Renouf and Lawson, 1986a; 1987; Wilson, 1974b), elephant (Rasa, 1971; Schusterman, 1968) and grey seals in previous studies (Lockley, 1966; Wilson, 1974b), behaviour acts which were highly aggressive when performed by adults or mothers, (e.g., HTH, FSR, HSW, BIT, CHA and RAW) were similar in form when performed by subadults, but altered (such as through reduced intensity) to cause no apparent physical injury. Or, in the case of CHA and RAW, subadults did not perform these (perhaps intentionally) for sufficient duration to elude their play partners. Unlike play behaviour of primates, which often incorporates elements of copulatory behaviour (e.g., Altmann, 1962b; Anzenberger *et al.*, 1986; Klein and Klein, 1971; Struhsaker, 1967; van Lawick-Goodall, 1968), I did not record any instances of subadults performing behavioural acts specifically characteristic of the copulatory process (e.g., OMD and PT). Even when clasping a play partner for example, subadults adopted different orientations than copulating adults, and the CLA lasted for a shorter duration.

At both breeding sites pups had the smallest repertoires (18 behaviour types). Most behaviour types were performed clumsily, without apparent vigour and usually at close range with the successor (e.g., EFF, NTN, PON, SNI, BIT, CLI, and NUR). Although Rasa (1971) observed it in weaned elephant seal pups, grey seal pups were never seen to perform reproductive (e.g., OMD, CLA or PT) or highly aggressive (e.g., HTH, FFW, FSB or HSW) behavioural acts. This may have resulted from the limited gregariousness of grey seal pups (e.g., Davies, 1949; Fogden, 1971; Kovaks, 1987b). Grey seal pups never interacted with other pups when they were nursing since mothers did not tolerate any pup other than their own. After weaning, grey seal pups did not seek the company of other seals, and so rarely interacted with any other age class and played on their own with objects (and see Kovaks, 1987b).

13) Sequence Type

Almost all behaviour types were performed in aggressive contexts, the most common setting for grey seal interactions (see Chapter Five and Table 36). The broadest, and most similar repertoires, were characteristic of aggressive (31 behaviour types) and copulatory (28 behaviour types) sequences. This was expected since female grey seals' normal responses to the sexual overtures of males were aggressive (and see Anderson *et al.*, 1975; Boness *et al.*, 1982; Boness and James, 1979; Davies, 1949; Hewer, 1960a; Twiss, 1991). In fact, while either sex performed HTH, FSR and BIT during aggressive interactions, only females performed them during attempted copulation. Like the males of the elephant seal (Christenson and Le Boeuf, 1977; Le Boeuf, 1972), Steller sea lion (Gentry, 1970; Jouventin and Cornet, 1980; Sandegren, 1970), South Australian fur seal (Stirling, 1971) and Antarctic fur seal (McCann, 1980), grey seal bulls attempted to circumvent these aggressive signals and were more likely to do so through AVF, RHV, CLI and ROA.

While PT was exclusively copulatory, the behaviour types FSS, FSW, FSB and NHS were recorded only during aggressive bouts (Tables 1 and 2). As noted in section 11, the three behavioural acts involving the foreflippers were primarily performed by females as defensive threats. Either sex was likely to perform an NHS, though this apparently "relaxed" behaviour type was performed only during aggressive sequences (see postulated function section, below).

The least number of behaviour types (22) were performed during mother/pup sequences, of which only two of the entire possible repertoire were predominantly performed in that context (PON and NUR; Tables 1 and 2). Many behaviour types common to aggressive or copulatory sequences were never performed during mother/pup sequences (e.g., OMD, HSW, HTH, FFW, FSB, FSS, FSW, CHA, CLA, CLI, RAW, or PT). While young have been seen to direct copulatory behaviour towards their mothers in ungulates (Franzmann, 1978; Geist, 1971; Meagher, 1978; Walther, 1984), cetaceans (e.g., Tavolga, 1966) and primates (Anzenberger *et al.*, 1986; Klein and Klein, 1971; Struhsaker, 1967), this was not the case for grey seal pups. Most behavioural acts were performed gently and sedately by mothers and pups when they interacted with each other.

The range of behaviour types used during play sequences was quite broad (25 types) and, like mother/pup sequences, exclusive of certain behavioural acts common to copulatory (PT) or aggressive interactions (FSB, FSS, FSW or OMD). CLI was a predominant behaviour type, particularly by subadult males at Miquelon, perhaps because there was no risk of the successor biting and injuring the performers' exposed foreflippers as would be the case in an aggressive context. Like other young pinnipeds (e.g., Gentry, 1974; Harestad and Fisher, 1975; Rasa, 1971; Renouf and Lawson, 1986a; 1987; Wilson, 1974b), playing grey seals performed behaviour types similar in form and pace to those used during aggressive and adult interactions. However, playful versions of behaviour types which were intense and potentially damaging in agonistic contexts (BIT, FSR, HSW) were obviously constrained, even when directed by larger animals towards smaller ones (Bekoff, 1974; Fagen, 1981; Smith, 1984).

Frequencies of Behavioural Categories

A stacked histogram of the relative frequencies of behaviour types (Figure 15) demonstrates the considerable differences among the three study sites. In most cases, a behavioural act was performed at a greater frequency at Miquelon and Sable Island, notwithstanding the greater number of seals within the Focal Area at these sites (and see Chapter Five).

The frequency of five behaviour types (EFF, FSR, HEX, GLA and ECL) was significantly greater at Miquelon than the other sites. The first four were usually performed by females at this site, and during aggressive responses to the movement or approach of another seal nearby (see section 11, above). Female grey seals (usually adult) at Miquelon were extremely bellicose, even when compared to those at breeding sites. They responded aggressively to all approaches, preferred the peripheral ends of the group in which to haul-out, and commanded a greater amount of space around them.

In contrast, the less "serious" nature of most interactions at this non-breeding site may have resulted in the significantly greater frequency with which male grey seals were willing to perform an ECL during interactions compared with North Rona and Sable Island.

The significantly larger frequencies of CHA and RAW at Sable Island (Figure 15) result from both the greater mobility of breeding males and the less stable social organization at this site (Boness, 1979; 1984; Boness and James, 1979; Twiss, 1991). The larger males frequently chased smaller males who were attempting to gain access to the females farther up the beaches. As part of this increased antagonism among breeding bulls, they performed OMDs at greater frequency than did the more stationary bulls at North Rona.

As mentioned previously, grey seals normally disliked physical contact with other individuals. Even pups did not welcome their mothers' nudges or attempts to prolong contact with the pups. Thus, the relative frequencies of those behaviour types requiring prolonged contact were low at all sites (FSR, PON, NTN, BIT, CLI, CLA, NUR and PT).

Postulated Messages in Behavioural Acts

The primary approach in this thesis to this point has been description and comparison of the topological aspects (physical nature of signals) of grey seal biocommunication. In this section I theorize what referent (the message in the signal, or semantic aspect) might have been contained in behavioural acts and, where possible, what component(s) of the acts were sign vehicles (the effective part of the signal).

In some cases I have also made suppositions about signal meaning (i.e., how the successor interpreted the signal). This task is laden with difficulties (e.g., Andrew, 1972; Dabelsteen, 1985; Halliday, 1983; Miller, 1973; Peters, 1980; Smith, 1965; 1968; 1969; 1977) since an observer must make such suppositions based solely on information from external cues such as context or the successor's responses to the behavioural act (pragmatic aspects). Further caution might be mandated if "No display that is used in more than one kind of circumstance has a single function ... [or] single meaning" (Smith, 1977).

While grey seal behaviour was sequentially predictable (see Chapter Four), in many cases behaviour types which seemed to indicate that the performer was agitated or angry (such as HTH, FFW, FSW or HSW) were rarely followed by a physical attack. Like harbour seals, grey seal "fights", particularly between females or males and females, often resulted in no actual contact (also Boness, 1979; Davies, 1949; Hewer, 1960a). Entire exchanges were mediated by vigorous visual and vocal signaling during head feinting and dodging. Except when bulls of similar size met at the breeding sites, or a bull attempted to copulate with a female, it was difficult to determine if the performers' acts were actually signaling an intent to attack. That is, the referent and meaning of signals in these situations were less clear; obviously the performers were agitated, but the extent to which they would press toward an actual physical attack were equivocal to me. Extrinsic features of the interactions, such as season or interactants' ages, size and sex, may have provided the added information necessary for the successor to correctly interpret the performers' signals.

The open mouth display {called "low open mouth threat" by Anderson (1975) and "challenging posture" by Hewer (1960a)}, unique to breeding grey seal bulls, was an example of a behavioural act which conveyed several messages depending on context. Miller and Boness (1979) termed this behaviour type a "distance threat" used by tenured males in response to activity by distant males. Certainly OMD was used as a longer range signal than most (up to 30m; this study and Boness, 1979; Boness and James, 1979; Miller and Boness, 1979), since the bright pink oral mucosa against the darker background of the bulls' faces provided easily-recognized visual information (Figure 12A; and see Anderson, 1978; Anderson *et al.*, 1975). The sign vehicle in the OMD was the open mouth, and to a lesser extent the extended neck and barely-audible exhalation. Between bulls the OMD certainly indicated that the performer was aggressively aroused. Its meaning as an apotreptic threat (Barnett, 1981) in this context was evident by the response in kind by similar-sized males, or retreat by smaller or subordinate bulls. Furthermore, OMD was never performed in playful or non-breeding situations. On the other hand, bulls often also directed this behaviour type at females whom they were approaching. In this context OMD may have indicated an ambivalent disposition on the part of the bull. The bull which approached a (usually) bellicose cow had to overcome the female's aggressive responses in order to successfully copulate with her (Anderson *et al.*, 1975). The bull was therefore torn between his reluctance to approach a combative consort and his desire to copulate. The OMD may have conveyed a message of arousal (sexually and aggressively) and intent to approach. As a result, females became more visibly agitated when bulls accompanied an approach with OMDs than without.

Using the otariid "bark" as an example, Miller (1991) stated that:

> *"Species that live at close quarters can use structurally graded signals and contextual information extensively, and often build parts of their structurally graded communication systems around 'keystone' signal types"* (p. 154).

Keystone signal types are basic behaviour patterns to which structural and temporal modifications are applied by the performer when it wishes to convey a different message. For grey seals, the "keystone" signal types would likely be HEX and EFF, which emphasized the seals' most mobile appendages, their heads and foreflippers.

The most unhurried behavioural act involving the head was HEX. This category was structurally homologous to an HTH, but its speed was less. HEX was similar to the static "gape" used during aggressive interactions of many otariid species (e.g., Gentry, 1970; 1975c; Harestad and Fisher, 1975; Marlow, 1975; Miller, 1975a; Sandegren, 1975; Sandegren, 1976b; Stirling, 1971) and Hawaiian monk seals (Kenyon and Rice, 1959). Depending on the context, however, it could convey a sense of either assertive or submissive threat. A dominant bull which performed a slow HEX towards a subordinate would often elicit the same panicked withdrawal response as if the performer had executed a vigorous HTH. Conversely, a subordinate bull would often extend his head towards a threatening, dominant bull while emitting loud open mouth whoos. In cases where the subordinate was very afraid, he would concurrently move away (behaviour much like the evasive, cut-off retreat by subordinate Steller sea lions; Sandegren, 1975).

HTH (also called "lunge" in Anderson, 1978; Anderson *et al.*, 1975; Cameron, 1969) was normally a defensive threat that was performed by the subordinate member of an interacting pair, and was frequently accompanied by loud vocalisations (open mouth whoo). This behaviour has also been reported as an agonistic signal in harbour (Allen, 1985; Sullivan, 1982), weddell (Kaufman *et al.*, 1975) and Hawaiian monk seals (Kenyon and Rice, 1959) as well as a number of otariid species (Gentry, 1970; 1974; 1975c; Harestad and Fisher, 1975; Marlow, 1975; Stirling, 1971). It was a graded act in that it could have been performed as a quick, quiet "stab" of the head (such as a pup towards its mother if she poked it awake), or at the opposite extreme, as a vigorous thrust of the head with loud vocalisation (such as by a female towards a male attempting to copulate with her). In aggressive contexts, the level of performers' arousal was reflected on this continuum. HTHs performed during play bouts were less vigorous than during agonistic interactions, and were never accompanied by audible vocalisations. This suggests that the sign vehicle, the open mouth and rapid head movement toward the successor, was augmented by vocalisation when the performer was most aggressively motivated.

A similar behavioural act performed at close range was HSW which may have been what Cameron (1967) observed at a great distance in another group of grey seals in Nova Scotia, and called "snout caressing". This behaviour type seemed to be relatively less threatening than HTH, a supposition supported by the fact that HSW was used relatively more frequently during playful interactions. Unlike a HTH, it was unlikely that a HSW would precede a BIT in any context; rather, a HSW was likely to be immediately copied by the successor.

Grey seals performed six behaviour types which involved the foreflippers (EFF, FSB, FFW, FSW, FSS and FSR). In most cases these were used in aggressive contexts by performers in response to the undesired approach of another seal. While I recorded more categories of foreflipper-based signaling than Sullivan (1982), I concur with his hypothesis that foreflipper displays could be arranged along an intensity scale. For these grey seals, EFF seemed to be the least aggressive form of foreflipper signal. At the opposite extreme, FSR was used only when the successor was in close proximity and the performer was highly agitated.

Arrayed from least to most aggressive, the categories might be arranged:

$$\textbf{EFF} \longrightarrow \textbf{FSB} \longrightarrow \begin{matrix}\textbf{FFW}\\ \textbf{FSW}\end{matrix} \longrightarrow \textbf{FSS} \longrightarrow \textbf{FSR}$$

FFW and FSW appear to be structurally similar, so the latter may just have been cases of FFW that happened to be performed in shallow water. As in most behaviour types, contextual cues extrinsic to the act probably modified the message conveyed by these signals. Both EFF and FSR[14] were performed by pups in response to investigative or playful attention from their mothers – contexts considerably less aggressive than between adult bulls at the breeding sites. In most cases, except perhaps play, these foreflipper-based behaviour types served as apotreptic signals that indicated the performer was displeased with the proximity or approach of a conspecific.

Three behaviour types were used as investigatory actions by grey seals of all ages and both sexes. NTN and SNI seemed to be a means whereby interactants could exchange olfactory or tactile information, and are common throughout the animal world. PON, documented in grey seals at Orkney (Fogden, 1971), and much like the "nudging" behaviour of young ungulates (Walther, 1984), seemed to be an attention-getting mechanism. Grey seal pups often performed it as a prelude to nursing in an apparent attempt to get the mothers to roll onto their sides and expose their nipples. Less frequently, mothers poked their pups as a way of gently playing, to wake the pups if the mothers wanted to move them away from harm, or initiate nursing. Subadults were occasionally seen to poke their play partners in an effort to resume the interaction after the partner had been distracted. That this behaviour type was only used among amicable partners was evidenced by the fact that adults, who usually interacted in an agonistic manner, never poked each other with their noses.

GLA and STA, often conveyed semantic information in addition to being behavioural acts required to see the successor. Like a number of primate species (e.g., Altmann, 1962a; Hinde and Rowell, 1962; Klein and Klein, 1971; Marler, 1976; Poirier, 1970; van Lawick-Goodall, 1968) some ungulate species (Park, 1969; Yoakum, 1978), and

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[14] As noted by (Fogden, 1971) mothers frequently performed FSR towards their pups after the mothers had rolled onto their sides, perhaps as a means to stimulate the pups to nurse.

other pinnipeds (Anderson, 1978; Gentry, 1975c; Miller and Boness, 1979; Sullivan, 1982), grey seal STAs often indicated an aggressive intent on the part of the performer. In close proximity, and particularly in agonistic encounters, the successor often reacted with hostility to a STA or GLA. The aggressive nature of these behaviour types in agonistic contexts was emphasised by the fact that the two acts which seemed to fulfill a "cut-off" role (Chance, 1962; Immelmann and Beer, 1989) during aggressive interactions were antithetical to STA. During AVF and LAW the performer's facial orientation was directed away from the successor, and the latter was less likely to attack.

It should be noted that AVF could still have indicated anger or aggressive intent as it was a common component during agonistic interactions between bulls at the breeding sites. In these cases AVF was interspersed with advances towards the successor (i.e. a mobile context providing additional semantic information) and may have been employed to emphasize the prominent snouts and rugous necks unique to adult bulls (Boness, 1979; Miller and Boness, 1979), much like the displays of specialized facial structures in hooded (Berland, 1958) and elephant seals (Sandegren, 1976a).

Biting was a behaviour type which could convey a number of messages. In aggressive and copulatory bouts a BIT was obviously meant as an agonistic threat which graded in intensity from small, brief BITs employed by females during copulation (which seemed to be a means of "complaining"; also seen in Steller sea lions (Sandegren, 1975; 1976b)), to vigorous, head-shaking bites by battling bulls. In other contexts, BIT could be used as a signal of playful intent or, when used by a bull during copulation, as a method to better hold onto the female and perhaps as a signal used to pacify her (see Boness and James, 1979).

Bulls performed a CLI onto a female when initiating a copulatory sequence. Like BIT, this often seemed to have a pacifying effect on the female. However, in a playful context, CLIs were performed during the most vigorous periods during the bouts, and judging by the exuberant responses, were an "intense" signal to continue play. Similarly, a CLA was a vigorous signal of intent to continue play at Miquelon. During copulatory bouts, the male clasped the female only during intromission (or while attempting to do so) and this behaviour type also indicated the male's intent to continue.

The behaviour type APT could have contained a number of messages. At the grossest level it signaled the performer's intent to reduce the distance between itself and the successor. If it was performed by a bull during an interaction with a female or subordinate male, its meaning was clearly perceived as threatening by the successor (as indicated by their hostile responses). Certainly breeding bulls used short APTs in an effort to supplant intruding males (or the more vigorous CHA; see below). That an approach was often perceived by grey seals as threatening in aggressive or copulatory bouts is consistent with reports in other pinnipeds (e.g., Anderson *et al.*, 1975; Harestad and Fisher, 1975), and ungulates {Yoakum, 1978; Walther (1984) stated that "... a[n] ... approach toward a partner often has a threat character."}. On the other hand, an approach could merely indicate a willingness to play when performed by one subadult towards another during a play bout.

The more vigorous type of approach behaviour, CHA, was used as either a highly aggressive or highly playful signal, depending on context. At the breeding colonies CHAs were performed by dominant, often resident, bulls (Boness and James, 1979).

Since subordinate or smaller bulls were obviously very vigilant when they entered areas occupied by larger bulls, the brief chases by dominant males may have functioned like the "run displays" of gorillas and chimpanzees (Schaller, 1965; van Lawick-Goodall, 1968). Run displays advertised the aroused state and dominant status of the performer. In the same way, CHA may have both signaled the bull's desire to force the successor from the area, and conveyed the performer's willingness to do this to any other males contemplating a similar incursion. Anecdotally, I frequently observed more than one subordinate male leaving the area when a more dominant bull chased one subordinate away.

When chased, either in play or aggressive sequences, the successor usually performed a RAW in an effort to maintain or increase the inter-seal distance. By rushing away, a breeding bull was signaling his submission (and fear) to the bull chasing him. In playful contexts at Miquelon, the performer was more likely to initiate a RAW spontaneously, rather than in response to an APT or CHA by the successor. In these cases a RAW was perhaps used by a performer to incite a playful CHA.

Like RAW, DPA was performed to increase the inter-seal distance between interactants. It was not simply a less rapid form of RAW since it was relatively more likely to occur spontaneously without following a CHA or APT by the successor.

While a ROA was often the most expedient way for seals (usually bulls at the breeding sites) to move laterally away from a successor in crowded quarters, other authors have suggested that it conveyed a message. ROA has been observed in grey seal colonies on both sides of the Atlantic (Cameron, 1967; Cameron, 1969; Hewer, 1960a) and often in the context of the final act of an agonistic exchange in which the performer has been victorious. Hewer (1960a) and Twiss (1991) both perceived that this was a "victory roll" and signaled the dominance of the performer. Evidence from this study is mixed in that bulls often rolled away from extremely aggressive females (having "lost" in their attempts to copulate) and mothers were also seen to roll away from their persistent pups if they no longer wished to nurse them. The message of this behavioural act, if there was one, was undoubtedly modified by the context in which it was performed.

When a seal performed a YAW, NHS or BSR, it was often during a lull in the pace of the interaction. Neither partner exhibited signs of agitation, so it seems unlikely that these behaviour categories could have functioned as "displacement activities" (e.g., Wilson, 1972). Further, it was difficult to determine if these behavior types signaled a grey seal's desire to slow the pace of the interaction, or were performed as a result of a behavioural hiatus.

A vertically raised head is a common behavioural act during aggressive interactions in many animal species (e.g., Bouckhout, 1972; Cameron, 1969; Gentry, 1975c; Kovacs, 1987a; Le Boeuf and Petrinovich, 1974b; Lockley, 1966; Rasa, 1971; 1970; Sandegren, 1976b; Schusterman, 1968; Stirling, 1970; 1971; Walther, 1984). Termed "full neck", and as a less intense act, "snobbing", in otariids (Harestad and Fisher, 1975; Marlow, 1975; Sandegren, 1970; Stirling, 1970), the RHV was a means whereby the performer tried to keep its head higher than the successor's. Unlike the "necking" (Harestad and Fisher, 1975) and "rearing" (Bartholomew, 1952; Le Boeuf, 1972; McCann, 1981; Sandegren, 1976a) behaviour of other seals, RHV did not seem to be a proactive aggressive behaviour. Rather, the performer seemed to express its reluctance to keep its face in close proximity to the threatening partner. This is probably because an aggressor was more likely to bite towards an opponent's face when they were oriented head-on. In this context a RHV was submissive behavioural act. During play, on the other hand, both partners were more likely to perform this behavioural act simultaneously and it could be viewed as a stationary version of the childhood game, "king of the mountain".

A grey seal was as likely to perform an ECL during any type of interaction. Since this behaviour type usually occurred when the pace of the interaction was lowest, it may have indicated a state of relative ease on the part of the performer (rather than being the displacement action of a distressed individual). Alternately, an ECL may have been the performer's attempt to discontinue the interaction (i.e., a cut-off signal). This supposition is supported by the fact that most ECLs occurred towards the end of interactive sequences.

Although ROS was occasionally performed in response to an aggressive approach by the successor, it was more usually executed by mothers prior to nursing their pups. In these cases it was either a response to PON by hungry pups, or an active solicitation of nursing (and see Fogden, 1971).

The messages and functions conveyed by NUR and PT were clear. Unlike mountain sheep which occasionally use PT as a means to assert dominance (Geist, 1971) or chimpanzees which use it to reassure subordinates (Trivers, 1985), grey seals seem to use this behaviour type only in a reproductive role. PT was never observed outside the breeding season, such as during play at Miquelon, or during same-sex interactions.

Clusters of Behavioural Categories

Discriminant analyses indicated that the two measures which best discriminated among the behaviour categories were the position of the seals' eyes and mouth at the onset of each type (Tables 16, 17 and 18). This emphasizes the importance of visual signals in grey seal communication, and in particular facial structures (see also Miller, 1975a; Miller and Boness, 1979). Since they lack specialised facial display structures like the inflatable proboscis of hooded (Berland, 1958) or elephant seals (Bartholomew, 1952; Le Boeuf, 1972; Le Boeuf, 1974), the tusks of walrus (Miller, 1975c; Salter, 1980) or the large mystacial vibrissae of many otariid species (e.g., King, 1983; Sandegren, 1976b; Trillmich, 1984), grey seal behaviour has evolved to emphasise their most obvious facial features, the eyes and mouth. The eyes are large and dark, with a white sclera which is clearly visible when the seal swivels its eyes laterally or opens them wider in fright or excitement. And as mentioned previously, the mouth's colouration renders it highly visible when opened.

Cluster analyses with complete linkage produced behavioural dendrograms for the behavioural repertoire at each site (Figures 16, 17 and 18). Each cluster had similar counterparts in the dendrograms of the other sites and these clusters appear to represent rational groupings of the behaviour types on the basis of the previous section on signal function.

At Miquelon there were six clusters, with the rare behaviour type YAW dissimilar to other types[15] (Figure 16). Cluster A and B's members were behaviour types commonly performed at short range, often aggressively and with greater vigour than most types in the other five clusters. They were characteristically brief, perhaps as these behavioural acts entailed approach or contact which grey seals disliked.

ECL, a low-intensity behavioural act, did not involve distance change and seemed to be relatively more autonomous (not a response to the prior behavioural act of the successor) than most behaviour types, except perhaps YAW.

The members of cluster D effected an increase in the distance between interactants. On the other hand, behaviour types in cluster E were used as gentle, closed-mouth investigatory contacts between playmates, rather than aggressive bouts.

The members of cluster F were related on the basis of the discriminative variables but did not seem to share a common function. STA, GLA and LAW were used to turn the performer's visual attention towards or away from the successor. APT decreased inter-seal distance and usually involved the performer watching the successor closely. Clusters E and F at Miquelon were similar in membership to clusters at the breeding sites: cluster C at North Rona (see Figure 17) and cluster B at Sable Island (see Figure 18).

The dendrogram of behaviour categories for North Rona contained five clusters, with behavioural act OMD dissimilar to most other types (Figures 17). The behavioural acts within cluster A could be characterised as relatively sedate behaviour types which were not normally elements of combative exchanges and, except for PT, the eyes were usually closed during these behavioural acts. While several types were performed during physical contact (NUR and PT), most members of this cluster were performed when the interactants were at least 29 cm apart (Tables 1 and 2). These behaviour types

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[15] YAW was an unusual combination of physical attributes since the mouth was always open, but the eyes were frequently closed, during its performance (Table 2).

were the same as those in the loosely-related cluster F of Sable Island (Figure 18), and similar to cluster C for Miquelon (Figure 16).

Cluster B's members were behaviour types commonly performed at short range, often in aggressive contexts and with greater vigour (i.e. both the eyes and mouth were usually open and the seal was vocalising) than most types in other clusters. They were characteristically brief, perhaps as these behavioural acts entailed close proximity or contact, which grey seals generally shunned. The members of clusters A of the Miquelon (Figure 16) and Sable Island dendrograms (Figure 18) contained subsets of the members of this cluster. At both breeding sites OMD was most closely related to the members of this cluster, perhaps supporting the previous interpretation that this behavioural act was an aggressive signal.

The members of cluster C were typically performed at close range and with both interactants in physical contact. None of these behaviour types would have resulted in physical injury to the successor, and three were usually performed sedately (PON, NTN and ROA).

BIT and RHV were closely related to each other at North Rona (cluster D; Figure 17), as well as at Sable Island (cluster E; Figure 18), and more loosely related within cluster B at Miquelon (Figure 16). The performer's eyes and mouths were always open at the start of these acts. In both cases the interactants were close to each other at the start of an BIT or RHV, and in fact the successors commonly performed an RHV in response to being bitten. The members of cluster E all resulted in distance changes between interactants (although AVF and ROS were subtler movements).

As mentioned above, the members of cluster A in Figure 18 (Sable Island) were very much like cluster A at Miquelon and B at North Rona (Figures 16 and 17). These behaviour types were usually aggressive and the most closely related to OMD.

Like cluster C for North Rona, cluster B of Sable Island types contained those generally used in an investigatory manner (GLA, STA and NTN). LAW may have been incorporated into this group since the performers' mouths were consistently open (as they were in the closely-related STA).

Clusters C and D were behavioural acts which resulted in changes in inter-seal distance (like cluster E for North Rona) and several were performed with open mouths (AVF, CLI, CHA).

The behaviour types in cluster F resembled those in cluster A of the North Rona dendrogram (Figure 17), but were not as strongly related. Except for BSR, they were usually performed at close range or in contact and were often performed sedately and with no chance of inflicting injury on the successor.

Summary

Like many other animals (Slater, 1981), pinnipeds are highly individualistic because of their intelligence, behavioural plasticity, and unique developmental experiences over many years (Miller, 1991). Even particular age-sex classes are extremely variable. In the Antarctic fur seal (*Arctocephalus gazella*), territorial "bulls are individually highly variable in their reaction to man ..." (Bonner, 1968; p. 40).

The grey seal is no exception to this and the inter-individual variation in quantitative measures of behaviour acts was often greater than that among the three study sites. The potential information conveyed within the broad behavioural repertoire of this species was augmented by the changes wrought by extrinsic factors such as context, season, age class and sex.

Ethogram Categories and Sample Completeness

- There was an excellent concordance between the behaviour types that I and a näive observer had coded. The structure of the ethogram was of sufficient precision to ensure inter-observer reliability, yet descriptive enough to accommodate the individual variability inherent in grey seal communication.

- Catalogue completeness estimates indicated the datasets in this study provided excellent sample coverage with which to build a comprehensive catalogue of terrestrial behaviour.

The Grey Seal Repertoire

- Grey seal behavioural types were diverse and regularly modified in subtle manners by performers depending on contextual factors such as site, interaction type or the age or sex of their partners.
- Comparisons of the grey seal repertoire with those from the few other pinniped species for which there has been descriptions of behaviour must be superficial since there are apparent differences in the emphasis researchers placed on creating comprehensive behavioural inventories.
- In the event ethologists undertake in-depth study of the communicative behaviour of other pinnipeds such as elephant seals, the grey seal repertoire will probably not appear comparatively broad.

Major Characteristics of Behavioural Acts

Eyes Condition

- Grey seals' eyes were predominantly open at the onset of behavioural acts.
- Where the risk of aggressive response was low, eyes were closed during the performance of behaviour types (e.g., YAW, ECL, NUR and BSR).

Mouth Condition

- Grey seals' mouths were open during performance of most behaviour types, particularly during agonistic or vigorously playful communication.
- Grey seals kept their mouths closed during only 10 behaviour types (NTN, PON, SNI, GLA, ROA, RAW, NHS, ECL, BSR and PT) which were less often performed during agonistic interactions and not liable to be responded to aggressively.

- Despite the frequency with which grey seal behavioural acts were performed with open mouths, they did not always do so in order to vocalise.
- Male grey seals commonly used their mouths solely as a visual display structure whereas females integrated both vocal and visual information.

Vibrissae Position

- With the exception of the behaviour types LAW, ROA and ECL, grey seals customarily kept their vibrissae protracted.
- Vibrissae may have performed a role in tonic communication by continuously transmitting information regarding the performer's level of arousal.

Nares Position

- Nares were clearly open at the onset of only five behaviour categories: OMD, FSS, NTN, PON and SNI.
- Due to grey seals' respiration pattern (during which the nares are closed for a large proportion of each cycle) and the difficulties in seeing the nares' position, I was more likely to record the nares as closed (or unknown).

Tail Position

- Grey seals only elevated their tails when they were executing a RAW, a locomotary behaviour type which was performed with great vigor.
- The tail of the grey seal was apparently not used as a signaling device .

Head Height

- Relative head height was highly variable among, and often within, behaviour categories. There were no consistent patterns among the three sites based on this measure, and relative head height was statistically unequivocal in only 33% of behaviour types.

Relative Orientation

- The most common body and head orientations adopted were either lying parallel to each other, facing the same direction, or facing each other head-on.

- Body or head orientations were seldom predictive of subsequent behaviour.
- Grey seal males have enlarged snouts which appear to be sexually-selected display organs and probably enhanced aerial displays.

Vocalisations

- Grey seals were usually quiet during communication, regardless of locale.
- At close range, and for socially subordinate seals (females or subordinate males), vocal accompaniment assumed a more prominent role. This was particularly true when behavioural acts were performed in agonistic contexts.
- Males at breeding sites occasionally accompanied an ECL with a distinctive, but difficult to localize, warbling vocalisation.

Behavioural Act Duration

- Behavioural acts performed by grey seals were of short duration in many instances, with most lasting less than five sec. However, act duration was exceedingly variable both within and among behaviour types.
- The briefest behaviour types were HTH, HSW and GLA, and usually performed in agonistic contexts.
- The behaviour types of greatest duration were NUR and CLA.
- The behaviour types with the lowest variability of act duration were OMD, YAW and NHS, which, with their invariant structural characteristics are typical of Modal Action Patterns.

Inter-seal Distance

- Grey seals began to perform behaviour at a variety of inter-seal distances (usually less than one m), and could be classified as either a contact or distance species depending on their current breeding status and locale.
- Inter-seal distances were more variable at the breeding sites, with more acts performed at greater inter-seal distances than at the non-breeding site. In

addition, there were more behaviour types involving contact performed at the breeding sites than at Miquelon.

- The variability of inter-seal distances at the breeding sites reflected the preponderance of long-range threat displays (such as the OMD) and close-contact fights, copulations and mother/pup interactions.
- Grey seals interacted at greater inter-seal distances than many other land-breeding pinnipeds, and were most similar to harbour seals in this respect.

Precedent's Sex

- Sixty percent of behaviour acts were as likely to be performed by either sex.
- The preponderance of instances of behavioural acts involving display or contact with foreflippers were performed by females.
- Males were more likely to perform behavioural acts used during copulatory (CLI, CLA, PT) or threatening interactions (OMD, APT, CHA, RHV, DPA and AVF). Bulls were more mobile within the breeding groups, and thus were more likely to perform behavioural acts which resulted in distance changes.

Precedent's Age

- Adult seals had the largest repertoire (31 behaviour types), and were seen to perform virtually all behaviour types. They were the exclusive performers of two behaviour types, OMD and PT, but did not perform NUR (performed by pups) or FSB (performed by mothers).
- Mothers had very similar repertoires (29 behaviour types) to other adults.
- Subadults' repertoires were almost 30 percent smaller than adults' (24 behaviour types) and included many relatively vigorous behaviour types performed during play.
- At both breeding sites pups had the smallest repertoire (18 behaviour types). They performed behaviour types clumsily, without apparent vigour and usually at close range with the successor (usually their mothers).

Sequence Type

- The broadest, and most similar repertoires, were characteristic of aggressive (31 behaviour types) and copulatory (28 types) sequences.
- The fewest behaviour types (22) were performed during mother/pup interactions.
- The range of behaviour types used during play sequences was quite broad (25 types) and, like mother/pup sequences, exclusive of certain behavioural acts common to copulatory or aggressive interactions.

Frequencies of Behavioural Categories

- In most cases, a behavioural act was performed at a greater frequency during communication at Miquelon and Sable Island.
- The greater frequencies of the aggressive acts CHA and RAW at Sable Island resulted from the greater mobility of breeding males and the less stable social organization at this site. As part of this increased antagonism among breeding bulls, they performed OMDs at greater frequency than did the more stationary bulls at North Rona.
- Grey seals normally disliked physical contact with other individuals, thus relative frequencies of behaviour types requiring prolonged contact were low at all sites.

Postulated Messages Incorporated in Each Behaviour Type

- While most behaviour types were performed in agonistic contexts, many were also used during play or copulatory interactions.
- Many grey seal behaviour types were meant as apotreptic, threatening signals to discourage the approach of a cohort, or force it to move away.
- Since grey seals "fights" infrequently resulted in actual physical contact, the referents and meanings of signals were conflicting. The performers were agitated, but it was difficult to predict if they would actually attack.

- The OMD conveyed a message of long-range threat in most cases, but was also used by bulls when approaching cows in some cases.
- Most threatening behaviour types emphasized performers' heads or foreflippers, and behaviour types EFF and HEX might be considered "keystone" signal types.
- A number of behaviour types were graded signals (e.g., FFW, HEX, BIT) and seemed to correlate with performers' degree of arousal, fear or anger.
- Behaviour types in which the performer approached (APT, CHA) or watched the successor (STA, GLA) usually conveyed a threat, whereas antithetical acts conveyed the opposite (DPA, ROA, RAW, LAW, AVF).

Clusters of Behavioural Categories

- On the basis of two measures, eye and mouth position, there were distinct groupings of behaviour types at all three sites, and in many cases the clusters contained similar members among sites. These groupings usually agreed with the postulated functions of member acts.
- At Miquelon there were six clusters, with YAW poorly related to any of them.
- OMD was distinctive from other clusters, but most closely related to aggressive behavioural acts at the breeding sites (North Rona: 5 clusters; Sable Island: 6 clusters).

Chapter Four: Behavioural Sequence Analyses

Subsequent to assembling matrices of preceding acts and responses to them (e.g., Altmann, 1965; Gokhale and Kullback, 1978; Lefebvre and Joly, 1982; Slater and Ollason, 1972; Sullivan, 1979; 1981; Wiepkema, 1961), I was able to calculate sequential dependencies (Caraco, 1972; Fagen and Young, 1978; Slater, 1973). In light of the relatively broad behavioural repertoire of grey seals' and the variety of contexts in which this repertoire is performed, I predicted that their behavioural systems would be flexible, and the likelihood of one behaviour type following another would be probabilistic rather than deterministic. Using these sequences I was able to evaluate behavioural predictability, both between individuals (inter-individual) and within the series of behavioural acts performed by one individual (intra-individual). In addition, I investigated the roles which the sexes of the interactants and the site of the interaction played in the degree of sequential dependency.

I calculated which behaviour types were predominantly facilitory or inhibitory to subsequent behaviour in each matrix by summing positive and negative standardised residual values from the log-linear analyses.

Inter-individual Sequential Analyses

This section describes results from the analyses of sequences of behavioural acts performed by interacting seal pairs. Tables 19 to 21 contain the first-order transition frequencies of behaviour types performed by precedents and successors at each site.

Significant transitions are indicated with "+" or "–" signs in their respective cells in the transition matrices. Cells with positive values indicate that the occurrence of those preceding act types increased the probability of particular responses (act A is said to direct response B; Fagen and Young, 1978). Negative transition cell values indicate that the occurrence of a preceding act type reduced the probability of that particular response type occurring (act A is said to inhibit response B).

Sequential Dependencies at Miquelon

1) First-Order Markov Interaction Sequences

The summary matrix for inter-individual behaviour transitions contains 1437 cases (Table 19). I defined ten structural zeros which were succeeding act types that could not occur and whose respective cells were given a weighting of zero during log-linear analyses (denoted with X's in the table). These were:

- a CHA following an NTN or a CLI.
- a FSR, NTN, PON or SNI following a ROA or RAW.

A log-linear analysis revealed the maximum difference between observed and fitted marginal totals was 0.001 and G was 1523.1 with 666 df_{adj}. This exceeded that required for significance at $p \leq .05$ ($\chi^2_{(666)} = 726.9$). Therefore the sequences were non-random and there was at least a first-order transitional dependence between preceding and succeeding acts by pairs of interacting grey seals at Miquelon.

Significant First-Order Transitions

Using the method of Bishop *et al.* (1975), I calculated the $Y_{critical}$ value to be 0.998 for first-order transitions at $p \leq .05$. There were 198 standardised residuals for transitions whose absolute values exceeded this $Y_{critical}$ value. These represented 27.5 percent of the total number of possible cells in the matrix. Significant transitions, and their facilitatory or inhibitory characteristics, indicated by "+" and "–" signs, respectively, are indicated in the transition matrix (Table 19).

I determined which behaviour types most frequently influenced subsequent responses by successors by summing these positive and negative signs (assuming the values represent +1 or -1, respectively, and noting only those totals greater than +2 or less than -2; Table 22). At Miquelon the behaviour types HTH, BIT, DPA, AVF, and particularly, HSW, were more inhibitory than other types. EFF, FFW, PON, GLA, STA, CHA, RAW and YAW were more often facilitatory.

2) Second-Order Markov Interaction Sequences

Subsequently, I tested a second-order Markov model using a three-way transition matrix with the axes being first preceding acts, succeeding acts, and next preceding acts. There were 1315 weighted cases (the same structural zeros were entered as for the first order model) incorporating 27 behaviour types.

The log-linear analysis produced a G of 5111.4 with 19604 df_{adj}. This did not exceed that required for significance at $p \leq .05$ ($\chi^2_{(19604)} = 19930.6$). Therefore, there was a poor fit of the second-order model to the actual transitional relationship, at Miquelon. The likelihood of occurrence of a particular second behavioural act was not significantly influenced by the identities of the first act and the response to it.

3) Significant Sequential Dependencies in Interactions Subdivided by Interactants' Sexes

I subdivided transition data from Miquelon into three categories on the basis of interactants' sexes (male-male, male-female and female-female). I used the same structural zeros in the female-female and male-female submatrices as for the overall matrix. The behaviour types SNI and NHS were not performed during male-male interactions, so there were an additional eight structural zeros for this submatrix.

There were no significant transitional dependencies between preceding and succeeding acts during male-female ($G = 371.9$, $df_{adj} = 431$, minimum $\chi^2_{(431)} = 480.1$) or female-female interactions ($G = 289.6$, $df_{adj} = 324$, minimum $\chi^2_{(324)} = 366.7$).

However, a log-linear analysis revealed a degree of sequential dependence ($G = 703.7$, $df_{adj} = 539$) between acts performed during male-male interactions which exceeded that required for significance at $p \leq .05$ (minimum $\chi^2_{(539)} = 593.8$). There was therefore at least a first-order transitional dependence between behavioural acts and responses to them (Table 23). A second-order model was not significant, however ($G = 2792.7$, $df_{adj} = 14321$, minimum $\chi^2_{(14321)} = 14600.5$).

Significant First-Order Transitions in Male-Male Interactions

The $Y_{critical}$ value for first-order male-male transitions at $p \leq .05$ was 0.903 and there were 153 standardised residuals whose absolute values exceeded this (representing 28.8% of the submatrix). Significant transitions are indicated as facilitatory ("+") or inhibitory ("–") in the transition submatrix in Table 23.

When two males interacted, the behaviour type LAW was more inhibitory than other types. GLA, STA, ROA and YAW were more often facilitatory (Table 22).

Sequential Dependencies at North Rona

1) First-Order Markov Interaction Sequences

The summary matrix for inter-individual behaviour transitions contains 4229 cases (Table 20). Before performing log-linear analyses, I defined 38 structural zeros (non possible response types; denoted with X's in Table 20). These were:

- an OMD following a NUR or a PT.
- a HTH following a NUR.
- a FSR following a ROA or RAW.
- a FSW following a NUR.
- a NTN following a ROA, RAW, or a NUR.
- a PON or SNI following a ROA or RAW.
- a CLI or CLA following a NUR or PT.
- a CHA following NTN, CLI, NUR or PT.
- a NUR following OMD, HTH, FSW, BIT, CLI, CLA, CHA, ROA, RAW, NUR or PT.
- a PT following a CHA, ROA, RAW, NUR, or PT.

The log-linear analysis indicated a maximum difference between observed and fitted marginal totals of 0.012 and a G of 3128.1 with 987 df_{adj}. This exceeded that required for significance at $p \leq .05$ (minimum $\chi^2_{(987)} = 1060.9$). There was therefore at least a first-order transitional dependence between preceding and succeeding behavioural acts at North Rona.

Significant First-Order Transitions

I derived a $Y_{critical}$ value of 0.987 for first-order transitions at $p \leq .05$. There were 412 standardised residuals for transitions whose absolute values exceeded the $Y_{critical}$ value. These represented 39.2% of the cells in the submatrix. The significant transitions are indicated with "+" or "−" signs in their respective cells in the transition matrix, Table 20. At North Rona, the behaviour types OMD, HTH, HSW, NTN, STA, LAW, CLA, APT, CHA, DPA, ECL, NUR, PT and AVF were more inhibitory than other types. SNI, CLI, YAW, NHS, ROS and BSR were more often facilitatory (Table 22).

2) Second-Order Markov Interaction Sequences

I tested a second-order Markov model using a three-way transition matrix with the axes being first preceding acts, succeeding acts, and second preceding acts. There were 3930 weighted cases (the same structural zeros were used as in the first-order model).

The log-linear analysis produced a G of 13423.8 with 35840 df_{adj}. This did not exceed that required for significance at $p \leq .05$ (minimum $\chi^2_{(35840)} = 36281.3$). Therefore, there was again an inadequate fit of a second-order model to the actual transitional relationships recorded at North Rona. The probability of occurrence of a specific type of second preceding act was not significantly influenced by the identities of the first preceding act and the act succeeding it.

3) Significant Sequential Dependencies in Interactions Subdivided by Interactants' Sexes

Transition data from North Rona was then subdivided into three categories on the basis of interactants' sexes. I used the same structural zeros for each of these submatrices as for the overall matrix except the behaviour types PT and OMD. These two behaviour types were coded as structural zeros in both the preceding and succeeding act axes of the female-female transition submatrix. A PT could not follow an OMD in male-male interactions.

There was no significant first-order transitional dependence between acts and responses to them during interactions between female grey seals ($G = 525.0$, $df_{adj} = 582$, minimum $\chi^2_{(582)} = 638.9$).

Log-linear analyses did reveal dependencies between acts performed during both male-male ($G = 639.6$, $df_{adj} = 460$) and male-female ($G = 1003.1$, $df_{adj} = 654$) interactions. These exceeded the minimum χ^2 values necessary for significance at $p \leq .05$ ($\chi^2_{(460)} = 510.9$ and $\chi^2_{(654)} = 714.3$, respectively). There was therefore at least a first-order transitional dependence between behavioural acts and responses to them (Tables 24 and 25, respectively).

There were no significant second-order models for sequences subdivided by sex: 1) male-male: $G = 2552.2$, $df_{adj} = 12136$, $n = 336$, minimum $\chi^2_{(12136)} = 12393.1$; 2) male-female: $G = 4142.7$, $df_{adj} = 17166$, $n = 1127$, minimum $\chi^2_{(17166)} = 17471.6$; 3) female-female: $G = 2131.5$, $df_{adj} = 15165$, $n = 543$, minimum $\chi^2_{(15165)} = 15452.3$.

a) Significant First-Order Transitions in Male-Male Interactions

The $Y_{critical}$ value for first-order male-male transitions at $p \leq .05$ was 0.685 and there were 172 standardised residuals (representing 32.8% of the cells in the submatrix) whose absolute values exceeded this. Significant transitions are indicated as facilitatory ("+") or inhibitory ("–") in the transition submatrix in Table 24.

During male-male interactions at North Rona the behaviour types OMD, STA, CHA, RAW and ECL were more inhibitory than other types. There were no behaviour types that were particularly facilitatory (Table 22).

b) Significant First-Order Transitions in Male-Female Interactions

The $Y_{critical}$ value for first-order male-female transitions at $p \leq .05$ was 0.810 and there were 266 standardised residuals (representing 28.5% of the cells in the submatrix) whose absolute values exceeded this. Significant transitions are indicated as facilitatory ("+") or inhibitory ("–") in the transition submatrix in Table 25.

During male-female interactions at North Rona the behaviour types OMD, APT, CHA and PT were more inhibitory than other types. EFF, FFW, FSR, HSW, LAW and ROS were more often facilitatory (Table 22).

4) A Test For Seasonal Stationarity in Sequences From North Rona

Interaction sequences from North Rona, as well as the other sites, contained too few behavioural transitions to permit a statistical test of sequential stationarity. Instead, I examined temporal variation in sequential dependency by subdividing the whole season's data for North Rona into two halves (by dividing the overall observation period in half), and used the halve identities as the third dimension in a HILOGLINEAR procedure. There were 3229 weighted cases (the same structural zeros were used as in the first-order model) encompassing 33 behaviour types.

The log-linear analysis produced a G of 1953.5 with 2112 df_{adj}. which did not exceed that required for significance at $p \leq .05$ (minimum $\chi^2_{(2112)} = 2220.3$). The probability of occurrence of a succeeding act type following a specific preceding act was not affected significantly by its temporal position during the sampling period.

Sequential Dependencies at Sable Island

1) First-Order Markov Interaction Sequences

The summary matrix for inter-individual behaviour transitions at Sable Island contained 1799 cases (Table 21). I defined 35 structural zeros which were given a weighting of zero during log-linear analyses (denoted with X's in Table 21):

- an OMD following a NUR or a PT.
- an HTH following a NUR.
- a FSR following an ROA or RAW.
- a NTN following an ROA, RAW, or a NUR.
- a PON or SNI following an ROA or RAW.
- a CLI or CLA following a NUR or PT.
- a CHA following NTN, CLI, NUR or PT.
- a NUR following OMD, HTH, BIT, CLI, CLA, CHA, ROA, RAW, NUR or PT.
- a PT following a CHA, ROA, RAW, NUR, or PT.

A log-linear analysis revealed that the maximum difference between observed and fitted marginal totals was 0.011 and the G was 1494.0 with 749 df_{adj}. This exceeded that required for significance at $p \leq .05$ (minimum $\chi^2_{(749)} = 813.5$), revealing at least a first-order transitional dependence between preceding and succeeding acts at Sable Island.

Significant First-Order Transitions

I derived a $Y_{critical}$ value of 0.983 for first-order transitions at $p \leq .05$. There were 246 standardised residuals, representing 30.5% of the total number of cells, for transitions whose absolute values exceeded the $Y_{critical}$ value. These significant transitions are indicated with "+" or "–" signs in their respective cells in the transition matrix, Table 21.

At Sable Island the behaviour types OMD, HTH, STA, LAW, APT and DPA were more inhibitory than other types. GLA, CLA and ROS were often facilitatory (Table 22).

2) Second-Order Markov Interaction Sequences

I tested a second-order Markov model using a three-way transition matrix with the axes being first preceding acts, succeeding acts, and second preceding acts. There were 1657 weighted cases (the same structural zeros were used as for the first-order model) encompassing 29 behaviour types.

The log-linear analysis produced a G of 6195.7 with 24304 df_{adj}. This did not exceed that required for significance at $p \leq .05$ (minimum $\chi^2_{(24304)} = 24667.5$). There was an inadequate fit of a second-order model to the actual transitional relationships at Sable Island. The likelihood of occurrence of a particular second preceding act was not influenced significantly by the identities of the preceding act and the act succeeding it.

3) Significant Sequential Dependencies in Interactions Subdivided by Interactants' Sexes

I subdivided transition data from Sable Island on the basis of interactants' sexes. I used the same structural zeros for each of these submatrices as for the overall matrix except the behaviour types PT and OMD. These two behaviour types were coded as structural zeros in both the behaviour and response axes of the female-female transition submatrix. PT was also coded as a structural zero in male-male interactions

There were no significant first-order transitional dependence between preceding and succeeding acts during interactions between females ($G = 87.4$, $df_{adj} = 127$, minimum $\chi^2_{(127)} = 154.0$) or between males and females ($G = 420.1$, $df_{adj} = 389$, minimum $\chi^2_{(389)} = 435.7$).

Log-linear analyses did reveal sequential dependencies between acts performed during male-male ($G = 812.7$, $df_{adj} = 511$) interactions. These exceeded the minimum χ^2 values necessary for significance at $p \leq .05$ ($\chi^2_{(511)} = 564.4$). There was thus at least a first-order transitional dependence between acts and responses.

There were no significant second-order models for sequences subdivided by sex: 1) male-male: G = 3231.9, $df_{adj} = 13794$, minimum $\chi^2_{(13794)} = 14068.1$; 2) male-female: G = 1764.2, $df_{adj} = 10501$, minimum $\chi^2_{(10501)} = 10740.2$; 3) female-female: G = 342.1, $df_{adj} = 3550$, minimum $\chi^2_{(3550)} = 3889.5$.

Significant First-Order Transitions in Male-Male Interactions

The $Y_{critical}$ value for first-order transitions in male-male interactions, at $p \leq .05$, was 0.819. There were 172 standardised residuals, representing 30.3% of the total number of cells, whose absolute values exceeded the $Y_{critical}$ value. These significant transitions are indicated with "+" or "–" signs in their respective cells in the submatrix (Table 26).

During male-male interactions at Sable Island the behaviour types OMD, STA, LAW, APT, CHA, RAW, DPA, RHV and AVF were more often inhibitory than other types. HEX and ROS were normally facilitatory (Table 22).

Intra-individual Sequential Analyses

This section describes results from analyses of sequences of consecutive behavioural acts performed by individual seals. Tables 27 to 29 contain the first-order transition frequencies among behaviour types performed by individual seals at each study site.

Significant transitions are indicated with "+" or "–" signs in the transition matrices. Cells with positive values indicate that the occurrence of the preceding behavioural acts increased the probability of those particular succeeding behavioural acts (act A_1 is said to direct act A_2; Fagen and Young, 1978). Negative transition cell values indicate that the occurrence of the preceding behavioural acts reduced the probability of those particular succeeding acts (act A_1 is said to inhibit act A_2). Log-linear G values were weighted for structural zeros in the LOGLIN procedure of SPSSx.

Sequential Dependencies at Miquelon

1) First-Order Markov Interaction Sequences

The summary matrix for intra-individual behaviour transitions at Miquelon contained 1385 cases. I defined 27 structural zeros on the descending diagonal of the transition matrix (denoted by grey cells in Table 27).

A log-linear analysis revealed a maximum difference between observed and fitted marginal totals of 0.151 and a G of 621.4 with 649 df_{adj}. This did not exceed that required for significance at $p \leq .05$ (minimum $\chi^2_{(649)} = 709.1$). There was no first-order transitional dependence between consecutive behavioural acts performed by individuals at Miquelon.

As suggested by these results, when I subdivided the transition data from Miquelon on the basis of precedent sex, log-linear analyses did not reveal sequential dependencies between acts performed by male (G = 524.6, $df_{adj} = 572$) or female (G = 306.2, $df_{adj} = 388$) seals (minimum chi-square values of $\chi^2_{(572)} = 628.5$ and $\chi^2_{(388)} = 434.6$, respectively).

Sequential Dependencies at North Rona

1) First Order Markov Interaction Sequences

The summary matrix for intra-individual behaviour transitions contained 4201 cases. Before performing log-linear analyses, I defined 37 structural zeros of which 33 lay on the descending diagonal of the transition matrix (denoted with grey cells in Table 28). The other four were:

- an OMD following a NUR.
- a FSW and NUR following a PT.
- a PT following a NUR.

The log-linear analysis revealed a maximum difference between observed and fitted marginal totals of 0.01 and a G of 1947.5 with 987 df_{adj}. This value exceeded that necessary for significance at $p \leq .05$ (minimum $\chi^2_{(987)} = 1060.9$) and indicated that there was at least a first-order transitional dependence between consecutive behavioural acts performed by individual seals at North Rona.

Significant First-Order Transitions

The $Y_{critical}$ value for first-order transitions at $p \leq .05$ was 0.987. There were 329 standardised residuals for transitions whose absolute values exceeded the $Y_{critical}$ value. These represented 31.4% of the cells in the submatrix. The significant transitions are indicated with "+" or "–" signs in their respective cells in the transition matrix, Table 28.

At North Rona the behaviour types OMD, LAW, CLA, DPA, ECL and PT were more inhibitory than others. EFF, FSR, FSW, FSB, CLI, CHA, YAW and ROS were more often facilitatory (Table 22).

2) Second Order Markov Interaction Sequences

I tested a second-order Markov model using a three-way transition matrix with the axes being first preceding acts, succeeding acts, and second preceding acts. There were 3832 weighted cases (the same structural zeros were entered as for the first-order model).

The log-linear analysis produced a G of 13717.9 with 35840 df_{adj}. This did not exceed that required for significance at $p \leq .05$ (minimum $\chi^2_{(35840)} = 36281.3$). The fit of a second-order model to actual intra-individual transitional relationships at North Rona was not significant. The likelihood of a grey seal performing a particular behavioural act was not significantly influenced by the identities of the two acts it had previously performed.

3) Significant Sequential Dependencies in Interactions Subdivided by Precedent's Sex

When transition data from North Rona were subdivided on the basis of precedent sex, there were 33 behaviour types on each axis. I used the same structural zeros (those values in the descending diagonal) for the male submatrix (Table 30). As females never performed OMD or PT, their submatrix contained 31 behaviour types (Table 31).

Log-linear analyses revealed sequential dependencies between acts performed by male ($G = 1085.6$, $df_{adj} = 746$) and female ($G = 967.1$, $df_{adj} = 776$) seals. These exceeded the minimum χ^2 values necessary for significance at $p \leq .05$ ($\chi^2_{(746)} = 810.4$ and $\chi^2_{(776)} = 841.6$, respectively). Thus there were first-order transitional dependencies between consecutive acts performed by both males and females at North Rona.

There were no significant models which fit the data for second-order act sequences by males ($G = 6201.6$, $df_{adj} = 23451$, minimum $\chi^2_{(23451)} = 23808.1$) or females ($G = 6592.5$, $df_{adj} = 25103$, minimum $\chi^2_{(25103)} = 25472.4$).

a) Significant First-Order Transitions in Consecutive Acts Performed by Males

The $Y_{critical}$ value for first-order transitions in consecutive behavioural acts performed by males, at $p \leq .05$, was 0.863. There were 237 standardised residuals, representing 29.3% of the total number of cells, for transitions whose absolute values exceeded the $Y_{critical}$ value. These significant transitions are indicated with "+" or "–" signs in their respective cells in the transition submatrix, Table 30.

During behavioural sequences performed by male grey seals at North Rona the behaviour types OMD, STA, CLA, APT and PT were more inhibitory than others. FFW, FSW, NTN, PON, BIT, ROS and BSR were more often facilitatory (Table 22).

b) Significant First-Order Transitions in Consecutive Acts Performed by Females

The $Y_{critical}$ value for first-order transitions in consecutive behavioural acts performed by females, at $p \leq .05$, was 0.936. There were 230 standardised residuals, representing 28.3% of the total number of cells, for transitions whose absolute values exceeded the $Y_{critical}$ value. These significant transitions are indicated with "+" or "–" signs in their respective cells in the transition submatrix, Table 31.

During behavioural sequences performed by female grey seals at North Rona, STA was more inhibitory than others. EFF, FFW, FSW, FSB, PON, CLI, ROA, YAW, ROS and BSR were more often facilitatory (Table 22).

4) A Test For Seasonal Stationarity in Sequences From North Rona

I tested for seasonal variation in intra-individual stationarity by subdividing the data set for North Rona into two halves, and used the halve identities as the third dimension in a HILOGLINEAR procedure.

There were 3176 weighted cases (the same structural zeros were used as in the first-order model) encompassing 33 behaviour types.

The log-linear analysis produced a G of 2153.5 with 2112 df_{adj}. This did not exceed that required for significance at $p \leq .05$ (minimum $\chi^2_{(2112)} = 2220.3$). The probability of a seal performing a specific behaviour type following another specific behavioural act was not influenced significantly by whether it occurred early or late during the sampling period.

Sequential Dependencies at Sable Island

1) First-Order Markov Interaction Sequences

The summary matrix for intra-individual behaviour transitions contained 1733 cases. Before performing log-linear analyses I defined 31 structural zeros of which 28 lay on the descending diagonal of the transition matrix (denoted with grey cells in Table 29). The other three were:

- an OMD following a NUR.
- an FSW and NUR following a PT.

- a PT following a NUR.

A log-linear analysis revealed a maximum difference between observed and fitted marginal totals of 0.25 and a G of 1159.9 with 725 df_{adj}. This value exceeded that necessary for significance at $p \leq .05$ (minimum $\chi^2_{(725)} = 788.5$). This indicated that there was at least a first-order transitional dependence between consecutive behavioural acts performed by individual seals at Sable Island.

Significant First-Order Transitions

The $Y_{critical}$ value for first-order transitions at $p \leq .05$ was 0.985. There were 195 standardised residuals for transitions whose absolute values exceeded the $Y_{critical}$ value. These represented 25.1 % of the cells in the submatrix. The significant transitions are indicated with "+" or "–" signs in their respective cells in the transition matrix, Table 29.

At Sable Island the behaviour types OMD, STA, LAW, APT, CHA, ROA, DPA, RAW and RHV were more inhibitory. FSR and HEX were more often facilitatory (Table 22).

2) Second-Order Markov Interaction Sequences

I tested a second-order Markov model using a three-way transition matrix with axes being the first, second and third behavioural acts in a sequence by a seal. There were 1518 weighted cases (the same structural zeros were entered as for the first-order model) encompassing 28, 29 and 29 behaviour types for each axis, respectively.

The log-linear analysis produced a G of 5753.3 with 22623 df_{adj}. This did not meet that required for significance at $p \leq .05$ (minimum $\chi^2_{(22623)} = 22973.8$). There was no significant fit of a second-order model to the intra-individual transitional relationships at Sable Island.

3) Significant Sequential Dependencies in Interactions Subdivided by Precedent's Sex

When transition data from Sable Island were subdivided on the basis of precedent sex, there were 29 behaviour types on each axis. I used the same structural zeros (those values in the descending diagonal) for the male submatrix (Table 32). Since females never performed OMD or PT, their submatrix was comprised of 27 behaviour types.

Log-linear analyses did not reveal significant sequential dependencies between acts performed by females ($G = 412.3$, $df_{adj} = 385$, minimum $\chi^2_{(385)} = 431.5$).

Data for males, on the other hand, did demonstrate a significant likelihood ratio chi-square value ($G = 877.8$, $df_{adj} = 594$). This exceeded the minimum χ^2 value necessary for significance at $p \leq .05$ ($\chi^2_{(594)} = 651.5$). Thus there was at least a first-order transitional dependency between consecutive acts performed by males at Sable Island.

There was a poor fit of second-order models to consecutive act sequences by both males ($G = 4000.3$, $df_{adj} = 16140$, minimum $\chi^2_{(16140)} = 16436.4$) and females ($G = 1837.7$, $df_{adj} = 10542$, minimum $\chi^2_{(10542)} = 10781.7$).

Significant First-Order Transitions in Consecutive Acts Performed by Males

The $Y_{critical}$ value for first-order transitions in consecutive behavioural acts performed by males, at $p \leq .05$, was 0.88. There were 197 standardised residuals, representing 29.3% of the total number of cells, for transitions whose absolute values exceeded the $Y_{critical}$ value. These significant transitions are indicated with "+" or "–" signs in their respective cells in the transition submatrix, Table 32.

During behavioural sequences performed by male grey seals at Sable Island OMD, STA, APT, CHA, ROA, DPA, RAW and RHV were more inhibitory than others (the only difference between this list and the overall analyses for Sable Island was LAW). FSR and HEX were more often facilitatory (Table 22).

Discussion

Substantial individual polyethism is a characteristic feature of grey seal communication, even that observed within apparently uniform contexts. In previous chapters I detailed aspects of grey seal behavioural variability by reporting sizable CVs of act duration (Table 4) and interseal distance (Table 6) as well as site and sex differences in other behavioural measures (see Chapters Three and Five). In this chapter I document an additional source of variability resulting from nominal sequence dependencies during behavioural interactions.

Animals in such diverse groups as insects (Fuchs, 1976; Rowe and Harvey, 1985; Wilson, 1975), fish (Baylis, 1975; Heiligenberg, 1973; Nelson, 1964), lizards (Cooper, 1977; Jenssen, 1971; 1977), birds (Rhijn, 1973; Thorpe, 1972), macropods (Jarman, 1991) and primates (Altmann, 1965; Chalmers and Locke-Hayden, 1981) exhibit predictable individual or interactive sequences. I have now demonstrated this for grey seals also.

Sequences of acts performed by two seals (inter-individual) demonstrated significant first-order dependencies at all three sites. Further analyses disclosed that these dependencies reflected the significant dependencies during interactions between adult males (as well as between males and females at North Rona). That is, an act performed by a male grey seal was normally predictable solely on the basis of the preceding act performed by its male partner (or female partner at North Rona).

Significant first-order dependencies were also evident during the series of acts performed by the same seal during an interaction (intra-individual) – but only at the breeding sites. Again, however, these dependencies were products of predictable male behavioural sequences (as well as females at North Rona). An act performed by a male grey seal at one of the breeding colonies was usually predictable only on the basis of the act immediately preceding the one it had just performed. This was true for females at North Rona as well.

Inter-individual Sequences

First-order sequential dependencies within inter-individual interaction sequences were evident at all three study sites (Tables 19 to 21), but models based on higher-order dependencies were not significant; succeeding acts were only predictable on the basis of immediately preceding acts. The lack of second-order, or greater, dependencies in grey seal interactive sequences may have been products of sub-optimal sample size. With R as repertoire size, Fagen and Young (1978) estimated that an immense number of acts, $10R^{(n + 1)}$, were the theoretical minimum number sufficient to ensure statistical reliability in examining n^{th} order Markov transitions. For second-order analyses, the calculated minimum sample size using this conservative formula for Miquelon, North Rona and Sable Island exceeded actual sample sizes.

The relatively short interaction sequences of grey seals did not permit an analysis of the effects, if any, of behavioural ergoticity[16] on sequential dependencies (e.g., Chatfield and Lemon, 1970). Dingle (1972) felt it unlikely that sequential dependencies would ever remain constant over the course of an interactive sequence, particularly an agonistic one; but he brevity of grey seal sequences might render stationarity a minor effect. Further, despite seasonal changes in a number of behavioural measues at North Rona, I found that the probability of occurrence of a succeeding act type following a specific preceding act was not affected by its temporal position during the breeding period.

The first-order inter-individual sequential dependencies supports Hinde's (1985) contention that signaling behaviour during interactions involving "negotiation"[17]

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[16] That is, whether instrinsic or extrinsic factors, such as changing motivational state, changed the degree of sequential dependency during the interaction.

[17] In this context "negotiation" should occur during situations such as a dominance struggle between two bulls, or a pup attempting to solicit milk from its mother.

should exhibit sequential dependencies. Hinde speculated that each partner must attend to, and in many cases react to, the messages conveyed in the other's signals.[18] This would be particularly true during potentially injurious agonistic exchanges, as were many of the aggressive interactions recorded during this study. In addition, it is an advantageous strategy to conserve energy by affecting actions by cohorts with postural or vocal signals rather than physical force (Walther, 1984).

A second rationale for sequential dependencies derives from a prediction of game theory. Animals engaged in agonistic interactions may behave to provide less information in terms of what the receiver can deduce about the sender's intentions (Caryl, 1979; 1982b; Miller, 1991; Smith, 1977), and are less likely to react to signals of cohorts (Dawkins, 1976; Moynihan, 1982; Smith, 1977; 1986b). In this way, signaling animals have an opportunity to manipulate associates to gain an advantage by providing less, or misleading, information about the signaler's current motivational state (e.g., Dawkins and Krebs, 1978; 1979; 1982; 1976; Maynard-Smith and Price, 1973).

If the benefits from manipulating cohorts are increased in breeding situations, such as males being able to increase their reproductive success by restricting access to females, the clarity of information transmitted during communication at grey seal breeding sites should have been minimal. And, since it has also been postulated that increased behavioural predictability, or redundancy, conveys less information to cohorts than unpredictable behaviour (e.g., Attneave, 1959), I predicted greater sequential dependencies at the North Rona and Sable Island breeding sites. However, sequences recorded at all three locales were equally predictable.

Using interaction matrices, preliminary measures of the amount of information per act that was transmitted (e.g. Wilson, 1975) also revealed that relatively little was

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[18] Alternatively, Altmann (1967) and Grier (1984) saw communication as a conditional process in which every individual communicatory event would not necessarily alter the probability of the *next* behavioural act by the recipient.

exchanged between grey seals at any site (0.3 to 0.8 bits•act^{-1}; compared with 6 to 12 bits•act^{-1} for humans; Dingle, 1969). There were differences among sequence types in the amounts of information contained in each behavioural act, with the least being exchanged during the predominant type - aggressive (see Chapter Five and Lawson, 1991). These relatively low information transmission rates common to all sites might be rationalized in three ways. The predominance of aggressive interactions at all sites renders a manipulative communication strategy beneficial at all times of the year. More likely, grey seals were sending and attending to subtle physical and contextual cues, with cohorts with which they may have been familiar, thereby providing a richer communication system than these analyses were able to measure. Finally, had I been able to define grey seal behaviour types on a more molecular level (resulting in a larger ethogram; but not to the extent of Golani, 1973), the amount of apparent information exchanged per act might have been higher than that measured. If true, this would provide further evidence to support Fentress' (1973) statement that "categories of behavior must be formed, but the investigator must not believe them!" (p. 163).

While sample sizes were insufficient to compare the impacts of the contexts of the four sequence types might have had on sequential dependencies, I was able to evaluate the effects of interactant sex (e.g., Harcstad and Fisher, 1975; Sullivan, 1982).

An earlier study of courtship displays of the cichlid genus *Cichlasoma* revealed the potential importance of subdividing sequences on the basis of interactants' sexes since they differed in the predictability of their behaviour (Baylis, 1975). Using a similar data treatment, I also found that the sex of the interacting seals had a significant impact on the degree of sequential dependency. Male-male interactions at all sites exhibited significant first-order sequential dependencies (Tables 23, 24 and 26). No other sequences, except those between male and female interactants at North Rona (Table 25), demonstrated significant predictability. Further, these significantly ordered male-male sequences probably accounted for the site dependencies discussed above (Tables 19 -21).

A plausible explanation for these results was that the males were behaving so as to limit how much their partners could perceive about their internal state or motivation during their interactions with other males. Stylized, and thus more predictable and less informative, behaviour is a common attribute of aggressive interactions, particularly between individuals capable of inflicting damage on each other (Andersson, 1980; Hazlett and Estabrook, 1974a; Rand and Rand, 1976; Sandegren, 1976a). The aforementioned game theory argument for cohort manipulation by information limitation could apply to male grey seals during their competitive interactions for access to females. This strategy would be adaptive for breeding grey seals since males were relatively mobile during the breeding season and frequently "settled" contests without actual combat (Boness, 1979) – an excellent context within which to evolve a manipulative communication system (Cheney and Seyfarth, 1985; Dawkins and Krebs, 1978; Grier, 1984; Hamilton, 1970; Krebs and Dawkins, 1984; Walther, 1984). Males could benefit by being able to bluff their opponents into leaving without combat - a function enhanced by not revealing their true motivational state.

While it was evident why males might choose to conceal their true intentions from male cohorts during the breeding season, the underlying cause for sequential dependency during inter-male bouts at Miquelon was ultimately different. In this non-breeding colony the haul-out substrate was only exposed at low tide and, despite the fact that there were several kms of sand bar on which to rest, the small area preferred as a haul-out was a limiting resource for which seals competed.[19] Large males are usually the first to arrive in the area, and most of their interactions are agonistic attempts to gain access to the preferred central area. Like harbour seals (Sullivan, 1982), those males able to aggressively supplant cohorts and assume resting positions in the centre of the haul-

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[19] Competition for haul-out space during non-breeding periods has also been documented in species such as harbour seals (Sullivan, 1982) and sea lions (Harestad and Fisher, 1975).

out group benefited by spending less time in energy-consuming altercations than those forced to occupy the bustling periphery.

Alternately, male grey seals might have been using this non-breeding period to maintain or augment their relative social status. Geist asserted that male ungulates learned to assess male opponents' relative strengths "during frequent, minor agonistic encounters outside the rutting season" (1966; p. 205). Geist concluded that this knowledge could serve as a basis for avoiding potentially injurious competition with superior males during the breeding season. If this were the case with grey seals, males might also behave "dishonestly" during this non-breeding period in an attempt to gain status that they could use to their advantage during subsequent breeding seasons.

That male-female sequences also exhibited first-order dependencies at North Rona is not so easily explained. Unlike Sable Island, males resident on the breeding grounds at North Rona maintained territories which they did not abandon for much of the season (Twiss, 1991), and females and their pups rarely changed locations. Over the course of the season there were fewer males within the Focal Area (Table 33) as males chased interlopers away with greater frequency (Tables 35). Thus most male-female interactions involved seals which were familiar with each other ("dear enemies"; e.g., Simpson, 1973). In this context, perhaps there was a decreased need for information exchange as expressed in sequential dependencies. And yet, Miller (1991) felt that:

> *"... long-term familiarity such as occurs in pinnipeds should reduce the efficacy of dishonest communication, and communication between experienced, familiar pinnipeds should be subtle and rich."* (p. 187)

Long-term studies of marked grey seals at North Rona (Anderson, 1978; Anderson and Fedak, 1987; Twiss, 1991) suggest that, in this colony at least, the same individuals returned to the same locations each year. It is thus reasonable to expect that they would be familiar with each other, in the context of Miller's statement.

Ultimately, the male-female sequential dependencies at North Rona may reflect an influence of larger sample size on the statistical results for sequential analyses. As I stated in Chapter Two, conclusions made using sequential dependencies from these datasets were interpreted with caution. Nonetheless, when augmented with extensive personal observation, these data support the conclusion that grey seal interactions, particularly between males, are non-random. That this order was not as great as that observed in other animal species (see section 2 below) was evidence of both this species' individuated behaviour and perhaps the influence of contextual cues that were important to grey seals, but not apparent to a skilled human observer.

1) Inter-individual Sequence Data Compared With Studies of Other Pinniped Species

Since this study was the first to apply sequence analysis techniques to seal behaviour, it was difficult to compare these results with other published accounts of pinniped communication. Previous descriptions of seal interactions were often anecdotal and usually focused on conspicuous acoustic displays used during breeding.

Miller and Boness (1979) observed that male grey seals have evolved morphological characteristics (enlarged snouts and heavier chests and necks) which they use during "elaborate parallel and antiparallel posturing" display behaviour when competing for females. It was unclear whether the term "elaborate" implied either a predictable series or a complex structure for these displays, or both.

To position grey seal communication within the assemblage of those few described for pinnipeds, I compared the results from this thesis with prolonged and stylized interaction sequences that have been documented in other pinniped families.

The best-quantified studies of seal behavioural sequences have been conducted on the spotted seal. Beier and Wartzok (1979) examined copulatory sequences and found that no single behaviour pattern or behaviour sequence always ended in copulation.

Rather, the behavioural sequences were highly variable with respect to behaviour types, with as many as 28 and as few as 8 behaviour events prior to termination. In addition, the behaviour types performed during the sequences were unpredictable. Gailey-Phipps (1984) later reported that captive male spotted seals engaged in "stylised" patterns of display and body contact during courting, but failed to disclose the structure of these sequences.

Extended sequences of aquatic rolling behaviour have been observed among pairs of harbour seals near breeding areas (Sullivan, 1979; 1981; Thompson, 1988; Venables and Venables, 1955; 1959), and among pairs of male and female Steller sea lions (Sandegren, 1975; 1976b). Similarly, male and female crabeater seals consorted in the water during which they "maintained almost constant physical contact ... through a number of typical postures." (Siniff *et al.*, 1979; p. 2249). If these are the same behaviour type repeated numerous times, then these likely represent higher-order Markov sequences. However, this remains to be determined since quantification of any aquatic interactions by pinnipeds is woefully lacking.

On land, some pinniped species also interact using stylised behaviour sequences, such as the male elephant seal:

> *"Highly formalized and elaborate vocal challenging and postural displays are an integral part of reproductive behaviour for which the snout of the male elephant seal has been evolutionarily modified"* (p. 149) (Sandegren, 1976a)

Males repeatedly rear and slam their necks against rivals as they defend, or attempt to invade, terrestrial territories. Complex interaction sequences also occur during "border displays" by males of many otariid species (see review by Krushinskaya and Lisitsyna, 1983).

Hamilton (1934) and Miller (1991) described interaction sequences between male and female Southern sea lions and Australian fur seals, respectively. Individuals spent considerable time repeatedly caressing each others' necks and mouths as they oriented face to face.

If we assume that the terms "stylised", "typical" and "formalised" used in the preceding quotes and paraphrased descriptions imply higher-order dependencies in these sequences, then grey seals appear to lie near the lower end of the spectrum of pinniped behavioural predictability. In addition to quantified results, which indicated first-order dependencies during interactions between males, extensive time spent observing them has revealed that grey seals are easily able to modify their behaviour in response to contextual variation. For example, a male at North Rona performed a long series of OMDs during aggressive interactions with a neighbouring male further inland, but would rarely perform more than three or four in a row while interacting with smaller males that entered from the seaward periphery of the group.

This species does perform stylized behaviour types, such as an OMD, NUR or PT, but these are not incorporated into particularly elaborate sequences such as have been described in several of the seal species described above, or other animals detailed in the next section.

2) Inter-individual Sequence Data Compared With Studies of Other Animal Species

Although studies of interactive sequences in pinniped behaviour are lacking, there are such studies for other species with which to compare the sequential dependencies in grey seal interactions. As expected, insect social interactions were often very predictable. The inter-individual communication sequences during periods of alarm in carpenter ant (*Camponotus*) colonies (Fuchs, 1976) were highly predictable – at times higher than third-order.

Analyses of fish (Nelson, 1964) and anoline lizard (Jenssen, 1977) courtship revealed second-order dependencies, which were important components of intra-specific identification.

Pair bonding is a primary function of the elaborate, and highly predictable, antiphonal and duetting song system used by breeding shrikes (*Laniarius aethiops*; Thorpe, 1972).

At least first-order sequential dependencies have been documented for mammals such as the larger Macropodoidea (kangaroos and wallabies; during male displays and fights; Jarman, 1991), and in playful interactions of the common marmoset (*Calithrix jacchus jacchus*; Stevenson and Poole, 1982) and timber wolf (*Canis lupus*) pups (McLeod, 1987). Similarly, Moran *et al.*, (1981) documented large individual behavioural variation during wolf fights, but found that behavioural sequences were constrained when interactive dyads were examined.

The greatest mammalian sequential dependencies have been documented in Rhesus monkey (*Macaca mulatta*) social interactions (Altmann, 1965). In this species, an individual's behaviour is predictable on the basis of at least the previous four behaviour types performed by a cohort (third-order), despite having a behavioural repertoire almost as large as man's (Table 8). Within the context of these examples, grey seals do not interact in a similarly predictable manner.

Golani rejected the concept of interactive behaviour as a sequence assembled one behaviour pattern at a time (as *per* Altmann, 1965). Instead, Golani viewed animal communication as a richly variable system, like Elsasser's (1966) "heterogeneous universe of discourse", with a high degree of openness. In an extremely detailed study of the golden jackal, Golani (1973; 1976; Golani and Mendelssohn, 1970) used a specialized form of behavioural coding to study pre-copulatory motor sequences. He viewed behaviour as a sequence of successive postural configurations or "system events" which were described by the posture and position of the jackals. These events demonstrated variability[20] at the level of the individual, the pair, the pair in successive years and over time in one year. Golani concluded that this contextual variability, in conjunction with tremendous event heterogeneity (98.5% of the 2,000 events had never been seen before), yielded a highly adaptable communication system capable of transmitting much information using a number of modes.

If this were true for grey seals, the fact that sequences were statistically predictable at the first-order level could reflect underlying behavioural and contextual richness (see comments on repertoire size in Chapter Three). On the other hand, such fine-scale analyses of animal behaviour as Golani has undertaken may reveal details to which the animals themselves are not attending or reacting. Redundant signals are a common component of many species' communication systems (Morton, 1982; Rand and Williams, 1970; Smith, 1977; Wilson, 1972).

3) Inhibitory And Facilitatory Behaviour Types in Inter-individual Sequences

Log-linear analyses permitted quantified determination of which behaviour types exhibited significant inhibitory or facilitatory influences on behavioural transitions.

There were a number of behaviour types which inhibited at least ten percent of the behavioural responses of cohorts (Table 22A; and see Chapter Three for detailed descriptions of these behaviour types and interspecific comparisons).

The behaviour types which were most often inhibitory were the OMD, AVF, LAW, HTH, HSW and BTC. These were usually performed during aggressive interactions and the first three may have acted as "cut off" behaviour types (Chance, 1962).[21] They may

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[20] Smith (1977) proposed instead that Golani's evidence of enormous variation may merely reflect different definitions of the term "display", and "variable" interactions may convey the same messages to the participants.

[21] Chance described "cut off" behavior types in his study of gulls. During aggressive interactions, one or both birds would occasionally face away from the other, thereby halting or reducing the intensity of the interaction.

have provided a means by which seals in social conflict could reduce distressing stimulation and hold their ground during an agonistic interaction by suppressing motivational tendencies to attack or flee.

The other predominantly aggressive behavioural acts (HTH, HSW and BIT) more often inhibited the occurrence of following acts since the recipient often tried to move away or avert its face or body. This was also the case for an APT. This latter result is not surprising if, like many ungulates, the mere approach of a cohort can be seen as a threatening action (Walther, 1984).

Two behaviour types were inhibitory at one site only; ROA was inhibitory at North Rona and EFF was predominantly inhibitory at Miquelon. Many males at North Rona terminated aggressive bouts by rolling away from their partners. Twiss (1991) termed these "victory rolls" when performed by a male who had just won a dominance interaction. However, I also recorded this behaviour by males when females had rebuffed their approaches, so the purpose of this behaviour is clearly different in these two contexts. Like harbour seal interactions (Sullivan, 1982), an EFF had the effect of slowing or pausing a sequence.

The other inhibitory behaviour types (DPA, ECL, PT and NTN) were slower-paced, performed without vocalisations and often indicated the onset of a very slow rate of behavioural activity in the sequence. Nursing was an inhibitory act because the mothers invariably relaxed and settled onto their sides when their pups began to nurse.

Many behaviour types which were predominantly facilitatory were performed sedately and without vocalisations. Further, most of these behaviour types involved either small changes in body position (ROS, ROA at Miquelon), or actions without physical contact (FFW, EFF, HEX, CHA, NHS, YAW, BSR, RAW and GLA).

The more vigorous of these facilitatory types (FSR, CLI, CHA and RAW) incited a reaction every time they were performed. Grey seals' dislike of physical contact in any context explains the response to the first two of these behaviour types. CHA and RAW were closely coupled in that one type often triggered the other.

As mentioned previously, an EFF was inhibitory at Miquelon in general, but facilitatory during interactions between males and females at all sites. While it was performed as an aggressive signal by females towards males at all sites, males nonetheless approached females who had extended their foreflippers (much as elephant seal bulls ignored the protests of females; Cox and Le Boeuf, 1977).

By examining cell values in the main diagonal of the interaction matrices for each site, it became apparent that there were certain behaviour types which evoked "mirror" or "mimic" responses. When one grey seal stared at another, this was most likely to evoke a similar response by cohorts at each site (Tables 19 to 21). An NTN (by definition) always resulted in the same behaviour type being performed in response.

During male-male interactions at the two breeding sites, one quarter of the acts succeeding OMDS and BITs were responses in kind. This was much the same as the "tit for tat" structure of fights between elephant seal bulls (Bartholomew, 1952; Cox, 1981; Sandegren, 1976a).

The most significant mirrored response occurred after one seal had performed a HSW at Miquelon (most of these occurred during playful interactions). Over 72% of the succeeding acts were also HSWs - and usually with little, or no, latency. By "tracking" the path of an opponent's swinging face the successor reduced the chances that the opponent would then be able to bite the successor's exposed neck.

Intra-individual Sequences

First-order sequential dependencies within intra-individual sequences were evident only at the breeding sites (Tables 28 and 29), and higher-order models of sequential dependency were not significant. As for the inter-individual sequences described previously, intra-individual behavioural acts were predictable on the basis of the one immediately preceding it (but see sex differences below).

I was able to test the seasonal dependency of sequences in the larger North Rona dataset. As was the case for inter-individual sequences, I found that the probability of occurrence of a succeeding act type following a specific preceding act was not affected by its temporal position during the sampling period; behaviour was as predictable during both halves of the season, despite changes in other measures (see Chapter Five).

It was not surprising that the sequences of behaviour performed by grey seals at Miquelon were not statistically predictable (Table 36). Play sequences of highly variable structure and duration were common at this site (Table 12). Younger seals (one to three years old) often spent considerable time playing, with individual differences in how they did so. It was considerably more difficult to predict what type of behaviour one of these younger seals was likely to perform in any context (which is a feature used in the definition of play; e.g., Fagen, 1981). Aggressive interactions between older seals were briefer and less intense than those at the breeding sites, with lower predictability as to which behaviour types were used and which animal won an altercation. Also, at the non-breeding site younger animals were regularly seen attempting to entice adult bulls to play or chase – and these bulls seemed less predictable in their responses to the playful harassment.

The behaviour of seals at the two breeding sites was significantly more predictable than at Miquelon (Table 28 and 29). However, in light of the previous inter-individual comparisons, I subdivided intra-individual sequences on the basis of interactant sex (Baylis, 1975). When subdivided this way, behaviour sequences by males at North Rona and Sable Island (Table 30 and 32), and females at North Rona (Table 31), exhibited significant first-order sequential dependencies. These sequences likely accounted for the overall site dependencies.

For the same reasons discussed in the inter-individual section above, males may have been behaving so as to exchange less information with cohorts.[22] And again, like the inter-seal first-order dependency found in male-female sequences at North Rona, the intra-seal first-order dependency found in the behavioural sequences of females at North Rona is difficult to explain. The fact that males and females are less mobile at North Rona, and therefore more likely to interact with a cohort with whom they are familiar, may result in a decreased necessity to exchange information (and adoption of more predictable behaviour). On the other hand, the female sequential dependencies at North Rona may reflect an influence of larger sample size on these analyses.

Like the inter-individual sequence analyses, these data corroborate the hypothesis that grey seal behavioural sequences, particularly those of males, are not random. However, high-order dependencies are probably restricted by individual variation in behaviour such as that which has been described for other species (Bonner, 1968; Hinde and Spencer-Booth, 1971; Nuechterlein, 1981; Shipley *et al.*, 1981). That this order was not as great as that observed in a number of other animal species (see section 2 below) is also evidence of this species' behavioural plasticity.

1) Intra-individual Sequence Data Compared With Studies of Other Pinniped Species

There are few quantitative studies of intra-individual behaviour of pinnipeds in the literature, and most of those were conducted on underwater breeding displays by walrus and bearded seals.

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[22] The majority of the largest cells were in the descending diagonal (auto-transitions) in the matrix for North Rona. In contrast, at Miquelon and Sable Island less than one third of the largest cell totals were auto-transitions. Thus, individual behaviour was more likely to occur in "bouts" at North Rona (Chatfield and Lemon, 1970; Lefebvre and Joly, 1982; Lemon and Chatfield, 1971; Smith *et al.*, 1977). These were removed in analyses (coded as structural zeros) since successive events cannot be "independent" in the usual sense required by Markov statistics (Bishop *et al.*, 1975; Chatfield and Lemon, 1970).

Adult male walrus engaged in "elaborate" display sequences in the water adjacent to breeding groups where the females resided (Fay *et al.*, 1984; Ray and Watkins, 1975; Stirling *et al.*, 1983; 1987). Both the swimming, and particularly the acoustic, behavioural displays were complex, repetitive and individually stereotyped. The underwater phonations of bearded seals were also repetitious and stereotyped (Cleator *et al.*, 1989; Stirling *et al.*, 1983). These results imply higher-order sequential dependencies, but behaviour that was individually rather than species-characteristic. Individual variability was a common feature of the calls of Northern elephant seal bulls (Shipley *et al.*, 1981).

Bonner (1968) reported that Antarctic fur seal bulls (*Arctocephalus gazella*) exhibited individual variation in behavioural acts and responses in interactive sequences. Although individual grey seals' sequences were not long enough to permit statistical comparisons of intra-individual sequential probabilities between individuals, there was anecdotal evidence of individual variation (noted in the inter-individual sequence section), in addition to the large CV measures described in Chapter Three.

In the only other study of seal behaviour which examined sequential predictability, Sullivan (1982) found a significant first-order relationship between behavioural acts during harbour seal agonistic interactions. However, less than two percent of the sequences he recorded contained behavioural triplets. These results, while perhaps exaggerated by the relatively limited number of behaviour types described (n=8), indicated that harbour seal intra-individual sequences exhibited a similar degree of predictability to those reported for grey seals.

While the intra-individual behavioural sequences of grey seals were not as orderly as the aquatic displays of those pinnipeds described at the beginning of this section, it was as ordered as harbour seal agonistic communication, and appeared to share the characteristic of individual variability with those seal species studied to date.

2) Intra-individual Sequence Data Compared With Studies of Other Animal Species

In an effort to place grey seal behaviour in the broader context, there was a quantitative basis for comparing grey seal intra-individual behavioural sequences with non-pinniped species. Grey seals again lie at the lower end of the spectrum of behavioural predictability represented by the species cited below.

As might be expected, behaviour patterns of many insects are very stereotyped relative to grey seals. Male fireflies (*Photinus* sp.) signal to females with species characteristic patterns of bioluminescent light flashes, each of which is composed of a highly-ordered sequence of pulses (Lloyd, 1977). The feeding sequences of newly emerged adult Colorado potato beetles were very stereotyped with fifth or higher-order dependencies (Harrison, 1987; pers. comm.). Dragonfly larvae and spider crabs also performed predictable chains of characteristic postures and behaviour types during interactions (Hazlett and Estabrook, 1974a; Rowe and Harvey, 1985).

Grey seal behaviour is also more individuated than that of certain other vertebrates. Nelson (1964) found second-order dependencies in individual behaviour during breeding interactions of glandulocaudine fish. The mating and agonistic displays of several lizard species was highly predictable (Cooper, 1977; Stamps and Barlow, 1973) with extended sequences of head bobbing being common.

Displays of birds such as the male Sage grouse, *Centrocercus urophasianus* (Wiley, 1973), wild turkey (Schleidt, 1964b), ruff, *Philomachus pugnax* (Rhijn, 1973) and zebra finch, *Taeniopygia guttata* (Slater and Ollason, 1972) were highly predictable with the lowest dependency values being first-order . Wood peewee song was predictable to at least second-order, although this value was artificially low because Chatfield and Lemon (1970) had removed triplets to control for "bout" effects. These authors subsequently found that Cardinal songs (*Richmondena cardinalis*) were first-order as well (Lemon and Chatfield, 1971).

In mammals there has been evidence of order in individual behaviour. Even during vigorous play of common marmosets (*Callithrix jacchus*), there were non-random, distinct patterns of behaviour (Chalmers and Locke-Hayden, 1981; Stevenson and Poole, 1982).

Like the underwater calls of the bearded seals (Cleator *et al.*, 1989; Stirling *et al.* 1983), the songs of the humpback whale, *Megaptera novaeangliae*, have proven to extremely repetitive with higher-order dependencies and individual stereotypy (Payne and McVay, 1971; Tavolga, 1983).

In the most extensive Markov study so far undertaken, Stuart Altmann (1965) described at least third-order intra-individual sequences during rhesus monkey interactions – despite their having a repertoire considerably larger than that described for any other animal species, with the exception of humans (Table 8).

These examples, and the grey seal behaviour described in this thesis, suggest that there is not a relationship between the reported complexity of animal repertoires and degree of sequential predictability. Even though they had a relatively large repertoire (Table 8), grey seals again lie at the lower end of the spectrum of behavioural predictability represented by the species cited in this section.

However, this may simply reflect both inconsistent levels of observer effort and the lack of standardized methods for describing animal communication. Further, in a good review of sequence analysis techniques, Slater (1973) warned that intra-individual sequence analyses assume no external or consistent influences on an animal's behaviour. This is obviously rarely true during animal interactions, and in the case of grey seals, their behaviour was certainly dependent on the preceding act of the seal with whom they were interacting. In effect, each behavioural act contained within itself the passage of behaviour and the seals were likely "aware" of the antecedents and consequents (there was temporal "thickness"). This social contextual factor, even in combination with individual behavioural variability, did not preclude first-order dependencies in the intra-individual sequences recorded at the two breeding colonies. Unlike Miquelon, there were advantages to individuals at the breeding colonies having more predictable, and less informative, behavioural sequences.

3) Inhibitory And Facilitatory Behaviour Types in Intra-individual Sequences

Using log-linear analyses, I was able to determine which behaviour types exhibited inhibitory or facilitatory influences on individuals' subsequent behaviour. Most behaviour types that were inhibitory or facilitatory in inter-individual sequences fulfilled the same role in intra-individual contexts (Table 22B).

Cells in the main diagonal (autotransitions) were removed to control for the effects of behavioural bouts (Chatfield and Lemon, 1970; Slater, 1973; Slater and Ollason, 1972) during intra-individual analyses, but I discuss these behaviour types at the end of the section.

The behaviour types which were most inhibitory to succeeding behaviour acts were the OMD, RHV and LAW. These were usually performed during aggressive interactions and, as mentioned in the inter-individual sequence section, may have acted as "cut off" behaviour types (Chance, 1962).

An APT, or STA, were also inhibitory and were highly related in that an APT was more often followed by a STA than any other behaviour type. Since these seemed to usually convey a sense of alertness or a threat (as they commonly do in harbour seals and ungulates; Sullivan, 1982; Walther, 1984), perhaps grey seals were less inclined to perform other behaviour types subsequent to these two.

DPA, ECL, CLA and PT were both more commonly inhibitory and slower-paced. DPA and ECL often indicated the onset of a hiatus in the seal's behavioural sequence – perhaps again acting as "cut off" signals. CLA and PT were closely associated in that the males would resume CLA when they stopped PT, or the female struggled in an effort to move away. During copulation males were evidently goal-directed and would normally ignore external events and perform few other behaviour types until they had finished.

The facilitatory behaviour types in intra-individual sequences were similar to those in inter-individual sequences. Many of the facilitatory behaviour types involved either small changes in body position (ROS and ROA), or actions without physical contact (FFW, EFF, FSW, FSB, HEX, CHA, NHS, YAW, BSR, RAW and GLA). It is interesting that all behaviour types involving use of the foreflipper (FFW, FSR, EFF, FSW, FSB and FSS) in both inter- and intra-individual sequences were more likely to be facilitatory. These categories were often performed in a deimatic role in situations where the performer was being approached by a more dominant individual, and the performer alternated relatively quickly amongst a number of behaviour types over the course of the interaction.

The facilitatory behaviour types, NHS, YAW, and BSR, seemed to play a role as "comfort movements" and had little pragmatic import on the performer's subsequent behaviour. Certainly they were more likely to be performed during either non-aggressive interactions, or by dominant animals.

All behaviour resulting in contact with the successor (FSR, PON, NTN, BIT and CLI) were facilitatory, particularly during playful interactions. Grey seals' sensitivity to physical contact may have made it more likely that they would perform further behaviour after an initial contact, or would have to react to the successors' reaction to being touched.

While it seems that most studies of display behaviour have been biased toward displays that are specialized in form, behaviour may instead be specialized through temporal patterning (e.g., rhythmic or bouted; Miller, 1991). This was not usually true of grey seal behavior since most behaviour types were performed singly. However, there were some behaviour types which were more likely than others to be executed a number of times consecutively (albeit not to the same extent as the vertebrate displays reviewed previously).

At the breeding sites, performance of an OMD or BIT by a male was often followed by another (Tables 30 and 31). Similarly, grey seals at North Rona or Sable Island were more likely to succeed a LAW with another (Tables 28 and 29). An HTH or a STA were likely to be followed by another at all sites (Tables 27, 28 and 29). As was the case for inter-individual sequences, a seal usually (68.4%) performed more than one HSW in succession at Miquelon (most of these occurred during playful interactions; Table 27). In all cases but OMD, consecutive behavioural acts were often performed in concert with similar behaviour by their partners. That is, the two seals seemed to be mimicking each others' behaviour, even to the extent of performing a series of the same behavioural acts themselves. Even when not copied by the partner, OMDs were often performed consecutively. Repetition would be a excellent way to augment the effectiveness of this behaviour type if it was being used to display status or intention (Radwan and Schneider, 1988; Wilson, 1972; 1975).

Summary

- In light of their relatively broad behavioural repertoire and variety of contexts in which they perform it, I predicted that grey seal behavioural systems would be flexible, and the likelihood of one behaviour type following another would be probabilistic rather than deterministic. Markov analyses of both signal-response and act A-act B matrices revealed first-order sequential dependencies during interactions at all sites - although this degree of predictability stemmed mainly from behaviour performed by adult males, and interactions between adult males (as well as males and females at North Rona). Since predictable behaviour conveys less information to cohorts, and many interactions were aggressive and potentially damaging, males may have adopted stylised postures to conceal their motivational state and intentions.

- Individual behaviour was zero-order at Miquelon since many bouts were either unpredictable play or brief, irregularly-structured agonistic exchanges.
- Within the context of animal species studied to date, grey seal behaviour yields further evidence against a relationship between the reported complexity of animal repertoires and degree of sequential predictability. Even with a relatively large repertoire, grey seals lay at the lower end of the spectrum of behavioural predictability represented by the species cited in this thesis. This may reflect inconsistent levels of observer effort in earlier studies, lack of standardised methods for describing animal communication and the fact that techniques of sequence analysis unrealistically assume no external influences on an animal's behaviour (i.e., stationarity).
- Although individual and interactive behavioural sequences were too brief to test statistically for changes in stationarity, there were no differences in inter- and intra-individual sequential probabilities between season halves of the at North Rona.
- Certain inter-individual behaviour types inhibited subsequent behaviour either through being interpreted by successors as threats, or by functioning as "cut off" behaviour to provide a means by which seals in conflict reduced distressing stimulation and held ground by suppressing tendencies to attack or flee.
- Most intra-individual behaviour types resulting in contact with the successor (FSR, PON, NTN, BIT and CLI) were facilitatory, particularly during play.
- Behaviour types involving use of the foreflipper (EFF, FFW, FSR, FSS, FSW and FSB) in both inter- and intra-individual sequences were more likely to be facilitatory.
- Most behavior types were not specialized through temporal patterning since they were usually performed singly. However, some acts were more likely to be executed a number of times by a seal consecutively (e.g., OMD, BIT, HTH, STA), perhaps as a means to augment its effectiveness if it was being used to display status or intention

Chapter Five: Comparisons Of Grey Seal Behaviour As A Function Of Demographic And Topographic Features

Behavioural changes associated with season, locale, demography, topography and climate have been reported in pinnipeds, but rarely between both breeding and non-breeding groups of the same species. As an exception to this, Miller (1975c, Miller and Boness, 1983) reported that walrus became more positively thigmotactic and less aggressive within summering groups. Carrick *et al.* (1962a) found that southern elephant seals of both sexes were more aggressive during the breeding season, than at other times of the year. Based on such findings in other pinnipeds, seasonality should also be an important factor influencing grey seal behaviour. However, virtually all previous research has been restricted to the breeding season when grey seals come ashore to give birth and mate (Anderson *et al.*, 1975; King, 1983; Ridgway and Harrison, 1981), I predicted, based on anecdotal observations I had made at the non-breeding site prior to this study, that seasonality would also be an important factor influencing this species' behaviour.

Testing seasonal changes in behaviour at one locale is impractical since most groups do not spend the entire year at one location, and the few that do are usually more difficult to approach in the non-breeding season. As an initial assay, I tracked seasonal changes on a smaller scale at North Rona, where I was on location long enough to examine trends in certain behavioural patterns from pre- to late-breeding.

Given that I could only large scale study seasonal changes in grey seal behaviour at different sites, I chose two sites representing similar stages in the breeding cycle, and one non-breeding. The dispersion of the groups ensured that I could also investigate the impact that site differences, in terms of locale and physical features, might have on this species' communication.

My *a priori* prediction that there would be site differences in behaviour was based on published inter-site comparisons found in other pinnipeds. Christensen and Le Boeuf (1977) reported inter-site differences in the incidence of aggressive behaviour by female Northern elephant seals at several breeding beaches. Southern sea lion bulls were more aggressively territorial at a site with variable substrate quality than at another more uniform site (Campagna and Le Boeuf, 1988). Researchers reported evidence of intersite differences in grey seal activity at British and Canadian sites. Davies (1949) found that females at North Rona were more active, and played more with their pups than females in Welsh breeding colonies. In a cursory comparison of colonies on Basque Islands, Nova Scotia and at several British sites, Cameron (1970) found that the former seals were consistently more active. In a more detailed study, Boness (1984) compared time budgets of breeding grey seals at Sable Island and the Monach Isles and found that the latter spent less time ashore, and more time engaging in locomotory, aggressive and sexual interactions. These studies did not specifically quantify communication, however.

Demographic factors were also predicted to have significant effects on grey seal communication. In other pinnipeds, females, in comparison to males, do not engage in the same types of combative interactions (e.g., Carrick *et al.*, 1962a; Cleator *et al.*, 1989; Kaufman *et al.*, 1975; Le Boeuf and Petrinovich, 1974b; Le Boeuf and Reiter, 1988; Miller, 1975a; Sandegren, 1976a; Smith, 1987; Stirling *et al.*, 1983; Trillmich, 1984) or territorial boundary displays (e.g., Gentry, 1970; Miller and Boness, 1979). Previous studies of grey seals have shown that males were more active and sought out combat, whereas females fought in response to others' approaches (Anderson and Fedak, 1987; Boness and James, 1979; Miller and Boness, 1979). Age-related differences in pinniped behaviour have also been described as part of studies of aggressive interaction (Harestad and Fisher, 1975; Sullivan, 1981; 1982) and play (Rasa, 1971; Renouf and Lawson, 1986a; Wilson, 1974b). In both contexts male pups and subadults were more likely to perform behaviour resembling that which they would later use as adults.

Group dispersion may also have significant effects on grey seals' behaviour since larger or more densely-packed groups of other species were less vigilant (Terhune, 1985; but see Renouf and Lawson, 1986b), more aggressive (e.g., Le Boeuf, 1986) and more highly polygynous (Jouventin and Cornet, 1980).

In several studies, topography has been implicated as a factor influencing behaviour. Subordinate male elephant seals, forced into the seaward periphery of colonies, were more active and less likely to copulate than those further up the beach (McCann, 1981). Hewer (1960a) postulated that breeding site topography affected the territorial strategy adopted by male grey seals and found that seals resident on the seaward periphery of the group were more active. Kovacs (1987b) also reported that topography governed females' diurnal time budgets with less time spent with pups when access to the sea was easy. As a means to assess this potential factor the breeding sites compared in this thesis have appreciably different topographies.

Another factor that might generate site differences in grey seal behaviour is variation in local weather patterns. While we (Renouf and Lawson, 1986b; 1987) found no significant meteorological effects on harbour seal play or vigilance, El Niño (a major climatic disturbance) has been demonstrated to cause changes in the behaviour patterns of California sea lions (Ono *et al.*, 1987). The three sites utilised in this investigation facilitate examination of climatic impact on behaviour as they have dissimilar climates.

Anderson (1978) discovered no diurnal pattern in the behaviour of a grey seal bull on the rocky breeding grounds of North Rona. On the other hand, substrate availability at Miquelon was strictly controlled by tidal action. I predicted that tidal action would have greater effects on grey seal communication at this site than at either North Rona or Sable Island where the substrate was available continuously .

Group Features

Age Class Characteristics

At the two breeding sites, most behavioural acts occurred during bouts involving interacting adults, or mothers and adults (see respective columns in Table 13). Other age classes accounted for considerably fewer interactions. At Miquelon, subadult-subadult and subadult-adult interactions accounted for a similar proportion to the mother-adult interactions at North Rona and Sable Island.

Early in my observations of grey seals at North Rona I perceived significant differences in the behaviour of two classes of adult females. In analyses, I subdivided data for adult females into that for mothers with pups and adult females without pups (as far as I was able to discern). These two types of adult female were indeed different on the basis of a number of measures (Table 37).

In bouts in which at least one of the interactants was a mother, the mean total duration and total number of acts in the bout were greater than bouts involving only adult females. The mean duration of a mother's behavioural act was also greater than that of an adult female (Table 37). On the other hand, females without pups performed behavioural acts more frequently than did mothers, both relative to the number of seals in the sample or to the number of adult females (Table 37).

A greater proportion of the seals within the Focal Areas around lone adult females were adult males than within the Focal Areas around mothers, despite the fact that the mean number of seals of all types within the Focal Areas near adult females or mothers were not significantly different. The mean vigilance level within Focal Areas containing mothers with pups was not significantly different than those with adult females only.

The only time females engaged in play was when mothers at North Rona and Sable Island played with their pups. Also, a greater relative proportion of bouts involving adult females without pups (85.4%) were aggressive compared to those bouts involving mothers (60.3%; $\chi^2 = 22.3$, df = 82, $p \leq .05$). There were no significant differences between these adult females and mother on the basis of interaction distance or response latency.

Focal Area

The mean number of seals within the Focal Area at Miquelon ($\bar{x} = 18.2$) and Sable Island ($\bar{x} = 17.0$), while not significantly different, were both greater than that at North Rona ($\bar{x} = 9.2$; F = 63.8, df = 2, 318, $p \leq .05$; $\hat{\omega}^2 = .76$).

Subdividing the Focal Area by sex also revealed significant differences between the three sites. I divided the Focal Male and Focal Female values by the Focal Area values for each case to derive relative proportions of each sex within the Focal Area.

The proportion of males within the Focal Area at Miquelon ($\bar{x} = 0.6$) was greater than at either North Rona ($\bar{x} = 0.1$) or Sable Island ($\bar{x} = 0.3$). Further, the relative proportion of males at Sable Island was also greater than that at North Rona (F = 104.7, df = 2, 8641, $p \leq .05$; $\hat{\omega}^2 = .83$).

The proportion of females within the Focal Area at North Rona ($\bar{x} = 0.5$) was greater than at either Sable Island ($\bar{x} = 0.3$) or Miquelon ($\bar{x} = 0.2$). The relative proportion of females at Sable Island was in turn greater than that at Miquelon (F = 1410.1, df = 2, 8641, $p \leq .05$; $\hat{\omega}^2 = .81$).

At the two breeding sites decreases in total bout duration were correlated with larger Focal Area values (Table 15). At all sites an increase in the number of seals was correlated with an increase in vigilance, whereas site duration, inter-seal distance and response latency were not.

Total Bout Duration

The shortest duration of a bout of behavioural interaction was 3 seconds and the longest 5000 seconds. There were no significant differences among the three sites in this regard (Miquelon: $\bar{x}$ = 115.6 seconds; North Rona: $\bar{x}$ = 237.6 seconds; Sable Island: $\bar{x}$ = 232.5 seconds; F = 2.0, df = 2, 321, p = .69).

At Sable Island, interaction between mothers and other adults (usually males; $\bar{x}$ = 470.6 seconds) lasted longer than if the adult dyad did not include a mother ($\bar{x}$ = 52.8 seconds; F = 16.0, df = 4, 131, $p \leq .05$; $\hat{\omega}^2 = .7$). However, there were no significant differences among the bout durations of different age classes at Miquelon (F = 0.2, df = 2, 61, p = .49) or North Rona (F = 2.0, df = 4, 95, p = .31).

Behavioural Act Duration

There were no significant differences between the sites on the basis of the duration of behavioural acts. Behavioural acts performed at Sable Island were no longer ($\bar{x}$ = 10.1 seconds) than those of North Rona ($\bar{x}$ = 5.4 seconds) or Miquelon ($\bar{x}$ = 4.2 sec; F = 11.6, df = 2, 8605, $p \leq .05$; but $\hat{\omega}^2 = .36$).

Cane (1959; 1961) attempted to explain the frequently observed negative linear relationship between the mean durations of a species' behavioural acts and the percentage of time they spent performing each of them. In this study there was no such relationship (Figure 19).

Weighted Behavioural Act Frequency

Averaged over all sites, the mean behavioural act frequency was 0.068 $\text{acts}\bullet\text{seal}^{-1}\bullet\text{min}^{-1}$. The smallest mean frequency during a bout was 0.002 $\text{acts}\bullet\text{seal}^{-1}\bullet\text{min}^{-1}$ (at Miquelon during a leisurely play bout and at North Rona during a copulatory bout) and the largest was 2.9 $\text{acts}\bullet\text{seal}^{-1}\bullet\text{min}^{-1}$ (at North Rona during an aggressive bout).

There were no differences among weighted frequencies at the study sites; the values for this measure at Miquelon ($\bar{x}$ = 0.082 $\text{acts}\bullet\text{seal}^{-1}\bullet\text{min}^{-1}$), Sable Island ($\bar{x}$ = 0.079 $\text{acts}\bullet\text{seal}^{-1}\bullet\text{min}^{-1}$) and North Rona ($\bar{x}$ = 0.060 $\text{acts}\bullet\text{seal}^{-1}\bullet\text{min}^{-1}$) were not sufficiently different (F = 16.9, df = 2, 8639, $p \leq .05$; but $\hat{\omega}^2 = .47$).

1) Sex Differences

At Miquelon, males did not perform behavioural acts at a different frequency ($\bar{x} = 0.097$ acts•seal^{-1}•min^{-1}) than females ($\bar{x} = 0.072$ acts•seal^{-1}•min^{-1}; F= 4.4, df = 1, 1483, $p \leq .05$; but $\hat{\omega}^2 = .23$). This was also the case at Sable Island (male: $\bar{x} = 0.098$ acts•seal^{-1}•min^{-1}; female: $\bar{x} = 0.038$ acts•seal^{-1}•min^{-1}; F = 40.0, df = 1, 2015, $p \leq .05$; but $\hat{\omega}^2 = .02$) and North Rona (male: $\bar{x} = 0.052$ acts•seal^{-1}•min^{-1}; female: $\bar{x} = 0.066$ acts•seal^{-1}•min^{-1}; F = 13.4, df = 1, 4557, $p \leq .05$; but $\hat{\omega}^2 = .27$).

2) Age Class Differences

The mean behavioural frequencies, subdivided by precedent age class, demonstrated significant differences at each site. Adult seals, at Miquelon, interacted at a greater rate ($\bar{x} = 0.131$ acts•seal^{-1}•min^{-1}) than either subadults ($\bar{x} = 0.042$ acts•seal^{-1}•min^{-1}) or weaned pups ($\bar{x} = 0.062$ acts•seal^{-1}•min^{-1}; F = 52.0, df = 2, 1656, $p \leq .05$; $\hat{\omega}^2 = .67$).

There were no sufficient differences among frequencies of behavioural acts by any age class at North Rona (weaned pups: $\bar{x} = 0.169$ acts•seal^{-1}•min^{-1}; adults: $\bar{x} = 0.059$ acts•seal^{-1}•min^{-1}; mothers: $\bar{x} = 0.058$ acts•seal^{-1}•min^{-1}; nursing pups: $\bar{x} = 0.066$ acts•seal^{-1}•min^{-1}; F = 5.7, df = 3, 4925, $p \leq .05$; but $\hat{\omega}^2 = .11$), or Sable Island (nursing pups: $\bar{x} = 0.032$ acts•seal^{-1}•min^{-1}; adults ($\bar{x} = 0.097$ acts•seal^{-1}•min^{-1}; mothers ($\bar{x} = 0.032$ acts•seal^{-1}•min^{-1}; subadults: $\bar{x} = 0.4$ acts•seal^{-1}•min^{-1}; F = 22.0, df = 3, 2058, but $p \leq .05$; $\hat{\omega}^2 = .1$).

Number of Behavioural Acts per Bout

There were significant differences among the number of behavioural acts performed during bouts at the three sites. Miquelon ($\bar{x} = 27.1$) and Sable Island ($\bar{x} = 25.7$) both had fewer behavioural acts per bout than North Rona ($\bar{x} = 50.1$; F = 18.5, df = 2, 237, $p \leq .05$; $\hat{\omega}^2 = .62$). The frequency values for Miquelon and Sable Island were not significantly different. A frequency distribution histogram of the number of behavioural acts performed per interaction (Figure 20) revealed a negative exponential distribution of cases near the mean.

Interaction Distance

There were no significant correlations between interaction distance and frequency of behaviour (Spearman's rho = 0.02, n = 8642, $p = 0.22$), duration of behavioural acts (Spearman's rho = 0.05, n = 8642, $p = 0.29$) or response latency (Spearman's rho = 0.01, n = 8642, $p = 0.57$).

There were differences in the distance between interactants at each study site; seals were further apart when they interacted at both North Rona ($\bar{x} = 99.8$ cm) and Sable Island ($\bar{x} = 99.7$ cm) than when they did so at Miquelon ($\bar{x} = 19.4$ cm; $F = 56.2$, df = 2, 6581, $p \leq .05$; $\hat{\omega}^2 = .74$). The mean distances between interacting seals at Rona and Sable were not significantly different.

1) Age Class Differences:

At Miquelon, the distance between interacting adults was greater than that between subadult pairs (Table 38). Also, adult-subadult pairs interacted at greater distances than subadults did with each other.

As at Miquelon, interactions between adults at North Rona occurred at greater inter-seal distances than between mothers, mothers and adults, and mothers and pups. Also, the distance between interacting mother-adult pairs was greater than between mothers and pups (Table 39).

Adult-adult interactions at Sable Island occurred at greater inter-seal distances than those between mothers, mothers and adults and mothers and pups (Table 40).

The mean inter-seal distances between adults at North Rona and Sable Island were greater than those at Miquelon (and not significantly different from each other; Table 9). Similarly, subadults interacted at a greater distance at Sable Island than those at

Miquelon. When mothers interacted with other mothers, pups or adults at North Rona, they did not do so at greater distances than at Sable Island.

Vigilance Level in the Group

The mean vigilance level (number of times per individual that a seal was seen to look about) the Focal Area at Miquelon ($\bar{x} = 2.6$) was higher than that at either North Rona ($\bar{x} = 1.5$) or Sable Island ($\bar{x} = 1.3$; $F = 1167.6$, $df = 2, 8640$, $p \leq .05$; $\hat{\omega}^2 = .88$). The mean vigilance level was not significantly greater at North Rona than Sable Island.

Behavioural act frequency, duration, distance between the interacting seals, response latency and total bout duration were not correlated with vigilance level (Table 41). There were also no significant differences in vigilance levels on the basis of head and body orientation, sex of the precedent or type of interaction sequence.

Simultaneous Behavioural Acts

Most responses occurred with a temporal interval of one second or more after the antecedent behavioural act of the precedent was completed. This was the situation at Miquelon ($\chi^2 = 22.3$, $df = 1618$, $p \leq .05$) and North Rona ($\chi^2 = 91.8$, $df = 4774$, $p \leq .05$).

On the other hand, at Sable Island, responses were as likely to occur with no interval between them and preceding acts as they would after a delay ($\chi^2 = 0.05$, $df = 2022$, $p = .8$).

1) Sex Differences

At Miquelon, when data were subdivided by successor sex, responses by males were more likely to occur after a delay of more than one second than within the same second as the preceding acts ($\chi^2 = 12.5$, $df = 1131$). However, females' responses were as likely to occur after a delay as to overlap preceding acts ($\chi^2 = 0.2$, $df = 318$, $p = .65$).

At North Rona, responses by males were more likely to occur after a delay than to overlap preceding acts ($\chi^2 = 40.5$, df = 2046, $p \leq .05$). On the other hand, female responses were more likely to overlap preceding acts ($\chi^2 = 87.6$, df = 2374, $p \leq .05$).

Responses by males, at Sable Island, were just as likely to occur after a delay as to overlap preceding acts ($\chi^2 = 0.09$, df = 1397, $p = .77$). This was also the case for females' responses, which were as likely to occur after a delay as to overlap preceding acts ($\chi^2 = 0.6$, df = 587, $p < .43$).

2) Age Class Differences

When subdivided by successor age class, responses by different age classes at Miquelon were more likely to occur after a delay than to temporally overlap preceding acts. This was the case for both adults ($\chi^2 = 4.4$, df = 718, $p \leq .05$) and subadults ($\chi^2 = 22.6$, df = 844, $p \leq .05$). Responses which temporally overlapped preceding acts were as likely to occur as delayed responses when performed by weaned pups ($\chi^2 = 2.5$, df = 56, $p = .11$).

Most responses by seals of different age classes at North Rona were more likely to occur after a delay than to temporally overlap preceding acts. This was the case for adults ($\chi^2 = 32.4$, df = 2526, $p \leq .05$) and mothers ($\chi^2 = 114.8$, df = 1876, $p \leq .05$). Alternately, responses which temporally overlapped preceding acts were more likely than delayed responses ($\chi^2 = 25.5$, df = 346, $p \leq .05$) when performed by nursing pups. Responses which temporally overlapped preceding acts were as likely as discrete responses ($\chi^2 = 1.0$, df = 25, $p = .3$), when performed by weaned pups at North Rona.

At Sable Island, responses which temporally overlapped preceding acts were as likely to occur as delayed responses, when performed by adults ($\chi^2 = 0.02$, df = 1435, $p = .9$), mothers ($\chi^2 = 1.3$, df = 545, $p = .2$), subadults ($\chi^2 = 1.0$, df = 4, $p = .3$) or nursing pups ($\chi^2 = 7.9$, df = 38, $p = .15$).

Cluster Analyses of the Study Sites Based on Behaviour Measures

The number of males and females ("Focal Male" or "Focal Female") within the Focal Area turned out to be the best variables to segregate the three study sites using discriminant analyses (see section on Quantified Variables, in Chapter Two). An initial discriminant analysis revealed that the variables "Focal Male" and Focal Area were highly intercorrelated (0.912); I removed the latter from subsequent analysis since it was simply the total for both sexes.

Nine variables failed the minimum tolerance test for inclusion (at $p \leq .05$) in subsequent analysis (vibrissae position, number of mother/pup pairs in the Focal Area, direction of approach relative to wind, sequence sex (whether interactants were male-male, female-female or male-female), sequence type, precedent sex, successor sex, multiact and whether the behaviour type was simultaneous). I excluded the variable "precedent nares status" due to its preponderance of unknown values.

Only the first orthogonal function resulting from the final discriminant analysis had an eigenvalue greater than 1.0 and accounted for 86.5% of the cumulative variance (Table 42). Within this function, the measures of the proportions of males and females within the Focal Area had adequately large standardized canonical function coefficients to differentiate the three sites.

Agglomerative clustering of the sites, using these two variables, produced the complete linkage dendrogram in Figure 21. In the dendrogram the two breeding sites clustered together at higher similarity levels than either did with the non-breeding group at Miquelon. Based on the relative proportion of males and females within the Focal Area, the breeding groups were more similar to each other than either was to Miquelon.

Sequence Type Features

Behavioural sequences were subdivided into four sequence types: aggressive, copulatory, play and mother/pup. Most (79.0%) interactions were aggressive with much fewer being copulatory (8.6%), play (6.2%) or mother/pup (6.2%; $\chi^2 = 504.6$, $df = 321$, $p \leq .05$). These relative proportions held true for individual study sites (Table 36) and precedent sex (Table 43). Play represented a greater proportion of the total number of behavioural acts at Miquelon.

At each study site, the sequence type did not have significant effects on the duration of behavioural acts, response latency, vigilance level of the group, Focal Area, frequency of behaviour by each precedent sex, and the frequency of behaviour at any head or body orientation (Table 44).

Total Bout Duration

At Miquelon, the mean durations of aggressive and play sequences were not sufficiently different ($F = 20.2$, $df = 1, 62$, $p \leq .05$; but $\hat{\omega}^2 = .43$; Table 45).

Within the breeding group at North Rona, copulatory bouts lasted longer than either mother/pup (usually nursing) or aggressive interactions ($F = 23.3$, $df = 3, 96$, $p \leq .05$; $\hat{\omega}^2 = .67$; Table 45). Mother/pup interactions were also of greater duration than aggressive types. The only two play bouts observed at this site had the shortest total duration, but differences between them and other sequence types were not significant.

Copulatory sequences at Sable Island also lasted longer than either mother/pup or aggressive interactions ($F = 61.2$, $df = 3, 156$, $p \leq .05$; $\hat{\omega}^2 = .74$; Table 45). Like North Rona, play bouts were again the shortest in total duration, but differences between them and other sequence types were not significant.

I found no sufficient differences when comparing the total durations of any similar sequence types among the three sites (Aggressive: $F = 4.1$, $df = 2, 252$, $p = .16$, Copulatory:

F = 9.2, df = 1, 27, p = .29, Play: F = 2.3, df = 2, 18, p = .33 or Mother/Pup: F = 1.4, df = 1, 20, p = .41).

Distance Between Interactants

Seals involved in aggressive interactions did so at much greater distances than during any other type of interaction at Miquelon (F = 211.1, df = 1, 1656, $p \leq .05$; $\hat{\omega}^2 = .81$), North Rona (F = 72.0, df = 3, 4922, $p \leq .05$; $\hat{\omega}^2 = .62$) and Sable Island (F = 58.1, df = 2, 2056, $p \leq .05$; $\hat{\omega}^2 = .61$; Table 45). However, differences among interseal distance values during mother/pup, play (Miquelon and North Rona) and copulatory (North Rona and Sable Island) sequence types were not significant.

I found no difference when comparing similar sequence types across the three sites. Site differences in interaction distances of aggressive (F = 37.7, df = 2, 5545, $p \leq .05$; but $\hat{\omega}^2 = .17$), mother/pup (North Rona and Sable Island; F = 0.6, df = 1, 621, p = .43), copulatory (North Rona and Sable Island; F = 3.4, df = 1, 1389, p = .06) and play sequences (Miquelon and North Rona; F = 0.2, df = 1, 1078, p = .64) were not significant.

Weighted Frequency of Behavioural Acts

At each site, there were no sufficient differences between the sequence types based on behaviour frequency (Miquelon: F = 253.0, df = 1, 1655, $p \leq .05$; but $\hat{\omega}^2 = .13$; North Rona: F = 74.6, df = 3, 4922, $p \leq .05$; but $\hat{\omega}^2 = .04$; Sable Island: F = 27.2, df = 2, 2056, $p \leq .05$; but $\hat{\omega}^2 = .02$; Table 46).

Within sequence types, there were no sufficient differences between the sites on the basis of frequency of behaviour (Aggressive: F = 29.9, df = 2, 5545, $p \leq .05$, but $\hat{\omega}^2 = .02$; Mother/pup: F = 1.6, df = 1, 621, p = .15; Copulatory: F = 23.1, df = 1, 1389, $p \leq .05$, but $\hat{\omega}^2 = .24$ or Play: F = 11.6, df = 2, 1077, $p \leq .05$, but $\hat{\omega}^2 = .15$).

Sex Differences in Sequence Features

Interaction sequences were subdivided into three categories on the basis of the sexes of the interactants: male-male, male-female and female-female.

Most the bouts recorded at Miquelon involved interacting males (64.1%; $\chi^2 = 27.2$, df = 62, $p \leq .05$), whereas most interactions at North Rona were between males and females (48.0%; $\chi^2 = 18.7$, df = 85, $p \leq .05$). At Sable Island interactions were more likely to involve either male-female or male-male pairs than female-female ($\chi^2 = 18.1$, df = 149, $p \leq .05$; Table 47).

Most interactions were aggressive, regardless of the sexes of the interactants (Table 47). Most male-male (95.4%; $\chi^2 = 109.1$, df = 131, $p \leq .05$), male-female (85.4%; $\chi^2 = 49.9$, df = 39, $p \leq .05$) and female-female (70.5%; $\chi^2 = 142.7$, df = 126, $p \leq .05$) interactive bouts were aggressive.

At each site, the sexes of the interacting seals did not have a significant effect on response latency, vigilance, Focal Area or the frequency of behaviour at any head or body orientation (Table 48).

Total Bout Duration

At Miquelon, mixed-sex bouts did not last longer ($\bar{x} = 226.2$ seconds) than either male-male ($\bar{x} = 64.4$ sec) or female-female bouts ($\bar{x} = 152.8$ sec). Male-male and female-female bouts were not sufficiently different in total duration (F = 4.3, df = 1, 55, $p \leq .05$; but $\hat{\omega}^2 = .22$). This was also the case at North Rona (male-male: $\bar{x} = 103.9$ sec, male-female: $\bar{x} = 315.0$ sec, female-female: $\bar{x} = 156.8$ sec; F = 2.1, df = 2, 85, $p = .24$) and Sable Island (male-female: $\bar{x} = 453.7$ sec, male-male: $\bar{x} = 50.1$ sec, female-female: $\bar{x} = 83.2$ sec; F = 7.7, df = 2, 136, $p \leq .05$; but $\hat{\omega}^2 = .11$).

There were no site differences in interaction differences in interaction distances for male-male (Miquelon: $\bar{x} = 64.4$ sec; North Rona: $\bar{x} = 103.9$ seconds; Sable Island: $\bar{x} = 50.1$

sec; F = 2.7, df = 2, 129, $p = .07$), male-female (Miquelon: $\bar{x} = 226.2$ sec; North Rona: $\bar{x} = 315.0$ sec; Sable Island: $\bar{x} = 453.7$ sec; F = 1.2, df = 2, 126, $p = .3$) or female-female pairs (Miquelon: $\bar{x} = 152.8$ sec; North Rona: $\bar{x} = 156.8$ sec; Sable Island: $\bar{x} = 83.2$ sec; F = 0.8, df = 2, 38, $p = .44$).

Age Class Differences

Male-male sequences were more likely to be comprised of adults (87.3%; $\chi^2 = 299.6$, df = 129, $p \leq .05$) than any other age classes. Interacting subadults were the next largest group, but represented only 9.2% of the total.

Female-female sequences were predominantly comprised of interacting mothers (46.3%; $\chi^2 = 40.5$, df = 35, $p \leq .05$).

Male-female sequences were usually comprised of mothers and adult males attempting to copulate with them (73.6%; $\chi^2 = 464.9$, df = 122, $p \leq .05$). Interacting adults were the next largest male-female group, but represented only 17.8% of the total.

Act Duration Differences

At Miquelon, durations of behavioural acts during mixed-sex ($\bar{x} = 4.9$ seconds), male-male ($\bar{x} = 4.5$ seconds) and female-female ($\bar{x} = 3.3$ seconds) interactions were not sufficiently different (F = 6.3, df = 2, 1302, $p \leq .05$; but $\hat{\omega}^2 = .15$).

This was also the case at North Rona (male-male: $\bar{x} = 2.6$ seconds; female-female: $\bar{x} = 3.3$ seconds and male-female: $\bar{x} = 5.2$ seconds; F = 0.7, df = 2, 4205, $p = .35$) and Sable Island (male-male:$\bar{x} = 4.3$ seconds; female-female: $\bar{x} = 5.5$ seconds, and male-female: $\bar{x} = 13.5$ seconds; F = 6.7, df = 2, 1963, $p \leq .05$; but $\hat{\omega}^2 = .09$).

Weighted Frequency of Behavioural Acts

At Miquelon, there were no sufficient differences in the frequencies of behavioural acts during male-male ($\bar{x} = 0.118$ acts$\bullet$seal$^{-1}\bullet$min^{-1}), female-female ($\bar{x} = 0.058$ acts$\bullet$

seal^{-1}•min^{-1}) and mixed sex pairs ($\bar{x} = 0.082$ acts•seal^{-1}•min^{-1}; F = 8.3, df = 2, 1305, $p \leq .05$; but $\hat{\omega}^2 = .14$). This was also the case at Sable Island (male-male: $\bar{x} = 0.138$ acts•seal^{-1}• min^{-1}; female-female: $\bar{x} = 0.052$ acts•seal^{-1}•min^{-1}, male-female: $\bar{x} = 0.035$ acts•seal^{-1}• min^{-1}; F = 57.2, df = 2, 1972, $p \leq .05$; but $\hat{\omega}^2 = .07$) and North Rona (male-male: $\bar{x} = 0.078$ acts•seal^{-1}•min^{-1}; female-female: $\bar{x} = 0.137$ acts•seal^{-1}•min^{-1}, and male-female: $\bar{x} = 0.043$ acts•seal^{-1}•min^{-1}; F = 163.4, df = 2, 4220, $p \leq .05$; but $\hat{\omega}^2 = .29$).

Interaction Distance Differences

At Miquelon, the mean distances between interacting males ($\bar{x} = 23.8$ cm), mixed sex ($\bar{x} = 29.0$ cm) or female-female pairs ($\bar{x} = 12.5$ cm) were not sufficiently different (F = 5.6, df = 2, 1305, $p \leq .05$; but $\hat{\omega}^2 = .01$).

The distances between seals during male-male interactions at North Rona ($\bar{x} = 483.3$ cm) were greater than those of mixed sex ($\bar{x} = 66.8$ cm) and female-female ($\bar{x} = 49.7$ cm; F = 381.9, df = 2, 4220, $p \leq .05$; $\hat{\omega}^2 = .72$). Mean distances between interactants in mixed sex and female-female pairs were not significantly different. The same was true for Sable Island, where males interacted with other males at greater distances ($\bar{x} = 175.2$ cm) than did male-female ($\bar{x} = 35.7$ cm) or female-female pairs ($\bar{x} = 42.9$ cm; F = 176.3, df = 2, 1972, $p \leq .05$; $\hat{\omega}^2 = .62$).

Distances between interactants during male-male (F = 184.5, df = 2, 2288, $p \leq .05$; but $\hat{\omega}^2 = .34$), male-female (F = 29.9, df = 2, 4428, $p \leq .05$; but $\hat{\omega}^2 = .11$) and female-female (F = 28.0, df = 2, 781, $p \leq .05$; but $\hat{\omega}^2 = .16$) were not sufficiently different between the study sites.

Seasonal Trends at North Rona

There were significant trends in a number of measures taken over the course of the breeding season at North Rona with fewer. longer bouts accompanied by an overall decrease in the frequency of behaviour. There were increasing trends in the daily mean values of total bout duration and the number of acts per bout (Table 33). These contrasted with decreasing trends in the daily frequency of behavioural acts (averaged over all sequence types) and the number of males within the Focal Area (using $p \leq .01$ to counter several tied ranks).

There were no significant trends in mean daily values of vigilance, total number of seals within the Focal Area, number of females within the Focal Area, interaction distance and duration and response latency (see respective columns in Table 33).

Weighted Frequency of Behavioural Acts

There were seasonal trends in the average daily frequency of a number of behaviour types (Tables 34 and 35). Both foreflipper waving and chasing occurred more frequently per seal per minute as the season progressed.

Nine behaviour types exhibited decreasing average daily frequencies over the course of the breeding season. Each of the behaviour types extend foreflipper, flipper scratch successor, nose-to-nose, glance, approach/turn towards, roll away, close eyes, roll on side and avert face were performed with decreasing frequency as the season progressed.

None of the remaining 22 behaviour types exhibited significant increasing or decreasing trends in their average daily frequencies.

Precedent Sex

After subdividing the North Rona dataset by precedent sex, I found a number of seasonal trends in both males' and females' interactions.

For bouts involving male precedents, there were decreasing numbers of males within the Focal Area and decreases in distance between interactants and response latency (Table 49).

With female precedents, there were also decreasing trends in the number of males within the Focal Area (using $p \leq .01$ to counter tied ranks) and the frequency of their behavioural acts. There was a large increase in the total duration of bouts over the course of the season (Table 50).

For bouts in which both precedents and successors were male, there was a decrease in the mean response latency over the season. There were no significant trends in vigilance, number of seals within the Focal Area, interaction distance, behavioural act duration, total bout duration, behavioural act frequency, and number of acts per bout (Table 51).

Bouts with female precedents and successors demonstrated a decrease in total bout duration over the course of the season. There were no significant trends in vigilance, Focal Area, number of females within the Focal Area, interaction distance, behavioural act duration, response latency, behavioural act frequency, and number of acts per bout (Table 52).

Among male-female interactions, there were no significant trends in measures of vigilance, number of seals within the Focal Area, number of females within the Focal Area, interaction distance, precedent behavioural act duration, response latency, total bout duration, behavioural frequency, and number of acts per bout (Table 53).

Topographic Features

Position of Interactants in the Group

At Miquelon, seals in the seaward side of the group interacted at a greater frequency ($\bar{x} = 0.2$) than those in the landward side ($\bar{x} = 0.1$; $F = 22.3$, $df = 1, 1622$, $p \leq .05$; $\hat{\omega}^2 = .66$; refer to Figure 7). This was likely due to the preponderance of seals which initially congregated in the seaward side during the haul-out process and interacted with a number of individuals as they made their way into the group. This was also the case when the group was divided into the six-celled grid (Table 54). Behavioural acts were performed more frequently in the right front quadrant than in any other location. Seals in the left and centre front quadrants also demonstrated greater behavioural act frequencies than those in the rear. This was also true at Sable Island, where seals in the seaward side of the group interacted at greater frequency ($\bar{x} = 0.2$) than those in the rear ($\bar{x} = 0.1$; $F = 94.3$, df = 1, 2057, $p \leq .05$; $\hat{\omega}^2 = .62$).

At North Rona, on the other hand, seals in the landward side of the group interacted with greater frequency ($\bar{x} = 0.498$) than those in the seaward side ($\bar{x} = 0.148$; $F = 4.3$, df = 1, 4925, $p \leq .05$; $\hat{\omega}^2 = .75$).

At Miquelon ($F = 6.1$, df = 5, 1649, $p \leq .05$; but $\hat{\omega}^2 = .46$), North Rona ($F = 0.4$, df = 1, 4907, $p = .73$) and Sable Island ($F = 1.1$, df = 1, 1937, $p = .46$) there were no sufficient differences among the mean durations of behavioural acts at any position.

At each study site, the relative position of the interacting seals within the group did not have significant effects on the duration of behavioural acts, total bout duration, distance between the interacting seals, and vigilance level of the group (Table 55).

Substratum Type

The majority of interactions occurred on either sand or grass, which corresponded to the predominant types of substrata found at the sites. Most (65.7%) of the acts recorded at Miquelon took place in shallow water near the haul-out group, with a smaller proportion (34.3%) on the sand beach ($\chi^2 = 162.5$, df = 1656, $p \leq .05$). The greatest proportion of bouts recorded at North Rona occurred on a grass substratum (62.5%), with smaller proportions on Cobble (33.4%) and in shallow, water-filled pools (4.1%; $\chi^2 = 2525.7$, df = 4925, $p \leq .05$). Bouts recorded at Sable Island occurred on the only available substrate - sand. At North Rona, the frequency of behavioural acts was not different whether it occurred in the shallow pools ($\bar{x} = 0.085$ acts•seal^{-1}•min^{-1}), on grass ($\bar{x} = 0.058$ acts•seal^{-1}•min^{-1}) or on cobble surfaces ($\bar{x} = 0.058$ acts•seal^{-1}•min^{-1}; $F = 12.3$,

$df = 2, 4925, p = .11$). This was also true at Miquelon where the frequency was not significantly different whether seals were interacting in the shallows ($\bar{x} = 0.055$ acts•seal^{-1}•min^{-1}) or on the beach ($\bar{x} = 0.135$ acts•seal^{-1}•min^{-1}; $F = 24.2$, $df = 1, 1656$, $p = .17$).

At each site, there were no significant effects of substratum type on act duration, total bout duration, response latency, inter-seal distance or vigilance level within the Focal Area or behaviour frequency (Table 56). This was true for bouts further subdivided by precedent sex, the type of interaction sequence performed or frequency of behaviour at various body and head orientations.

Substratum Slope

Most interactions (73.6%) occurred on substrata with little slope (values between zero and 15 degrees from horizontal). At North Rona, the frequency of behavioural acts was higher on flatter terrain ($\bar{x} = 0.067$ acts•seal^{-1}•min^{-1}) than on slopes of more than 15 degrees ($\bar{x} = 0.034$ acts•seal^{-1}•min^{-1}; $F = 18.1$, $df = 1, 4924$, $p \leq .05$; $\hat{\omega}^2 = .6$). The same was true for Sable Island (0 to 15 degrees: $\bar{x} = 0.096$ acts•seal^{-1}•min^{-1}; greater than fifteen degrees: $\bar{x} = 0.029$ acts•seal^{-1}•min^{-1}; $F = 36.5$, $df = 1, 2057$, $p \leq .05$; $\hat{\omega}^2 = .71$).

All interactions recorded at Miquelon occurred on haul-out substrata with slope values less than 15 degrees from horizontal.

At each site, there were no significant effects of substratum slope on act duration, total bout duration, response latency, inter-seal distance, vigilance level within the Focal Area or number of seals within the Focal Area (Table 57). This was true for bouts further subdivided by frequency of behaviour per precedent sex, frequency of behaviour per type of interaction sequence performed or frequency of behaviour at various body and head orientations.

Meteorological Features

Weather Type

At each site, there were no significant effects of weather type on act duration, total bout duration, response latency, inter-seal distance, vigilance level within the Focal Area, number of seals within the Focal Area or behaviour frequency (Table 58). This was true for bouts further subdivided by frequency of behaviour per precedent sex, frequency of behaviour per type of interaction sequence performed or frequency of behaviour at various body and head orientations.

Wind Velocity and Direction

All three study sites were windy locales; during most interactions there was a greater chance of a wind of moderate strength blowing (44.3%) than strong (18.5%), light (28.9%) or no wind (8.2%; $\chi^2 = 2460.8$, $df = 8638$, $p \leq .05$). Again, however, this result reflects the predominant conditions at each site.

At each site, there were no significant effects of wind velocity (Table 59) or wind direction (Table 60) on act duration, total bout duration, response latency, inter-seal distance, vigilance level within the Focal Area, number of seals within the Focal Area or behaviour frequency. This was true for bouts further subdivided by frequency of behaviour per precedent sex, frequency of behaviour per type of interaction sequence performed or frequency of behaviour at various body and head orientations.

Direction of Seals' Approaches Relative to Apparent Wind Direction

At each site, there were no significant effects of the precedents' approaches relative to wind direction on act duration, total bout duration, response latency, inter-seal distance, vigilance level within the Focal Area, number of seals within the Focal Area

(Table 61). This was true for bouts further subdivided by frequency of behaviour per precedent sex, frequency of behaviour per type of interaction sequence performed or frequency of behaviour at various body and head orientations.

Chronological Features

Time of Day

Grey seals interacted during the night as I was able to hear movement and vocalisations during this time at all sites and, at Miquelon and North Rona, I observed nocturnal activities using a Javelin light amplification device although, without sufficient resolution to describe them quantitatively.

A plot of the number of bouts per hour (Figure 22) shows that most interactions took place in the late morning, regardless of sequence type. A larger proportion of aggressive bouts occurred in the morning at North Rona ($\chi^2 = 4.4$, df = 76, $p \leq .05$).

During daylight periods at each site, there were no significant correlations between time of day and act duration, total bout duration, response latency, inter-seal distance, vigilance level within the Focal Area or number of seals within the Focal Area (Table 62). The time of day also had no correlation with frequency of behaviour when bouts were subdivided by precedent sex.

Time Relative to High Tide

Miquelon was the only site at which the behaviour of grey seals was measurably affected by the tide state. The majority of animals would only haul-out when the tide level had fallen enough to expose the sand. Adult males were normally the first seen in the tidal channels near the haul-out sites, and the first to come ashore to establish a haul-out aggregation.[23]

While it appears that the frequency of behavioural acts was greatest in the hour preceding peak high tide (for data aggregated over all age classes; Figure 23A), the only differences were that the frequency in the third hour after peak high tide ($\bar{x} = 0.103$ acts•seal^{-1}•min^{-1}) was greater than that in the first hour ($\bar{x} = 0.059$ acts•seal^{-1}•min^{-1}; F = 24.3, df = 4, 1656 $p \leq .05$; $\hat{\omega}^2 = .67$). The differences between any other time relative to high tide were not significant.

The differences between the frequencies of behaviour by adults at any time relative to high tide were not sufficient (F = 8.6, df = 3, 742, $p \leq .05$; $\hat{\omega}^2 = .24$; Figure 23B). This was also true for subadults (F = 30.0, df = 3, 862 $p \leq .05$; $\hat{\omega}^2 = .21$; Figure 23C).

Weaned pups interacted at greater frequencies during the second hour after high tide ($\bar{x} = 0.4$ acts•seal^{-1}•min^{-1}) than during the first ($\bar{x} = 0.1$ acts•seal^{-1}•min^{-1}; F = 169.1, df = 1, 50 $p \leq .05$; $\hat{\omega}^2 = .68$; Figure 23D).

There were no significant differences between the frequencies of behavioural acts performed by males (F = 3.7, df = 3, 1163 $p \leq .05$; but $\hat{\omega}^2 = .09$) or females (F = 1.8, df = 3, 320, $p = .22$) at any time relative to high tide.

The frequencies of behavioural acts, subdivided by either precedent age class or sex, at any time relative to high tide at were not significant at North Rona (age class: F = 1.2, df = 3, 4925, $p = .24$; sex: F = 2.2, df = 1, 4901, $p = .21$) or Sable Island (age class: F = 1.5, df = 3, 2058, $p = .36$; sex: F = 1.9, df = 1, 2002, $p = .42$).

During daylight periods at the breeding sites, there were no large correlations between time of day relative to high tide[24] and act duration, total bout duration,

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[23] For up to two hrs prior to haul-out, seals could be seen swimming near the haul-out site. There were few visible interactions between individuals during these times and most seemed to maintain a static position against the current, often with their eyes closed.

[24] While the time relative to high tide was subdivided into one hr intervals for some analyses, it was recorded as a continuous variable.

response latency, inter-seal distance, vigilance level within the Focal Area or number of seals within the Focal Area (Table 63). This was true for frequency of behaviour for bouts further subdivided by precedent sex.

At Miquelon, on the other hand, as time relative to high tide increased, there were correlated increases in inter-seal distance and Focal Area, and decreases in total bout duration (Table 63). Like the breeding sites, there were no significant correlations between time relative to high tide and act duration, response latency and vigilance.

Discussion

Quantitative comparisons (see also Chapters Three and Four) indicated that, as predicted, there were differences in grey seal behaviour among the three study sites. It was reasonable to expect grey seal behaviour to vary over the course of a year, or between locales at the same time of year, since such behavioural differences have been noted in other pinnipeds (e.g., Cameron, 1970; Godsell, 1988; Harestad and Fisher, 1975; Miller, 1975c; Riedman, 1990; Sandegren, 1976a; Thompson, 1989; Thompson *et al.*, 1989). For example, many male pinnipeds are more aggressive towards each other (Sandegren, 1970; Wartzok, 1991) and vocalise more frequently during the breeding season {bearded (Burns, 1981; Stirling *et al.*, 1983); harp (Terhune and Ronald, 1986); ringed (Stirling *et al.*, 1983) and spotted (Beier and Wartzok, 1979) seals; and walrus (Ray and Watkins, 1975)}.

Intra-seasonal behavioural differences among sites have been documented in relatively few pinnipeds. Christenson and Le Boeuf (1977) reported dissimilarities in the incidence of aggressive behaviour by female Northern elephant seals at different breeding beaches. Activity levels and behaviour structure varied qualitatively among breeding grey seal groups in the British Isles (Davies, 1949), and between these and colonies in Canada (Boness, 1984; Cameron, 1970).

There were significant differences between Miquelon, North Rona and Sable Island based on a variety of behavioural measures. Grey seal behaviour was influenced by contextual factors such as sequence type, interactant sex and age. Conversely, extrinsic physical factors such as substrate slope or type, weather, wind velocity and direction or horizontal visibility (Appendix E and Table 64) had little apparent impact. Chronological factors seemed important only at Miquelon, where the presence of a substrate, and thus the haul-out group, was ruled by the state of the tide. Notable individual behavioural variation rendered certain statistical comparisons of aggregate values insignificant.

Sample Group Features

There were a number of significant differences in behaviour depending on certain characteristics of the group sampled at each site. Age- and sex-related differences have been described during studies of aggressive (Harestad and Fisher, 1975; Sullivan, 1981; 1982), vigilant (Renouf and Lawson, 1986b) and play (Rasa, 1971; Renouf and Lawson, 1986a; Wilson, 1974b) behaviour by pinnipeds.

At the two breeding sites interactions were predominantly between adults (including mothers; Table 13). At Miquelon, on the other hand, subadults engaged in over a third of the recorded interactions. This reflects both the larger relative proportion of subadult seals present in the Miquelon samples and this age group's greater playfulness. Like young Steller sea lions (Harestad and Fisher, 1975), Northern elephant (Rasa, 1971) and harbour seals (Renouf and Lawson, 1986a; 1987), subadult grey seals were relatively more boisterous and frequent in their behavioural interactions relative to other age classes (see also Wilson, 1974b).

Breeding seals were extremely intolerant of the presence of subadults and at Sable Island, for instance, subadults were aggressively excluded from breeding areas if they were male, or sexually harassed if they were female. When subadults were able to enter a group such as at Miquelon, they were as playful as young seals in other locales (Rasa, 1971; Renouf and Lawson, 1986a; Wilson, 1974b).

With grey seals, any future behavioural analyses should treat adult females and mothers (females with pups) as distinct classes. Interactions involving mothers lasted longer, contained more behavioural acts, and these acts were of greater duration than those bouts involving adult females (Table 37). When males attempted to approach a mother with her pup, they normally spent more time near her - perhaps assessing her reproductive condition. On the other hand, bouts with adult females were more often combative, there were more males nearby and the frequency of behaviour was greater. Males were more likely to gather near, and attempt to copulate with lone females, and were more quickly rebuffed. Vigorous rebuffs by all females, even those with weaned pups, may function like the protests of female Northern elephant seals which ensure that only the most dominant males copulate with them (Christenson and Le Boeuf, 1977; Cox and Le Boeuf, 1977; Le Boeuf, 1972).

Like harbour seal (Godsell, 1988) and walrus (Miller, 1976) herds at different sites, one of the most apparent differences between the three sites was the number of seals within the Focal Area during interactions. This value was significantly greater at either Miquelon and Sable Island than at North Rona. However, subdividing the seals within the Focal Area based on sex revealed seasonal variation in the proximity tolerance of both sexes.

The number of males within the Focal Areas at Miquelon was greater than at the breeding sites (and Sable Island was greater than North Rona). On the other hand, the number of females within the Focal Areas at the breeding sites were greater than at Miquelon. Evidently, males tolerated each other to a greater extent outside the breeding season (see also Harestad and Fisher, 1975; Miller, 1975c). The converse was true for females - like Northern elephant seals, female grey seals were less likely to tolerate another female nearby in a non-breeding context than they would at the breeding sites

(Sandegren, 1976a). This preference for the company of other mother/pup pairs might explain why female grey seals congregate in colonies rather than singly like ringed (Hammill, 1987; Smith, 1987) or bearded seals (Burns, 1981).

The proportions of males and females within the Focal Area were the best variables to discriminate among the study sites (Table 42 and Figure 21); the two breeding sites were more similar to each other than they were to Miquelon. Further, an increase in the size of the Focal Area was correlated with an decrease in total bout duration at the two breeding sites only (Table 15). Despite these differences between breeding and non-breeding seals, act duration, interseal distance or response latency (all of which exhibited great variance) were not correlated with the number of seals within the Focal Area at any site (Table 15). Group density had little apparent impact on these highly variable measures.

As an example, the total duration of interactive bouts ranged from a brief three seconds to over 5,000 seconds. Bout length exhibited such large variability that mean values for the three sites were not significantly different. There was a greater proportion of lengthy bouts at North Rona and this was probably facilitated by the lower group density, and resultant opportunities for individuals to have extended interactions without being disturbed by others. On the other hand, at Miquelon, and to a lesser extent Sable Island, group densities were higher and most bouts were less than 200 seconds long.

The three sites did not differ in their mean values of behavioural act duration (Table 3), response latency (Appendix E) or frequency of behaviour (Table 7). This absence of statistical difference between sites also applied when these measures were subdivided by interactant sex or age class. Only adult grey seals at Miquelon conducted their behaviour at a higher frequency than their counterparts at the breeding sites; probably as a result of the close grouping and frequent position changes by the central core of adult bulls caused by the entire group having to repeatedly reform after being dispersed for the duration of each high tide.

Although total bout length and frequency of behaviour at the sites were not statistically different, the mean number of acts per bout was greater at Rona than either Miquelon or Sable Island (which were themselves not different). Again, the greater levels of disturbance at Miquelon and Sable Island may have limited the extent and complexity of interactions at these sites. Alternately, the more stable dominance hierarchies at North Rona relative to Sable Island may have permitted resident pairs of seals to interact more affiliatively with more acts performed.

The durations of behavioural acts did not exhibit the frequently-observed negative linear relationship with proportion of time spent performing them (Figure 19; Cane, 1959; 1961). That is, grey seals did not spend proportionately less time performing behavioural acts of greater duration. This likely reflects the preponderance of brief acts in the grey seal repertoire (Tables 1 and 2); behavioural acts rarely lasted much longer than 10 seconds (e.g., CLA, ECL and NUR). There was also no evidence of a division among interaction sequences with respect to the number of acts performed, as has been found in grooming bouts of American kestrels (Lefebvre and Joly, 1982). The number of acts per bout was negative exponentially distributed near the mean for data from all sites (Figure 20). The usual reluctance of adult grey seals to interact with one another, and then often aggressively, would certainly explain the majority of bouts with few acts.

While the interseal distance tolerated by females remained relatively large throughout the year (in contrast with female elephant seals which became highly thigmotactic during the breeding season; e.g., Christenson and Le Boeuf, 1977), males became much more tolerant of the presence of other males during the non-breeding season. The tightly-packed arrangement of the non-breeding "bachelor" group at Miquelon is a common feature of other mammalian species (e.g., Altmann, 1956; Fay, 1982; Feist and McCullough, 1976; Geist, 1971; Harestad and Fisher, 1975; Miller and Boness, 1983; Peterson, 1968; Rideout, 1978; Walther, 1984).

Grey seals were further apart when they interacted at the two breeding sites than Miquelon. At breeding sites males often confronted each other at relatively long distance using OMDs (at greater distances than any other behaviour type; Table 1; and see Miller and Boness, 1979). Many interactions between males and females at the breeding sites were also performed at relatively large inter-seal distances as the females aggressively kept the males away from their pups. The distance between interacting seals was highly variable, however, and I found no statistical correlations between inter-seal distance and behavioural frequency, act duration or response latency. Perhaps grey seal communication, whose signals have significant visual components (Chapter Three), is less affected by inter-individual distance than those species which engage in higher proportions of physical contact. Interactions between adults, a situation where the risk of injury was greater, were done at greater distances than those involving other age classes, at all sites (Tables 38, 39 and 40). A possible reason that subadults interacted at greater distances at Sable Island than Miquelon (Table 9) was that subadults were usually engaged in contact play at Miquelon, but aggressively challenging each other at Sable Island.

The vigilance level within the Focal Area was unrelated to behavioural frequency, act duration, inter-seal distance and response latency at any site (Table 41), although it did increase in conjunction with larger Focal Area values at all sites (Table 15). Further there were no differences in vigilance levels depending on relative orientation, interactant sex or sequence type. At the breeding sites only, an increase in vigilance was correlated with a decrease in total bout duration (Table 41). Vigilance levels were higher at Miquelon than either breeding site (which themselves were equal); I suspect this was due to both the recurrent reformation of the group caused by tidal action and the higher levels of external disturbance documented at Miquelon (Renouf *et al.*, 1981). Interactive bouts were more likely to be curtailed by changes in vigilance at the relatively less-vigilant breeding groups.

Male harbour seals became increasingly vigilant as the time when females usually came into oestrous approached (Renouf and Lawson, 1986b). This result was not replicated at North Rona as males (indeed all seals within the Focal Area in general) were no more vigilant as the breeding season progressed (Table 33). Since there were changes in other measures of male behaviour, vigilance was likely a poor measure of reproductive activity. That females did not enter oestrous synchronously at North Rona (Twiss, 1991) may have obviated males' needs to increase their vigilance as the season progressed. In general then, extrinsic factors such as group disturbance seemingly had greater effects on grey seal vigilance than did social events within the group.

While response latency varied inconsistently among the sites, and between sexes at each site, there were common age class attributes. All age classes (including pups) were more likely to exhibit a measurable delay before they responded to the action of another seal (Appendix E). Thus even young seals seemed to use "standard" rules of social intercourse in this respect (Bekoff, 1972).

Sequence Type Features

During times of the year when they are not breeding, grey seals become more gregarious and gather to form tightly packed haul-out groups (Anderson *et al.*, 1975; Beck, 1983; Bonner, 1981; Cameron, 1967; Mansfield, 1967). While not quantitatively investigated before this study, it was known that grey seals interact frequently in both aggressive and playful manners during these periods (Wilson, 1974b).

Grey seal behaviour at all sites shared many behavioural features, the most obvious of which was an aggressive temperament. This is an obstreperous species with almost 80 percent of sequence types being agonistic (Table 36). Even when subdivided by sex, this preponderance of aggressive interactions remained (Table 43). Grey seals must accrue some benefits for them to form tightly-packed haul-out groups in the non-breeding site with a homogeneous substrate, where they expend more energy during altercations than they would if hauled out alone. This may be a ecologically ancient characteristic from an earlier stage in grey seal evolution when it was thought that grey seals were predominantly ice breeders (Hewer, 1960a); the chances of detecting a predator (such as polar bears) is increased in larger groups (e.g., Krebs and Davies, 1978).

Play represented a larger proportion of bouts at Miquelon, but this was mainly a function of the concurrently larger proportion of young, playful seals in this group. Compared across all sites (and even amongst age classes at Miquelon), grey seals behaved like harbour seals in that they played less as they got older and increasingly interacted in an aggressive manner with other seals (Eliason, 1986; Renouf and Lawson, 1986a; 1987).

Comparisons of the duration and interseal distances during the different sequence types revealed significant differences. Grey seals were further apart during aggressive sequences than during any other type (Table 45), and this was true for all sites. These results support previous studies (Boness, 1979; Davies, 1949; Hewer, 1960a; Twiss, 1991) which claimed that agonistic interactions rarely involved physical contact; grey seals employed visual and acoustic displays to intimidate opponents. In addition, aggressive bouts normally did not last as long as other sequence types (Table 12). Even when males decided to engage in physical conflict, it was usually of limited duration relative to copulatory or (subadult) play sequences. Restricting aggressive exchanges reduced energy expenditures crucially important during the breeding season when reproductive individuals must fast for the duration of this period (Anderson and Fedak, 1987; Twiss, 1991).

Copulatory bouts lasted the longest, whereas the two sequence types (aggressive and play) recorded at Miquelon were not different. During copulation, once intromission was achieved, the pair would often lie together motionless for more than 30 minutes (and see Twiss, 1991). Prolonged copulation may be one mechanism which males employed to increase the chances that their sperm would fertilize the females (Twiss, 1991), since females usually copulated with more than one bull as they left the colonies.

Even though the four sequence types likely served different functions, the frequencies of behavioural acts within each were not significantly different, and these values were not different when similar sequence types were compared between sites (Table 46). Thus although this measure was highly variable, these seals communicated at a similar pace in all contexts. Sequence type had little effect on measured variables at any site (Table 44). Both the high level of individual behavioural variability in this species, and the preponderance of one sequence type (aggressive) may have obscured any sequence type effects.

Sex Differences in Sequence Features

Sex differences in the behaviour of pinnipeds have been documented in a number of species. Males have usually been found to be more aggressive and mobile (e.g., Carrick *et al.*, 1962a; Le Boeuf, 1972; 1974; Sandegren, 1976a), and often more vocally active than females during breeding (e.g., Cleator *et al.*, 1989; Kaufman *et al.*, 1975; Le Boeuf and Petrinovich, 1974a). While I found some sex-related behavioural differences (and see Chapter Three and Four for other sex differences), overall, male and female grey seals behaved similarly with respect to the measures detailed in this section.

Most bouts at Miquelon involved males (in particular subadults - see Table 13), whereas bouts were more likely to involve male-female pairs at North Rona and either male-female or male-male Sable Island (Table 47). It was apparent that female grey seals maintained a greater distance between themselves and cohorts at Miquelon, and frequently did so by hauling out at the periphery of the group. Adult males, on the other hand, arranged themselves in an intimate mass at the centre of the haul-out group. Thus adult males were more likely to interact with a male cohort. Subadult males were active for much of the haul-out and frequently seemed to solicit playful interactions with other subadults while the adult seals slept. At the breeding sites, adult females frequently interacted with adult males in search of copulations (Boness, 1979; Twiss, 1991). Perhaps owing to their reluctance to leave their sedentary pups, females rarely interacted with other females at the breeding sites (although if they did it was usually between mothers rather than single females). That male-male bouts were as frequent as male-female at Sable Island is probably due to the same reasons that Sable Island bulls differ from those breeding on the Monach Isles in Britain (Boness, 1984): there were proportionately more males present in the group and they moved about more frequently.

Irrespective of sex, the majority of pairs engaged in agonistic interactions (Table 12). Contrary to expectations, interactant sex had no significant impact on total bout duration, response latency, vigilance or Focal Area, or behavioural frequency at any head or body orientation (Table 48). Either the large individual behavioural variability overshadowed any sex-related differences in these measures, or the sexes were actually alike . In fact, I could identify no gender characteristic postures or orientations (except the clasping behaviour males utilised during copulation).

While the distance between interactants was not different between sequences involving either sex at Miquelon, there were differences at the breeding sites.[25] By maintaining greater inter-seal distances, and utilizing long-range displays such as the OMD, males were able to reduce the number of tiring physical altercations they engaged in at the breeding sites. This contrasted with the smaller distances between interacting males and females (males only approached females in an attempt to copulate with them), or females and females. Boness (1979) also reported that the mean distance between bulls was greater than that between cows at Sable Island.

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[25] Even though the distance between seals in bouts with male precedents decreased over the course of the season at North Rona (Table 51), they still interacted at greater distances than females.

I was able to measure temporal changes in certain categorical measures over the course of an entire breeding season at North Rona. These revealed a distinct change in the social dynamic of the group and the behaviour patterns of bulls. The amount of sexual activity increased over the course of the season as mothers weaned their pups and males became more persistent in their efforts to copulate. While the total duration of interactive bouts and the number of acts performed during those bouts increased, the rate of behaviour and the number of males with the Focal Area decreased (Tables 33 and 50). Thus males became increasingly aggressive towards each other as the end of the season approached and most females began entering oestrous. Male grey seals spent more time in close proximity (Table 49), and interacting with, females in an attempt to copulate with them, while becoming decreasingly tolerant of other males nearby {decreasing response latency during interactions with other males (Table 51); and also indicated by generally decreasing response latencies (Table 49) and increasing frequency of chasing (Table 34)}. While bouts involving female precedents became longer (Table 50), female-female pairs spent shorter periods interacting with each other (Table 52), perhaps as the bond with between mother and pup weakened near weaning {implied by Kovaks (1987b) and similar to harbour seals (Lawson and Renouf, 1987)}.

Females responded by Foreflipper Waving more frequently in efforts to reject the males' advances (Table 34). Decreasing energy reserves through lactation (Fedak and Anderson, 1982) likely forced females to reduce their frequency of behaviour (Table 50). They were more lethargic as the season passed – a cue bulls may have used (in addition to the females' obvious thinness) in assessing their readiness to copulate and which may have stimulated their approach as it does male otariids (Miller, 1991).

Certain behavior types decreased in frequency over the season (EFF, FSR, NTN, GLA, APT, ROA, ECL, ROS and AVF; Tables 34 and 35). These behaviour types might be categorised broadly as "sedate" and, except for APT and AVF, were less likely to be performed during the copulatory or male-male interactions which predominate later in the season.

Measures of male-female bouts were too variable to detect trends (Table 53). And, as mentioned previously, there was no seasonal trend in vigilance (Table 33). We found that adult male harbour seals became increasingly vigilant as the time when most females entered oestrous approached (Renouf and Lawson, 1986b). That male grey seals did not exhibit a change in this measure was perhaps related to their terrestrial copulatory practice where potentially available females and male competitors were more apparent, or the fact that female oestrous was not highly synchronized at this site (Twiss, 1991).

Topographic Features

Topography has been previously implicated as a factor influencing breeding behaviour in grey seals (Anderson *et al.*, 1975; Hewer, 1960a; Kovaks, 1987b). Bulls were better able to maintain territories at those colonies with restricted access to the sea, and cows were less likely to remain ashore with their pups if the sea was readily accessible. In this thesis I was able to look in greater detail at the influence of topographic features, and at a non-breeding site as well. At all sites grey seal behaviour was not measurably affected by relative group position, substratum type or slope.

At both Miquelon and Sable Island the seaward side of the group was most active (Figure 7 and Table 54). This area was the point of continuous exchange as newly-arrived members came to haul-out, and others left or were chased from the group. At Miquelon 65.7 percent of the interactions occurred in the shallow water in front of the main haul-out group. This was the favoured area in which subadults often played with each other. At Sable Island, the land/sea interface was an area of extreme activity as males competed with each other during attempts to copulate with females as they came and went to the sea (Boness, 1979). At North Rona, on the other hand, the most active part of the group was the landward side. Caution is advised in interpreting this last point as I was unable to record underwater interactions immediately adjacent to the limited access points to North Rona's breeding flats. Observations from elevated viewpoints suggest that, like Sable Island, the sea/land interface may be the site of intense competition and interaction amongst males.

However, the relative position of an interaction within the group did not have any impact on act or bout duration, inter-seal distance or vigilance (Table 55). In addition, the substratum type had no impact on any quantified measure at any site (Table 56). While most (73.6%) behavioural interactions occurred on surfaces with slopes of less than 15 degrees from horizontal, this variable had no significant impact on any measure at any site (Table 57). As a species with a broad thermoneutral range (Gallivan and Ronald, 1979) and relatively good mobility on land, these results indicate that grey seals were not behaviourally constrained by the nature of the substrate they chose to interact on. As an example, I observed seals of all ages sleeping with apparent lack of distress in ice-filled freshwater ponds or snowdrifts at Sable Island. Several females gave birth to and nursed their pups on slopes at North Rona that were so steep that I had difficulty negotiating them. This is possibly one reason why they are able to breed successfully on ice, rock, grass and sand in many locales around the Atlantic.

Meteorological Features

Like Renouf and Lawson (1986b; 1987), this study found no significant effects of meteorological conditions on grey seal behaviour. In particular, weather type (Table 58), wind velocity (Table 59) or direction (Table 60), and horizontal visibility (Table 64; Appendix E) did not have any measurable effect on grey seal behaviour at any site. Unlike species whose activities were regulated by temperature (e.g., Arnold and Trillmich, 1985; Shipley and Strecker, 1986), the temperate environments of these study areas seemed to place no such limitations on grey seals.

While most seals at North Rona approached each other from a crosswind orientation, the approach relative to wind direction had no effect on any measure at any site (Table 61). This, and the observation that bulls were never seen to investigate females' perineal regions like otariids (Gentry, 1975c), suggests that olfactory cues were relatively unimportant in invoking an interaction.

Chronological Features

Diel patterns in activity have been reported for other pinnipeds (e.g., Arnold and Trillmich, 1985; Chwedenczuk and Frysz, 1983; Cleator *et al.*, 1989; Erickson *et al.*, 1989; Rasa, 1971; Shipley and Strecker, 1986; Thomas and Kuechle, 1982), with most of these species exhibiting a crepuscular cycle.

While there were no correlations between time of day and most parameters (Table 62), there was evidence of a late morning peak in behavioural interactions using data from all sites (Figure 22). As indicated in Figure 22, most aggressive and play bouts occurred during the midday period. Although not quantified in this study, several nights spent watching these seals with a light amplification device provided evidence to support Anderson's (1978) observation that grey seals continued to interact throughout the night. However the midday peak in activity I observed was not matched by the cruder measures of Anderson's study.

As with time of day, time relative to high tide had no significant impact on any of the selected variables shown in Table 63. for the breeding sites This was also the case when data were subdivided by interactant sex.

Miller (1991) felt that diel rhythms in haul-out behaviour influenced pinniped communication (e.g., Tedman and Bryden, 1979; Thomas and DeMaster, 1983; Yochem *et al.*, 1987). Although I did not detect any such rhythms at the two breeding sites, grey seal activity at Miquelon was constrained by tidal action. When compiled over all age classes, the frequency of behaviour was greatest during the hour immediately preceding high tide (Figure 23A). This represented the time when seals were congregating in the shallow waters covering the intended haul-out area, and individuals were beginning to assume preferred spots.

When subdivided by age class, there were no significant differences in behavioural frequency at any time relative to high tide by adults (Figure 23B) or subadults (Figure 23C). Weaned pups, on the other hand, exhibited a sharp increase in frequency of behaviour in the second hour after high tide (Figure 23D). At this time, older seals had settled down to sleep and the pups were able to haul out and move about with reduced risk of being threatened.

As time passed after high tide, seals at Miquelon were more closely grouped, but interacted at greater distances and the bouts were briefer (Table 63). The latter two changes were probably due to the increased relative number of play bouts involving chases (usually performed at greater-inter-seal distances) into and out of the water by subadults and pups.

While a tide-related pattern in certain measures of activity level was apparent at the non-breeding site, most measures of grey seal behaviour were not subject to variation in relation to time at the breeding sites.

Summary

The individual variation in grey seal behaviour overshadowed many intra- and intersite comparisons. Nonetheless, behaviour patterns were significantly affected by extrinsic factors such as locale, season, context, age class and interactant sex. Social features had generally greater impact on behaviour patterns at all sites than did topographic, meteorological or temporal characteristics of the sites. On a number of measures the breeding sites were more similar to each other than they were to the non-breeding site.

Sample Group Features

- While adult grey seals performed most interactions at all sites, which partly reflected the greater number of adults, at the non-breeding site subadults engaged in over one third of the bouts.
- The seal types "female without pup" and "mother with pup" were distinctive in that interactions involving the latter lasted longer, were less combative, had lower rates of behaviour and there were usually more adult males within the Focal Area.
- Males tolerated each others' presence to a greater degree outside the breeding season, while the reverse was true for females.
- The relative proportion of male and female seals within the focal area were the best measures to discriminate the sites on a demographic basis. The breeding sites were more similar.
- Higher group densities were not correlated with a number of measures at any site (frequency of behavior, act duration and interseal distance). However, increased Focal Area density was correlated with increased vigilance at all sites, and a decrease in total bout duration at the breeding sites (indicating that breeding interactions may be more susceptible to disturbance).
- Large variation rendered site differences in act duration, frequency of behaviour and response latency non-significant.
- The mean number of acts per bout was greater at North Rona, but at all sites generally low thus reflecting grey seals' normal reluctance to interact with one another.
- While the interseal distance females tolerated remained large throughout the year, males became much more gregarious outside the breeding season.
- Seals were further apart when they interacted at the breeding sites than Miquelon, and adults at all sites also communicated over greater distances than other age classes.

- Extrinsic factors such as group disturbance seemingly had greater effects on vigilance than did social events within the group.

Sequence Type Features

- The bellicose temperament of this species resulted in most interactions being agonistic.
- Play was more common at Miquelon, where there were also more subadults present.
- Perhaps to conserve energy and reduce risk of injury, grey seals were further apart when they engaged in aggressive interactions than any other sequence type.

Sex Differences in Sequence Features

- Male-male bouts were more common at Miquelon, while the highly mobile and numerous bulls at Sable Island interacted as frequently with each other as they did with females (male-female bouts were the predominant type at North Rona).
- Despite their higher frequency, male-male interactions were carried out at greater range by emphasizing visual and auditory signals.
- There were significant changes in male and female behaviour over the course of the season at North Rona which were probably linked to the onset of oestrous.

Topographic, Chronological and Meteorological Features

- Local topographic features had no measurable effects on grey seal behaviour.
- Only at Miquelon, where haul-out activity was governed by tide state, was there evidence of any temporal patterns in seal behaviour. Observations suggested there were no diel patterns in behaviour at any of the three sites.
- The grey seals' broad thermonuetral range rendered meteorological conditions (weather type, wind velocity or direction, and horizontal visibility) relatively ineffective as factors controlling this species' behaviour.

Chapter Six: Future Research Directions

The strength of this study is not that it is a quantitative study of pinniped behaviour, but that it has demonstrated the merit of using a consistent comparative method across several populations (and see Gentry, 1975c). Uniform observational and analytical techniques at all three sites eliminated the effects that differences in these approaches have when comparing different seal groups using data from several studies. Thus the data revealed genuine, significant differences among all three sites. Researchers undertaking future studies should be more aware of this and try to include more than one locale.

By observing grey seals in three varied locations I was able to construct an extensive description of their terrestrial behaviour. Nonetheless, I concur with Miller (1991) who stated that:

> *"Despite the obvious difficulties of obtaining meaningful observations on pinniped behaviour at or below the water surface, much important communication occurs there (e.g., Sullivan, 1979; 1981; Miller and Boness, 1983; Gailey-Phipps, 1984)."* (p. 200)

Therefore, an important supplement to this work would be to obtain video records of underwater behaviour. North Rona would be an ideal site for this since I have observed that the water has low turbidity and many seals of all age classes congregate in the narrow fjords around the coast of the island. The success of the underwater blind Dr. G. Kooyman has been using in the Antarctic to study penguins and leopard seals suggests that this is feasible.

Grey seals maintain a fairly constant pattern of activity on land during the day and at night (Anderson, 1978; Shipley and Strecker, 1986). Using readily-available image amplification equipment it should also be possible to obtain data on nocturnal communication.

As I postulated in Chapter Four, the nominal sequential predictability of grey seal behavioural is likely a product of both a relatively large behaviour repertoire and an abundance of contextual cues. However, the influence of individual behavioural variability, a characteristic receiving attention in ethological studies only recently[26], was doubtless also significant.

If one could repeatedly identify individual seals between bouts, using marked or photographically identified animals, it would be possible to assess the impact that interactants' familiarity with each other, or individual differences in behaviour, may have on how they interact with others. For instance, do males who are familiar with each other spend less time in agonistic communication than they do with strangers - the "dear enemy" effect (Simpson, 1973). This certainly seems to be the case with elephant seals (Shipley *et al.*, 1981) and some otariid species (e.g., Bonner, 1968; Gentry, 1975c).

With larger sample sizes and individually identifiable seals, future work could also more precisely appraise the impact that seasonal, daily or intra-bout differences in individual behaviour may have on sequential analyses. One could test a prediction that changes in in aggressive motivation would be faster during agonistic interactions between seals of dissimilar size than between equally-matched opponents (Rand and Rand, 1976; Sullivan, 1982; Wagner, 1989; but see Turner and Huntingford, 1986).

Stochastic analyses do not take into account the variation in duration of actions or intervals between them, which may be just as significant as the order of events in behavioural sequences (Immelmann and Beer, 1989). For instance, grey seals may have attended to inter-act intervals as a means to assess their partners' motivational states. I was unable to undertake continuous-time transition analysis (time intervals between

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[26] For example, Moran *et al.*, (1981) described marked individual variation in wolf behaviour during fight sequences, but their behaviour was constrained when interactive dyads were examined.

behavioural acts are used as an additional dimension in transition matrices) since Fagen and Young (1978) stipulated that there must be a sample size of at least $30R^2$ acts in order to perform first-order continuous-time transition analyses. Further studies of grey seal communication could address this question through analyses of a much larger, narrowly-focused dataset.

Further sequential and information estimate studies could do much to test current theories regarding reproductive strategies in pinnipeds. Preliminary estimates of information transmission provided indications that grey seals were "manipulative" communicators during the breeding season. Further data would strengthen these estimates, and allow measurement of information transmission in dissimilar contexts (e.g., is less information exchanged during aggressive than playful communication ?).

Finally, work should be undertaken to obtain records of interactions among younger age classes of grey seals. Their attendance was relatively rare in all three groups, but particularly at the breeding sites. From the perspective of behavioural ontogeny, a study of subadult males could reveal how and when they begin performing the stereotyped behavioural acts (OMD) and postures of adult bulls. Do they perform their first OMDs "perfectly", or must they practice ? The fact that subadults are rarely seen on breeding grounds suggests that young males do not learn this behavioural act by watching adults.

More data from young seals could reveal whether the sex differences in behaviour exist from birth. Fagen's functional model of play (Fagen, 1981), in which playing animals gain valuable experience and strength, predicts that in species in which the variance in reproductive success is greater in males than females, males should spend more time playing (and see Wartzok, 1991).

The grey seal provides a good subject on which to continue behavioural studies of individual behavioural variation, behavioural ontogeny, sequential dependency and information transfer. With a quantitative, consistent approach ethologists should be able to compare a number of pinniped species in different habitats and seasons.

Table 1: Summary of major characteristics of the first 17 behaviour types (data aggregated from all sites).

	Behaviour Type																
	OMD	HTH	EFF	FFW	FSR	FSS	FSW	FSB	HSW	HEX	NTN	PON	SNI	GLA	STA	LAW	BIT
Eyes Condition	Open	Open	Open	Open	Open	Open	Open	Open	Open	Open	Open	Open	Open	Open	Open	Open	Open
Mouth Condition	Open	Open	Open	Open	Open	Open	Open	Open	Open	Open	Closed	Closed	Closed	Open/ Closed	Open	Open	Open
Vibrissae Position	Protr.	Protr.	Protr.	Protr.	Protr.	Protr.	Protr.	Protr.	Protr.	Protr.	Protr.	Protr.	Protr.	Protr.	Protr.	Retr.	Protr.
Nares Position	Open	Closed	Closed	Closed	Closed	Open	Closed	Open/ Closed	Closed	Open	Open	Open	Open	Closed	Closed	Open/ Closed	Closed
Tail Position	Down	Down	Down	Down	Down	Down	Down	Down	Down	Down	Down	Down	Down	Down	Down	Down	Down
Head Height	Higher /Same	Any	Lower	Lower	Lower /Same	Lower	Same	Higher /Same	Same	Lower /Same	Any	Higher /Lower	Any	Any	Any	Any	Any
Body Orientation																	
Head Orientation													Any				
Vocalisations	None	None/ OMW	None/ OMW	OMW	None/ OMW	None/ OMW	OMW	OMW	OMW	None/ OMW	None/ OMW	None	None	None	None	None	None
Mean Duration (sec)	2.8	1.3	5.1	4.2	7.1	4.7	1.9	3.8	1.5	3.8	4.2	7.1	4.0	1.0	5.7	10.8	3.0
Interseal Distance (cm)	307.7	19.0	19.4	33.7	3.7	84.4	46.1	51.2	16.3	37.4	3.1	2.5	28.9	51.5	110.7	64.2	5.3
Precedent's Sex	Male	Male/ Female	Female	Male/ Female	Male/ Female	Female	Female	Female	Male/ Female	Male/ Female	Male/ Female	Male/ Female	Male/ Female	Male/ Female	Male/ Female	Male/ Female	Male/ Female
Precedent's Age	Adult	Adult/ Subadult	Adult/ Pup	Adult	Mother/ Pup/ Subadult	Adult/ Mother	Mother	Mother	Mother/ Adult/ Subadult	Adult	Mother/ Adult/ Subadult	Adult/ Subadult /Pup	Mother/ Adult	Adult	Adult/ Mother	Mother/ Adult/ Subadult	Adult/ Subadult
Sequence Type	Aggr.	Aggr.	Aggr.	Aggr.	Aggr.	Aggr.	Aggr.	Aggr. /Cop.	Aggr.	Aggr.	Aggr.	Mother & Pup	Any	Any	Aggr.	Aggr.	Aggr.

Orientation Symbol Key (Body or Head): **Posterior**  **Anterior**

Table 2: Summary of major characteristics of the second 16 behaviour types (data aggregated from all sites).

	Behaviour Type															
	CLI	CLA	APT	CHA	ROA	DPA	RAW	YAW	NHS	RHV	ECL	ROS	NUR	BSR	PT	AVF
Eyes Condition	Open	Open	Open	Open	Open	Open	Open	Open/ Closed	Closed	Open	Closed	Open	Closed	Open/ Closed	Open	Open
Mouth Condition	*Open*	Open/ Closed	Open/ Closed	*Open*	*Closed*	Open/ Closed	*Closed*	*Open*	*Closed*	*Open*	*Closed*	Open/ Closed	*Open*	*Closed*	*Closed*	*Open*
Vibrissae Position	Protr.	Protr./ Retr.	Protr.	Protr.	Retr.	Protr.	Protr./ Retr.	Protr.	Protr./ Retr.	Protr.	Retr.	Protr.	Protr.	Protr./ Retr.	Protr.	Protr.
Nares Position	Open/ Closed	Open/ Closed	Closed	Open/ Closed	Closed	Closed	Open/ Closed	Open/ Closed	Open/ Closed	Open/ Closed	Closed	Closed	Unk.	Unk.	Open/ Closed	Open/ Closed
Tail Position	Down	Down	Down	Down	Down	Down	Up/ *Down*	Down	Down	Down	Down	Down	Down	Down	Down	Down
Head Height	Higher	Higher	Any	Same	Lower/ Same	Lower/ Same	Any	Any	Higher	Higher	Lower/ Same	Any	Higher	Any	Higher	Lower/ Same
Body Orientation									Any					Any		
Head Orientation									Any					Any		
Vocalisations	None	None	None	None	None	None	None	None	None	None	None	None	None	None	None	None
Mean Duration (sec)	8.1	49.5	3.2	6.5	4.0	3.9	4.1	1.9	2.0	2.6	27.0	2.9	143.5	4.4	18.4	3.4
Interseal Distance (cm)	2.3	0.5	144.3	251.1	198.8	79.7	219.5	28.8	61.3	11.5	166.6	40.9	8.8	106.5	0.0	31.8
Precedent's Sex	Male	Male	Male	Male	Male/ Female	Male	Male/ Female	Male/ Female	Male/ Female	Male	Male/ Female	Male/ Female	Male/ Female	Male/ Female	Male	Male
Precedent's Age	Adult/ *Subadult*	Adult/ *Subadult*	Adult	Adult/ Subadult	Adult/ Mother/ Subadult	Adult/ *Subadult*	Adult/ *Subadult*	Adult/ *Mother*	Adult/ *Mother*	Adult	Adult	Adult/ Mother/ Subadult	Pup	Mother /Adult	Adult	Adult
Sequence Type	Aggr./ Play	Aggr./ Play	Aggr.	Any except Mother/Pup	Aggr.	Aggr.	Any except M/P	Any except Cop.	Aggr.	Any	Any	Any	M/P	Any except Play	Cop.	Aggr.

Orientation Symbol Key (Body or Head): Posterior  Anterior

Table 3: Mean duration (sec) of each behaviour type at each study site.

	Mean Duration (SD)			ANOVA (Scheffé [1])		
Behaviour Type	**Miquelon**	**North Rona**	**Sable Island**	M vs R	M vs S	R vs S
Open Mouth Display	--	2.8 (0.8)	3.1 (1.0)	--	--	
Head Thrust	1.3 (1.1)	1.2 (0.7)	1.6 (2.5)			
Extend Fore Flipper	4.4 (4.1)	4.3 (7.9)	9.7 (12.5)			
Fore Flipper Wave	5.7 (8.4)	3.2 (3.7)	5.7 (7.4)			
F. Fl. Scratch Succ.	6.8 (8.1)	6.8 (8.0)	7.6 (9.3)			
F. Fl. Scratch Sub.	--	2.4 (0.5)	6.1 (9.3)	--	--	
F. Fl. Slap Water	--	1.9 (1.1)	--	--	--	--
F. Flipper Slap Body	--	3.8 (3.1)	--	--	--	--
Head Swing	1.2 (1.2)	1.9 (1.9)	1.7 (1.5)	5.6		
Extend Head	4.0 (3.0)	3.2(3.1)	5.0 (5.7)			7.2
Nose-to-Nose	2.5 (0.7)	4.0 (3.5)	13.6 (13.2)		13.3	13.2
Poke with Nose	3.0 (2.6)	6.3 (8.4)	12.3 (13.1)			
Sniff	2.0 (--)	4.5 (5.2)	1.6 (0.7)			
Stare	6.9 (7.4)	5.0 (6.6)	6.5 (6.2)			6.1
Look Away	7.0 (8.6)	7.6 (31.4)	19.7 (94.0)			3.8
Bite	4.5 (4.6)	2.2 (3.0)	2.7 (2.7)	12.6	5.7	
Climb	5.7 (6.9)	8.4 (9.4)	12.5 (13.2)		9.3	
Clasp	7.3 (6.0)	34.5 (197.6)	80.6 (263.7)			
App. / Turn Toward	2.8 (2.8)	2.9 (3.5)	4.1 (2.9)		5.3	8.7
Chase	24.4 (26.1)	5.0 (4.4)	3.9 (2.2)	10.6	12.2	
Roll Away	3.3 (1.2)	2.7 (3.5)	4.9 (2.2)			
Depart/Turn Away	3.3 (4.4)	3.4 (4.7)	5.2 (4.9)		7.0	9.6
Rush Away	3.8 (2.7)	3.9 (3.4)	4.5 (4.3)			
Yawn	2.0 (0.8)	1.9 (0.6)	--		--	--
Neck and Head Shake	3.0 (--)	1.7 (0.6)	--		--	--
Raise Head Vertical	3.4 (3.4)	1.9 (1.7)	2.0 (1.8)	7.6	4.5	
Eyes Closed	11.0 (16.8)	24.5 (147.2)	40.7 (154.3)			
Roll on Side	1.4 (1.0)	2.3 (2.5)	5.2 (6.6)	5.4		5.4
Nurse	--	100.2 (189.7)	370.8 (236.9)	--	--	6.4
Body Scratch/Rub	2.0 (--)	4.0 (3.9)	6.0 (3.4)			
Penile Thrust	--	15.8 (14.6)	24.6 (38.9)			
Avert Face	4.1 (7.1)	2.8 (3.5)	3.9 (3.3)			
N = 33	$\bar{x} = 4.2$ [2] (6.3)	$\bar{x} = 5.4$ [2] (39.7)	$\bar{x} = 10.1$ [2] (60.0)			

[1] Sufficiently different at $p \leq .05$ and $\hat{\omega}^2 \geq .60$. Empty cells signify non-significant differences.

[2] These values incorporate unlisted MultiAct or Unknown behavioural types

Table 4: Mean coefficients of variation (CV; expressed as percentages) of duration for each behaviour type at each study site.

	Miquelon	North Rona	Sable Island
Behaviour Type	CV %	CV %	CV %
Open Mouth Display	--	28.6	32.3
Head Thrust	84.6	58.3	156.3
Extend Fore Flipper	93.2	183.7	128.9
Fore Flipper Wave	147.4	115.6	129.8
F. Fl. Scratch Succ.	119.1	117.6	122.4
F. Fl. Scratch Sub.	--	20.8	152.5
F. Fl. Slap Water	--	57.9	--
F. Flipper Slap Body	--	81.6	--
Head Swing	100.0	100.0	88.2
Extend Head	75.0	96.9	114.0
Nose-to-Nose	28.0	87.5	97.1
Poke with Nose	86.7	133.3	106.5
Sniff	0.0	115.6	46.7
Stare	107.2	132.0	95.4
Look Away	122.9	413.2	477.2
Bite	102.2	136.4	100.0
Climb	121.1	200.0	105.6
Clasp	82.2	572.8	327.2
App. / Turn Toward	100.0	120.7	70.7
Chase	107.0	88.0	56.4
Roll Away	36.4	129.6	44.9
Depart/Turn Away	133.3	138.2	94.2
Rush Away	71.1	87.2	95.6
Yawn	40.0	31.6	--
Neck and Head Shake	0.0	35.3	--
Raise Head Vertical	100.0	89.5	90.0
Eyes Closed	152.7	600.8	379.1
Roll on Side	71.4	108.7	126.9
Nurse	--	189.3	63.9
Body Scratch/Rub	0.0	97.5	56.7
Penile Thrust	--	92.4	158.1
Avert Face	173.2	125.0	84.6
Overall [1]	$\bar{x} = 83.5$ SD=48.6	$\bar{x} = 133.2$ SD=137.1	$\bar{x} = 124.2$ SD=102.5

[1] The site values were not significantly different (F = 1.8, df = 2, 86, $p = 0.35$).

Table 5: Mean values of distance (cm) between interacting seals during each behaviour type at each study site.

	Mean Distance (SD)			ANOVA (Scheffé [1])		
Behaviour Type	**Miquelon**	**North Rona**	**Sable Island**	M vs R	M vs S	R vs S
Open Mouth Display	--	364.4 (700.2)	161.3 (165.9)	--	--	13.0
Head Thrust	9.1 (17.7)	24.4 (45.5)	17.2 (22.4)			
Extend Fore Flipper	15.3 (19.8)	22.6 (34.7)	12.1 (23.4)			
Fore Flipper Wave	30.0 (87.5)	42.9 (89.0)	8.4 (9.4)			
F. Fl. Scratch Succ.	6.6 (14.7)	1.3 (3.8)	5.5 (8.0)			
F. Fl. Scratch Sub.	--	53.0 (32.7)	26.3 (21.0)	--	--	9.9
F. Fl. Slap Water	--	46.1 (32.6)	--	--	--	--
F. Flipper Slap Body	--	51.2 (51.1)	--	--	--	--
Head Swing	6.4 (10.6)	34.3 (41.9)	16.5 (15.5)	40.4	5.8	
Extend Head	29.7 (38.3)	37.1 (70.3)	42.4 (79.0)			
Nose-to-Nose	1.5 (3.8)	3.3 (9.2)	2.0 (2.7)			
Poke with Nose	1.7 (2.9)	1.9 (5.4)	6.0 (7.6)		11.3	12.4
Sniff	0.0 (--)	27.9 (65.6)	51.0 (69.3)			
Glance	27.5 (35.2)	49.4 (80.1)	83.2 (138.9)			
Stare	43.1 (71.9)	113.3 (214.3)	143.0 (180.0)	10.0	16.9	
Look Away	18.0 (25.2)	53.4 (141.3)	111.4 (221.6)		13.7	10.3
Bite	2.7 (11.1)	6.4 (20.8)	6.6 (15.2)			
Climb	2.4 (4.9)	2.5 (7.3)	1.7 (7.3)			
Clasp	1.7 (2.9)	0.3 (1.6)	0.9 (4.8)			
App. / Turn Toward	46.3 (85.2)	149.2 (337.1)	178.5 (193.1)	4.9	8.9	
Chase	63.0 (79.4)	306.8 (430.6)	243.7 (243.8)			
Roll Away	18.6 (19.7)	33.3 (50.1)	343.1 (348.3)		6.5	9.5
Depart/Turn Away	24.3 (56.9)	86.9 (297.6)	106.0 (202.3)	8.4	6.6	
Rush Away	75.8 (115.9)	273.2 (361.1)	176.5 (206.2)			
Yawn	32.5 (30.1)	25.0 (32.4)	--		--	--
Neck and Head Shake	25.0 (--)	73.3 (23.1)	--		--	--
Raise Head Vertical	11.4 (14.0)	13.0 (14.6)	8.9 (11.8)			
Eyes Closed	48.0 (73.6)	218.7 (650.0)	110.3 (159.3)			
Roll on Side	7.5 (8.4)	45.8 (133.7)	52.3 (193.9)			
Nurse	--	10.5 (10.2)	0.0 (0.0)	--	--	
Body Scratch/Rub	30.0 (0.0)	141.7 (352.8)	28.8 (30.1)			7.9
Penile Thrust	--	0.0 (0.0)	0.0 (0.0)	--	--	
Avert Face	12.2 (13.1)	46.1 (43.4)	15.3 (19.1)		8.8	
N = 33	$\bar{x}$ =19.4 [2] (46.2)	$\bar{x}$ =99.8 [2] (323.9)	$\bar{x}$ =99.7 [2] (175.9)	59.2	43.7	

[1] Sufficiently different at $p \leq .05$ and $\hat{\omega}^2 \geq .60$. Empty cells signify non-significant differences.

[2] These values incorporate unlisted MultiAct or Unknown behavioural types

Table 6: Mean coefficients of variation (CV; expressed as percentages) of distances for each behaviour type at each study site.

Behaviour Type	Miquelon CV %	North Rona CV %	Sable Island CV %
Open Mouth Display	--	192.2	102.9
Head Thrust	194.5	186.5	130.2
Extend Fore Flipper	129.4	153.5	193.4
Foreflipper Wave	291.7	207.5	111.9
Forefl. Scratch Successor	222.7	292.3	145.5
Forefl. Scratch Substrate	--	61.7	79.8
Foreflipper Slap Water	--	70.7	--
Foreflipper Slap Body	--	99.8	--
Head Swing	165.6	122.2	93.9
Extend Head	129.0	189.5	186.3
Nose-to-Nose	253.3	278.8	135.0
Poke with Nose	170.6	284.2	126.7
Sniff	--	235.1	135.9
Glance	128.0	162.1	166.9
Stare	166.8	189.1	125.9
Look Away	140.0	264.6	198.9
Bite	411.1	325.0	230.3
Climb	204.2	292.0	429.4
Clasp	170.6	533.3	533.3
App. / Turn Toward	184.0	225.9	108.2
Chase	126.0	140.4	100.0
Roll Away	105.9	150.5	101.5
Depart/Turn Away	234.2	342.5	190.8
Rush Away	152.9	132.2	116.8
Yawn	92.6	129.6	--
Neck and Head Shake		31.5	--
Raise Head Vertical	122.8	112.3	132.6
Eyes Closed	153.3	297.2	144.4
Roll on Side	112.0	291.9	370.7
Nurse	--	125.2	110.1
Body Scratch/Rub		249.0	104.5
Avert Face	107.4	311.1	124.8
Overall [1]	$\bar{x} = 160.3$ SD=83.7	$\bar{x} = 208.7$ SD=102.7	$\bar{x} = 169.0$ SD=106.0

[1] The site values were not significantly different ($F = 2.1$, df = 2, 83, $p = 0.24$).

Table 7: Mean, weighted frequencies (number of behavioural acts per sampled seal per sampled minute) of each behaviour type at each study site.

		Mean Frequency (SD)			**ANOVA**		
					Scheffé Value[1]		
Behaviour Type	N	Miquelon	North Rona	Sable Island	M vs R	M vs S	R vs S
Open Mouth Display	566	--	0.038 (0.052)	0.077 (0.142)	--	--	22.2
Head Thrust	454	0.052 (0.087)	0.064 (0.081)	0.067 (0.102)			
Extend Fore Flipper	157	0.145 (0.205)	0.057 (0.068)	0.042 (0.090)	7.5	5.1	
Fore Flipper Wave	164	0.091 (0.108)	0.073 (0.100)	0.073 (0.100)			
F. Fl. Scratch Succ.	141	0.071 (0.098)	0.037 (0.061)	0.026 (0.024)		6.4	
F. F. Scratch Sub.	13	--	0.019 (0.007)	0.012 (0.016)	--	--	
F. Fl. Slap Water	28	--	0.086 (0.040)	--	--	--	--
F. Flipper Slap Body	20	--	0.048 (0.040)	--	--	--	--
Head Swing	328	0.009 (0.039)	0.074 (0.072)	0.087 (0.117)	38.0	20.3	
Extend Head	348	0.153 (0.330)	0.057 (0.113)	0.075 (0.108)	8.1	4.8	
Nose-to-Nose	124	0.075 (0.076)	0.078 (0.129)	0.023 (0.030)			
Poke with Nose	109	0.028 (0.025)	0.049 (0.186)	0.019 (0.017)			
Sniff	18	0.222 (--)	0.048 (0.095)	0.040 (0.014)			
Glance	357	0.163 (0.331)	0.063 (0.134)	0.056 (0.074)	9.5	6.4	
Stare	1163	0.138 (0.272)	0.068 (0.171)	0.082 (0.202)			
Look Away	828	0.065 (0.109)	0.049 (0.139)	0.065 (0.196)			
Bite	321	0.033 (0.045)	0.042 (0.073)	0.047 (0.074)			
Climb	224	0.021 (0.029)	0.023 (0.043)	0.020 (0.061)			
Clasp	118	0.008 (0.005)	0.011 (0.009)	0.009 (0.009)			
Appr. / Turn Toward	670	0.136 (0.178)	0.097 (0.242)	0.084 (0.109)			
Chase	48	0.100 (0.184)	0.119 (0.144)	0.352 (0.262)		12.1	9.7
Roll Away	63	0.142 (0.306)	0.040 (0.049)	0.204 (0.584)			
Depart / Turn Away	703	0.106 (0.266)	0.145 (0.213)	0.170 (0.217)			
Rush Away	76	0.254 (0.352)	0.134 (0.156)	0.325 (0.516)			
Yawn	16	0.101 (0.149)	0.056 (0.085)	--		--	--
Neck / Head Shake	5	0.034 (--)	0.041 (0.008)	--		--	--
Raise Head Vertical	209	0.077 (0.149)	0.074 (0.079)	0.087 (0.126)			
Eyes Closed	251	0.199 (0.202)	0.050 (0.152)	0.108 (0.321)	6.6		
Roll on Side	107	0.059 (0.095)	0.069 (0.223)	0.040 (0.040)			
Nurse	25	--	0.022 (0.009)	0.008 (0.003)	--	--	9.8
Body Scratch/Rub	16	0.005 (--)	0.081 (0.079)	0.022 (0.020)			
Penile Thrust	65	--	0.013 (0.011)	0.005 (0.004)	--	--	9.7
Avert Face	418	0.063 (0.140)	0.054 (0.072)	0.057 (0.074)			
N = 33	8153	$\bar{x} = 0.082$[2] (0.183)	$\bar{x} = 0.060$[2] (0.141)	$\bar{x} = 0.079$[2] (0.199)	11.4		10.1

[1] Sufficiently different at $p \leq .05$ and $\hat{\omega}^2 \geq .60$. Empty cells signify non-significant differences.

[2] these values incorporate unlisted MultiAct or Unknown behavioural acts

Table 8: Reported minimum repertoire sizes of a number of species.

Species	Minimum Repertoire Size	Source
Non-pinnipeds:		
Southern Right Whales	"few" Behaviour Types	Cummings, 1972
Spider Crab	15 Behaviour Types	Hazlett, 1974
Fish	15 to 26 Behaviour Types	Moynihan, 1970
Squirrel Monkey	17 Behaviour Types	Maurus, 1973
Bighorn Sheep	18 Behaviour Types	Geist, 1971
Rabbit	18 Behaviour Types	Peters, 1980
Deer	20 Behaviour Types	Peters, 1980
Pika	20 Behaviour Types	Peters, 1980
Wolf	25 Behaviour Types	Peters, 1980
Ruff (male)	22 Behaviour Types	Rhijn, 1973
Black-Capped Chickadee	30 Vocalizations	Ficken *et al.*, , 1987
Rhesus Monkey	37 Behaviour Types	Moynihan, 1970
Cat	56 Behaviour Types	Fagen, 1978
Rhesus Monkey	120 Behaviour Types	Altmann, 1965a
Human	150+ Behaviour Types	Peters, 1980
Golden Jackel	2,000 Behaviour Types ("system events")	Golani, 1973; 1976; Golani and Mendelssohn, 1970
Pinnipeds:		
Walrus	8+ Behaviour Types	Miller, 1975; Stirling, 1987
Harbour Seal	8+ Behaviour Types	Sullivan, 1982
Grey Seal (European)	9+ Behaviour Types	Anderson and Harwood, 1985
Grey Seal (European)	17 Behaviour Types	Twiss (1991)
Steller Sea Lion	34 Behaviour Types	Harestad and Fisher, 1971; Harestad, 1973
Weddell Seal	34 Vocalizations	Thomas and Kuechle, 1982
Grey Seal (European/Canadian)	33 Behaviour Types	This Study

Table 9: A comparison of the mean distance (cm) between interactant age classes subdivided by study site.

<table>
<tr><th>Interactant Class</th><th>Miquelon
Mean (SD, N)</th><th>North Rona
Mean (SD, N)</th><th>Sable Island
Mean (SD, N)</th></tr>
<tr><td>Adult-Adult</td><td>33.1 (64.2, 677)</td><td>227.0 (598.5, 1183)</td><td>168.6 (219.5, 1018)</td></tr>
<tr><td colspan="4">North Rona was greater than Miquelon (F = 25.6, df = 1, 1858, $p \leq .05$; $\hat{\omega}^2 = .65$)
Sable Island was greater than Miquelon (F = 22.6, df = 1, 1693, $p \leq .05$; $\hat{\omega}^2 = .71$)
North Rona was not sufficiently different than Sable Island (F = 49.0, df = 1, 2199, $p \leq .05$; but $\hat{\omega}^2 = .2$)</td></tr>
<tr><td>Adult-Subadult</td><td>22.4 (26.3, 115)</td><td>–</td><td>95.6 (180.0, 9)</td></tr>
<tr><td colspan="4">Sable Island was greater than Miquelon (F = 16.1, df = 1, 122, $p \leq .05$; $\hat{\omega}^2 = .6$)</td></tr>
<tr><td>Mother-Mother</td><td>–</td><td>43.9 (89.1, 179)</td><td>42.6 (78.7, 70)</td></tr>
<tr><td colspan="4">North Rona was not significantly different than Sable Island (F = 0.019, df = 1, 247, $p = 0.56$)</td></tr>
<tr><td>Mother-Pup</td><td>–</td><td>13.3 (29.1, 704)</td><td>10.6 (21.9, 83)</td></tr>
<tr><td colspan="4">North Rona was not significantly different than Sable Island (F = 0.3, df = 1, 785, $p = 0.36$)</td></tr>
<tr><td>Mother-Adult</td><td>–</td><td>72.6 (120.8, 2798)</td><td>32.9 (54.1, 879)</td></tr>
<tr><td colspan="4">North Rona was not sufficiently different than Sable Island (F = 56.7, df = 1, 3675, $p \leq .05$; but $\hat{\omega}^2 = .13$)</td></tr>
</table>

Table 10: Mean distance (cm) between interactants subdivided by body orientation categories (data aggregated from all sites).

Body Orientation	Mean Distance	N
1 - Facing towards, from directly ahead	141.3	1621
2 - Facing away, from anterior	166.5	496
3 - Parallel, same direction	28.6	1712
4 - Parallel, opposing direction	43.1	872
5 - Facing towards, from obliquely ahead	70.3	1112
6 - Facing towards, from obliquely behind	55.4	641
7 - Facing away, from obliquely posterior	152.7	142
8 - Facing towards, perpendicular	73.5	1402
9 - Facing away, perpendicular	60.8	486
10 - Facing towards, from directly behind	415.9	149

Significantly Different Mean Distance Values According to Body Orientation:

1 is significantly greater than **3, 4, 5, 6, 8** and **9.**
2 is significantly greater than **3, 4, 5, 6, 8** and **9.**
5 is significantly greater than **3** and **4.**
7 is significantly greater than **3, 4** and **6.**
8 is significantly greater than **3** and **4.**
10 is significantly greater than **1, 2, 3, 4, 5, 6, 7, 8** and **9.**
(F = 77.6, df = 9, 8623, $p \leq .05$; $\hat{\omega}^2 = .73$)

Table 11: Mean distance (cm) between interactants subdivided by head orientation categories (data aggregated from all sites).

Head Orientation	Mean Distance	N
1 - Facing towards, from directly ahead	127.8	1927
2 - Facing away, from anterior	96.0	809
3 - Parallel, same direction	38.8	1309
4 - Parallel, opposing direction	46.3	1021
5 - Facing towards, from obliquely ahead	104.6	623
6 - Facing towards, from obliquely behind	55.3	706
7 - Facing away, from obliquely posterior	82.9	293
8 - Facing towards, perpendicular	70.3	939
9 - Facing away, perpendicular	57.9	828
10 - Facing towards, from directly behind	356.0	173

Significantly Different Mean Distance Values According to Head Orientation:

1 is significantly greater than **3, 4, 6, 7, 8** and **9.**
2 is significantly greater than **3** and **4.**
5 is significantly greater than **3** and **4.**
10 is significantly greater than **1, 2, 3, 4, 5, 6, 7, 8** and **9.**
(F = 57.6, df = 9, 8616. $p \leq .05$; $\hat{\omega}^2 = .6$)

Table 12: Mean total durations (sec) for each sequence type at each site.

Sequence Type	Miquelon		North Rona		Sable Island	
	Mean	SD/N	Mean	SD/N	Mean	SD/N
Aggressive	**48.4**	86.8/47	**134.9**	165.9/78	**81.9**	138.7/130
Copulatory	--	--	**842.9**	667.6/9	**1169.3**	1075.3/19
Play	**301.5**	363./17	**281.0**	319.6/2	**65.0**	--/1
M/P Interaction	--	--	**462.8**	399.3/11	**427.4**	299.6/10

Table 13: Proportions of interactions subdivided by age class at each study site.

Age Class	Miquelon		North Rona		Sable Island	
	Percent	N	Percent	N	Percent	N
Adult - Adult	62.5	40	32.0	32	48.12	77
Adult - Mother	-		43.0	43	36.9	59
Adult - Subadult	15.6	10	-		0.6	1
Adult - Pup	-		1.0	1	-	
Adult - Weaned Pup	3.1	2	-		-	
Subadult - Subadult	15.6	10	-		-	
Subadult - Weaned Pup	3.1	2	-		-	
Mother - Mother	-		8.0	8	7.6	12
Mother - Pup	-		15.0	15	6.9	11
Weaned Pup - Weaned Pup	-		1.0	1	-	
Total		64		100		160

Table 14: Sequence sex categories subdivided by study site.

	Miquelon		North Rona		Sable Island	
Sequence Sexes	**N**	**Percentage**	**N**	**Percentage**	**N**	**Percentage**
Male-Male	41	64.1	16	16.0	75	46.9
Female-Female	6	9.4	23	23.0	12	7.5
Male-Female	17	26.6	48	48.0	64	40.0
Unknown	-	-	13	13.0	9	5.6

Table 15: Spearman Correlation values between the number of seals within the Focal Area (independent variable) and selected dependent variables.

Dependent Variable	Spearman Correlation Values (rho/df)		
	Miquelon	North Rona	Sable Island
Act Duration	-0.01/1657	0.02/4926	-0.01/2059
Total Duration	0.08/1657	-0.09*/4926	-0.15*/2059
Response Latency	-0.02/1657	0.02/4926	0.02/2059
Interseal Distance	-0.10/1657	0.28/4926	0.27/2059
Group Vigilance	0.21*/1657	0.07*/4926	0.42*/2059

* indicates correlation values significant at $p \leq .05$.

Table 16: Discriminant analyses of behaviour types at Miquelon.

Behaviour Type	Number of Cases Tested	Behaviour Type	Number of Cases Tested
Head Thrust	79	Bite	57
Extend Fore Flipper	26	Climb	40
Fore Flipper Wave	26	Appr. / Turn Towards	56
Fore Fl. Scratch Successor	18	Roll Away	2
Fore Flipper Slap Body	38	Depart / Turn Away	67
Extend Head	35	Rush Away	3
Nose-to-nose	9	Yawn	6
Poke With Nose	2	Neck and Head Shake	54
Glance	35	Close Eyes	33
Stare	109	Roll on Side	9
Look Away	81	Avert Face	63
		Total	**848**

Canonical Discriminant Functions

Function	Eigenvalue	% of Variance	Cumulative % Variance	Canonical Correlation	Wilks' Lambda	χ^2	Degrees of Freedom
1	4.6086	58.9	58.9	0.9065	0.0873	2010.5	440 $p \leq .05$
2	1.5875	20.3	79.1	0.7833	0.2259	1226.7	399 $p \leq .05$

Variable	Standardised, Canonical Discriminant Function Coefficients Function 1	Function 2
Vigilance	-0.07608	-0.11855
Focal Area	0.04400	0.01660
Social Female	-0.00417	-0.02691
Interaction Distance	0.11714	0.14947
Precedent Type	-0.06277	-0.19936
Interactant Sex	0.06181	0.17592
Interaction Duration	0.13938	0.06366
Precedent Vocals	-0.00720	-0.21030
Vibrissae Position	0.10706	0.17698
Eye Position	**0.94740**	-0.32545
Mouth Position	0.15599	**0.83125**
Tail Position	0.00780	-0.00937
Precedent Height	0.05349	0.00533
Body Orientation	-0.04905	-0.00294
Head Orientation	-0.02634	-0.02806
Respondent Type	-0.01176	-0.03921
Respondent Sex	0.03600	-0.01842
Respondent Height	-0.07762	-0.12268
Response Latency	0.09110	-0.04807
Total Duration	-0.00427	0.13872
Weighted Frequency	0.05573	0.09125

Table 17: Discriminant analyses of behaviour types at North Rona.

Behaviour Type	Number of Cases Tested	Behaviour Type	Number of Cases Tested
Open Mouth Display	235	Climb	33
Head Thrust	150	Clasp	41
Extend Fore Flipper	50	Approach / Turn Towards	186
Fore Flipper Wave	47	Chase	3
Fore Fl. Scratch Successor	36	Roll Away	10
Fore Fl. Scratch Substratum	3	Depart / Turn Away	183
Fore Flipper Slap Water	9	Rush Away	8
Fore Flipper Slap Body	10	Neck and Head Shake	2
Head Swing	66	Raise Head Vertical	41
Extend Head	131	Eyes Closed	123
Nose-to-nose	86	Roll on Side	39
Poke With Nose	60	Nurse	12
Glance	148	Body Scratch or Rub	7
Stare	389	Penile Thrust	26
Look Away	296	Avert Face	130
Bite	59	**Total**	2624

Function	Eigenvalue	Canonical Discriminant Functions % of Variance	Cumulative % Variance	Canonical Correlation	Wilks' Lambda	χ^2	Degrees of Freedom
1	1.9634	45.3	45.3	0.8140	0.1461	4997.8	522 $p \leq .05$
2	1.0117	23.3	68.6	0.7092	0.2938	3181.8	476 $p \leq .05$

	Standardised Canonical Discriminant Function Coefficients	
Variable	**Function 1**	**Function 2**
Vigilance	0.01637	-0.06024
Focal Area	0.03299	-0.03615
Social Female	-0.04273	0.04920
Interaction Distance	0.09808	-0.02848
Precedent Type	-0.20041	0.16524
Interaction Duration	-0.01231	0.06802
Precedent Vocals	0.40348	-0.44162
Vibrissae Position	-0.02746	0.43396
Eye Position	**0.87023**	0.27028
Mouth Position	-0.44802	**0.67507**
Tail Position	0.04184	-0.09776
Body Orientation	0.02295	-0.03703
Head Orientation	0.00150	0.00741
Respondent Type	0.07139	-0.02845
Response Latency	0.09171	0.11710
Total Duration	0.01035	0.05896
Weighted Frequency	-0.03518	-0.06697

Table 18: Discriminant analyses of behaviour types at Sable Island.

Behaviour Type	Number of Cases Tested	Behaviour Type	Number of Cases Tested
Open Mouth Display	98	Climb	26
Head Thrust	32	Clasp	14
Extend Fore Flipper	14	Approach / Turn Towards	111
Fore Flipper Wave	23	Chase	8
Fore Fl. Scratch Successor	27	Roll Away	28
Fore Fl. Scratch Substratum	7	Depart / Turn Away	101
Head Swing	22	Rush Away	9
Extend Head	69	Raise Head Vertical	31
Nose-to-nose	3	Eyes Closed	58
Glance	28	Roll on Side	14
Stare	211	Body Scratch or Rub	3
Look Away	112	Penile Thrust	6
Bite	28	Avert Face	53
		Total	1138

		Canonical Discriminant Functions					
Function	Eigenvalue	% of Variance	Cumulative % Variance	Canonical Correlation	Wilks' Lambda	χ^2	Degrees of Freedom
1	2.0885	42.5	42.5	0.8223	0.0297	2659.0	500 $p \leq .05$
2	1.0443	22.1	64.7	0.7149	0.2701	2078.1	456 $p \leq .05$

	Standardised Canonical Discriminant Function Coefficients	
Variable	Function 1	Function 2
Vigilance	-0.01323	0.22076
Focal Area	-0.04796	0.07796
Social Female	-0.03998	0.01257
Interaction Distance	-0.15265	0.22474
Precedent Type	-0.03375	0.19240
Interaction Duration	-0.08718	-0.01962
Precedent Vocals	0.00100	-0.00439
Vibrissae Position	0.26851	0.10736
Eye Position	**0.86901**	-0.50694
Mouth Position	0.19469	**0.65591**
Tail Position	-0.01759	-0.04292
Body Orientation	-0.03400	0.04060
Head Orientation	-0.05568	0.01971
Respondent Sex	-0.00512	-0.06578
Respondent Reaction	0.00765	-0.03072
Respondent Height	-0.06912	0.05651
Response Latency	-0.04657	0.00695
Total Duration	0.06838	-0.04226
Weighted Frequency	-0.02454	-0.01017

Table 19: The transition frequencies between behaviour types of interacting seals at Miquelon.

Succeeding Act

Preceding Act	HTH	EFF	FFW	FSR	HSW	HEX	NTN	PON	SNI	CLA	STA	LAW	BIT	CLI	CLA	APT	CHA	ROA	DPA	RAW	YAW	NHS	RHV	ECL	ROS	BSR	AVF	Sums
HTH	35+	3	5+	3	6-	6	-			1-	4-	2-	6	7		1-			9				19+	-	2		18+	127
EFF	5	2+	2+	1	2-	1		1+		1	5	3	4+	3		1			3				2				1	37
FFW	-	1	2+		1-	1				1	7+	5+	2	2		1			7+				1				4+	35
FSR	5+				-					1	3	-	1+	3	1				7+				3+				3	27
HSW	2-	3	2-	-	138+	-	-	1		2-	3-	4-	3-	10	1+	-		1	2-		-		9	-	2		8-	191
HEX	8+	-	1	1	-	6+					8	4	-	1-		-			2-	1+			7+	-			10+	49
NTN	-				-		7+				1	1	1			1	X	1+	-								1	13
PON				1+						1+									1+									3
SNI																1+												1
CLA	6	2	3+	1	4-	1				5+	5	2-	4	4		5+	1+	1+	4		2+		-	3+			-	53
STA	19	5	6	1-	3-	15+	3+		1+	9+	37+	9	7-	11		8+			17	1			-	7+	2	1+	4-	166
LAW	9	5+	-	4+	4-	2				9+	13	24+	5	9		5			11		1+		3-	4	-		5	113
BIT	4-	1	-	3+	5-	-				1-	5-	6	19+	7		1-			9				8+	-	1		14+	84
CLI	8	3	4+	7+	10	-				-	6-	5	10+	4		-	X	1+	24+	1+			2-	-	3+		6	94
CLA	1+	1+																										2
APT	4-	5+	6+	2	4-	2				8+	19+	1-	4	2-		2			3-				10+	1	2		4	79
CHA		1+								1+		1+					1+			1								5
ROA	1			X			X	X	X		2+	2+											1					6
DPA	4-	-	-	1	6-	4	-	1+		2	32+	12	5-	17+		11+	1		12		3+		-	7+	-		1-	119
RAW				X			X	X	X	1+	2+					+	2+											5
YAW	1				-					1+	2+	1							1		1+			1+				8
NHS											1+																	1
RHV	9	4+	3	1	5-	7+				2	6-	9+	2-	3-		3			6				9+	4+			9+	82
ECL	-				+						4	3	2			5+			1-				1	5+	+		-	21
ROS	1				2		1+			1	2	-	3+	2		2			2					1			-	17
BSR										1+																		1
AVF	8	1	2	3	2-	-	1			4	9	16+	10+	12+	1+	1-		2+	9			1+	5	1	2		8	98
Sums	130	37	36	29	192	45	12	3	1	52	176	110	88	97	3	48	5	6	130	4	7	1	80	34	14	1	96	1437

Structural zero transition values are indicated by an " X". Significant transitions are indicated by " +" (facilitatory) or "-" (inhibitory).

Table 20: The transition frequencies between behavioural acts of interacting seals at North Rona.

Succeeding Act

Preceding Act	OMD	HTH	EFF	FFW	PSR	PSS	PSW	PSB	HSW	HEX	NTN	PON	SNI	GLA	STA	LAW	BIT	CLI	CLA	APT	CHA	ROA	DPA	RAW	YAW	NHS	RHV	ECL	ROS	NUR	BSR	FT	AVF	Sums
OMD	22-	28+	8	15+	1-		-	-	4-	23+	-	1-	-	14	98+	47+	1-	-	-	24	1	1	23-	3			-	15	4	X	1	X	16	350
HTH	11-	9-	6	15+	1-		1	-	3-	28+	1-	-		16	12-	6-	1-	3	4	10-	-	3+	27+	1+			22+	-	4	X		5+	52+	261
EFF	14+	5	-	-	4+		4+		1	5	1	6+	1+	8+	10	6-	2	-	5+	1-			8				2	-	2			1	4	90
FFW	15+	6	1	6+			2+		4+	4	-	-		4	10-	5-	-	3+	1	3-	1		17+	1			-	-	1			-	11+	95
PSR	1-	1-	3+	-	1				2	-	-	6+	1+	3	2-	3-	6+	3+	5+	1-		1+	6				2+	-				1	8+	56
PSS															3+					1													1+	5
PSW	-	2	3+				11+			1				2	3	-				-			2						1	X			2	27
PSB	2	1												2+	8+	2				-			2										2+	19
HSW	5-	8	3	3	-	1+		1	19+	16+	1	2		7	10-	2-	-	-	-	2-			8				6+	1-	1			-	5	101
HEX	18	23+	4	3	-	1+	-	1	13+	10	7+	3		12	16-	18	2-	2	9+	5-			6-	-			8+	6	6+	-		4+	14+	191
NTN	1-	1-	1	1	4+				3	-	50+	-		1-	6-	13+	1-	5+	1	1-	X		6				-	1-	3+		2+	-	1-	102
PON	-	-	7+	-	4+				1	2	8+	4+		4	6-	17+	1	1	-	8		1	14+		1+		-	3	6+				-	88
SNI	-		1+	1+										2+	1	4+				-			3+											12
GLA	18	19+	8+	3	5+		1	7+	10+	9	3	8+	2+	25+	24-	14-	4	1-	2	15	1	1	21	-			2	5	1-	-	1	4+	6-	220
STA	91+	34	10	11	2-		4	5+	16	18-	6-	6-	3	28	105+	69+	4-	4-	7	68+	-	-	35-	3-	3+		4-	30+	3-	-	1	2-	15-	587
LAW	56+	3-	6-	3-	4		-	1	4-	9-	6-	21	3+	16-	79-	73+	9-	13+	11+	27	1	3	28-	1-	3+	1+	-	22+	4	10+	2	16+	4-	439
BIT	3-	1-	2	2	5+				2	1-	1-	1-		2-	-	5-	19+	5+	5+	4-	1		20+	7+			10+	1-	1	X		6+	17+	121
CLI	-	5	3+	1	4+				-	3	1	1		8+	6	6	4+			-	X	1+	10+				-	1	4+	X			-	58
CLA	-	7+	2	-	8+				-	7+	-	-		3	4-	15+	8+		-	-		4+	7				-	1	4+	X			1-	71
APT	22-	16	6	6	2-	1	3	2	3-	12	6	5	-	24+	83+	20-	7-	2-	1-	49+	-	-	40+	8+			6	16+	6	-	1	-	17	364
CHA	1	-												-	3	2				-			1	13+						X		X	-	20
ROA	1	-			X				1	2+	X	X	X	4+	4	1	1		1+	1		1+	2					1		X		X	-	20
DPA	30	22	6	10	6		-	2	6	8-	4-	8	3+	19	59+	25-	17+	11+	7	58+	3	-	14-	-		1+	2-	10	1-	1	1	1-	10-	345
RAW	5	1		1	X					-	X	X	X	1	3-	1-	7+			4+	10+		-					-		X		X	1	34
YAW												2+			2+	2+												1+						7
NHS																							1+			1+		1+						3
RHV	-	11+	3+	3+	1	2+			6+	4	-	-		-	5-	4-	11+	3+	2	3-			7				6+	-	1				5	77
ECL	20+	4-	1-	-	1				1-	7	1-	9+		2-	18	21+	2-	-	1	7	1		11	-			-	12+	3	5+		2	3-	132
ROS	3	2	2	-					-	3	-	3+		5+	9	3-	-	2+	2+	9+	+		4				+	1		4+		2+	3	57
NUR	X	X					X			-	X			-	-	14+		X	X	-	X		1					5+		X		X	-	20
BSR	1	1										1+		1	3+								2+											9
FT	X	7+	2	1	1				-	3	1	-		3	3-	14+	7+	X	X	-	X		1-					2	1	X		X	-	46
AVF	21	29+	2-	11+	4		1	1	2-	14+	2-	1-	1	9	18-	14-	10+	-	2	9-	-	4+	20	3			4	8	5	-	2+	1	24+	222
Sums	361	246	90	96	58	5	27	20	101	189	99	88	14	225	613	426	124	58	66	310	19	20	347	40	7	3	74	143	62	20	11	45	222	4229

Structural zero transition values are indicated by an " X". Significant transitions are indicated by " +" (facilitatory) or "-" (inhibitory).

Table 21: The transition frequencies between behavioural acts of interacting seals at Sable Island.

	Succeeding Act																												
Preceding Act	OMD	HTH	EFF	FFW	FSR	FSS	HSW	HEX	NTN	PON	SNI	GLA	STA	LAW	BIT	CLI	CLA	APT	CHA	ROA	DPA	RAW	RHV	ECL	ROS	NUR	BSR	PT	AVF	Sums
OMD	28+	1-	3+	-	1-		3	8		-		4	44+	16	1-	-	-	15	-	5+	11-	2	-	5	-	X	2+	X	-	149
HTH	-	-	1	4+	1		1	1				1	2-	3	2	1	1	-	1		2-		10+	-	1	X			13+	45
EFF	-	1	1-					1					3	1		6+	1+	2		1+	1				1+					19
FFW	-	1		1				3+				2+	2-	4	1	2+	2+	1-		1	3		1		2+				1	27
FSR	2			1	1			-		2+		1	7	5	2	3+	4+	-	1	1	6+			1					2	39
FSS													2					1						4+					1+	8
HSW	3							3+				3+	2-	1-				1-			2		5+						8+	28
HEX	8	3	2+	2	1		4+	5	1+			3	13	7	4	-	2	4-	1	-	9	-	5+	3	1			1	8+	87
NTN					1+				2+				1	1					X											5
PON	-				4-								1-	2				1			2			1	3+		1+			15
SNI													1+					1+												2
GLA	4	4+		1	2+		2	2				2	7	5	2	3+	1	6		1	3-	1	1	4+				3+	1	55
STA	47+	8	2	4	4-	4+	6	13		-	1+	6-	59	36	6-	8	1-	39+	3	5	27	4	1-	12	3		1	1-	8-	312
LAW	16	2-	-	1-	3	2+	-	10	1	2		5	27-	21	2-	13+	15+	16	3	10+	20	1-	-	11+	1-	2+		8+	5-	197
BIT	1-	3+		1	3+		2	-				2	2-	1-	12+	7+	3+	2-	1	-	7	2	8+	-	1	X		2+	8+	68
CLI	1-	2	6+	4+	3+			2				3+	4-	13+	3+	1-	-	-	X	+	5	1	1	3	1	X			1	54
CLA	-	1	3+	2+	3+			-				1	-	14+	6+	-		-			6+			1	2+	X			+	39
APT	8-	5	2	2	1-		3	11		2		11+	48+	13-	4	1-	1-	19	2	-	35+	2	3	3-	5+			-	8	187
CHA	1							-					1-	1-							4+	13+	2+			X		X	-	22
ROA	2				X			-	X	X	X	1	9+	9+	-	-		-		2+	3	1		2	1	X		X	-	30
DPA	18	2-	-	1-	6		3	4-		3-		1-	45+	11-	7	5	5	27+	2	5	15	1-	-	4	1-			1	1-	168
RAW	4+	1			X			-	X	X	X	1	5	2		1		-	7+	2+	2					X		X	-	25
RHV	3	3+					2+	4+				-	6	3	4+	1		1-			3		1	-					8+	39
ECL	2-	-		-	3+	1+	-	5+		2+	1+	3	5-	8	2	1	-	4+	1	-	8	-	-	5+	1	1+			-	53
ROS	1	2+						1		3+		2+	3	5+		1		1			2			1		1+		1+	-	24
NUR	X	X							X					1		X	X		X		1			2+		X		X		4
BSR										1+			1	2+																4
PT	X							2+					2	9+	2+	X	X	-	X		2					X		X		17
AVF	1-	4+		4+	3+	1+	3+	7+				4+	13	11	4	-	-	3-	-	-	10	2	-	-	2			1	4	77
Sums	148	43	20	28	40	8	29	82	4	15	2	56	315	208	64	54	36	144	22	33	189	30	38	62	26	4	4	18	77	1799

Structural zero transition values are indicated by an " X". Significant transitions are indicated by " +" (facilitatory) or "-" (inhibitory).

Table 22: Summary tables indicating those behaviour types which were usually either inhibitory or facilitatory to succeeding behaviour types in **(A)** inter- or **(B)** intra-individual sequences at all sites unless otherwise indicated.

(A) Inter-individual Sequences:

Inhibitory	Facilitatory
open mouth display	foreflipper wave
raise head vertical	extend foreflipper (between males and females)
look away	foreflipper scratch successor
clasp (at North Rona)	extend head
depart or turn away	chase (at Miquelon)
stare	roll on side
chase (at North Rona)	roll away (at Miquelon)
roll away (between males at Sable Island)	poke with nose (at Miquelon)
approach or turn towards	neck and head shake
close eyes	yawn
penile thrust	body scratch or rub
head thrust	climb
extend foreflipper (at Miquelon)	rush away
bite	glance
head swing	sniff
avert face	clasp (at Sable Island)
nose-to-nose	
nurse	

(B) Intra-individual Sequences:

Inhibitory	Facilitatory
open mouth display	foreflipper wave
raise head vertical	extend foreflipper
look away	foreflipper slap water
clasp	foreflipper slap body
depart or turn away	foreflipper scratch successor
stare	extend head
approach/turn towards (at Sable Island)	chase (at North Rona or Sable Island)
close eyes	roll on side
penile thrust	roll away (at Sable Island/by females)
	poke with nose
	neck and head shake
	yawn
	body scratch or rub
	climb
	rush away (at Sable Island)
	bite (by males)
	nose-to-nose (by males)

Table 23: The transition frequencies between behavioural acts of interacting male seals at Miquelon.

Preceding Act	HTH	EFF	FFW	FSR	HSW	HEX	NTN	PON	GLA	STA	LAW	BIT	CLI	CLA	APT	CHA	ROA	DPA	RAW	YAW	RHV	ECL	ROS	BSR	AVF	Sums
	Succeeding Act																									
HTH	10 +	2	4 +	3 +	2	2			-	2 -	2 -	4	1		1 -			2 -			13 +	-	1		10 +	59
EFF	3 +	2 +	1	1	1				1	3	1	3 +	1		1			2			2				-	22
FFW	-		1		1	1			1	3	5 +	1	1		-			3 +			1	-			3	21
FSR	5 +									2	-	-	1		1			6 +			2				3	20
HSW	1 -	2 +	2 +	-	7 +			1 +	2	1 -	-	2	-	1 +	-			-			6 +	-	2 +		3	30
HEX	3 +								-	2	2	-						2			2				8 +	19
NTN							5 +			-	1				1 +	X	1 +								1	9
PON									1 +									1 +								2
GLA	1 -	1	2 +	1	3 +	1			3 +	4	1 -	4 +	1		5 +	1 +	1 +	4		2 +	-	1			-	36
STA	13 +	2	2	1 -	3	7 +	2 +		5	21 +	5 -	4	3		10			7	1 +		2 -	7 +	2	1 +	3 -	101
LAW	5	3	-	3	1 -	2			6 +	10	15 +	2 -	-		8			5	1	1	2 -	2			4	70
BIT	2	1	-	1	1	-			1	2 -	3	6 +	4 +		2			2			6 +	-	1		13 +	45
CLI	3	2 +	1	4 +	2 +				-	1 -	2	2			-	X		2			1	-			3	23
APT	2 -	3 +	5 +	2	1 -				5 +	10 +	-	2	1		1			3			11 +	1	2 +		2 -	51
CHA																			1 +							1
ROA	1 +			X			X	X		1	1 +										1 +					4
DPA	1 -	-	-	1	1	3 +		1 +	1 -	20 +	7 +	1 -	4		7			4		2 +	-	6 +			-	59
RAW				X			X	X	1 +	1 +					1											3
YAW	1								1 +	1								1		1 +		1 +				6
RHV	-	4 +	2	1	4 +	2			1 -	5 -	6	1 -	3		3			4			9 +	4 +			9 +	58
ECL	-					1			1	4	2	2	1		11 +			1			-	5 +	1		-	29
ROS					1		1 +		1	1	-	2 +			2 +			1				1 +			-	10
BSR									1 +																	1
AVF	6	-	1	3	2	-			4	8	10 +	8 +	5 +		1 -		2 +	6			5	1 -	1		8	71
Sums	57	22	21	21	30	19	8	2	36	102	63	44	26	1	55	1	4	56	3	6	63	29	10	1	70	750

Structural zero transition values are indicated by an " X". Significant transitions are indicated by " +" (facilitatory) or "-" (inhibitory).

Table 24: The transition frequencies between behavioural acts of interacting male seals at North Rona.

	Succeeding Act																						
Preceding Act	OMD	HTH	EFF	FFW	FSR	HSW	HEX	NTN	GLA	STA	LAW	BIT	CLI	CLA	APT	CHA	DPA	RAW	RHV	ECL	ROS	BSR	AVF	Sums
OMD	19 +	1 -		-		-	1 -	-	1 -	8 +	1	-			7 +	1 -	7	3 -	-	13 +	2 +	1 +	3 -	68
HTH	-	-		1 +			1		5 +	-		1 -			3 +	-	7 +	-	1	-			4 +	23
EFF							1 +																	1
FFW	-					1 +											-						3 +	4
FSR												1 +							1 +					2
HSW	-	1 +	1 +	1 +			1 +					-					1		1 +				-	6
HEX	-	3 +				2 +		2 +	3 +	-		1			-		1	-		-			1	13
NTN	-							2 +	1 +							X	-						1 -	4
GLA	1 -	5 +					1			-	1 +	-			1		6 +	-	1 +				1	17
STA	9 +	-							-	2 +		-			5	-	1 -	3 +	-	2 +			-	22
LAW	1 -										1 +	1				1 +	1						1 +	6
BIT	-	1 -		1 +		-	-		1	-		13 +	2 +		2	-	9 +	4	5 +	-			9 +	47
CLI					1 +											X	1 +							2
CLA												1 +												1
APT	5	2				1 +	-		-	3 +	2 +	1 -			1 -	-	7 +	6 +	-	2			1 -	31
CHA	1 -	-								2 +		-			-		1	9 +		-			-	13
DPA	10	6 +		-		1	2	-	2	4	-	12 +		1 +	8 +	1	2 -	-	2	-			7	58
RAW	5	-			X		-	X	1	2		5 +			6 +	8 +	-	-	-	-			-	27
RHV	-	1				1 +				-		4 +			-		2	-	1 +	-			3 +	12
ECL	13 +	-							-	1 -		-			1 -	1 +	1 -	-		-			-	17
ROS	1 +									1 +														2
BSR	1 +																							1
AVF	4 -	4 +		1 +		-	6 +		2	-	1	5			1 -	-	8 +	3	-	-			7 +	42
Sums	70	24	1	4	1	6	13	4	16	23	6	45	2	1	35	12	55	28	12	17	2	1	41	419

Structural zero transition values are indicated by an " X". Significant transitions are indicated by " +" (facilitatory) or "-" (inhibitory).

Table 25: The transition frequencies between behavioural acts of interacting male and female seals at North Rona.

Succeeding Act

Preceding Act	OMD	HTH	EFF	FFW	FSR	FSS	FSW	FSB	HSW	HEX	NTN	PON	SNI	GLA	STA	LAW	BIT	CLI	CLA	APT	CHA	ROA	DPA	RAW	NHS	RHV	ECL	ROS	NUR	PT	AVF	Sums
OMD	X	27-	8	15+	1-	·	·	·	4-	20+	·	1		15	90+	46+	1-			20	·	1-	16-			·	2-	2-	X	X	14	283
HTH	11+	4	6+	10+	1+				2	24+				9-	7-	4-	·	3	4	6		2	19	1		19		2+	X	5	43+	182
EFF	14+	4+					4+			4-				3+	4	4-	1		5				3+			1		1+		1	5+	54
FFW	*16+*	*2-*	*1+*	*6+*			*2+*		*1+*	*2-*				*1*	*8+*	*4-*		*3*	*1*	*3-*	*1+*		*11+*	*1*							*8+*	71
FSR	1	1							1					2+				3+	5+				3+			1				1	7+	25
FSS															3+					1											1	5
FSW		1	3+				6+								1-	·							1+					1+	X		2	15
FSB	2+	1												2+	7+	2							2								2	18
HSW	5+	2	2+	1-		1+		1+	11+	12+	1	1		3+	5+	1-				·			6+			5+		1+			2	60
HEX	19+	19+	2	1-	·	1+		1	6+	7+	3+	1	1	5-	13+	12-	1	2	9	3			5-			7	6-	3+		4	11+	142
NTN	1	1							3+	·	10+				2-	1	1-	4	1		X		·									24
PON		·									1				2	2	1+						2+				1+					9
SNI				1+												1+																2
GLA	11	12+	3	1-	3+			7+	6+	5	1			13+	15-	10-	4-	1	2	6	1	1	8				3-	·	1	4	4	122
STA	88+	23	6	8	1-		3+	4+	10+	11	1-	1	1	21+	69	44	4-	5	7	59+		·	24+			4-	20	1-		2	9-	426
LAW	56+	1-	3	3	1			1	4	8		3+	1	7	57+	36+	7	10	12	15+		3+	14	1+	1+		17+	·	2	16+	2-	281
BIT	3	1-	1	1-	1+				2-	1-	1+			1-	·	4+	4+	3	5	2-	1		9+	3		4+	1	1+	X	6	7+	62
CLI		5	3+	1	1				·	3		2+		7+	5-	6	4-			1	X	1+	3				1	4+	X		·	47
CLA		7	2	·	8+			·	·	7+				3	4-	15+	7+			·		4-	7				1	4+	X		1-	70
APT	15-	11-	2-	4	2	1	·	2	1-	9	·			14	59+	8-	5	1	1	30+		·	20	1		6-	3-	3			14+	212
CHA															1+	2+								4					X	X		7
ROA	1	·			X					1+	X	X	X	4+	3	1	1		1	2		1	1				1		X	X		17
DPA	19+	16+	2	5+	3			2	5	5-	1	1		9	34	16	5	6	6	35+	2+	·	6-				7+	1		1	3-	190
RAW		1		1+	X					·	X	X	X		1	1	2+			2+	2+		·						X	X	1	11
NHS																									1		1+					2
RHV		9+	1	3	1	2+			3+	4				·	5-	4-	6+	3	2	3			4			5+	·	·			2	57
ECL	7	4-	1	·	·			·	1	7+		1		2-	18+	13+	1-		1	6-			6+				10+	2		2	3	85
ROS	2+		1+							1				1	5	1		2	2	3			3				1			2	4+	28
BSR		1+												1	1								2+									5
PT	X	7	2	1	1			·	·	3	1+			3-	3-	14+	7	X	X	·	X	·	1				2+	1	X	X	·	46
AVF	17+	25+	2	9+	4+		·	1	2-	8	2-	1		5-	15-	9-	5		2	6-		4+	12			2+	8	4+	2	1	16+	162
Sums	288	185	51	71	28	5	15	19	62	142	22	12	3	131	437	261	67	46	66	203	7	17	188	11	2	54	85	31	5	45	161	2720

Structural zero transition values are indicated by an " X". Significant transitions are indicated by " +" (facilitatory) or "-" (inhibitory).

Table 26: The transition frequencies between behavioural acts of interacting male seals at Sable Island.

Succeeding Act

Preceding Act	OMD	HTH	EFF	FFW	FSR	HSW	HEX	NTN	SNI	GLA	STA	LAW	BIT	CLI	APT	CHA	ROA	DPA	RAW	RHV	ECL	ROS	BSR	AVF	Sums
OMD	29 +	-			-	1 -	5			3	38 +	13 +	1 -	-	15	-	5 +	9 -	2 -	-	5 +			-	124
HTH	-			1 +		1 +	1			1 +	-	-	2 +		-	1 +		-		7 +					14
EFF											1			1 +	1 +										3
FFW													1 +							1 +					2
FSR	-				1 +						1		1 +			1 -		2 +							6
HSW	3						1			2 +	-	-	-		1			1 -		5 +				5 +	18
HEX	4		1 +		1 +	1	2	1 +		2 +	5	2	4 +		2	1	-	3	-	1	3 +			1	34
NTN											1 +					X									1
SNI											1 +														1
GLA	4	1 +				1	1			1	3	1	-		4 +		1	1 -	1	1	2 +			-	22
STA	38 +	-			-	4	3 -		1 +	3	42	22 +	4 -	-	28 +	3	2 -	19	4	1 -	4		1 +	1 -	180
LAW	9	1				-	4 +			3	6 -	5	2 -		11 +	3 +	8 +	7	1	-	1	1 -		-	64
BIT	-	3 +			3 +	2 +	-			1	-	-	12 +	4 +	1 -	1	-	6	2	8 -	-	1 +		7 +	51
CLI	-		1 +								-	1	1 +		-	X		2 +	1 +			1 +			7
APT	6 -	1	1 +	1 +	-	2	5	1		3	26 +	4 -	4	-	7 -	1 -	-	30 +	2	3	1 -			4	102
CHA	1 -						-				1 -	1	-		1 -			4 +	13 +	1				-	22
ROA	2				X		-	X	X	1	9	7 +	-		-		1	1 -	1						22
DPA	14	1			-	3	3			-	29 +	5	7	1	25 +	2	3	7 -	1 -	-	2			1 -	104
RAW	4	1 +			X		-	X	X	1	5	2	-		1 -	7 +	2 +	2	-	-				-	25
RHV	3	3 +				2 +	3 +			-	4	-	4 +		1 -	-	-	2 -	-	1	-			8 +	29
ECL	1 -						4 +			2 +	3 -	-	1		5 -	1 +		3			4 +				24
ROS														1 +							1 +				2
BSR											1 +														1
AVF	1 -	1 +			1 +	1	1			-	8	1	4 +		1 -	-	-	7 +	1	-	-			2 +	27
Sums	119	12	3	2	6	18	33	2	1	23	182	64	48	7	104	21	22	106	29	29	23	3	1	27	885

Structural zero transition values are indicated by an " X". Significant transitions are indicated by " +" (facilitatory) or "-" (inhibitory).

Table 27: The transition frequencies between consecutive behavioural acts of the same seal at Miquelon.

	Succeeding Act																											
Preceding Act	HTH	EFF	FFW	FSR	HSW	HEX	NTN	PON	SNI	GLA	STA	LAW	BIT	CLI	CLA	APT	CHA	ROA	DPA	RAW	YAW	NHS	RHV	ECL	ROS	BSR	AVF	Sums
HTH	37	2	2	4	1	6				4	14	14	7	14		2			6				3	1	3		12	132
EFF	4	4	2	2	2						4	3	4						2	1		1	1				1	31
FFW	2	1	4	2						3	6	6	2	1				2	4				2	1			1	37
FSR	2	2	1	4	2					2	3	4	3	4										2				29
HSW	2		1	1	128		1			1	12	8	1	11	1	2		2	10				1	1			4	187
HEX	6		1		2	7				1	7	5	3	2		1		1	8				1				2	47
NTN	2						1				2	1	2			1		1									2	12
PON											1					1					1							3
SNI																											1	1
GLA	7		5	1	2	2				3	6	3	1	1		1	1		4	1			4	3		1	3	49
STA	12	5	7	3	5	9	5			3	21	10	11	7		9			17				10	8			14	156
LAW	6	2	4	4	10	3				10	7	9	4	11		4			13		3		5		1		7	103
BIT	2	2	2	3	3		1			3	7	7	16	6		1			13				6	3	4		9	88
CLI	5	2	1		11	1		1			6	12	16	11	2	3	2		13				3				5	94
CLA					1			1				1																3
APT	5	1	1	1	6	5	2	1	1	4	14	4	4	1		9			10				6	1	1		6	83
CHA											1	2	1	1														5
ROA																1			2									3
DPA	16	1		1	7	5				1	14	8	7	9		4	1		12	1	1		4	5	2		3	102
RAW		1								1										1								3
YAW											1			1					3						1		1	7
NHS											1																	1
RHV	4	1	1	2	1	1				1	13	4	2	8		5			7				19	4	1		8	82
ECL			1		1	1				1	4		3	1		1			1				1					15
ROS		3	2		1		1			1	1		1	1		2							1	1				15
BSR										1																		1
AVF	13		1		7	4	1			4	10	10	6	3		2			7	1	2		6	1	2		16	96
Sums	125	27	36	28	190	44	12	3	1	44	155	111	94	93	3	49	4	6	132	5	7	1	73	31	15	1	95	1385

Structural zero transition values are indicated by grey cell colouration.

Table 28: The transition frequencies between consecutive behavioural acts of the same seal at North Rona.

Succeeding Act

Preceding Act	OMD	HTH	EFF	FFW	FSR	FSS	FSW	FSB	HSW	HEX	NTN	PON	SNI	GLA	STA	LAW	BIT	CLI	CLA	APT	CHA	ROA	DPA	RAW	YAW	NHS	RHV	ECL	ROS	NUR	BSR	PT	AVF	Sums
OMD	207		1-	-	-		-		-	8	1-	-		12	30	23	4	6+	5+	38+	1	-	16	3+			6+	5	3	X		-	16+	385
HTH	2-	70	8+	12+	3	2+	1	2+	10+	21+	1-	-		6-	19-	25	9+	2	1	7-	1	1	21+	1			4	2-	3		1	-	19+	254
EFF	-	12+	17	6+	5+		2+	2+	1	2	6+	1		4	4+	8	2	1		4		4+	3-				2	-	1		1-		4	92
FFW	1-	10+	10+	22	1		2+	2+	1	2	-	-		4	6-	5-	1			3	1+		7	1			-	1	1				5	86
FSR	-	3	8+	-	13				-	2	2	2		3	2-	3-	9+	1		3		2+	6				1	-	4+				1-	65
FSW		1+							2+	1+						1																		5
FSW	-	1	4+	1+			10	1+		1				-	2	2				1		1+	2						1+				1	28
FSB		3+	4+	1+				3	1+	1					1	1				2			-								2+			19
HSW	-	5	-	1	-				27	10+	1	2		2-	14+	10	3	-		2-		1	7				3+	1	5+				5	99
HEX	4-	13+	3	3	2	1+	2+	1	5	50	10+	2	1	7	21	19	4	2	-	9-		2+	15	-			6+	1-	2				17+	202
NTN	3	4	1	2	2				4+	-	7	6+		7	18+	20+	2	2	2	3-			9				1	2	3		2+		1-	101
PON	-	-	1	-	3+				-	1-	10+	21	1+	2	4-	16+	1	3+	1	10+			4		1+		-	1	2	6+			-	88
SNI	1									1		1+	2		3	2		2+		1			2											15
GLA	10	16+	1-	2	2		1	1	6	9	4	1-	1	51	30+	21	4	1-	-	12	1	-	19	1		1+	4	8+	3			-	12	222
STA	35+	28	7-	11	2-	1	2	-	9	26	8-	8	1	33+	180	65+	6-	1-	-	54+	-	-	36	3			9	16	9	-	3+	-	22	575
LAW	13-	13-	6	5-	6		-	-	8	20	12	12+	3+	23	68+	110	9	3-	2-	32	2	3	39+	3	3+	1+	2-	23+	6	-	-	1	8-	436
BIT	-	3-	6+	3	9+				2	5	1-	2	1	3-	3-	10	34	5+	4+	5-	3+		11	2+			7+	-	-				17+	136
CLI	3	1	2+		2+					-	5+	2+	1+	-	1-	1-	3+	7	5+	5+			2				1	-					2	43
CLA	2	1								-	-			2	2-	2-	4+	3+	17	1-			2					-				16+	-	52
APT	49+	27+	3-	6	3		3	1	5	18	13+	19+	2	10-	52+	22-	10	6	2	62	7+	1	10-	1			4-	7	6	3+	-	-	11-	363
CHA	3+			1+											4+	-	4+			4+	1		-									X		17
ROA	1	2	1		1+					-				1	1-	8+	1			1			-					1	1+			X	1	20
DPA	17	15	2-	7	2		-	-	2-	9	10	2-		14	39	40+	9	3	-	16	-	2	80	7+	1		6	10	7+			-	9-	309
RAW				1+											5+	1	1			-			6+	14								X		28
YAW											1+					1							2+		2			2+						8
NHS															1													2+						3
RHV	2	5	2	1	1				4+	2	-	-		3	12	2-	5+	1	1	2-			14+				11	2	-			2+	7+	79
ECL	6	2-	2	1	-				-	1-	2	1	1-	20+	14	19+	1-	-	-	6		1	6	1	1+	1+	3	37	-				1-	127
ROS	1-	3	3+	3+	2+		1+	2+	3+	1-	3	-		1-	9	10+	1		1	4		1+	3				-	4+	1		1+		2	60
NUR	X											3+				1							2+							11		X		17
BSR	1							2+			1+				-	-							1					3+					1	9
PT	1	-					X			-	1			-	-	-	1	5+	10+	-			-				1	1	1	X		16	1	38
AVF	12+	12	1-	1-	3		3+		10+	10	3	-		17+	19	13-	8	1	1	11	2+		18+	-			6+	3	-		1		65	220
Sums	374	250	93	90	62	4	27	17	100	201	102	85	14	225	564	461	136	55	52	298	19	19	343	37	8	3	77	132	59	20	11	35	228	4201

Structural zero transition values are indicated by grey cell colouration or "X".

Table 29: The transition frequencies between consecutive behavioural acts of the same seal at Sable Island.

	Succeeding Act																												
Preceding Act	OMD	HTH	EFF	FFW	FSR	FSS	HSW	HEX	NTN	PON	SNI	GLA	STA	LAW	BIT	CLI	CLA	APT	CHA	ROA	DPA	RAW	RHV	ECL	ROS	NUR	BSR	PT	AVF	Sums
OMD	57		-	-	-	-		7 +				2	23 +	11	2	-	1	10 +	4 +	5 +	12	-	2	3	-	X			6	145
HTH	2	7	2 +		2 +		1	5 +				1	8	6	1	1		-			3	1	3 +	-					5 +	48
EFF	-	2 +	3	2 +	2 +							1	2	4 +	1			-			1			1	1 +		1 +			21
FFW	-	1	1 +	4	6 +			1					4	4	1			-		1 +	1		1						2	27
FSR	-	-		4 +	5			2				3 +	3 -	10 +	2	2		2		1	4		1	1	1				-	41
FSS						1							1	2 +				1			1			1 +						7
HSW	1	2 +			1		5	2					7 +	2	-			1		1 +	4								3 +	29
HEX	2 -	1		-	2	2	2 +	14				-	17 +	15 +	4	-	-	4	-	1	3 +	2	4 +	3	2				7 +	85
NTN					1 +					1 +				2 +								1 +								5
PON										7			1								1					4 +			1	14
SNI	1 +												1 +																	2
GLA	2	2			2		1	1				8	9	5	2	-		3	1	1	9 +			3 +		-			3	52
STA	25 +	11 +	2	4	1 -	3 +	2 -	16		1 +	1 +	12 +	76	30 -	4 -	-	1 -	40 +	4	7 +	30	4	6	11	7 +		2 +	-	11	311
LAW	11	3	2	3	5	1	-	13 +	2 +	1	1 +	8 +	25	36	5	1 -	3	13	-	1 -	32 +	5 +	-	11 +	4			-	2 -	188
BIT	2 -	1	2 +		2		4 +	3				1	6 -	5 -	13	7 +	-	3	1		8	1	4 +	-	2 +				6 +	71
CLI	-	-	1		1			1				-	-	6	3 +	6	11 +	1 -	1		8 +							4 +	-	43
CLA	-							-					-	3	-	11 +	7	1			3							8 +		33
APT	25 +	9 +	-	2	2		4	13 +		4 +		5	25	12 -	15 +	7 +	2	37	5 +	1 -	1 -	2	2	2 -	1 -		1	-	13 +	190
CHA	6 +	2 +										1	2	1	1	1		1	1		1	1 +						X	1	19
ROA	4 +												2	3				1	1 +	11	2			1	2 +			X		27
DPA	9	-	1	1	4		5 +	6	1 +			3	26	27 +	5	3	-	9	1	3	32	4 +	5 +	2	2			-	1 -	150
RAW	1			1 +								2 +	4	3	1			1	1 +		3	4	1					X		22
RHV	-		1 +		1			-		1		3 -	9 +	4 +				4			5 +	1 +	17						2	48
ECL	1 -	1	3 +	3	1			-					3 +	4 +	1	-		1 +		1	1			1					1	22
ROS			3 +					-						1										1						5
NUR	X												1	2 +										1 +	1			X		5
PT													-	-		5 +	6 +				-					X		2	1	14
AVF	1 -	3		1	-	1 +	5 +	1 -				2	20 +	8	5 +	3	-	3	1	-	4 -	-	2	2	1			1	13	77
Sums	150	45	23	25	38	8	29	85	3	15	2	52	275	206	66	47	31	136	21	34	169	26	31	61	24	4	4	15	78	1703

Structural zero transition values are indicated by grey cell colouration or "X".

Table 30: The transition frequencies between consecutive behavioural acts of male seals at North Rona.

Preceding Act	Succeeding Act																													
	OMD	HTH	EFF	FFW	FSR	FSW	HSW	HEX	NTN	PON	SNI	GLA	STA	LAW	BIT	CLI	CLA	APT	CHA	ROA	DPA	RAW	NHS	RHV	ECL	ROS	BSR	PT	AVF	Sums
OMD	209	-	1	-			-	8	1 -	-		10	28 +	23 +	4 -	6	5	38 +	1	-	16	3		6	5	3 +		-	15	382
HTH	2 -	7		1				5 +				-	1 -	1	3 +	2 +	1	1 -			9 +	1		1	-				5 +	40
EFF	-		2	1 +		1 +						1	1					-			2 +								2 +	10
FFW	1 -	2 +	1 +	2		1 +						1	2	1				1			3 +	1 +							2	18
FSR												1 +			1 +															2
FSW			2 +			2								1 +							1 +									6
HSW	-						5	3 +	1 +	2 +		1	3	3 +	3 +			-			1								1	23
HEX	3 -	-		2 +		1 +	2 +	29	4 +			3	3 -	4	3	1	-	4		1 +	3	-		6 +	-				8 +	77
NTN	3	1 +					1 +		2	1 +		2 +	1	1		1 +	2 +	1			-								1	17
PON	-							1 +								1 +	1 +	3 +												6
SNI	1												1 +								1 +									3
GLA	8	4 +		1			4 +	1 -	1			21	8	3	1 -	1	-	5	1		9 +	1		3	7 +			-	9 +	88
STA	32 +	5	1	1		1	4 +	8 +	-	-		10	42	11	2 -	-	-	20 +	-		10 -	3		7	8 +	1	3 +	-	9 -	178
LAW	13	-		-			1	3	-		1 -	6	14 +	11	-	2	2	8	2 +	2 +	5 -	2	1 +	2	10 +			1	5	91
BIT	-	1			1 +		2 +	2		1 +	1 +	1 -	1 -	1 -	16	4 +	4 +	3 -	1		7 +	2 +		5 +	-			-	15 +	68
CLI	3	1						-	3 +	1 +		-	-	-	3 +	7	5 +	3			1			1	-				2	30
CLA	2 -	1						-				2	2 -	2	4 +	3 +	17	1 -			2			-	-			16 +	-	52
APT	50 +	2	-	3			-	9 +	2	1		6 -	22	6 -	5	4	2 -	27	6 +	1	6 -	1 -		3 -	3 -			-	9 -	168
CHA	3 +												3 +	-	2 +			4 +	1		-							X	-	13
ROA	1		1 +										1	3 +														X		6
DPA	17	4 +	1	4 +			1	2 -	1			4 -	11	9	7 +	2	-	7	-	1	32	6 +		5	4	1 +		-	6	125
RAW	-			1 +								-	4 +	1	1			-			6 +	14						X	-	27
NHS																									1 +					1
RHV	2 -	3 +		1			2 +	2				2	9 +	-	3	1	1	2 -			12 +	-		10	2			2 +	5	59
ECL	6	-		1				-		1 +		10 +	8 +	7 +	-	-	-	3			-	1		3 +	32				1 -	73
ROS	1												1				1 +			1 +					1 +					5
BSR	1																				1 +				1 +				1 +	4
PT	1 -							-	1 +			-	-	-	1	5 +	10 +	-			-			1	1	1 +		16	1	38
AVF	11 -	5 +		1			3 +	4	1			14 +	9 -	6	8 +	1 -	1 -	7 -	2 +		15 +	-		4	1 -		1 +	-	48	142
Sums	370	36	9	19	1	6	25	77	17	7	2	95	175	94	67	41	52	138	14	6	142	35	1	57	76	6	4	35	145	1752

Structural zero transition values are indicated by grey cell colouration or "X".

Table 31: The transition frequencies between consecutive behavioural acts of female seals at North Rona.

Succeeding Act

Preceding Act	HTH	EFF	FFW	FSR	FSS	FSW	FSB	HSW	HEX	NTN	PON	SNI	GLA	STA	LAW	BIT	CLI	APT	CHA	ROA	DPA	RAW	YAW	NHS	RHV	ECL	ROS	BSR	AVF	Sums
HTH	63	8	11 +	3	2 +	1	2	10 +	16 +	1 -	-	-	6	18 -	23	6	-	6 -	1	1	12				3 +	2 -	3 -	1	14 +	213
EFF	12 +	15	5 +	5 +		1	2 +	1	2 -	5 +	1		3	3 -	8	2	1	4		4 +	1 -				2 +	-	1	1 +	2	81
FFW	8 +	9 +	20	1		1 +	2 +	1	2	-			3	4 -	4 -	1		2	1 +		4					1	1		3 +	68
FSR	3	8 +	-	11				-	2	2	2 +		1	1 -	3 -	8 +	1 +	3		2 +	5				1	-	4 +		-	57
FSS	1							2 +	1 +						1															5
FSW	1	2 +	1			8	1 +		1					2	1			1		1 +	1						1		1	22
FSB	3 +	4 +	1				3	1	1					1	1			2 +			-							2 +		19
HSW	5	-	1	-				22	7 +	-			1 -	11 +	7	-		2		1	6				3 +	1	5 +		4 +	76
HEX	13	3 +	1 -	2	1 +	1	1	3	21	5 +	-	1	4	18	14	1 -		5		1	12 +				-	1 -	2		9	119
NTN	3	1	2	1				3 +	-	3			1 -	8	13 +	2	1 +	1 -			7 +				1	1	3 +	2 +	-	53
PON	-	1		3 +				-		3 +	4	1 +	1	-	8 +		2 +	2			3		1 +			1	2 +		-	32
SNI	-								1		1 +	2		2	2		2 +	1			1									12
GLA	12 +	1 -	1 -	2		1	1	2	6	2	1	1	28	23 +	16	2		3 -			9			1 +	-	1 -	2		3	118
STA	23	5 -	10	2 -	1	1	-	5 -	18	5 -	4	1	22 +	131	48 +	4 -	1	27 +		-	20				2	8	8	-	14 +	360
LAW	12 -	5 -	5	4		-	-	7	14	7	8 +	2	15	49 +	91	9	1	18		1	27 +	1 +	2 +		-	12 +	6	-	2 -	298
BIT	2 -	6 +	3 +	8 +				-	3	1			2	2 -	8	15	1 +	2	2 +		4				2 +	-	-		2	63
CLI	-	2 +		2 +						2 +	1 +	1 +		1	1			2 +			-									12
APT	24 +	3 -	3	2		3 +	1	5	8	6	6 +	2 +	4 -	24	15 -	5	2 +	24	1 +	-	2 -				1	4	6		2 -	153
CHA			1 +											1		2 +														4
ROA	2			1 +									1	-	4 +	1 +		1			-					1 +	1 +		1	13
DPA	11	1 -	3	1 -		-	-	1 -	7	5	1		7	24 +	19	2	1	8		1	35	1 +	1 +		-	6 +	6 +		2 -	143
RAW														1 +																1
YAW										1 +					1						1 +		2			2 +				7
NHS														1 +												1 +				2
RHV	2	2 +		1				2 +	-				1	3	1 -	2 +		-			1				1				2 +	18
ECL	2 -	2	-	-				-	1 -	1		1 +	10 +	6	12 +	1		3		1 +	4		1 +	1 +		5	-		-	51
ROS	3	3	3 +	2		1	2 +	3 +	1 -	3 +			1 -	8	10	1		4			3					3 +	1	1 +	1	54
BSR							2 +			1 +																2 +				5
AVF	7	1	-	3 +		3 +		7 +	6 +	2	-		3	10	6 -	-		4			3				2 +	2	-		17	76
Sums	212	82	71	54	4	21	17	75	118	55	29	12	114	352	317	64	13	125	5	13	161	2	7	2	18	54	52	7	79	2135

Structural zero transition values are indicated by grey cell colouration.

Table 32: The transition frequencies between consecutive behavioural acts of the male seals at Sable Island.

Preceding Act															Succeeding Act												
	OMD	HTH	EFF	FFW	FSR	HSW	HEX	NTN	PON	SNI	GLA	STA	LAW	BIT	CLI	CLA	APT	CHA	ROA	DPA	RAW	RHV	ECL	ROS	BSR	PT	AVF	Sums
OMD	57	-				-	7 +				2	23 +	11	2 -	-	1 -	10	4 +	5 +	12	-	2	3	-		-	6	145
HTH	2	3					1					-	-	1			-			1	1 +	3 +					4 +	16
EFF		1 +		1 +								-	1							1				1 +	1	1 +		7
FFW				1								1							1 +	1							2 +	6
FSR							1 +					1		1 +						2 +		1 +						6
HSW	1					3	2 +					5 +	-				-		1 +	4 +							2 +	18
HEX	2 -	1			1 +	1	4				-	10	5	3	-	-	2 -	-	1	2 -	2 +	3 +	3 +				5 +	45
NTN																					1 +							1
SNI	1 +											1 +																2
GLA	2					1	1				6	7	4	2	-	-	3	1	1	3		-	3 +				3 +	37
STA	25 +	1	1	1	-	1 -	8			1 -	7	62	22	3 -	-	1 -	32 +	4	7 -	23	4	6	9	4 +		-	6 -	228
LAW	11	1				-	5			1 +	4 +	12	9	1 -	1 -	3	8	-	1	13 +	5 +	-	8 +	1		-	2 -	86
BIT	2 -	1	1 +		1 +	4 +	2				-	6 -	1 -	8	3 +	-	3	1	-	8 +	1 +	4 +	-	2 +			6 +	54
CLI	-				1 +			-				-	4	1	5	11 +	1-	1		5 +		-	-			4 +	-	33
CLA	-						-					-	3	-	11 +	7	1 -			3			-			8 +	-	33
APT	25 +	3 +				3	7				4	20	8 -	14 +	6 +	2	31	5 +	1-	-	2	1 -	2 -	-		-	10 +	144
CHA	6 +	2 +									1	2	1	1	1		1	1		1	1 +					X	1	19
ROA	4 +											2	2				1	1 +	11	1			1	2 +		X	-	25
DPA	9	-			2 +	1	5	1 +			3	17	13 +	4	2	-	9	1	2	23	3	4 +	2	1		-	1 -	103
RAW	1			1 +							2 +	4	2	1			1	1 +		3	4	1				X	-	21
RHV	-		1 +		1 +		-					8 +	1 -	6 +	-		1 -			8 +	1	8	-				1	36
ECL	-						-		1 +		3 +	9 +	2	-	-		2			5 +	1		14				2	39
ROS	1		1 +	1 +								1	1	1			1		1 +	1							1	10
BSR												1																1
PT	-											-	-		5 +	6 +	-			-						2	1	14
AVF	1 -	1		1 +		4 +	1				2	16 +	5	5 +	3 +	-	2 -	1	-	4	-	2	2			1	13	64
Sums	150	14	4	6	6	18	44	1	1	2	34	208	95	54	37	31	109	21	32	124	26	35	47	11	1	16	66	1193

Structural zero transition values are indicated by grey cell colouration or "X".

Table 33: Seasonal trends in a number of measures from North Rona.

Date[1]	Mean Vigilance	Mean Focal Area	Mean Focal Male	Mean Focal Female	Mean Distance (cm)	Mean Duration (sec)	Response Latency (sec)	Total Duration (sec)	Weighted Behaviour Frequency	Acts per Bout
266	1.2	7.1	0.4	1.9	221.9	5.1	1.4	124	0.186	17.6
267	1.0	8.2	0.9	2.3	120.8	2.0	2.2	136	0.079	18.9
268	1.4	8.1	1.4	1.3	48.1	2.3	1.3	149	0.154	23.1
272	1.7	6.6	0.8	1.4	75.7	12.3	1.5	289	0.141	18.4
273	1.3	13.0	0.0	0.0	40.0	2.0	0.9	8	0.577	4.5
275	1.3	8.0	0.0	0.9	51.3	1.5	2.3	53	0.167	15.7
278	1.3	20.0	3.3	0.7	28.1	5.7	2.2	215	0.018	16.2
279	1.5	8.8	2.2	0.4	110.4	3.6	2.5	864	0.017	89.3
285	3.0	6.6	1.0	0.2	374.4	3.3	1.5	243	0.061	43.7
286	3.2	13.2	1.4	0.0	98.0	2.4	1.1	69	0.173	26.3
287	0.5	8.0	1.0	0.0	20.6	1.7	1.4	480	0.016	60.5
289	0.5	9.2	1.8	0.4	60.0	15.8	2.4	1073	0.071	39.7
298	2.0	6.0	1.0	1.0	141.7	2.0	3.1	115	0.087	9.5
299	1.6	7.6	1.0	0.6	32.3	3.8	1.5	314	0.026	50.1
301	1.0	9.6	1.1	0.0	183.1	5.2	1.8	255	0.05	30.6
302	1.1	8.5	1.5	0.6	66.9	4.3	1.6	311	0.044	41.8
303	1.7	9.3	1.1	0.0	57.3	5.9	1.7	458	0.045	40.0
304	1.8	8.6	1.5	0.1	34.0	5.2	1.6	615	0.023	67.9
309	1.0	7.0	1.0	0.1	21.3	8.4	1.5	985	0.026	91.3
311	0.3	6.7	1.0	0.2	61.1	2.3	1.0	28	0.337	10.9
$L_{variable}$	**2286.5**	**2082.5**	**2274.0** [D]	**2580.0**	**2376.0**	**2400.0**	**2166.0**	**2239.0** [I]	**2220.5** [D]	**2483.0** [I]

[1] Note that the Date column assumes January 1st = 1, and does not represent a complete series.

[D] Significant decreasing trend. [I] Significant increasing trend

Table 34: Seasonal trends in mean daily weighted behavioural act (1-17) frequencies at North Rona.

Date[1]	OMD	HTH	EFF	FFW	FSR	APT	BIT	RAW	RHV	ROA	ROS	BSR	CHA	CLA	CLI	DPA	ECL
266	0.112	0.18	0.179	0.056	0.046	0.362	0.056	0.317	0.179	--	0.05	0.054	--	--	--	0.268	0.144
267	0.022	0.081	0.098	0.068	--	0.094	0.108	0.108	0.062	0.062	0.022	0.108	0.108	--	--	0.073	0.038
268	0.081	0.059	0.051	0.051	0.063	0.223	0.024	0.03	0.127	0.051	0.651	--	0.031	0.043	--	0.167	0.562
272	0.075	0.069	0.034	0.06	0.017	0.251	--	--	0.074	--	0.017	--	--	--	--	0.19	0.032
273	--	--	--	--	--	0.577	--	--	--	--	--	--	--	--	--	0.577	--
275	--	0.195	0.195	0.211	0.211	0.14	0.083	0.083	0.083	0.179	0.211	0.211	--	--	--	0.12	0.083
278	0.017	0.036	--	--	--	0.036	0.036	0.024	0.036	--	--	--	0.011	0.011	--	0.03	--
279	0.016	0.023	0.025	0.038	0.009	0.018	--	0.114	0.009	0.058	0.016	--	0.114	--	0.009	0.02	0.014
285	0.049	0.042	0.041	0.043	0.042	0.101	0.049	0.061	0.055	0.042	0.04	0.174	0.061	--	0.053	0.049	0.077
286	--	0.301	0.046	0.407	0.046	0.284	0.469	0.407	0.046	0.046	0.046	0.046	0.407	--	--	0.252	0.046
287	0.016	0.016	0.016	0.016	0.016	0.016	0.016	--	0.016	--	0.016	--	--	--	--	0.016	0.016
289	0.036	0.076	0.084	0.092	--	0.081	0.002	--	0.002	0.01	0.106	--	0.496	0.002	0.002	0.094	0.002
298	--	--	0.087	--	--	0.087	--	--	--	0.087	--	--	--	--	--	0.087	--
299	0.022	0.028	0.026	0.046	--	0.03	0.025	--	0.022	0.036	0.032	--	--	0.025	--	0.033	0.033
301	0.035	0.055	--	0.037	0.039	0.053	0.015	0.086	0.208	--	0.021	--	0.097	--	0.109	0.1	0.015
302	0.063	0.023	0.128	0.031	0.025	0.048	0.014	--	0.014	0.048	0.028	0.027	--	0.014	0.014	0.073	0.062
303	0.031	0.102	0.012	0.048	0.022	0.033	0.037	0.067	0.083	0.007	0.016	--	0.062	0.007	0.017	0.04	0.007
304	0.027	0.029	0.013	0.061	0.013	0.029	0.028	0.051	0.033	0.007	0.011	--	0.048	0.008	0.013	0.027	0.031
309	0.008	0.052	0.007	0.068	0.007	0.02	0.039	--	0.069	0.007	0.008	0.06	--	0.007	0.007	0.037	0.024
311	0.444	0.303	--	0.303	0.303	0.35	0.303	--	0.303	--	--	--	--	--	0.303	0.338	--
L_{var}	1199.0	1699.5	1354.0 **D**	1380.0 **I**	851.0 **D**	2524.0 **D**	1224.0	415.0	1669.0	773.0 **D**	1350.0 **D**	122.0	313.0 **I**	182.0	238.0	2413.0	1343.0 **D**

[1] Note that the Date column assumes January 1st = 1, and does not represent a complete series.

D Significant decreasing trend. **I** Significant increasing trend.

Table 35: Seasonal trends in mean daily weighted behavioural act (18-33) frequencies at North Rona.

Date[1]	FSB	FSS	FSW	GLA	HEX	HSW	LAW	NHS	NTN	NUR	PON	PT	SNI	STA	YAW	AVF
266	--	--	--	0.494	0.169	0.056	0.138	--	0.494	0.046	0.046	--	0.046	0.139	0.267	0.119
267	--	--	0.129	0.094	0.078	0.135	0.089	--	0.094	--	--	--	--	0.086	--	0.091
268	0.063	--	0.051	0.144	0.144	0.144	0.536	--	0.144	--	10.25	0.063	--	0.089	--	0.099
272	--	--	--	0.057	0.232	0.054	0.098	0.032	0.057	0.017	0.017	--	--	0.244	--	0.032
273	--	--	--	--	--	--	--	--	--	--	--	--	--	0.577	--	--
275	--	--	--	0.187	0.19	0.179	0.128	--	0.187	--	--	--	--	0.184	--	--
278	--	--	--	0.011	0.011	--	0.011	--	0.011	--	0.011	--	--	0.017	--	--
279	0.02	0.006	0.064	0.017	0.011	0.008	0.012	--	0.017	0.009	0.009	--	0.008	0.017	--	0.02
285	0.174	--	--	0.038	0.05	0.08	0.076	--	0.038	--	0.037	--	--	0.094	--	0.051
286	0.046	--	--	--	0.046	0.046	0.146	0.046	--	--	--	--	--	0.162	--	0.046
287	0.016	--	--	0.016	0.016	0.016	0.016	--	0.016	--	--	--	--	0.016	--	0.016
289	--	--	0.042	0.084	0.119	0.042	0.031	--	0.084	--	0.002	0.002	0.086	0.09	--	0.115
298	--	--	--	0.087	0.087	--	0.087	--	0.087	--	--	--	--	0.087	--	0.087
299	--	0.022	--	0.033	0.024	0.022	0.028	--	0.033	0.026	0.026	0.025	0.026	0.025	0.03	0.022
301	--	--	--	0.021	0.046	0.039	0.029	--	0.021	0.015	0.046	--	--	0.048	--	0.026
302	0.027	--	--	0.042	0.055	0.09	0.029	--	0.042	--	0.081	0.014	0.357	0.047	--	0.031
303	--	--	--	0.046	0.007	0.14	0.044	--	0.046	0.022	0.02	0.007	--	0.054	--	0.077
304	--	--	--	0.016	0.031	0.035	0.017	--	0.016	--	0.022	0.008	0.017	0.022	0.017	0.037
309	--	0.023	--	0.032	0.027	0.047	0.019	--	0.032	0.008	0.008	0.007	0.008	0.039	--	0.013
311	--	--	--	--	0.444	--	0.303	--	--	--	--	--	--	0.409	--	0.303
L_{var}	81.0	14	29	1589.5 D	2066	1277	1985.5	5	1591.5 D	127	676	123	118.5	2410	14	1472 D

[1] Note that the Date column assumes January 1st = 1, and does not represent a complete series.
D Significant decreasing trend.

Table 36: Sequence type categories subdivided by study site.

Sequence Type	Miquelon		North Rona		Sable Island	
	N	Percentage	N	Percentage	N	Percentage
Aggressive	47	73.4	79	79.0	130	81.2
Copulatory	--	--	9	9.0	19	11.9
Play	17	26.6	2	2.0	1	0.6
M/P Interaction	--	--	10	10.0	10	6.2

Table 37: Differences between the seal types "Adult female" and "Mother".

Variable	Adult Female Mean (SD)	Mother[4] Mean (SD)	ANOVA F value[1] (df; $\hat{\omega}^2$)
Acts Per Bout	27.7 (11.7)	52.3 (20.5)	124.0 (1, 67; 0.67)
Act Duration (sec)	3.6 (4.9)	7.6 (24.6)	14.5 (1, 3114; 0.61)
Total Duration (sec)	185.0 (106.3)	581.4 (236.0)	339.3 (1, 67; 0.82)
W. Behav. Av.[2]	0.094 (0.2)	0.052 (0.01)	43.5 (1, 3114; 0.79)
W. Behav. Ty.[3]	0.4 (0.1)	0.2 (0.2)	92.6 (1, 3114; 0.62)
Focal Area	9.6 (4.6)	9.7 (4.0)	Not Significantly Different
Focal Male	2.5 (1.1)	1.7 (1.4)	29.4 (1, 3114; 0.71)
Group Vigilance	1.4 (0.7)	1.5 (0.9)	Not Significantly Different
Inter-seal Distance (cm)	47.2 (50.1)	53.1 (21.7)	Not Significantly Different
Response Latency (sec)	1.6 (2.4)	1.7 (1.4)	Not Significantly Different

[1] Values significantly different at $p \leq .05$.

[2] Number of acts per sampled seal (irrespective of type) per sampled minute.

[3] Number of acts per sampled adult female, or mother, per sampled minute.

[4] This did not include interactions between mothers and their pups.

Mean
Standard Deviation
Number of Cases

Interactant Type	Adult	Subadult	Mother	Pup	Weaner
Adult	33.0 cm 64.0 683				
Subadult	22.6 cm 26.2 109	7.4 cm 19.0 758			
Mother	No Cases	No Cases	No Cases		
Pup	No Cases	No Cases	No Cases	No Cases	
Weaner	37.9 cm 54.6 17	10.6 cm 33.8 90	No Cases	No Cases	No Cases

Respondent Type

Significant Differences *

Adult-Adult > Subadult-Subadult
Adult-Adult > Weaned Pup-Subadult
Subadult-Adult > Subadult-Subadult

* (F = 34.6, df = 4,1653, $p \leq .05$; $\hat{\omega}^2 = .71$)

Table 38:
Mean distances between interacting seals, subdivided by the seal types involved, at Miquelon.

Mean
Standard Deviation
Number of Cases

Interactant Type	Adult	Subadult	Mother	Pup	Weaner
Adult	227.0 cm 598.5 1183				
Subadult	No Cases	No Cases			
Mother	72.6 cm 151.4 2798	No Cases	43.9 cm 50.5 179		
Pup	8.3 cm 7.5 6	No Cases	13.3 cm 44.0 704	No Cases	
Weaner	No Cases	No Cases	No Cases	No Cases	16.6 cm 9.4 26

Respondent Type

Significant Differences *

Adult-Adult > Mother-Mother
Adult-Adult > Mother-Adult
Adult-Adult > Weaned Pup-Weaned Pup
Adult-Adult > Mother-Pup
Adult-Mother > Mother-Pup

* (F = 49.2, df = 5,4891, $p \leq .05$; $\hat{\omega}^2 = .62$)

Table 39:
Mean distances between interacting seals, subdivided by the seal types involved, at North Rona.

Mean
Standard Deviation
Number of Cases

Interactant Type	Respondent Type				
	Adult	**Subadult**	**Mother**	**Pup**	**Weaner**
Adult	168.6 cm 219.5 1018				
Subadult	95.6 cm 180.0 9	No Cases			
Mother	32.9 cm 68.9 879	No Cases	42.6 cm 91.6 70		
Pup	No Cases	No Cases	10.6 cm 19.3 83	No Cases	
Weaner	No Cases	No Cases	No Cases	No Cases	No Cases

Significant Differences *

Adult-Adult > Mother-Mother
Adult-Adult > Mother-Adult
Adult-Adult > Mother-Weaned Pup
Adult-Adult > Mother-Pup

* ($F = 87.4$, df = 4,2055, $p \leq .05$; $\hat{\omega}^2 = .8$)

Table 40:
Mean distances between interacting seals, subdivided by the seal types involved, at Sable Island.

Table 41: Spearman Correlation values between group vigilance level (independent variable) and selected dependent variables. Also, F-test (ANOVA) values for the effects of selected independent variables on group vigilance level.

Dependent Variable	Spearman Correlation Values (rho/df)		
	Miquelon	North Rona	Sable Island
Act Duration	-0.01/1657	0.01/4926	0.03/2059
Total Bout Duration	0.06/1657	-0.07*/4926	-0.10*/2059
Response Latency	0.03/1657	0.007/4926	-0.07/2059
Interseal Distance	0.01/1657	0.03/4926	0.03/2059
Behaviour Frequency	-0.02/1657	0.04/4926	0.0004/2059

* indicates correlation values significant at $p \leq .05$.

Dependent Variable	F Values (F/df/p)		
Precedent Sex	.2/1, 1485/.5	.2/1, 4559/.6	.7/1, 2016/.47
Body Orientation	1.0/9, 1648/.6	.7/9, 4907/.52	1.8/9, 2050/.37
Head Orientation	1.9/9, 1647/.43	3.1/9, 4904/.34	2.7/9, 2050/.3
Sequence Type	4.9/1, 1485/$p \leq .05$/$\hat{\omega}^2 = .11$	2.3/3, 4923/.4	2.7/3, 2056/.32

Table 42: Discriminant analyses of the three study sites on the basis of 20 selected variables.

Study Site		Number of Cases Tested
Miquelon		1227
North Rona		3052
Sable Island		1653
	Total	5932

		Canonical Discriminant Functions					
Function	Eigenvalue	% of Variance	Cumulative % Variance	Canonical Correlation	Wilks' Lambda	χ^2	Degrees of Freedom
1	2.4338	86.5	86.5	0.8419	0.7253	1901.1	19 $p \leq .05$

Variable	Standardised Canonical Discriminant Function Coefficients Function 1
Vigilance	0.25785
Focal Male	**0.68138**
Focal Female	**0.63162**
Interaction Distance	-0.11574
Precedent Type	0.20444
Interactant Behaviour	-0.02015
Interaction Duration	-0.07100
Precedent Vocals	0.17733
Eye Position	-0.10354
Mouth Position	-0.14032
Tail Position	0.15617
Precedent Height	-0.03709
Body Orientation	0.04506
Head Orientation	0.00781
Respondent Type	0.11784
Respondent Reaction	-0.00897
Response Latency	-0.01135
Total Duration	-0.17365
Weighted Frequency	0.13914

Table 43: Sequence type categories subdivided by sex of the precedents.

Sequence Type	Male [1]		Female [2]	
	N	Percentage	N	Percentage
Aggressive	217	63.1	126	74.1
Copulatory	28	10.7	28	16.5
Play	14	5.4	12	7.1
M/P Interaction	2	0.8	4	2.3

[1] These include Male-Male and Male-Female interactions

[2] These include Female-Female and Female-Male interactions

Table 44: F-test (1 and 2 Factor ANOVA) values for the effects of sequence type (independent variable) on selected dependent variables.

Dependent Variable	F Values (F/df/p)		
	Miquelon	North Rona	Sable Island
Act Duration	8.8/1, 1656/$p \leq .05/\hat{\omega}^2 = .01$	9.8/1, 4925/$p \leq .05/\hat{\omega}^2 = .01$	47.2/2, 2057/.12
Response Latency	18.4/1, 1656/$p \leq .05/\hat{\omega}^2 = .08$	1.6/3, 4923/.18	25.2/2, 2057/$p \leq .05/\hat{\omega}^2 = .1$
Group Vigilance	0.45/1, 1656/$p = .5$	30.9/3, 4923/$p \leq .05/\hat{\omega}^2 = .02$	4.1/2, 2057/$p \leq .05/\hat{\omega}^2 = .1$
Focal Area	6.1/1, 1656/$p \leq .05/\hat{\omega}^2 = .22$	144.9/3, 4923/$p \leq .05/\hat{\omega}^2 = .08$	26.7/2, 2057/$p \leq .05/\hat{\omega}^2 = .11$
Behaviour Freq. per Interactant Sex	2.0/2, 1474/.24	2.3/4, 4922/.3	0.9/2, 2016/.7
Behaviour Freq. / Body Orientation	2.3/11, 1646/.17	.5/12, 4914/.23	2.6/10, 2050/.21
Behaviour Freq. / Head Orientation	1.8/11, 1646/.15	1.4/12, 4914/.32	6.4/10, 2050/.2

Table 45: Mean interaction distances (cm) for each sequence type at each site.

Sequence Type	Miquelon		North Rona		Sable Island	
	Mean	SD/N	Mean	SD/N	Mean	SD/N
Aggressive	37.1	62.8/722	149.2	395.9/3137	117.1	187.5/1689
Copulatory	--	--	14.4	55.2/1105	21.4	65./286
Play	5.8	17.7/935	5.0	21.9/145	--	--
M/P Interaction	--	--	12.5	40.7/539	16.5	56.7/84

Table 46: Mean weighted frequency of behaviour in each sequence type category subdivided by study site.

Sequence Type	Miquelon		North Rona		Sable Island	
	Mean	**SD/N**	**Mean**	**SD/N**	**Mean**	**SD/N**
Aggressive	0.158	0.257/722	0.08	0.15/3137	0.094	0.217/1689
Copulatory	--	--	0.01	0.01/1105	0.007	0.005/286
Play	0.023	0.028/935	0.026	0.028/145	--	--
M/P Interaction	--	--	0.053	0.2/539	0.025	0.017/84

N = number of cases

Table 47: Sequence type categories subdivided by sequence sexes.

Sequence Type	Male-Male		Female-Female		Male-Female	
	N	Percentage	N	Percentage	N	Percentage
Aggressive	126	95.5	35	85.4	91	70.5
Copulatory		-		-	28	21.7
Play	6	4.5	4	9.8	8	6.2
M/P Interaction		-	2	4.9	2	1.6

Table 48: F-test (1 and 2 Factor ANOVA) values for the effects of sequence sexes (independent variable) on selected dependent variables.

Dependent Variable	**F Values (F/df/p)**		
	Miquelon	**North Rona**	**Sable Island**
Response Latency	11.2/2, 1308/$p \leq .05$/$\hat{\omega}^2 = .11$	12.3/2, 4222/.06	4.2/2, 1975/.21
Group Vigilance	2.3/2, 1308/.3	1.0/2, 4222/.62	3.1/2, 1975/.29
Focal Area	31.3/2, 1308/$p \leq .05$/$\hat{\omega}^2 = .3$	2.0/2, 4222/.6	18.1/2, 1975/$p \leq .05$/$\hat{\omega}^2 = .2$
Behaviour Freq. per Body Orien.	1.1/12, 1298/.26	0.7/12, 4912/.26	1.8/12, 1965/.25
Behaviour Freq. per Head Orien.	0.7/12, 1298/.3	1.3/12, 4912/.31	3.2/12, 1965/.4

Table 49: Male precedent trend data from North Rona.

Date[1]	Mean Vigilance	Mean Focal Circle	Mean Focal Male	Mean Distance (cm)	Mean Duration (sec)	Response Latency (sec)	Total Duration (sec)	Weighted Behaviour Frequency
266	1.2	8.3	2.0	941.0	5.0	2.4	106	0.128
267	1.0	9.9	2.0	269.0	2.1	3.5	189	0.052
268	1.4	8.9	1.7	51.5	2.4	1.5	184	0.057
272	1.6	6.6	1.0	102.2	2.3	2.0	121	0.164
278	1.3	20.0	3.4	39.9	5.3	1.8	185	0.022
279	1.4	9.7	2.8	171.6	3.3	3.4	764	0.023
285	3.0	7.0	1.2	686.5	2.7	1.2	239	0.055
286	3.1	12.7	1.5	148.5	2.6	1.1	67	0.185
287	0.5	8.0	1.0	19.7	1.6	1.7	480	0.016
289	0.5	9.4	2.0	87.1	16.1	1.4	1078	0.093
298	2.0	6.0	1.0	140.5	1.8	3.3	115	0.087
299	1.8	9.0	1.7	34.2	3.4	1.1	294	0.022
301	1.0	9.9	1.2	254.9	2.9	1.1	213	0.054
302	1.1	8.6	1.6	67.7	5.1	1.6	348	0.044
303	1.7	10.5	1.6	65.8	5.6	1.4	425	0.038
304	1.8	9.5	1.6	39.6	4.3	1.4	546	0.03
309	1.0	7.0	1.0	20.7	5.6	1.4	974	0.029
311	0.3	6.7	1.0	59.7	1.9	0.9	29	0.336
Lvariable	**1690.5**	**1698.0**	**1846.5** D	**2292.0** D	**1770.0**	**1920.0** D	**1416.0**	**1686.5**

[1] Note that the Date column assumes January 1st = 1, and does not represent a complete series.

D Significant decreasing trend.

Table 50: Female precedent trend data from North Rona.

Date [1]	Mean Vigilance	Mean Social Circle	Mean Social Male	Mean Distance (cm)	Mean Duration (sec)	Response Latency (sec)	Total Duration (sec)	Weighted Behaviour Frequency
266	1.2	7.3	2.7	53.8	4.4	1.3	111.6	0.226
267	1.0	7.2	2.5	40.4	1.9	1.5	107.9	0.095
268	1.4	6.8	0.8	45.1	2.2	1.0	92.7	0.245
272	1.9	6.9	1.8	73.0	11.0	1.4	280.6	0.102
273	1.3	13.0	0.0	27.5	2.0	0.7	8.0	0.577
275	1.3	8.0	0.9	51.3	1.5	2.3	53.8	0.167
278	1.3	20.0	1.0	5.8	6.5	2.8	275.0	0.011
279	1.5	8.8	0.4	82.8	3.7	1.8	886.2	0.015
285	3.0	6.2	0.2	64.3	3.2	1.7	245.7	0.07
286	3.1	13.7	0.0	38.5	2.1	1.1	72.7	0.159
287	0.5	8.0	0.0	21.4	1.9	1.0	480.0	0.016
289	0.5	9.0	0.4	32.9	15.4	3.3	1068.6	0.05
298	2.0	6.0	1.0	142.8	2.2	2.8	115.0	0.087
299	1.5	7.3	0.6	35.8	3.4	1.7	307.4	0.029
301	1.0	9.6	0.0	147.2	4.3	2.4	268.0	0.047
302	1.1	8.4	0.7	67.5	3.8	1.5	293.9	0.039
303	1.7	8.1	0.0	56.2	5.7	2.1	521.3	0.059
304	1.8	8.0	0.0	33.4	5.8	1.8	749.1	0.015
309	1.0	7.0	0.1	21.3	8.1	1.6	984.3	0.026
311	0.3	6.7	0.2	62.5	2.7	1.0	28.5	0.338
Lvariable	**2300.5**	**2214.0**	**2583.0** [D]	**2221.0**	**2403.0**	**2371.5**	**2489.0** [I]	**2471.0** [D]

[1] Note that the Date column assumes January 1st = 1, and does not represent a complete series.

[D] Significant decreasing trend. [I] Significant increasing trend.

Table 51: Male-male interaction trend data from North Rona.

Date [1]	Mean Vigilance	Mean Focal Circle	Mean Distance (cm)	Mean Duration (sec)	Response Latency (sec)	Total Duration (sec)	Weighted Behaviour Frequency	Acts per Bout
266	1.2	8.3	941.0	5.0	2.4	106.4	0.128	12.1
267	1.0	9.0	525.8	2.6	4.7	310.0	0.022	16.0
268	1.5	10.3	64.0	2.5	1.3	243.7	0.024	28.1
278	1.3	20.0	72.2	4.1	1.6	84.0	0.036	9.0
279	1.7	12.0	1152.9	2.9	1.9	44.0	0.114	9.0
285	3.0	10.0	2886.7	2.6	1.8	166.0	0.036	23.0
286	3.2	6.0	983.3	8.7	0.8	29.0	0.345	3.5
289	0.5	7.6	257.5	2.7	1.0	22.6	0.401	7.6
301	1.0	10.0	768.7	3.7	1.6	62.0	0.097	8.5
303	1.6	12.1	51.4	1.8	1.1	90.5	0.06	29.5
304	1.8	10.9	42.9	2.0	1.1	102.2	0.055	37.0
$L_{variable}$	**423.5**	**377.5**	**434.0**	**435.0**	**475.5** [D]	**448.0**	**428.0**	**406.5**

[1] Note that the Date column assumes January 1st = 1, and does not represent a complete series.

[D] Significant decreasing trend.

Table 52: Female-female interaction trend data from North Rona.

Date[1]	Mean Arousal	Mean Social Circle	Mean Social Male	Mean Distance (cm)	Mean Duration (sec)	Response Latency (sec)	Total Duration (sec)	Weighted Behaviour Frequency
267	1.0	10.6	1.0	20.2	1.6	2.3	72.4	0.083
268	1.4	7.2	1.0	42.8	2.3	1.8	104.1	0.101
272	1.6	6.6	1.0	106.7	2.2	2.2	123.6	0.139
278	1.3	20.0	3.0	11.1	6.5	2.0	275.0	0.011
279	1.4	9.5	2.8	105.6	3.4	3.5	817.6	0.016
285	3.0	6.2	1.0	77.7	2.7	1.1	260.5	0.061
286	3.1	13.6	1.4	41.9	1.8	1.2	71.8	0.165
287	0.5	8.0	1.0	19.7	1.6	1.7	480.0	0.016
289	0.5	9.8	2.0	46.9	19.2	1.5	1327.1	0.02
298	2.0	6.0	1.0	140.6	1.8	3.3	115.0	0.087
299	1.8	9.0	1.1	34.2	3.4	1.1	294.2	0.023
301	1.0	9.9	1.1	182.8	2.8	1.1	234.4	0.048
302	1.1	8.6	1.6	69.4	5.2	1.6	357.9	0.035
303	1.8	9.0	1.0	80.0	9.3	1.7	753.4	0.016
304	1.8	8.4	1.4	37.2	6.0	1.6	861.9	0.012
309	1.0	7.0	1.0	20.7	5.5	1.4	973.8	0.029
311	0.3	6.7	1.0	59.7	1.9	0.9	28.8	0.336
$L_{variable}$	**1444.0**	**1469.0**	**1415.5**	**1424.0**	**1523.0**	**1558.0**	**1513.0** D	**1434.0**

[1] Note that the Date column assumes January 1st = 1, and does not represent a complete series.
D Significant decreasing trend.

Table 53: Male-female interaction trend data from North Rona.

Date[1]	Mean Vigilance	Mean Social Circle	Mean Social Female	Mean Distance (cm)	Mean Duration (sec)	Response Latency (sec)	Total Duration (sec)	Weighted Behaviour Frequency	Acts per Bout
267	1.0	10.6	3.9	20.2	1.6	2.3	72.4	0.083	15
268	1.4	7.2	1.0	42.8	2.3	1.8	104.1	0.101	21
272	1.6	6.6	0.9	106.7	2.2	2.2	123.6	0.139	16
278	1.3	20.0	1.0	11.1	6.5	2.0	275.0	0.011	19
279	1.4	9.5	0.5	105.6	3.4	3.5	817.6	0.016	97
285	3.0	6.2	0.3	77.7	2.7	1.1	260.5	0.061	50
286	3.1	13.6	0.0	41.9	1.8	1.2	71.8	0.165	27
287	0.5	8.0	0.0	19.7	1.6	1.7	480.0	0.016	61
289	0.5	9.8	0.5	46.9	19.2	1.5	1327.1	0.02	46
298	2.0	6.0	1.0	140.6	1.8	3.3	115.0	0.087	9
299	1.8	9.0	0.7	34.2	3.4	1.1	294.2	0.023	58
301	1.0	9.9	0.0	182.8	2.8	1.1	234.4	0.048	35
302	1.1	8.6	0.6	69.4	5.2	1.6	357.9	0.035	49
303	1.8	9.0	0.0	80.0	9.3	1.7	753.4	0.016	52
304	1.8	8.4	0.0	37.2	6.0	1.6	861.9	0.012	83
309	1.0	7.0	0.1	20.7	5.5	1.4	973.8	0.029	101
311	0.3	6.7	0.2	59.7	1.9	0.9	28.8	0.336	10
L_{variable}	**1467.5**	**1402.0**	**1435.0**	**1523.0**	**1465.0**	**1388.0**	**1410.0**	**1504.0**	**1377.0**

[1] Note that the Date column assumes January 1st = 1, and does not represent a complete series.

Table 54: Mean frequency of behavioural acts for interacting seals in each position in the haul-out group, at Miquelon, subdivided into a six-celled grid (Figure 7).

Position in Group	Frequency	SD	N
1 - Left Front	0.155	0.182	235
2 - Left Rear	0.031	0.064	703
3 - Centre Front	0.229	0.161	54
4 - Centre Rear	0.108	0.184	269
5 - Right Front	0.357	0.601	63
6 - Right Rear	0.034	0.076	300
7 - Isolated	0.107	0.120	33

Significantly different frequency values:

1 is significantly greater than **2** and **6**.
3 is significantly greater than **2**, **4** and **6**.
4 is significantly greater than **2**.
5 is significantly greater than **1**, **2**, **3**, **4**, **6** and **7**.

$(F = 79.8, df = 6, 1650, p \leq .05; \hat{\omega}^2 = 0.69)$

Table 55: F-test (ANOVA) values for the effects of interactant's position within the group (independent variable) and selected dependent variables.

Dependent Variable	F Values (F/df/*p*)		
	Miquelon	North Rona	Sable Island
Act Duration	2.7/6, 1650/.2	2.4/1, 4924/.7	1.2/1, 2057/.4
Total Duration	$12.1/6, 1650/p \leq .05/\hat{\omega}^2 = .07$	$241.9/1, 4924/p \leq .05/\hat{\omega}^2 = .07$	$289.4/1, 2057/p \leq .05/\hat{\omega}^2 = .12$
Interseal Distance	2.3/6, 1650/.24	$21.1/1, 4924/p \leq .05/\hat{\omega}^2 = .15$	$9.4/1, 2057/p \leq .05/\hat{\omega}^2 = .01$
Group Vigilance	$21.2/6, 1650/p \leq .05/\hat{\omega}^2 = .26$	$30.2/1, 4924/p \leq .05/\hat{\omega}^2 = .01$	$579.5/1, 2057/p \leq .05/\hat{\omega}^2 = .32$

Table 56: F-test (1 and 2 Factor ANOVA) values for the effects of substratum type (independent variable) on selected dependent variables.

Dependent Variable	**F Values (F/df/p)**	
	Miquelon	**North Rona**
Act Duration	0.7/1, 1655/.42	1.4/2, 4925/.25
Total Duration	364.3/1, 1655/$p \leq .05/\hat{\omega}^2 = .18$	202.6/2, 4925/$p \leq .05/\hat{\omega}^2 = .26$
Response Latency	0.25/1, 1655/.62	1.6/2, 4925/.2
Interseal Distance	17.7/1, 1655/$p \leq .05/\hat{\omega}^2 = .01$	46.2/2, 4925/$p \leq .05/\hat{\omega}^2 = .06$
Group Vigilance	315.6/1, 1655/$p \leq .05/\hat{\omega}^2 = .16$	58.9/2, 4925/$p \leq .05/\hat{\omega}^2 = .09$
Focal Area	62.0/1, 1655/$p \leq .05/\hat{\omega}^2 = .04$	18.8/2, 4925/$p \leq .05/\hat{\omega}^2 = .13$
Behaviour Frequency	75.5/1, 1655/$p \leq .05/\hat{\omega}^2 = .06$	3.4/2, 4925/$p \leq .05/\hat{\omega}^2 = .1$
Behaviour Frequency per Precedent Sex	29.2/3, 1481/$p \leq .05/\hat{\omega}^2 = .08$	14.2/3, 4557/.27
Behaviour Frequency per Body Orientation	18.1/9, 1648/$p \leq .05/\hat{\omega}^2 = .14$	2.4/9, 4907/.41
Behaviour Frequency per Head Orientation	2.8/9, 1648/.22	4.6/9, 4904/.36
Behaviour Frequency per Sequence Type	6.9/2, 1655/.12	7.9/5, 4921/.1

All interactions at Sable Island were performed on a sand substratum.

Table 57: F-test (1 and 2 Factor ANOVA) values for the effects of substratum slope (independent variable) on selected dependent variables.

Dependent Variable	**F Values (F/df/p)**	
	North Rona	**Sable Island**
Act Duration	0.7/1, 4925/.42	0.23/1, 2057/.63
Total Duration	$364.3/1, 4925/p \le .05/\hat{\omega}^2 = .18$	$965.0/1, 2057/p \le .05/\hat{\omega}^2 = .18$
Response Latency	0.25/1, 4925/.62	0.27/1, 2057/.6
Interseal Distance	$17.7/1, 4925/p \le .05/\hat{\omega}^2 = .01$	$87.3/1, 2057/p \le .05/\hat{\omega}^2 = .14$
Group Vigilance	$315.6/1, 4925/p \le .05/\hat{\omega}^2 = .16$	$107.2/1, 2057/p \le .05/\hat{\omega}^2 = .22$
Focal Area	$62.0/1, 4925/p \le .05/\hat{\omega}^2 = .04$	$203.5/1, 2057/p \le .05/\hat{\omega}^2 = .41$
Behaviour Frequency per Precedent Sex	12.4/1, 4559/.23	8.5/1, 2017/.21
Behaviour Frequency per Body Orientation	1.2/9, 4909/.44	$24.3/9, 2051/p \le .05/\hat{\omega}^2 = .33$
Behaviour Frequency per Head Orientation	5.7/9, 4903/.2	4.7/9, 2051.31
Behaviour Frequency per Sequence Type	$10.1/3, 4926/p \le .05/\hat{\omega}^2 = .24$	3.1/2, 2057/.28

All interactions at Miquelon occurred on virtually flat substrata.

Table 58: F-test (1 and 2 Factor ANOVA) values for the effects of weather type (independent variable) on selected dependent variables.

Dependent Variable	F Values (F/df/p)		
	Miquelon	North Rona	Sable Island
Act Duration	1.3/1, 1655/.2	0.59/3, 4922/.62	1.1/4, 2054/.37
Total Duration	3.1/1, 1655/.1	256.9/3, 4922/$p \leq .05$/$\hat{\omega}^2 = .29$	18.8/4, 2054/$p \leq .05$/$\hat{\omega}^2 = .33$
Response Latency	1.5/1, 1655/.51	2.7/3, 4922/.16	0.19/4, 2054/.95
Interseal Distance	18.4/1, 1655/$p \leq .05$/$\hat{\omega}^2 = .11$	39.1/3, 4922/$p \leq .05$/$\hat{\omega}^2 = .05$	6.3/4, 2054/$p \leq .05$/$\hat{\omega}^2 = .07$
Group Vigilance	221.4/1, 1655/$p \leq .05$/$\hat{\omega}^2 = .11$	136.0/3, 4922/$p \leq .05$/$\hat{\omega}^2 = .17$	108.1/4, 2054/$p \leq .05$/$\hat{\omega}^2 = .09$
Focal Area	51.0/1, 1655/$p \leq .05$/$\hat{\omega}^2 = .19$	96.9/3, 4922/$p \leq .05$/$\hat{\omega}^2 = .27$	190.2/4, 2054/$p \leq .05$/$\hat{\omega}^2 = .22$
Behav. Frequency	0.8/1, 1655/.22	1.9/3, 4922/.41	1.4/4, 2054/.36
Behav. Frequency per Precedent Sex	1.5/1, 1475/.34	2.1/1, 4559/.29	0.9/1, 2017/.43
Behav. Frequency per Body Orien.	0.7/9, 1648/.48	1.1/9, 4907/.46	1.2/9, 2051/.4
Behav. Frequency per Head Orien.	12.1/9, 1648/$p \leq .05$/$\hat{\omega}^2 = .06$	2.3/9, 4904/.36	2.9/9, 2051/.36
Behav. Frequency / Sequence Type	5.1/1, 1656/.29	0.7/3, 4923/.67	2.0/2, 2057/.33

Table 59: F-test (1 and 2 Factor ANOVA) values for the effects of wind velocity (independent variable) on selected dependent variables.

Dependent Variable	**F Values (F/df/*p*)**		
	Miquelon	**North Rona**	**Sable Island**
Act Duration	0.96/1, 1655/.32	2.5/1, 4925/.06	1.0/1, 2057/.31
Total Duration	538.9/1, 1655/$p \leq .05/\hat{\omega}^2 = .24$	210.6/1, 4925/$p \leq .05/\hat{\omega}^2 = .24$	53.0/1, 2057/$p \leq .05/\hat{\omega}^2 = .13$
Response Latency	5.1/1, 1655/$p \leq .05/\hat{\omega}^2 = .01$	4.4/1, 4925/.06	.20/1, 2057/.66
Interseal Distance	1.6/1, 1655/.21	43.2/1, 4925/$p \leq .05/\hat{\omega}^2 = .15$	72.6/1, 2057/$p \leq .05/\hat{\omega}^2 = .07$
Group Vigilance	796.3/1, 1655/$p \leq .05/\hat{\omega}^2 = .32$	2.7/1, 4925/.2	38.1/1, 2057/$p \leq .05/\hat{\omega}^2 = .1$
Focal Area	382.9/1, 1655/$p \leq .05/\hat{\omega}^2 = .19$	126.7/1, 4925/$p \leq .05/\hat{\omega}^2 = .17$	294.2/1, 2057/$p \leq .05/\hat{\omega}^2 = .29$
Behav. Frequency	2.7/1, 1655/.20	0.9/1, 4925/.11	0.4/1, 2057/.06
Behav. Frequency per Precedent Sex	3.1/1, 1475/.2	1.3/1, 4559/.35	44.4/1, 2017/$p \leq .05/\hat{\omega}^2 = .32$
Behav. Frequency per Body Orien.	2.3/9, 1648/.28	0.2/9, 4907/.57	1.3/9, 2051/.41
Behav. Frequency per Head Orien.	4.1/9, 1648/.31	1.1/9, 4904/.22	32.9/9, 2051/$p \leq .05/\hat{\omega}^2 = .18$
Behav. Frequency / Sequence Type	2.1/1, 1656/.14	1.3/3, 4923/.46	2.2/2, 2057/.22

Table 60: F-test (1 and 2 Factor ANOVA) values for the effects of wind direction (independent variable) on selected dependent variables.

Dependent Variable	F Values (F/df/p)		
	Miquelon	North Rona	Sable Island
Act Duration	1.7/2, 1654/.19	1.0/5, 4920/.77	0.04/1, 2057/.85
Total Duration	759.3/2, 1654/$p \leq .05/\hat{\omega}^2 = .38$	111.0/5, 4920/$p \leq .05/\hat{\omega}^2 = .2$	51.4/1, 2057/$p \leq .05/\hat{\omega}^2 = .13$
Response Latency	1.3/2, 1654/.88	2.2/5, 4920/.06	0.05/1, 2057/.47
Interseal Distance	5.2/2, 1654/$p \leq .05/\hat{\omega}^2 = .12$	6.2/5, 4920/$p \leq .05/\hat{\omega}^2 = .02$	15.7/1, 2057/$p \leq .05/\hat{\omega}^2 = .1$
Group Vigilance	12.2/2, 1654/$p \leq .05/\hat{\omega}^2 = .09$	369.6/5, 4920/$p \leq .05/\hat{\omega}^2 = .07$	156.5/1, 2057/$p \leq .05/\hat{\omega}^2 = .28$
Focal Area	175.8/2, 1654/$p \leq .05/\hat{\omega}^2 = .16$	313.7/5, 4920/$p \leq .05/\hat{\omega}^2 = .5$	484.6/1, 2057/$p \leq .05/\hat{\omega}^2 = .31$
Frequency	1.6/2, 1654/.38	6.3/5, 4906/$p \leq .05/\hat{\omega}^2 = .03$	0.9/1, 2057/.07
Behav. Frequency per Precedent Sex	7.0/2, 1474/.1	2.3/5, 4920/.32	0.7/1, 2017/.13
Behav. Frequency per Body Orien.	22.3/10, 1647/$p \leq .05/\hat{\omega}^2 = .05$	0.4/14, 4902/.5	1.1/9, 2051/.42
Behav. Frequency per Head Orien.	0.2/10, 1647/.58	4.1/14, 4902/.14	29.8/1, 2057/$p \leq .05/\hat{\omega}^2 = .33$
Behav. Frequency / Sequence Type	3.2/2, 1657/$p \leq .05/\hat{\omega}^2 = .09$	1.1/8, 4918/.49	2.6/2, 2057/.2

Table 61: F-test (1 and 2 Factor ANOVA) values for the effects of orientation relative to the prevailing wind (independent variable) on selected dependent variables.

Dependent Variable	F Values (F/df/p)		
	Miquelon	North Rona	Sable Island
Act Duration	1.4/2, 1653/.25	3.5/2, 4922/$p \leq .05$/$\hat{\omega}^2 = .07$	2.7/2, 2055/$p \leq .05$/$\hat{\omega}^2 = .2$
Total Duration	53.0/2, 1653/$p \leq .05$/$\hat{\omega}^2 = .23$	48.3/2 4922$p \leq .05$/$\hat{\omega}^2 = .08$	2.6/2, 2055/.17
Response Latency	2.2/2, 1653/.08	1.5/2, 4922/.21	1.1/2, 2055/.24
Interseal Distance	22.3/2, 1653/$p \leq .05$/$\hat{\omega}^2 = .18$	30.2/2, 4922$p \leq .05$/$\hat{\omega}^2 = .07$	41.6/2, 2055/$p \leq .05$/$\hat{\omega}^2 = .3$
Group Vigilance	8.0/2, 1653/$p \leq .05$/$\hat{\omega}^2 = .15$	63.4/2, 4922$p \leq .05$/$\hat{\omega}^2 = .13$	7.2/2, 2055/$p \leq .05$/$\hat{\omega}^2 = .24$
Focal Area	40.0/2 1653/$p \leq .05$/$\hat{\omega}^2 = .3$	21.8/2, 4922/$p \leq .05$/$\hat{\omega}^2 = .07$	20.3/2, 2055/$p \leq .05$/$\hat{\omega}^2 = .14$
Behav. Frequency per Precedent Sex	1.6/3, 1254/.57	1.1/3, 3775/.6	2.8/3, 1682/.55
Behav. Frequency per Body Orien.	0.3/2, 1255/.74	6.1/2, 4008/$p \leq .05$/$\hat{\omega}^2 = .04$	1.3/2, 1725/.71
Behav. Frequency per Head Orien.	0.3/2, 1254/.75	1.1/2, 4006/.7	0.9/2, 1725/.78
Behav. Frequency / Sequence Type	3.9/3, 1254/$p \leq .05$/$\hat{\omega}^2 = .2$	2.0/4, 4012/.56	4.1/5, 1720/.13

Table 62: Pearson Correlation values between time of day (independent variable) and selected dependent variables.

Dependent Variable	Pearson Correlation Values (r/df)		
	Miquelon	North Rona	Sable Island
Act Duration	0.05/1657	-0.004/4926	0.03/2059
Total Duration	0.24*/1657	0.37*/4926	0.31/2059
Response Latency	0.01/1657	-0.01/4926	0.04/2059
Interseal Distance	0.01/1657	-0.05/4926	-0.1/2059
Group Vigilance	-0.17/1657	0.12/4926	0.42*/2059
Focal Area	-0.3*/1657	-0.25*/4926	-0.4*/2059
Male Behaviour Frequency	-0.11/1164	0.03/2112	0.01/1424
Female Behaviour Frequency	0.002/321	0.22/2447	0.01/593

* indicates correlation values significant at $p \leq .05$.

Table 63: Spearman Correlation values between the time relative to high tide (independent variable) and selected dependent variables.

Dependent Variable	Spearman Correlation Values (rho/df)		
	Miquelon	North Rona	Sable Island
Act Duration	0.01/1657	0.01/4926	-0.02/2059
Total Duration	-0.07*/1657	-0.025/4926	0.03/2059
Response Latency	0.01/1657	0.008/4926	-0.06/2059
Interseal Distance	0.28*/1657	0.07/4926	0.01/2059
Group Vigilance	0.04/1657	0.03/4926	0.04/2059
Focal Area	0.05*/1657	0.007/4926	0.3/2059

* indicates correlation values significant at $p \leq .05$.

Table 64: Spearman correlation values between horizontal visibility (independent variable) and selected dependent variables.

Dependent Variable	Spearman Correlation Values (rho/df)		
	Miquelon	North Rona	Sable Island
Act Duration	-0.08/1657	0.03/4926	0.07/2059
Total Duration	0.02/1657	0.031/4926	0.02/2059
Response Latency	0.01/1657	-0.03/4926	0.04/2059
Interseal Distance	0.02/1657	0.04/4926	0.01/2059
Group Vigilance	-0.03/1657	-0.06/4926	0.001/2059
Focal Area	0.02/1657	0.01/4926	-0.04/2059
Behaviour Frequency	-0.06/1657	0.04/4926	0.02/2059
Male Behaviour Frequency	-0.02/1164	0.01/2112	0.01/1424
Female Behaviour Frequency	-0.03/321	-0.01/2447	0.01/593

* indicates correlation values significant at $p \leq .05$.

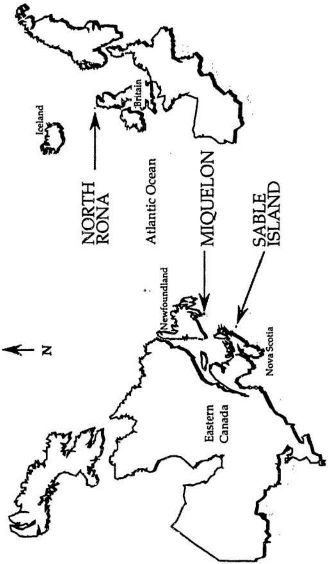


Figure 1:
Map showing the three study sites (Miquelon, North Rona and Sable Island) on the north Atlantic Ocean. Note that this projection renders the relative orientation of the continents inexact.

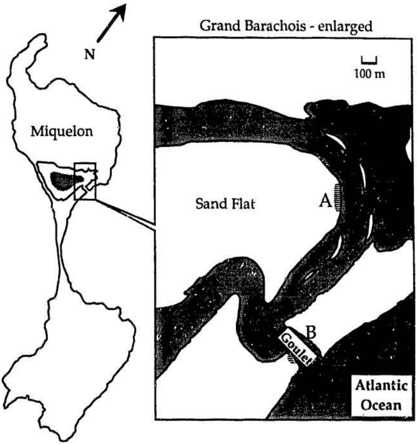


Figure 2:
Map of the island of Miquelon with an enlargement of the large tidal lagoon, the Grand Barachois. The locations of the grey seal group haul-outs (▤) and the two observation blinds (**A** and **B**) are indicated.

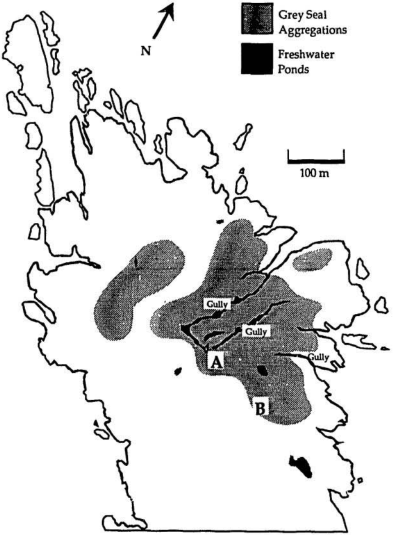


Figure 3:

Map of the northern tip of the island of North Rona, Scotland indicating the grey seal aggregations in this locale and the two consecutive locations of the observation blind (A and B).

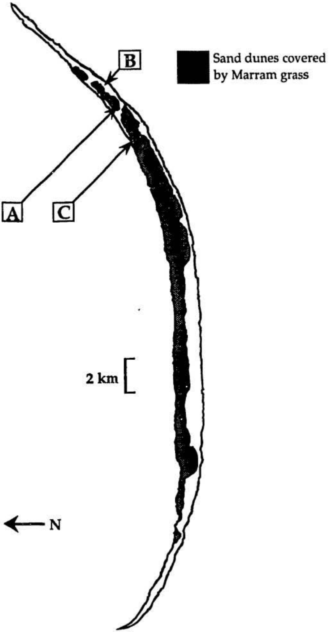


Figure 4:

Map of Sable Island, Nova Scotia with the three observation sites indicated (**A**, **B** and **C**).

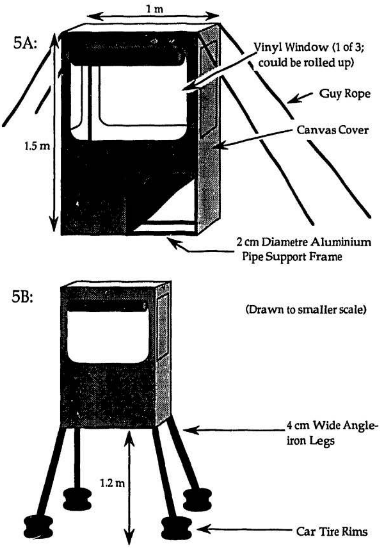
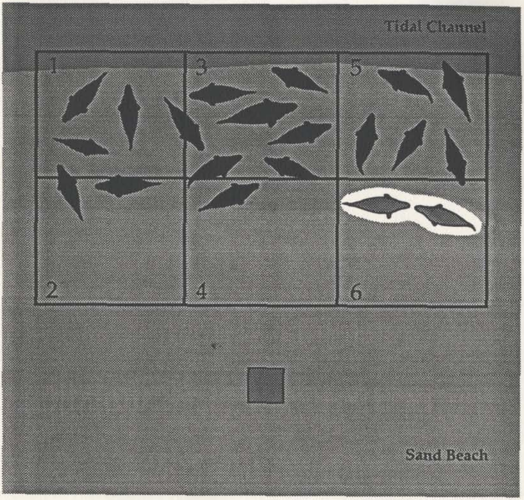


Figure 5:
The observation blinds used on North Rona (**5A**) and Miquelon (**5B**).

Figure 6:
A view of the landward periphery of a typical grey seal haul-out group at Miquelon.



(Grid dimensions are not drawn to scale)

Figure 7:

This figure illustrates the use of an imaginary six-celled grid established within a haul-out group of grey seals at Miquelon. The total width of the grid was continuously adjusted so that its left and right edges corresponded to the positions of seals on the left and right ends of the haul-out group. Note the interaction in cell six (denoted by lighter-coloured silhouettes). Cells were chosen for sampling using either the roll of a six-sided die or a random number table; new cells were selected if either the original interaction ceased, or if no interactions occurred in the first cell. The observation blind is represented by the smaller square on the landward side of the grid.

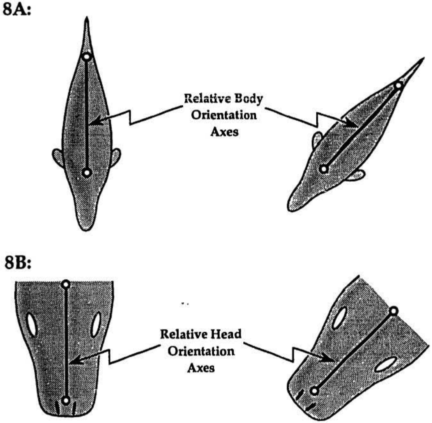


Figure 8:

A) Body Orientation was defined as the relative orientation of the the interactants' bodies and was determined by comparing the relative positions of imaginary lines drawn from the two seals' shoulders to the bases of their hind flippers. This category took its first and subsequent values relative to the position of the first interactant.

B) Head Orientation was defined as the relative orientation of the the interactants' heads and was determined by comparing the relative positions of imaginary lines drawn from the two seals' noses to the bases of their skulls. This category took its first and subsequent values relative to the position of the first interactant.

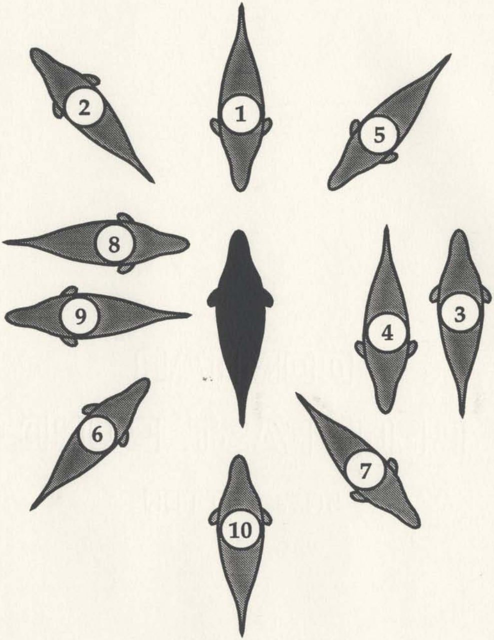


Figure 9:

The relative orientation of the the interactants' bodies. 1 - facing towards, from directly ahead, 2 - facing away, from anterior, 3 - parallel, same direction, 4 - parallel, opposing direction, 5 - facing towards, from obliquely ahead, 6 - facing towards, from obliquely behind, 7 - facing away, from posterior, 8 - facing towards, perpendicular, 9 - facing away, perpendicular and 10 - facing towards, from directly behind.

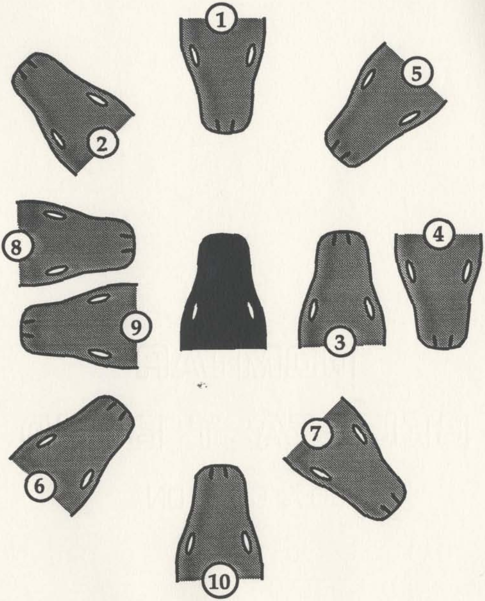


Figure 10:

The relative orientation of the the interactants' heads. **1** - facing towards, from directly ahead, **2** - facing away, from anterior, **3** - parallel, same direction, **4** - parallel, opposing direction, **5** - facing towards, from obliquely ahead, **6** - facing towards, from obliquely behind, **7** - facing away, from posterior, **8** - facing towards, perpendicular, **9** - facing away, perpendicular and **10** - facing towards, from directly behind.

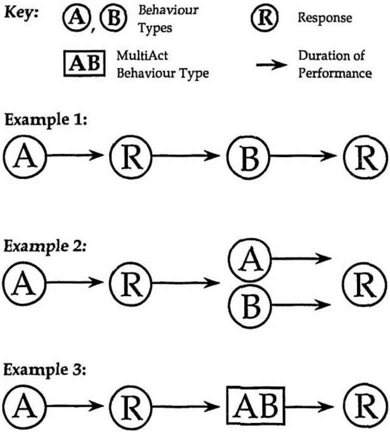
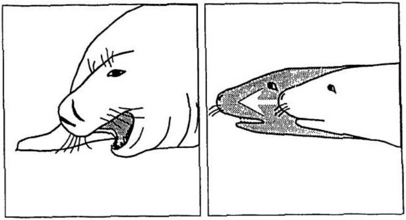
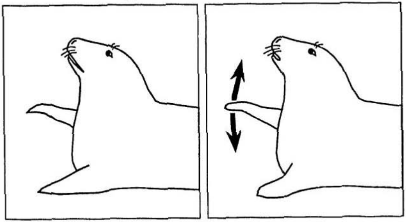


Figure 11:
This figure demonstrates the approach used to code a behavioural act in which a seal performed more than one defined behaviour act at the same time. In most cases (**Example 1**), a seal performed a single behaviour act to which the respondent reacted. In rare instances (**Example 2**) a seal performed more than one defined behaviour act at the same time. These sequences were coded with a set of provisional MultiAct behaviour labels (***Example 3***).



(A) Open Mouth Display

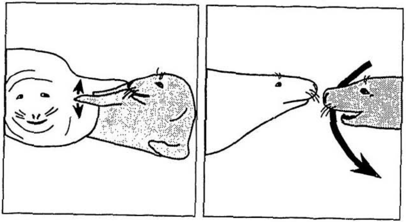
(B) Head Thrust



(C) Extend Foreflipper

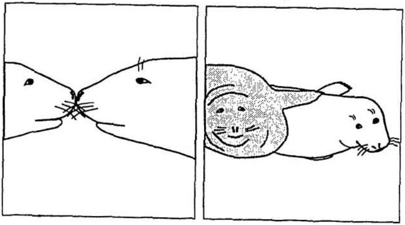
(D) Foreflipper Wave

Figure 12:
Figures illustrating the behaviour types: (A) Open mouth display, (B) Head thrust (C) Extend Foreflipper and (D) Foreflipper wave.



(A) Foreflipper scratch successor

(B) Head swing

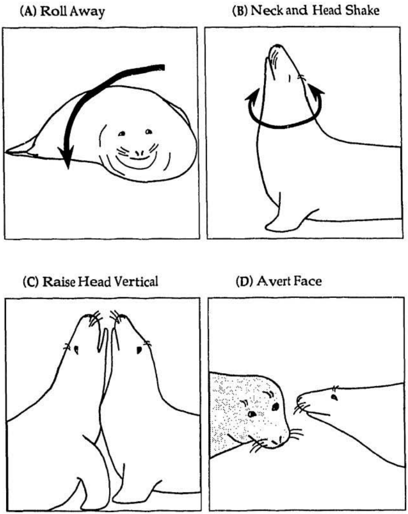


(C) Nose-to-nose

(D) Clasp

Figure 13:

Figures illustrating the behaviour types: (A) Foreflipper scratch successor, (B) Head swing, (C) Nose-to-nose and (D) Clasp.



(A) Roll Away

(B) Neck and Head Shake

(C) Raise Head Vertical

(D) Avert Face

Figure 14:

Figures illustrating the behaviour types: (A) Roll Away, (B) Neck and Head Shake, (C) Raise Head Vertical, and (D) Avert Face.

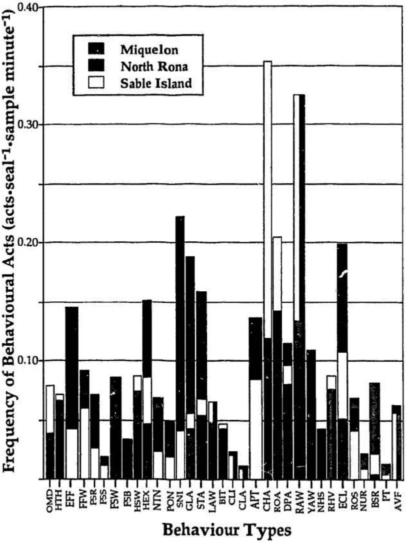


Figure 15:

Mean, behavioural act frequencies for each behaviour type at each study site. In this stacked histogram each column is a sandwich of mean values for each site with smaller values in the foreground. Similar values are arrayed side by side.

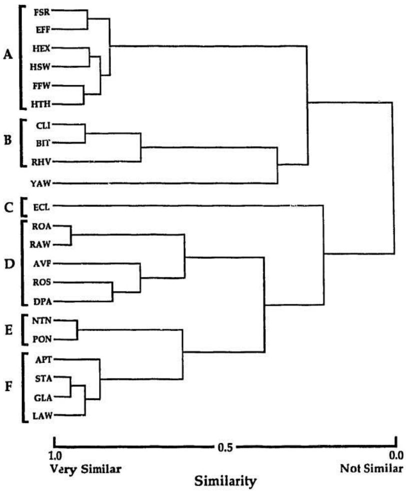


Figure 16:

Eye and mouth position were used as variables in complete linkage cluster analyses, using the distance method, of behaviour types at Miquelon. Clusters are indicated to the left of the tree diagram and discussed in the text.

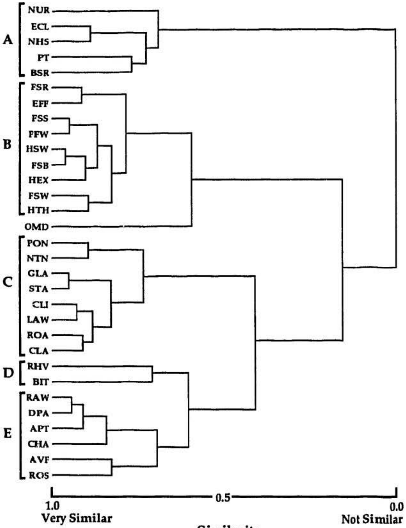


Figure 17:

Eye and mouth position were used as variables in complete linkage cluster analyses, using the distance method, of behaviour types at North Rona. Clusters are indicated to the left of the tree diagram and discussed in the text.

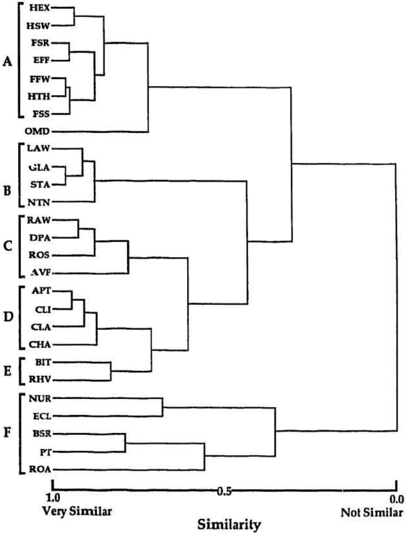


Figure 18:

Eye and mouth position were used as variables in complete linkage cluster analyses, using the distance method, of behaviour types at Sable Island. Clusters are indicated to the left of the tree diagram and discussed in the text.

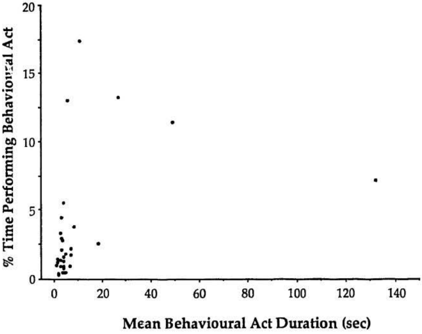


Figure 19:

Plot illustrating lack of relationship between the percent time spent performing a behavioural act and its mean duration (using data aggregated from all study sites). This was true for each study site as well.

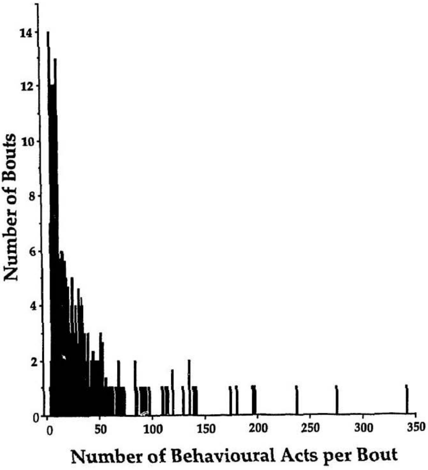


Figure 20:

This histogram displays interactive bouts subdivided on the basis of the number of acts performed per bout (using data aggregated from all sites).

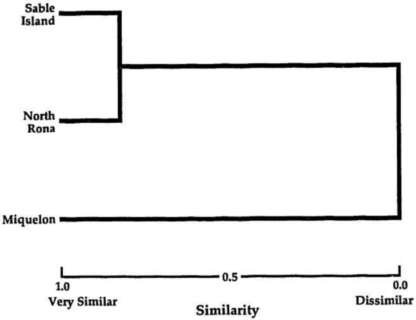


Figure 21:

The relative proportion of male and female seals within the Focal Area were selected as variables in a complete linkage cluster analyses, using the distance method, of the three study sites.

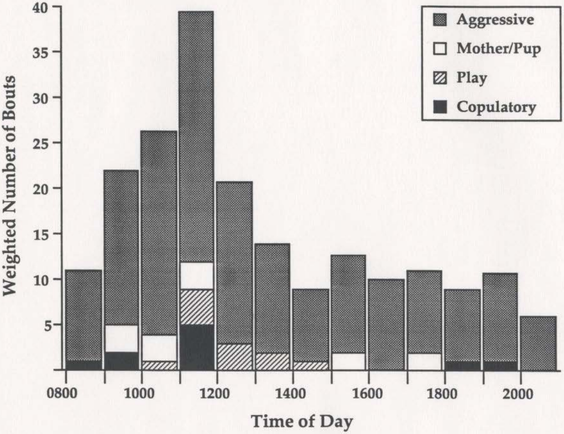


Figure 22:

This figure displays the total number of bouts subdivided, by sequence type, that occurred in indicated time intervals (using data from all study sites). The amount of observation effort for each interval was not significantly different and each interval count was weighted by dividing it by the total observation effort (time) in that interval.

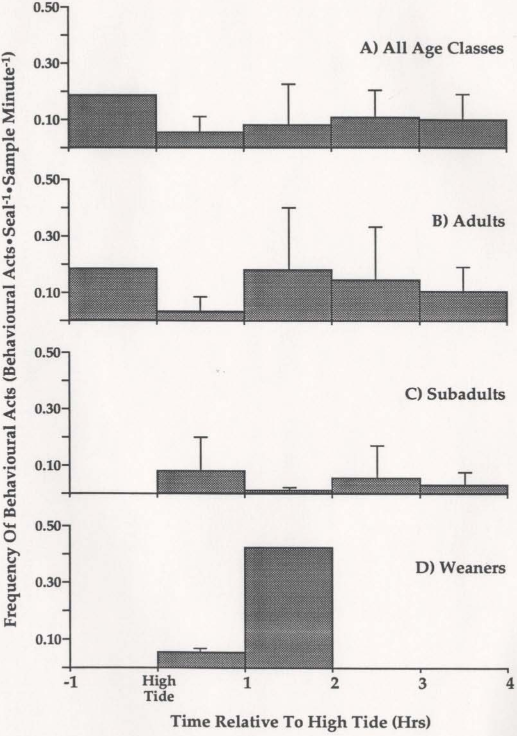


Figure 23:
Weighted frequencies of behavioural acts at Miquelon relative to the time of high tide (overall, and subdivided by age class). Error bars represent SD values.

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Appendix A: Detachable Reference Card Listing Grey Seal Behaviour Types

Appendix B: Chi-square Test Estimates and Corrections

In cases where the degrees of freedom exceeded 100 (the maximum in tables of chi-square values such as those in Rohlf and Sokal (1969), I used the following formula to calculate the necessary minimum chi-square quantiles:

$$\chi^2_{\alpha\,(\infty)} = \frac{1}{2}\left\{t_{2\alpha\,(\infty)} + \sqrt{2\surd - 1}\right\}^2$$

where the value $t_{2\alpha\,(\infty)}$ is derived from a table of the Student's *t* distribution with $df = \infty$ and $p = (2 \times \alpha)$, and $\surd$ is the desired degrees of freedom (Patel *et al.*, 1976; Powell, 1982; Rohlf and Sokal, 1969).

For example, to calculate the minimum chi-square value in the case where the degrees of freedom are 120 and $p \leq .05$:

$$\chi^2_{0.05\,(120)} = \frac{1}{2}\left\{1.645 + \sqrt{2(120) - 1}\right\}^2 = 146.3$$

This method has proven to be far more precise than extrapolation from tables of chi-square quantiles of df < 100 (Patel *et al.*, 1976). The derived chi-square values are listed as "minimum χ^2(df value)" in the Results sections.

Corrections for small expected frequencies were made during calculations of chi-square statistics. Where the df = 1 and the expected frequencies for any cell were smaller than 10, or the total number of occurrences of the behaviour type was equal to or less than 40, I applied a Yates correction for continuity (Keppel and Saufley, 1980; Yates, 1934). Since guide-lines are inconsistent with regards to performing chi-square tests with sample sizes less than 20 (Losey, pers. comm.), I used a Yates-corrected value in these instances as well.

Where I compared three or more values using the chi-square test, I first performed an overall assessment. If this was significant, I determined individual values' contributions by collapsing the smaller values into a single cell and partitioning the degrees of freedom. These (df - 1) *post-hoc* chi-square tests compared the collapsed cell values with the largest single value (Abraham Ross, pers. comm.; Keppel and Saufley, 1980). For example, where:

Cell Number	Observed Values	Expected Values
1	45	20
2	5	20
3	10	20
	$\chi^2 = 47.5$, df = 2, $p \leq .05$	

The smaller chi-square value indicates that there is a deviation of observed from expected values. A (2- 1 df) *post-hoc* chi-square test with partitioned degrees of freedom is then used to determine if the first cell value is larger than the others:

Cell Number	Observed Values	Expected Values
1	45	20
2 + 3	15	40
	$\chi^2 = 32.5$, df = 1, $p \leq .05$	

In this example, the value of cell 1 is larger than 2 or 3.

Appendix C: Partitioning Variance During ANOVA Using Omega Squared

The primary problem with the F ratio is that its size is directly related to that of the sample (Keppel and Saufley, 1980; Maxwell and Delaney, 1990), and more importantly, nothing can be said about the magnitude of the variation that can be attributed to the treatment. In the context of this thesis, the categories within the independent variables are "treatments". A comparison of dependent variable values of subjects assigned to groups on the basis of an independent variable is an "experiment".

While rarely cited in the animal behaviour literature (Keppel, 1982; Keppel and Saufley, 1980), the omega squared index ($\hat{\omega}^2_A$) provides an invaluable estimate of the magnitude of treatment effects: its value represents the percentage of the total variance accounted for by the experimental treatments. If both the F value and the omega squared index are large, then the difference between the treatment conditions is statistically significant (a significant F value), and this difference represents a sizable effect (a large omega squared value).

A formula for calculating the omega squared index is:

$$\text{Estimated magnitude of treatment} = \text{omega squared } (\hat{\omega}^2_A) = \frac{\hat{\sigma}^2_A}{\hat{\sigma}^2_A + \hat{\sigma}^2_{S|A}}$$

where $\hat{\sigma}^2_A$ = the estimated population treatment effects, and
$\hat{\sigma}^2_{S|A}$ = the estimated population error variance

For further discussion of this estimate, see Keppel and Saufley (1980), Kirk (1982), Maxwell and Delaney (1990) or Yaremko *et al.* (1982).

Appendix D: Page's $L_{critical}$ Values

With a single column of data, I used a formula, detailed in Page (1963), to derive the following $L_{critical}$ values for one column with $p \leq .05$. Note that the formula requires a minimum of four row values.

Number of Rows (number of ranked values)	**$L_{critical}$ Value**
4	29.8
6	86.4
7	130.9
8	188.2
9	260.0
10	347.9
11	457.2
13	723.7
14	835.4
16	1300.8
17	1545.3
18	1818.4
19	2115.8
20	2456.7

Appendix E: Other Site Comparisons

Response Latency

The mean response latency was 1.7 sec (SD = 3.4), with the smallest value being zero sec and the largest 104 sec.

There were no significant differences among the study sites on the basis of the mean time between the precedent's behavioural act and the successor's. The response latency at North Rona ($\bar{x} = 1.8$ sec) was not different than that of the other sites, which were also not sufficiently different (Miquelon:$\bar{x} = 1.5$ sec; Sable Island: $\bar{x} = 1.6$ sec; $F = 5.6$, df = 2, 8639, $p \leq .05$; but $\hat{\omega}^2 = .11$).

1) Sex Differences

At Miquelon, the response latency was unrelated to successor sex (male: $\bar{x} = 1.6$ sec; female: $\bar{x} = 1.4$ sec; $F = 0.9$, df = 1, 1485, $p = 0.14$). This was also true at North Rona (male: $\bar{x} = 1.8$ sec; female: $\bar{x} = 1.8$ sec; $F = 0.01$, df = 1, 4535, $p = 0.22$) and Sable Island (male: $\bar{x} = 1.5$ sec; female: $\bar{x} = 1.7$ sec; $F = 3.1$, df = 1, 2016, $p = 0.09$). Results were virtually identical when response latency differences were assessed using precedent sex instead.

2) Age Class Differences

Amongst non-breeding seals at Miquelon, the response latency of adult seals ($\bar{x} = 1.7$ sec), subadults ($\bar{x} = 1.3$ sec) and weaned pups ($\bar{x} = 1.1$ sec) were not sufficiently different ($F = 4.1$, df = 2, 1656, $p \leq .05$; but $\hat{\omega}^2 = .24$). This was also the case for the breeding sites {North Rona (adult: $\bar{x} = 1.7$ sec; mother: $\bar{x} = 1.9$ sec, nursing pup: $\bar{x} = 1.5$ sec; weaned pup: $\bar{x} = 3.8$ sec; $F = 3.6$, df = 4, 4895, $p \leq .05$; but $\hat{\omega}^2 = .14$) and Sable Island (adult: $\bar{x} = 1.5$ sec; subadult: $\bar{x} = 1.0$ sec; mother: $\bar{x} = 1.8$ sec; nursing pup: $\bar{x} = 1.3$ sec; $F = 1.5$, df = 3, 2055, $p = 0.26$).

Appendix E: Other Site Comparisons (cont.)

3) Interaction Distance Differences

There was no correlation between the distance between interacting seals and response latency at Miquelon ($r^2 = 0.02$, df = 1657, $p = 0.35$), North Rona ($r^2 = 0.01$, df = 4926, $p = 0.18$) or Sable Island ($r^2 = 0.2$, df = 2059, $p = 0.27$).

4) Sequences' Interactant Sex Differences

When subdivided on the basis of the sex of the interacting seals, the response latencies during bouts at Miquelon (male-male: $\bar{x} = 1.7$ sec; male-female: $\bar{x} = 1.4$ sec; female-female: $\bar{x} = 1.3$ sec; F = 1.8, df = 2, 1306, $p = .15$), North Rona (male-male: $\bar{x} = 1.6$ sec; male-female: $\bar{x} = 1.8$ sec; female-female: $\bar{x} = 1.7$ seconds; F = 0.8, df = 2, 4221, $p = .49$) and Sable Island (male-male: $\bar{x} = 1.5$ sec; male-female: $\bar{x} = 1.6$ sec; female-female: $\bar{x} = 1.2$ sec) were not significantly different (F = 0.8, df = 2, 1973, $p = .47$).

Multiple (Coincident) Acts

Most grey seals performed only one behavioural type at any one instant. A very small proportion performed more than one defined behaviour category coincidentally (multiact). This was true of Miquelon ($\chi^2 = 1422.1$, df = 1631, $p \leq .05$), North Rona ($\chi^2 = 4154.0$, df = 4877, $p \leq .05$) and Sable Island ($\chi^2 = 1764.6$, df = 2035, $p \leq .05$).

Horizontal Visibility

The estimated horizontal visibility was not sufficiently different at Miquelon ($\bar{x} = 975.1$ m), Sable Island ($\bar{x} = 964.2$ m) or North Rona($\bar{x} = 905.4$ m; F = 88.0, df = 2, 8641, $p \leq .05$; but $\hat{\omega}^2 = .21$). At each site, there were no significant correlations between horizontal visibility and act duration, total bout duration, response latency, inter-seal distance, vigilance level within the Focal Area or number of seals within the Focal Area (Table 64). This was also true for frequency of behaviour in bouts subdivided by precedent sex.