NOSING BEHAVIOUR IN CAPTIVE HARBOUR SEALS (Phoca vitulina concolor): IMPLICATIONS FOR OLFACTION AND AFFILIATION

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Nosing Behaviour in Captive Harbour Seals (*Phoca vitulina concolor*): Implications for Olfaction and Affiliation

by

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Abstract

Nosing behaviour has been shown to be an important component of social behaviour in a variety mammals. Some forms of social nosing are thought to serve as affiliative behaviours which promote group cohesion or tolerance; the olfactory and tactual senses may play a role in mediating these affiliative behaviours. In pinnipeds, nosing is thought to aid mothers in identifying their offspring, but little is known about nosing behaviours in contexts unrelated to mother-pup interaction. The objective of the present study was to examine the role of nosing in the social behaviour of captive harbour seals (*Phoca vitulina concolor*). Rates and types of nosing behaviour were expected to differ between individuals and between the breeding and non-breeding seasons.

In this study, general activity and nosing behaviour of six captive harbour seals were observed over 43 weeks. A significant triple interaction between type of nosing (solo and dyadic), seal, and season (breeding and non-breeding) was found [$F(5, 48)= 6.35$, $p<.05$]; some seals showed strong seasonal differences in solo and dyadic nosing rates while others did not. Dyadic nosing rates increased in the breeding season, while solo rates declined. Distinct individual differences were evident for most types of nosing, and seasonal patterns among males emerged for some types; for example, nose-to-nose and nose-to-body acts were more frequent during the breeding season, while nose-to-object acts were less frequent during this season. Solo and dyadic nosing acts were found to occur frequently and most often involved both open nares and protracted vibrissae, which may be indicative of olfactory and tactual involvement. A large proportion of nosing interactions, particularly nose-to-nose acts appeared to be mutually initiated and distinct partner preferences were evident, suggesting that some forms of nosing behaviour in harbour seals are affiliative. Quantification of affiliative behaviours, in conjunction with other measures, may help investigators address uncertainties regarding the social organization of wild seals. Further investigation is required to determine the exact role played by the olfactory and tactual senses in nosing behaviour.

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Chapter One: Introduction

The main goal of this study was to examine the role of nosing in the social behaviour of captive harbour seals (*Phoca vitulina concolor*). This goal raised a number of issues which are presented in this introductory chapter. First, because the study animals were captive, the ways in which a captive environment might influence social interactions were considered. These potential influences of captivity led to consideration of the concepts of social cohesion and affiliative behaviour as they might apply to captive harbour seals. In fact, various forms of nosing behaviours have been shown to serve an affiliative function in a broad range of mammals. Because both the olfactory and tactual senses are thought to mediate some nosing behaviours, it was also important to include a summary of information regarding olfactory and tactual communication in seals. This first chapter integrates the above ideas with respect to what is known about harbour seals and what can be learned by conducting observations of nosing events among a small number of captive individuals.

Behaviour and Social Cohesion in Captivity

Background. Observations of and experiments with captive animals are often the best means by which to directly investigate specific behavioural phenomenon. Particular questions may arise only from research with captive animals because of the possibility of frequent, short-range, or long-term observations of known animals. For instance, the subtleties of many types of social interaction may be best investigated with captive animals because the identity, sex, age and history of each individual can be taken into account in the behavioural analyses. However, whether or not the behaviour of interest is social in nature, it is necessary to acknowledge that some behavioural patterns of captive animals may differ significantly from those of their free-living counterparts. Ideally, then, captive research should be conducted in conjunction with field work (i.e., before, after or during) in order to assess the external validity of the inferences drawn from behavioural data from captive animals. Nonetheless, the behavioural patterns of captive animals are of inherent interest for a number of reasons, among which is that particular patterns may indicate methods by which individual animals cope with both the special challenges and opportunities of a captive environment.

<u>Constraints and Opportunities</u>. That captivity places constraints on an individual's behaviour is a well-known fact. For instance, choice of sexual or play partners is limited, territorial behaviours or migration patterns may be suppressed or altogether prevented, and some locomotory actions may be restricted due to the physical parameters of the captive environment. However, it is important to recognize that captivity also presents opportunities for individuals to create an environment utterly unlike that found in the wild. The captive individual is generally freed from survival pressures, such as the risk of predation, foraging requirements, food competition, and environmental variability (Markus & Croft, 1995). Thus, the captive animal is probably presented with the mixed

blessing of more free time. As a result, behavioural patterns of captive individuals can be expected to differ in quality or quantity from behaviours found in free-living members of the same species (Carlstead, 1996).

Boredom. Boredom, "the psychological response to an environment that fails to meet the animal's needs for stimulation due to low stimulus diversity" (Carlstead, 1996, p.326), may cause an individual to become lethargic or to seek changes in stimulation. As a result, captive animals may develop abnormal self-directed behaviours, such as autoaggression, self-mutilation, regurgitation/reingestion, food manipulation and coprophagy (Carlstead, 1996; Goosen & Ribbens, 1980). Stereotyped movement patterns, and occupational behaviours, such as food-begging, may also develop in captive animals (Morris, 1964; Odberg, 1978). However, even in a relatively impoverished physical environment, boredom may be significantly alleviated by the inclusion of social partners because, as stated by Carlstead, "social partners are an infinite source of response contingent stimulation, allowing an individual to interact with its surroundings to a much greater degree than if it were alone." (1996, p. 328).

Social Cohesion. Social interaction provides more than mere sensory stimulation to otherwise bored captive animals; the quality and quantity of social interactions may be integral to determining the degree of cohesion that exists within the captive population. Social cohesion is a concept that is often used to describe the social organization of a particular species – a species can be 'cohesive' and form groups, or be 'dispersive' and increase inter-individual space (e.g., see Wilson, 1974a). Clearly, there are flaws inherent in the use of such a dichotomous categorization, especially if it is used in its most absolute sense (e.g., see Fagan, 1981). However, social cohesion is a worthwhile construct when used to characterize a group of animals that are contact-prone or that are tolerant of close proximity with other individuals. In captivity, social cohesion is especially important because an individual has few, if any, of the options available to free-living animals for avoiding conflict. For example, a captive animal cannot avoid being in close proximity to another individual, at least not for an extended time period, so ignoring one another is rarely an option. In short, captive animals have the choice of either tolerating or harming one another, and tolerance requires the development of some degree of social cohesion.

It would appear that captive animals in most successful breeding colonies have opted for tolerance, but just how this is achieved is not always obvious. All too often, human observers focus their attention on the most conspicuous behaviours (e.g., fighting and mating), while failing to note the importance of the more frequently occurring but less striking affiliative behaviours which promote social cohesion. It is possible to distinguish between *general* affiliative behaviours that are often performed mutually, are contact-promoting, and allow individuals within a group to maintain a relatively 'friendly' and peaceful atmosphere (Mikulica & Labem, 1991; Peters, 1980; Salo, Shapiro & Dewsbury, 1993), and *specific* affiliative behaviours that occur for the purposes of obtaining a mate and in the context of parental care. At a recent conference on the integrative neurobiology of affiliation, affiliation was viewed as providing "a social matrix within which other behaviours, including reproduction and aggression, may occur" (Carter, Lederhendler & Kirkpatrick, 1997, p.xiii). Although reproductive and aggressive behaviours may also reduce distance between individuals, their expression is partially regulated by "a positive social fabric based on affiliations" (p.xiii). If this is true, then research into the social behaviour of a particular population, whether captive or free-living, is incomplete without considering the role of affiliative behaviours.

Implications for the Present Study. The present study addressed questions regarding affiliative behaviour in a captive breeding colony of harbour seals. This particular colony of seals has resided in an outdoor enclosure at the Ocean Sciences Centre (O.S.C.) in Logy Bay, Newfoundland since 1972. During this period, these seals have been subject to a number of scientific investigations on their behaviour, physiology, and sensory perception. These studies have been used to corroborate observations of the behaviour of free-ranging harbour seals or, sometimes, to infer the behaviour of wild seals at times when they cannot be observed (e.g., while at sea). Although the O.S.C. seals have bred successfully a number of times, no study has yet focused on the behavioural mechanisms by which these seals manage to live in relative peace in a restrictive environment. However, such a study is merited because captive environments can be regarded as an extreme point of the environmental range within which a species can survive and breed

(Rowell, 1967). Accordingly, questions of how behavioural variability relates to captivity and how it relates to ecological factors are merely two aspects of the same problem. In order to clarify the rationale for conducting the present study, it was necessary to provide both a brief summary of the life history of wild harbour seals and a description of the captive environment of the O.S.C. harbour seals.

Life History of Wild and Captive Harbour Seals

Wild Harbour Seals. Although harbour seals copulate and feed in the water, parturition occurs on land. Females aggregate at pupping grounds to give birth and nurse their pups, while males gather in the vicinity to await mating which occurs at the time of weaning; the moult occurs annually in late summer, shortly after the breeding season (Bigg, 1981). Pups are capable of swimming immediately following birth and are weaned within 23 or 24 days (Muelbert & Bowen, 1993). During the breeding season, a group of hauled-out wild harbour seals generally includes adult males, females with pups, juveniles, and pregnant females (Davis & Renouf, 1987). Despite the fact that most observations of wild harbour seals occur during this breeding/mating season when seals spend much of their time on land, the social organization of seals aggregated at haul-out grounds is unclear (Davis & Renouf, 1987; Godsell, 1988). However, during this approximately six-week period, documented social interactions include: (i) conflicts involving lactating females prior to weaning, (ii) mother-pup interactions, (iii) conflict between adults of both sexes, during and after weaning, (iv) adult-juvenile and juvenile-juvenile conflict,

(v) male display behaviour, and (vi) social play, predominately between yearlings (Davis & Renouf, 1987; Godsell, 1988; Perry, 1993; Renouf, 1991; Renouf & Lawson, 1986; Wilson, 1974a; Wilson & Kleiman, 1974).

As is the case with many species, investigations into the behaviour of harbour seals often focus on agonistic and aggressive behaviour; the former is defined as social fighting among conspecifics and includes threat, submission, chasing, and physical combat, but excludes predation, while the broader term of 'aggression' generally includes predation, defensive attacks on predators by prey, and attacks on inanimate objects (Drickamer & Vessey, 1982). In free-living harbour seals, agonistic behaviours appear to be common during the breeding season, which is the period when behavioural observations are usually made (Davis & Renouf, 1987; Evans & Bastian, 1969; Godsell, 1988; Walker & Bowen, 1993). During pupping, agonistic interactions commonly occur between females on land, while after weaning, most agonistic behaviours occur between males in the water. Some females may also respond agonistically in the water to approaches by males during the mating season. Based on a breeding season estimated to be 6 weeks in duration for Sable Island harbour seals (Walker & Bowen, 1993), an individual spends almost 90 percent of its life outside of the breeding season; however, very little is known about behavioural patterns of wild harbour seals during this non-breeding period. In addition, no study to date has investigated the relative frequency of affiliative to agonistic interactions in free-living harbour seals so that it is difficult to determine the role that agonism and affiliation play in their social structure.

There is little agreement about the social organization of free-living harbour seals. Some investigators consider them to be loosely gregarious on land but solitary when foraging (Bigg, 1981; Button, 1975; Scheffer & Slipp, 1944). Sullivan (1982) stated that harbour seals are a "distance species" (p.564); that is, they are highly intolerant of prolonged contact with conspecifics and if an individual's threshold distance is exceeded by an approaching seal, agonistic behaviour invariably ensues. Furthermore, Sullivan suggested that harbour seals develop strong linear dominance hierarchies based on sex and age. In contrast, Wilson (1974a; 1978) characterized harbour seals as highly cohesive and cooperative foragers with no overt competition between males for access to mates (cf. Perry, 1993). Wilson also proposed that harbour seals form a long-term network of social relationships and that seals foraging together at sea, stay together as groups when hauled-out. However, Davis and Renouf (1987) rejected both Wilson's notion that harbour seals participate in cooperative feeding activities and Sullivan's proposal of a dominance hierarchy. Instead, based on evidence for a consistent hauling-out pattern and a high degree of site fidelity, Davis and Renouf suggested that "the seals reunite during the breeding season to carry out the pupping and mating rituals in a manner dictated by the rules of their social organization" (1987, pp. 4). Thus, some form of social organization appears to exist in free-living harbour seals but its exact nature remains unclear.

Although some of the above discrepancies regarding harbour seal social behaviour may reflect different interpretations of the observed behavioural patterns (e.g., a tendency to see dominance hierarchies where they may not in fact exist), others may reflect population differences. Sullivan observed Pacific harbour seals (*Phoca vitulina richardsi*) in California, Wilson studied Atlantic harbour seals (*P. vitulina vitulina*) in Scotland and Ireland, while Davis and Renouf conducted their observations of Atlantic harbour seals (*P. vitulina concolor*) on the French Island of Miquelon. There is evidence that the social organization of a species may vary in the different habitats of its natural range (Rowell, 1967). Indeed, Davis and Renouf (1987) speculated that one reason they may not have found evidence of a dominance hierarchy as proposed by Sullivan (1982) is because at Miquelon there was enough space on the sand flats to accommodate all individuals. According to Perry (1993), the physical features of Miquelon may also explain her finding that males establish territories in water; that is, because the haul-out area at Miquelon was small enough, it could be easily defended. That two separate research teams interpreted the influence of the spatial constraints of Miquelon in an apparently contradictory manner highlights the difficulties associated with determining dominance and territoriality in harbour seals. At this time, there is insufficient data to speculate on possible population differences underlying the question of social structure and cooperative foraging in harbour seals.

<u>The O.S.C. Harbour Seals</u>. The degree of social complexity that exists in free-living harbour seals may be somewhat extraneous to a study of captive seals given the behavioural constraints of captivity. The O.S.C. harbour seals lived in an outdoor

enclosure consisting of three tanks of ambient sea water, surrounded by wooden decking for hauling-out and an adjacent gravel path by which technicians accessed a storage shed and another enclosure containing harp seals, *Phoca groenlandica* (see Methods for further details). During the present study six adults (5 males and 1 female) remained in this enclosure year-round (except for the female, following the birth of a pup). On occasion, seals left the tank/deck area and traversed the gravel strip either in the context of a social interaction, or in order to hide underneath the shed or deck. A daily feeding session, usually performed by a technician, occurred on deck and lasted for a minimum of 30 minutes. In addition, technicians frequented the enclosure daily in order to monitor the seals and maintain the enclosure.

Based on my observations, agonistic interactions appeared to be relatively rare in the O.S.C. seals, and when they did occur, they were most often of low intensity and rarely resulted in laceration or even physical contact. Apart from occasional agonism during feeding (e.g., a head thrust or growl/snort), most agonistic behaviours within the captive colony occurred during the breeding season and followed the same general pattern as that found in the wild (i.e., the mother was intolerant of other adults and inter-male conflict occurred). Of course, in captivity, it is more difficult for males to avoid conflict with other males during the breeding season, and particular signaling patterns (e.g., flipper-slapping and bubble-blowing) may play a role in determining the most likely candidate for mating with the sole captive female (Peddigrew, 1997; Perry, 1993; Sullivan, 1981). However, outside of the breeding season when agonistic behaviours were infrequent, social cohesion within the captive group was probably determined, to a great extent, by general affiliative behaviours.

That the O.S.C. seals have bred successfully a number of times (i.e., ten live births and two stillbirths since 1985) probably indicates that they are not overly-stressed or unhealthy. Nonetheless, these seals reside in a relatively impoverished captive situation. That is, the enclosure is considerably less complex than the dynamic wild environment and no attempt has been made to enrich the environment[1] through the inclusion of 'toys' or by naturalistic feeding methods (e.g., the presentation of live fish). At least two of the behaviours thought to reflect boredom in captivity, have been observed in the O.S.C. harbour seals: (i) a fish is sometimes played with extensively rather than being eaten or outright rejected (e.g., it is torn apart with the foreflippers and/or teeth, tossed in the air and caught again, or may be taken surreptitiously out of the feeding area and into one of the swimming tanks for further antics which may then include an additional seal or two), and (ii) regurgitation and reingestion of fish may occur either in the feeding area (whole fish only) or in the water, where regurgitation of partially digested fish is not usually followed by reingestion and may simply reflect overeating.

In general, there is very little change in the seals' physical environment, if at all, aside from naturally occurring changes in weather. Sensory stimulation, external to the

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[1] According to Carlstead (1996), "... 'environmental enrichment' means providing a complex and diverse environment that increases the possibility that the captive animal's own behavior will produce what it needs: finding food, demarcating a territory, building a nest, maintaining its physical condition, escaping conspecifics, or hiding." (p.327)

seal compound, included the sights, sounds and smells of people on the adjacent audience viewing platform, vehicles in the area surrounding the compound, activity of employees of the O.S.C., gulls and other bird-life in the vicinity, and aircraft flying overhead. Although sounds and smells also likely emanated from the other pinniped species in a nearby compound, these animals were not within visual or tactual range. In addition, seal technicians and researchers entered and exited the harbour seal compound regularly throughout the day, either to attend to the harbour seals themselves or to access adjacent facilities. These sources of stimulation may have activated the seals' visual, olfactory or auditory sensory systems. Despite these small daily events, no major changes in the seals' environment occurred during my period of observation.

Implications for the Present Study. The most regular sources of "excitement" for the seals included their daily feeding of herring and the daily activities of technicians within the compound. The seals' activity patterns appeared to revolve to a great extent around the daily feeding event; for instance, before their daily feeding, the seals were especially active and attentive to human activity outside the compound, presumably in anticipation of the arrival of food. However, apart from the feeding event and technician activity which occurred at any time during daylight, the seals had to provide much of their own diversion or sensory stimulation. Two possible options were: (i) tactual stimulation achieved, for example, through social interaction or object manipulation and (ii) chemical stimulation, either from sources external to the compound or from changing physiological states of other individuals within the same compound. The degree to which these sources of stimulation were utilized by each seal was largely under individual control and hence, could be considered true sources of environmental enrichment. Tactual and chemical stimulation may be of greater relative importance for captive harbour seals than for their free-living counterparts who, of course, have many other potential stimulatory diversions.

In brief, I suggest here that many behavioural patterns exhibited by the captive harbour seals at the O.S.C. reflect their unique environmental circumstances. Although the behaviour of these seals may not be qualitatively different than that seen in the wild, it was expected that behaviours which served to increase chemical and tactual stimulation would occur frequently, because these behaviours would provide a source of stimulation over which the captive seals had some control. Additionally, I proposed that because many of the behaviours that involve tactual and chemical sensation are social in nature, these behaviours would also serve the purpose of promoting social cohesion within the captive group. However, no direct comparisons of the frequency of particular behaviours between captive and free-living harbour seals were undertaken since the latter are only accessible to observers for a brief period each year during which time social interactions are specialized for the purposes of pupping, weaning and breeding. Hence, the main objective of this study was to describe and collate the behaviours that were thought to provide both sensory stimulation and a sense of social cohesion or tolerance to captive harbour seals residing in an otherwise impoverished and restrictive environment.

Affiliative Behaviours and Their Role in Promoting Social Cohesion

Background. Judging from the published scientific literature on social behaviour, the general affiliative behaviours that allow animals to maintain a sense of peace do not garner much attention (Harris & White, 1992). Instead, the literature is dominated by accounts and analyses of agonistic or aggressive behaviours for both free-living and captive animals. Exceptions include specific types of affiliative behaviours that occur between potential mates, in the context of offspring care, and submissive behaviours that allow an individual to avoid a conflict. The disproportionate attention given to the relatively infrequent agonistic events over affiliative ones may be due to their relative degree of conspicuousness. It is also possible that, as Klopfer (1985) suggested, human preoccupation with aggression is simply a reflection of the degree of violence in contemporary life. Certainly, the scientific literature reveals a bias towards observing aggression; for example, in one study of wolf (*Canis lupus*) social behaviour (see Zimen, 1982), 60% of the behavioural codes applied to aggressive encounters although only 21% of observed social interactions were aggressive (R. E. Anderson, personal communication, 1996). More attention needs to be given to those behavioural mechanisms that are used frequently and universally by individuals within a group in order to maintain a peaceful coexistence. This seems especially apparent given that some research has revealed a higher frequency of affiliative behaviours in a captive population than in free-living animals, but that no similar change was found for aggressive behaviour (Rowell, 1967). Because aggressive events are generally rare, affiliative behaviours are likely to be important in determining the 'mood' of a group of animals, particularly captive ones.

Defining Affiliative Behaviours. What specifically is meant by the term affiliative behaviour? Most often, no clear criteria are offered when particular behaviours are referred to as affiliative, or sometimes the behaviours classified as affiliative are determined via their exclusion from other categories. Such practices may reflect the fact that research is rarely primarily focused on affiliative behaviour; that is, affiliation is usually included as a behavioural category in the development of an ethogram or as part of an investigation into other social behaviours such as mating or aggression. For example, Wrangham and Rubenstein (1986) studied avian species with closed foraging groups and more than one breeding female, and found that the affiliative relationships between breeding females were poorly developed. The authors, however, did not elaborate on what exactly was meant by affiliative relationships. In an investigation into reproductive strategies in yellow-bellied marmots (*Marmota flaviventris*), the formation of amicable relationships was found to be dependent on kinship and sex (Armitage, 1986). Just what constituted marmot amicable behaviours, though, was never made clear.

Mutual grooming or allogrooming is often considered a form of affiliative behaviour. For instance, Rubenstein (1986) revealed that strong affiliative bonds, as measured by preferred grooming partners, form among free-ranging feral female horses (*Equus przewalskii* and *E. caballus*), and suggested that because amicable behaviours outnumbered aggressive ones, the formation of permanent harems was possible. Within a pack of dwarf mongooses (*Helogale parvula*) affiliative behaviours were common between adult males and females and between adults and juveniles; the strongest social bonds, as determined by allogrooming and allomarking, were between adults of the opposite sex (Rood, 1986). In silverbacked and golden jackal pairs (*Canis mesomelaa* and *C. aureus*), affiliative behaviours encompassed not just mutual grooming but also food sharing, and feeding and protecting sick or injured partners (Moehlman,1986).

Sometimes allogrooming may even be the only type of affiliative behaviour measured, as was the case with Harris and White's (1992) study of dispersal in red foxes (*Vulpes vulpes*). Harris and White used the extent of chewing on plastic ear tags as an indirect measure of the cumulative affiliative experiential history of free-ranging red foxes. This indirect measure of social grooming was necessary because of difficulties associated with direct behavioural observation of these elusive, nocturnal canids. In contrast to the commonly held view that increased aggression causes dispersal of subdominant members from a group, Harris and White found that dispersal in males was related to decreased affiliative behaviour, as measured by tag-chewing.

In general, it would appear that primatologists are more likely than most ethologists to investigate the nature of affiliative behaviours rather than to merely use the term as a convenient behavioural category. Nonetheless, primatologists seem no more inclined either to define what is meant by an affiliative interaction or to justify the inclusion or exclusion of particular behaviours. Thus, when Wrangham (1986) stated that "female bonobos have more frequent affiliative interactions than female chimpanzees do" (p.376), he makes clear that the behaviours considered to be affiliative include: homoerotic behaviours (i.e., mutual rubbing of sexual swellings), allogrooming, food-sharing and close proximity; yet he does not make clear the basis for their inclusion. Wrangham also acknowledged that that female bonobo (*Pan paniscus*) relationships may merely be tolerant rather than truly affiliative and indicated that this issue had not yet been examined.

In a study of captive liontail macaques (*Macaca silentus*), affiliative behaviours included huddling, embracing, nuzzling, crouching and head-bobbing with crouching (Skinner & Lockard, 1979). Despite these relatively few types of affiliative behaviours (i.e., compared to agonistic behaviours), these behaviours were displayed with relative high frequency. In contrast, considerably more behaviours were categorized as affiliative for a captive group of De Brazza's guenons (*Cercopithecus neglectus*) (Oswald & Lockard, 1980). Four categories of affiliative behaviour were defined: (i) grooming (auto- and allogroom); (ii) approach-contact (embrace, huddle, mouth-to-mouth muzzle, and nuzzle); (iii) social play (bounce, chase, grab, and grapple); and (iv) sexual behaviour (present, perineal inspect, mount and intromission). Threat-submission and contact aggression were relatively rare and the social organization of the De Brazza guenon was characterized as being very cohesive and stable. Unfortunately, the nature of Oswald and Lockard's study makes it difficult to discern the relative importance of affiliative behaviours in maintaining the group's social cohesion.

In a captive colony of breeding cotton-top tamarins (*Saguinus oedipus*), sniffing (excluding the anogenital region), nuzzling or licking the partner's fur were all considered affiliative behaviours (Price, 1992). Allogrooming appears not to have been included as an affiliative behaviour; rather it was considered a form of investment in the pair relationship. Likewise, anogenital sniffs and approaching/leaving were considered to be sexually-related, rather than affiliative behaviours. Male investment in the pair relationship in terms of promoting proximity and affiliative behaviours (e.g., nuzzling) was greatest during the first weeks post-partum when the female was most likely to conceive. This finding brings into question the author's separation of allogrooming from (other) affiliative behaviours, as both categories were related to investment in the pair relationship. This example highlights the difficulties involved in distinguishing between affiliative acts for the purpose of group cohesion versus for the purposes of obtaining a mate or another resource. However, it seems that primatologists generally consider close proximity, allogrooming, mutual help, nuzzling, kissing and social play to be affiliative behaviours, while maternal and sexual behaviours are usually considered separately (Fragaszy, Schwarze & Shimosaka, 1982; Robbins, 1996).

It may be the case that for group-living species with complex social relationships, such as many primates and canids, that it is impossible to classify affiliative acts based on presumed function, because *all* affiliative behaviours may be viewed as having an impact on, for instance, future reproductive success. In primates, recognition of the subtleties and diversity of social relationships among species has meant that it is impossible to define one set of criteria to identify affiliative relations (Boinski, 1994; Hill & Van Hooff, 1994). Although Boinski (1994) suggested that the most useful measure may be spatial association, he also acknowledged that even this measure can vary greatly between closely-related species.

Van den Bos and de Cock Buning (1994) made use of proximity as a measure of affiliation in a study that was one of the few to emphasize the role of affiliative behaviours in social organization. In this investigation into the social behaviour of a captive group of ten female domestic cats (*Felis lybica f. Catus L.*), the following behaviours were considered to be affiliative: social licking, social rubbing, social sniffing (of body), sniffing rear (anogenital region), nosing, lordosis, rolling in front of partner, mounting, and social play. The authors found, not surprisingly, that social licking, social sniffing and sniffing rear all correlated positively with proximity, measured in approximate body lengths, between individuals. In addition, the rank order of the cats, determined by means of actor/receiver matrices, was related to both spatial distribution of the cats and proximities between them. For instance, higher-ranking cats occupied the floor area (where food and litter boxes could be accessed) while lower-ranking individuals usually remained in a 16-compartment complex from which food and litter boxes were less accessible. Proximity scores were probably affected by physio-chemical factors [i.e., "a common attraction to or repulsion from a site" (p. 32)] or social factors (i.e., attachment/repulsion between group members). For example, social repulsion mechanisms may have led to the high proximity scores between lower-ranking cats in that these individuals were forced to stay in the complex in order to avoid higher-ranking cats. However, high proximity scores between the two highest ranking cats may have resulted from attachment. Further analyses and comparison to other research led to the conclusions that: (i) social licking played a role in regulating tension between group members and in strengthening bonds between individuals; and (ii) proximity was indicative of either tolerance or attachment between individuals.

Considerations for Determining Categories of Affiliative Behaviour. One consideration for researchers of social behaviour is that the captive environment should be viewed in terms of the ecological constraints it imposes on the animals. This view suggests that patterns of individual and social behaviour within the captive group will reflect the group's unique set of circumstances. As mentioned previously, harbour seal social organization may vary considerably from one wild population to the next, and these variations may reflect the ecological features of each population's geographic location (Davis & Renouf, 1987; Renouf, 1991; Wilson, 1974a, 1978). Similar variation may occur in captive environments depending on their physical parameters. In fact, Renouf (1993) has suggested that the small tank size of the O.S.C. harbour seal enclosure was responsible for the lack of vigour found in some types of locomotor-rotational play (e.g., porpoising and torpedoing) in the captive seals relative to a free-living population. There is also some evidence that a richer inventory of affiliative behaviours may exist in some captive animals than in their counterparts living in the wild (e.g. in white rhinoceros, Miulica & Labern, 1991). Likewise, a recent CBC report suggested that free time in captivity may facilitate unusual behavioural patterns, such as problem-solving in primates. These findings indicate that perhaps behaviour patterns are best determined for each individual population of animals, whether captive or free-living.

Another consideration is that of terminology. Often unwarranted implications are produced by the casual selection of a particular term for some affiliative behaviour. For instance, while 'association' implies only that two or more animals spend time together, 'alliance' implies mutual support during agonistic contexts (Hill & Van Hooff, 1994). One way to avoid such problems is to define behavioural units in terms of form rather than function, and then to use discriminant analysis to classify behaviours objectively into major functional categories (Packard & Ribic, 1982). But even this method requires some degree of interpretation on the part of the researcher.

Affiliative behaviours may be either more or less difficult to define for captive animals belonging to species who, when free-living, are normally not highly social outside of the breeding season. More difficult because social interactions may be subtle or infrequently observed, or less difficult because the complexity of social behaviour may be somewhat reduced (especially when behaviour has become stereotyped). However, this consideration is somewhat of a moot point when applied to harbour seals whose social order in the wild is variable (Davis & Renouf, 1983; Evans & Bastian, 1969; Winn & Schneider, 1977). Significantly, all examples of affiliative behaviour mentioned above are drawn from social species that need to cooperate for hunting, foraging, protection from predators, or rearing of young. It is unlikely that any of the phocid species, including harbour seals, exhibit the degree of social organization and cooperation found in, for example, a pack of jackals or a harem of feral horses. It is not my intention to imply that the harbour seals are a cooperative social group in the same sense as these other species. Because the O.S.C. colony of breeding seals represents a far from natural grouping of individuals in which the likelihood of social interaction is high, I was interested in knowing what behaviours these seals exhibit and how they maintain relative peace. Because agonistic events are infrequent, affiliative behaviours and spatial distribution within the enclosure are likely to be the primary mechanisms for group maintenance. However, all examples of affiliative behaviours discussed in the preceding text have been drawn from terrestrial or arboreal species which may have little in common with aquatic or amphibious species (i.e., due to their different environments or to adaptations to these environments). Thus, examples of affiliative interactions specific to amphibious and aquatic species should also be considered.

Affiliative Behaviour in Aquatic and Amphibious Species. In a behavioural survey of trainers of captive cetaceans, the following behaviours were categorized as affiliative/social/contact behaviours: breathing in unison, leaping in unison, pair swimming (pectoral fin touching), male-female pair formation, stroking another animal, and soliciting strokes from a human (Defran & Pryor, 1980). Care-giving, social play and sexual behaviour were all considered separately, but as usual, no explanation was offered regarding the basis for each functional categorization. In contrast, a classification of behaviours observed in free-living sea otters *(Enhydra lutris)* made clear the basis for the behavioural distinctions; that is, discrete action patterns based on form were clustered according to time sampling of individual animals (Packard & Ribic, 1982). This method resulted in a cluster of action patterns ("interaction activities") that included many affiliative behaviours, such as: "social interactions with a playful quality" (e.g., tumbling, wrestling and mutual porpoising); "more subdued interactions" (e.g., nosing, pawing and riding); and "interactions with a possible agonistic function" (e.g., gape and leave) (p. 1369). Some behaviours belonging to the feeding and grooming clusters also occurred during interactions, emphasizing the imperfections of a form-before-function type of behavioural analyses.

Implications for the Present Study. Affiliative behaviours that appear to be common to terrestrial, arboreal, aquatic and amphibious species include social play, social sniffing/nosing, and nuzzling. Most investigators appear to consider these three behavioural patterns to be affiliative in that they all involve close physical interaction without agonistic components, between two or more animals, in which each individual must 'trust' that no harm will be done to them. Therefore, for consistency and comparative purposes, the present investigation focused on social play, social nosing and nuzzling. In harbour seals, social play has been described in both captive and wild populations, and is thought to involve the exchange of olfactory and tactual stimulation

(Renouf & Lawson, 1986; Wilson, 1974a; Wilson & Kleiman, 1974). In the O.S.C. harbour seals, social nosing and nuzzling, as well as social play, have been frequently observed. Thus, it is possible that these particular behaviours play an important factor in the maintenance of social cohesion or tolerance within the captive colony of O.S.C. harbour seals.

The Role of Social Play, Social Nosing and Nuzzling in Group Cohesion

Social Play. Social play has been hypothesized to play a role in promoting social cohesion in a number of species, although this view has been contentious (see e.g., Fagan, 1981; Thompson, 1996). While acknowledging the various controversies surrounding play theory, the view espoused in the present study is that play likely serves multiple functions and that social play probably serves social functions, including the promotion of social cohesion. The idea that social play increases social bonds and, therefore, group cohesion has found support from research involving a variety of species. For instance, social play behaviour in captive white-fronted parrots (*Amazona albifrons*) appears to increase social ties between birds and to introduce and develop adult behaviours used in epigamic and agonistic contexts (Skeate, 1985). Bekoff (1974) suggested that social play in canids serves to facilitate the formation and continued maintenance of social relationships within the group. Poirer and Smith (1974) proposed that primate play facilitates the development of social abilities, establishes the basis for social communication, and partially determines an individual's dominance rank. In addition, qualitative and quantitative differences in social play behaviour between captive and free-living populations of common chimpanzees (*Pan troglodytes*) have been used to assess the well-being and group cohesion of the captive animals (Markus & Croft, 1995).

Harbour seal social play has been studied both in the wild and in captive populations, including the O.S.C. seals. Wilson (1974a) described two types of aquatic social play in juvenile harbour seals: (i) dyadic play, in which two animals combine exuberant somersaulting movements with mutual muzzle-to-body and body-contact; and (ii) group play, in which several individuals leap and splash simultaneously with each seal temporarily orienting towards one another and briefly coming into contact. Wilson found that dyadic play was often initiated by nose-to-nose or nose-to-face contact and that bouts usually involved individuals of similar size. Group play occurred less frequently than dyadic play and, on occasion, a pair would opt out of group play in favour of dyadic play. With a known captive population (3 juvenile males, 2 juvenile females, and 1 yearling female), there were discernible individual and dyadic patterns in terms of preferred play partners and play vigour. Females rarely took part in dyadic play bouts, but except for the yearling, did participate in group play. The dyadic play of captive individuals was qualitatively different than that of free-living seals; for example, there was more slow rolling, less pre-rolling and the bout duration was longer for captive animals (Wilson, 1974a).

Wilson (1974a) concluded that one function of social play is to bring individuals into close physical contact so that they become acquainted and integrated into a unified group. That dyadic play patterns (e.g., somersaulting/rolling) result in almost continuous body contact between seals and do not resemble behaviours found in other contexts, such as fighting or mating (cf. Renouf, 1993), further supports Wilson's proposal that a major function of social play in harbour seals is to promote social cohesion rather than some other function (e.g., predator avoidance). In addition, Wilson noted that nose-to-tail contact is maximized during those dyadic play bouts in which head-to-tail rolling is the predominant feature and that such contact may be associated with scent production from the anal gland. One particularly interesting suggestion was that the exuberant movements that characterize the social play of juvenile harbour seals "may have a catalytic effect on the formation of social affinities,...that is, if young seals merely nuzzled each other in a tranquil manner, the bond between them might not be so strong" (Wilson, 1973, p.57). If this is true, then should we expect dyadic play between adult seals to be as exuberant, because social bonds presumably are already well established? Or should exuberance characterize the dyads regardless of age because social bonds need to be maintained?

Renouf and Lawson (1986; 1987; Renouf, 1993) investigated social and solitary play in harbour seals across all age categories. For free-ranging seals, Renouf and Lawson (1986) described five types of social play including: climbing, chasing, mouthing, chin-sparring and rolling, a behaviour consistent with Wilson's (1974a) 'somersaulting' or 'head-to-tail rolling'. In the captive O.S.C. seals, however, Renouf (1993) described four partially overlapping types of social play: nipping, chasing, hugging, and rolling. No explanation was offered for this discrepancy (i.e., whether the differences in social play categories reflected qualitative variation between captive and wild harbour seals). Unlike Wilson (1974a), Renouf and Lawson did not describe any occurrences of group play.

In free-living seals, Renouf and Lawson (1986) determined that only 20% of play bouts were social in nature but that social play was significantly longer in duration in comparison with solitary play bouts. Social play was slightly less frequent among adults than among juveniles and yearlings, and juveniles exhibited less social play than yearlings. Although most play was rated as relatively intense (i.e., vigourous or moderately vigourous), no patterns were reported regarding the relationship between social play intensity and age of individuals. Apparently, most social play occurred in younger seals and involved seals within the same age class, and it would have been interesting to know, in light of Wilson's (1973) above suggestion, whether younger seals played more 'exuberantly' than older seals. Among the captive seals, most play was considered of low vigour (Renouf, 1993) but again, the data were not used to assess social play patterns in relation to age or the establishment of social bonds.

Social Nosing and Nuzzling. Social cohesion is also thought to be facilitated by social nosing and nuzzling. For example, Wilson (1973) provided evidence that conspecific body odours, in particular, the odour produced by the skin at the back of the head, served as a play signal in spring-born, short-tailed voles (*Microtus agrestis*) and, as such, ensured frequent olfactory and tactual contact. This contact promoted cohesion and tolerance towards each other, and towards autumn-born young who incidentally lacked the scent which stimulates play. Hence, autumn-born young interacted and played less frequently than spring-born young and were less tolerant and cohesive when they became sexually mature. Thus, Wilson managed, rather ingeniously, to establish a link between odour, social play, group cohesion and the annual population cycle of short-tailed voles. As pointed out by Fagan (1981), the potential of odour cues to act as a play-signal has only recently been recognized in canids, mongooses, rodents and pinnipeds, and certainly deserves further investigation given the importance of olfaction to many mammals.

One interesting aspect of Wilson's (1973) vole study was her finding that the skin at the back of the vole head was especially salient as a source of an odoriferous play signal. In both grey seals (*Halichoeurs grypus*) and harbour seals (*P. v. concolor*), dyadic play bouts were often initiated by one seal leaning its chin or head and shoulders over its partner's body (Wilson, 1974a; Wilson & Kleiman, 1974). This behaviour, called the "head-over-back play solicitation signal" by Wilson and Kleiman (1974, p.353) may be the same as "chin sparring" as described by Renouf and Lawson (1986; p.75), "where one seal rapidly thrusts its head forward toward another, often dropping the chin on the other's shoulder". Reciprocation of this presumed play signal was common during particular dyadic play bouts of 'rolling'[2] and this was true for both captive and free-living

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[2] For the present study, rolling will be considered in accordance with Renouf and Lawson's definition: "Two or more seals engage in a series of fluid somersaulting rolls near the surface. Seals usually roll in pairs oriented either head to head as they roll around each other's longitudinal axis, or the head of one animal will be adjacent to the

harbour and grey seals (Wilson, 1974a; Wilson & Kleiman, 1974).

Interestingly, the regions of the body (i.e., back of head and neck) that are contacted most frequently during the head-over-back play signal are some of the most odoriferous skin regions of the harbour seal (Wilson & Kleiman, 1974). As well, these regions are most likely to be above the water surface and hence, accessible for olfactory investigation. However, there is no empirical evidence, as yet, to substantiate the notion of an odoriferous play cue in harbour seals. Regardless, the fact that the back-of-head scent stimulated play among juvenile voles so that play and nosing contacts were mutually perpetuating (Wilson, 1973) suggests that the notion of a play signal mediated by chemoreception merits further study – a proposal echoed more recently by Thompson (1996).

In a study focusing on contact-promoting behaviour (i.e., affiliation) in captive degus (*Octodon degus),* Wilson (1982) revealed again that odour emanating from the neck region had attractive qualities. However, in this case, the neck odour did not appear to stimulate play; rather, it seemed to offer a sense of reassurance to young degus. According to Wilson, body-nosing contacts between individuals were the dominant mode of juvenile social interaction, and were thought to involve olfactory and tactile exchange. Body-nosing was identified as a contact-promoting behaviour in juvenile degus and was

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other's flippers as they somersault in a cartwheel." (1986, p. 75). In the current study, rolling is referred to as 'nose-to-tail rolling' to emphasize the predominant style of interaction.

shown to increase immediately in frequency when they were separated from their parents and put in an unfamiliar enclosure. Furthermore, these juveniles in the new cage did not groom or play as they did while in their home cage with parents present; instead, they engaged in more vocalizing, forepaw-clasping and neck-nosing. That neck-nosing was more frequent than snout-nosing in the unfamiliar environment, but not in the home cage, suggested that increased neck-nosing was a response to a familiar and attractive stimulus in an otherwise unfamiliar situation. These results indicate that contact-promoting or affiliative behaviours may be differentially activated as a function of an animal's age, and the social and physical context within which the behaviours occur. Thus, interpretations of observed affiliative interactions should take these factors into account.

One of the environmental factors that has been shown to affect social play is the scent of the 'playground'. For instance, Byers (1985) showed that free-ranging collared peccaries (*Tatassu tajacu*) played at high frequencies at a well-worn, scent-marked space located within the herd's bedground. At this 'playground', play bouts involved more herd members and were almost four times longer in duration than play performed elsewhere. It is not known whether this site was popular for play because the animals were relatively safe from predators or risk of injury. However, since collared peccaries are a species in which olfaction plays an important role for many social behaviours, including the maintenance of social cohesion (Byers, 1983; Byers, 1985; Byers & Bekoff, 1981), it is possible that the scent of the playground itself acted as a type of play signal. Another particularly interesting finding is that collared peccaries, a species with herds that are highly social and cohesive (i.e., an average inter-individual distance of only 3.9 m), exhibit a high frequency of olfactory-related behaviour. Byers (1985) found that 20% of all social or socially-related acts were olfaction-related, and that social nosing and nuzzling occurred at particularly high frequencies. Nosing another individual in the nose, mouth, eye, face, ear, and head accounted for almost half of all social nosing contacts, implicating the head as a particularly salient region for olfactory investigation.

Although, social nosing and nuzzling have not been the primary focus of many behavioural investigations, it is probable that these behaviours serve a chemosensory or tactual function, depending upon the species being studied. For instance, in the gray short-tailed opossum (*Monodelphis domestica*), nuzzling is a chemosensory exploratory behaviour, mediated by the vomeronasal system, that enables individual recognition of conspecifics (Poran, Tripoli & Halpern, 1993; Poran, Vandoros & Halpern, 1993). In contrast, Poole (1985) characterized mammalian nuzzling as a common affectional and sexual behaviour in which vibrissae, in those species where they are highly developed, are used for tactually mediated social communication.

Most pinnipeds are considered to have a well-developed tactual sense in which contact and rubbing of the vibrissae are a conspicuous component of greeting behaviour (Caudron, 1994; Evans & Bastian, 1969). Typically, nose-to-nose greetings in seals involve both the opening of the nares and the forward projection of the vibrissae (Miller, 1975; Lawson, 1983; 1993), which may implicate the dual involvement of the olfactory and tactual senses. This concurrent action of the nares and vibrissae is also common during many occurrences of social nosing (e.g., the nosing of another seal's body, head, or flippers), at least in harbour seals (Renouf, 1979). However, it is difficult to ascertain the degree to which nuzzling or nose-to-nose greeting, and social nosing involve olfactory and tactual communication. As stated by Miller (1975), "simply because tactile information is exchanged...is insufficient evidence for assuming a signal function: the 'whiskers-forward' response may occur indiscriminately whether a conspecific or a rock is being smelled." (p.280).

It appears that nose-to-nose and nuzzling behaviours occur in all three families of pinnipeds, Phocidae, Otariidae and Odobenidae. Furthermore, anecdotal observations have revealed that these behaviours occur in the context of mother-pup greeting displays, adult greeting, pre-copulatory behaviour and social play in all age classes (Ross, 1972; Wilson & Kleiman, 1974). However, few researchers have addressed the potential for nuzzling and nosing to have an important function in seal social behaviour. One exception is Ross's (1972) investigation of nuzzling behaviour in captive Cape fur seals (*Arctocephalus pusillus*) which led the author to speculate that nose-to-nose nuzzling plays a more significant role in pinniped social structures than was previously believed. Ross suggested that observed changes in nuzzling activity prior to parturition and copulation may be related to the seal's hormonal state. In addition, Ross hypothesized that olfactory cues transmitted during nose-to-nose nuzzling may be of more importance in aquatic mammals than in terrestrial ones since these cues cannot be transmitted by other areas of the body (e.g., the genital regions) while underwater. Unfortunately, Ross's recommendation to use nuzzling activity as a quantitative behavioural criterion in studies of captive pinnipeds has, thus far, been unheeded.

Implications for the Present Study. The behavioural mechanisms that drive social cohesion have rarely been the primary focus of scientific inquiry. Nonetheless, it appears that there is sufficient evidence to support the notion that social play, social nosing and nuzzling help promote group cohesion or tolerance in some species, including harbour seals. Furthermore, these behaviours may involve olfactory and tactual communication which suggests that these sensory modalities may play an important role in the mediation of affiliative behaviours. However, neither olfactory nor tactual senses are well understood in pinnipeds – largely as a result of the difficulties associated with studying these sensory systems, but also as a result of some long-held, human misconceptions, particularly with respect to chemical communication in marine mammals. The following section is a brief summary of the current state of knowledge regarding olfactory and tactual communication in pinnipeds.

Olfactory and Tactual Communication in Pinnipeds

Background. Along with humans and the anthropoid primates, the marine mammals are most often suspected of living in a scent-deprived sensory world (Eisenberg & Kleiman, 1972; Harrington, 1972; Schusterman, Thomas & Wood, 1986). Typically it is thought that the more aquatic a mammal is, the less important the olfactory sense is to that species

(Fobes & Smock, 1981; Harrington, 1972). Thus, completely aquatic mammals, such as cetaceans (whales, dolphins and porpoises), have been labeled ‘anosmatic’ or ‘anosmic’ while amphibious mammals, such as pinnipeds (seals, sea lions and walrus), have been labeled ‘osmatic’ and ‘micronosmic’ (Fobes & Smock, 1981; Lowell & Flanigan, 1980). However, because most of the literature regarding the role of olfaction in marine mammal behaviour is based on anecdotal or unsystematic observations, such labeling is, at best, speculative.

This notion that marine mammals have limited olfactory sensitivity simply because they are primarily aquatic is even more questionable when one considers the long-established evidence demonstrating the importance of chemical senses in fish behaviour (Bardach & Todd, 1970; Colgan, 1983; Liley, 1982; Reebs, 1994). For instance, chemical signals have been shown to be involved in a variety of social behaviours in fish, including schooling, homing, territorial marking, courtship, parent-offspring interactions, and species, sex and individual recognition (Bardach & Todd, 1970, Liley, 1982; Reebs, 1994). Given that research on chemical communication in fish has been ongoing since the 1940s (see Liley, 1982), there exists a great deal of empirical evidence for its importance in fish social behaviour. Thus, with respect to fish, statements such the following can be made with confidence: “the chemical senses of olfaction and taste are highly developed and play a major role in mediating physiological and behavioural responses to the chemical environment” (Liley, 1982, p.22). Unfortunately, based on our present state of knowledge, such a generalization cannot be made for other aquatic or semi-aquatic animals such as marine mammals.

Until recently, almost all scientific investigation of the chemoreceptive capacity of marine mammals has been restricted to histological and anatomical examinations of the nasal pathways and gustatory systems of cetaceans with little or no effort directed towards these systems in the other orders of marine mammals (Pinnipedia, Carnivora and Sirenia) or towards the role of olfaction and gustation in marine mammal social behaviour. A review of the recent literature regarding olfactory communication in marine mammals has indicated a general lack of knowledge in this field (Brown, 1985; Evans & Bastian, 1969; Fobes & Smock, 1981; Lowell & Flanigan, 1980; Schusterman, Thomas & Wood, 1986; Watkins & Wartzok, 1985). This failure to examine the chemosensory abilities of marine mammals scientifically is underscored by a recent publication entitled "Marine Mammal Sensory Systems" (Thomas, Kastellein & Supin, 1992); in over 750 pages of text there is no mention of either olfactory or gustatory systems. The tactual senses of pinnipeds did not fare much better in this publication; there are only two brief statements of the importance of vibrissae for tactile identification.

<u>The Role of Olfaction in Pinniped Behaviour</u>. Although most studies relevant to marine mammal chemoreception have been histological or anatomical[3] in nature, a few

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[3] Pinniped neuroanatomy is thought to be similar to that of terrestrial carnivores except that pinniped brains are more spherical, the cerebrum more convoluted, and the olfactory area somewhat reduced (Lowell & Flanigan, 1980). Olfactory bulbs and tracts are probably less developed in phocids than in otariids (Fobes & Smock, 1981). The

behavioural investigations have been undertaken in pinnipeds and cetaceans. For example, olfaction is speculated to play an important role in mother-pup recognition in California sea lions, *Zalophus californianus* (Peterson & Bartholomew, 1967), Stellar sea lions, *Eumatopias jubata* (Ono, 1972), Cape fur seals, *Arctocephalus pusillus* (Ross, 1972), grey seals, *Halichoerus grypus*, (Burton, Anderson & Summers, 1975), Weddell seals, *Leptonychotes weddelli* (Kaufman, Siniff & Reichle, 1975), and harp seals, *Phoca groenlandica* (Kovacs, 1987). It has been suggested that although auditory and visual cues may be used in the initial stages of mother-pup reunion, final recognition is made via the olfactory system in many seals (Evans & Bastian, 1969; Kaufman et al., 1975; Perry & Renouf, 1986). Tactile sensation, by means of vibrissae, is also thought to be used by some pinniped species, particularly the Otariids (sea lions and fur seals: Evans & Bastian, 1969).

Much of the evidence supportive of the notion that odour is important for mother-pup recognition is derived solely from observations of the immediacy (i.e., following birth) and high frequency of nose-to-nose or nose-to-body contact between mothers and their offspring. Additional support may be found in some unsystematic observations of Weddell seals made by Hammond (1970; personal communication to Kaufman et al., 1975). During some studies on thermoregulation, Hammond transported several pups in

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olfactory epithelium of otariids is typically mammalian (Lowell & Flanigan, 1980). Taste buds are reduced in number but do consist of the four typical mammalian papillae. (Brown, 1985; Lowell & Flanigan, 1980).

the same canvas bag which soon became impregnated with the pups' fecal odours and probably with other types of odours, as well. After the pups were returned to their mothers, the mothers appeared to be confused and one pup was abandoned. The following year, when separate bags were used to transport each pup, no confusion or abandonment occurred.

Hammond also attempted to promote the adoption of orphaned pups by (i) tying the skin of a dead newborn pup to an orphan and (ii) rubbing feces from a stillborn pup onto an orphan; and then presenting the orphan to the mother of the dead pup. Although in both cases the mothers initially accepted the orphans, ultimately the pups were rejected, but under very different conditions. In the first case, the pup lost the skin and the female abandoned it, and in the second case, the orphaned pup left the adoptive female to return to its dead mother. Despite the fact that the aforementioned examples suggest that odour communication is important for mother-pup social interaction, there appears not to have been any empirical investigations of this phenomenon. Perhaps this deficit reflects the extreme sensitivity of seal colonies to human disturbance or the difficulties associated with studying olfaction in free-range animals.

More recently, however, there has been some systematic investigation focusing on the role of odour in seal signaling behaviour. For instance, Hardy, Roff, Smith and Ryg (1991) suggested that the facial skin glands of both ringed seals, *Phoca hispida*, and grey seals, *Halichoerus grypus*, may play an important role in visual and olfactory sexual signaling during the breeding season (from late February to the end of May). In mature male ringed seals, facial sebaceous and apocrine glands were larger and more actively secreting than the same types of glands in the neck region, as well as being larger and more active than the facial glands of immature males, mature females and immature females. As well, the facial glands of mature males were found to secrete melanin in the sebum. The greater size, secretory activity, and melanin production of the facial glands of mature male Ringed seals is thought to account for the strong odour and dark colour of their faces during the breeding season. Similar results were found for dominant bull grey seals; however, comparative data from female and immature male grey seals are required before any conclusions can be drawn. Unfortunately, the authors made no mention of any behaviours, such as social nosing, associated with the odoriferous facial regions.

Another study has indicated that odour emanating from the faces of male ringed seals may play an important role in territory defense (Ryg et al., 1992). During the rut, odoriferous substances from the facial skin of mature male ringed seals were analyzed by means of gas chromatography. The results indicated that the strong scent of rutting male ringed seals is caused by a mixture of various organic nitrogen and sulphur compounds and at least two hydrocarbons. It appears that these substances are deposited in a lipid solution at breathing holes and subnivean lairs to mark the territory of the male. Unlike most other phocids, male ringed seals defend underwater territories during the rutting season. The likely function of the lipid solution is to prevent the scent from being dissolved and diluted in water (i.e., the scents will lie in a film on the water surface of the breathing holes.). These conclusions were strengthened by the finding that nitrogen, sulphur and some of the lipids were absent from the facial skin extract of sexually immature seals.

Based on research in other mammals and on their own findings, Ryg et al. (1992) have suggested some possible functions, other than sexual signaling and territory defense, of the odoriferous facial skin glands of rutting male ringed seals. These include: (i) inducing gonadal development, ovulation, and estrus in females during late lactation; (ii) producing an olfactory camouflage that serves to mask the scent cues emitted by the females and their young, thereby protecting them from potential predators: (iii) individual recognition; and (iv) protecting the males from predator attacks, since polar bears will recognize, by scent, which lairs contain an unpalatable quarry. None of these suggestions, however, have been empirically investigated. Nor has the possibility that the facial odours may serve a more general purpose, such as promoting social cohesion, been addressed.

Although, the question of whether animals use odours to discriminate individuals on the basis of sex, age, social status, reproductive status, familiarity, species (or subspecies), etc., has received a great deal of attention in terrestrial mammals, particularly rodents, this question has rarely been addressed for any of the marine mammals (Brown & Macdonald, 1985; Muller-Schwarze, 1983; Wilson & Kleiman, 1974). However, anecdotal reports suggest that olfactory cues are used by pinnipeds for a variety of social behaviours not directly related to reproduction (i.e., not related to mother-pup recognition, territory defense or sexual signaling). One such behaviour includes the ability of seals to detect the presence of humans, a potential predator, by olfactory cues alone. For example, in 1874, Scammon reported that sealers tended to approach seal herds downwind in order to avoid detection by the animals as they approached (in Evans & Bastian, 1969). As well, some trainers of sea lions consider this animal's olfactory sensitivity to be sufficient to detect the presence of non-visible humans (Evans & Bastian, 1969; Lowell & Flanigan, 1980).

Captive harbour seals have been observed by myself to make nose contact with various body parts (e.g., face, hands) and clothing (e.g., footwear, pant-legs) of familiar technicians and unfamiliar visitors when they are present in the seals' enclosure. Typically, this nosing behaviour involves extension of the neck in the direction of the person to be sniffed/nosed, a rapid opening and closing of the nares and a simultaneous forward projection of the vibrissae. Although, it is not thought that the seals depend on olfaction in this situation in order to detect the presence of the humans, it is possible that the individual technicians can be recognized in this manner. The role of the vibrissae in this context is also unclear; that is, tactually-mediated information may or may not be used. However, it is known that harbour seal vibrissae are important sensory receptors which are highly sensitive to low frequency vibrations (Renouf, 1979) and can be used for detecting low-amplitude water movements produced by moving organisms (Dehnhardt, Mauck & Bleckmann, 1998).

Along with Wilson (1974a), I have observed that nose-to-nose, nose-to-head, nose-to-body and nose-to-tail contact occur at a high frequency in dyadic play bouts (i.e., rolling) of captive harbour seals. Similar patterns of contact occur during play bouts in free-living harbour seals (Wilson, 1974b; Wilson & Kleiman, 1974). During dyadic play, different parts of the body were nosed selectively, with the muzzle and nape regions receiving the most attention and the trunk, hind flipper, anus and genital regions receiving very little. These findings were consistent with my own preliminary observations of the O.S.C. seals. Wilson and Kleiman (1974) also found that the 'head-over-back' play solicitation signal correlated with: (i) the total amount of body contact during play between two adolescents, and (ii) the total amount of nose-to-body contact during mother-pup play. In addition, these authors noticed that the parts of the body most often nosed during social play were also the focus of attention in other functional contexts such as during mother-pup reunions after a brief separation and during sand-rubbing. This observation led the authors to hypothesize that social interactions such as play serve to increase the amount of nose-to-body contact and, hence, the amount of odour input. Thus, it was thought that the nosing animal can select different body regions to sniff within the different functional contexts, and thereby control the quality and quantity of olfactory input. Unfortunately these ideas were never fully investigated. Also, not investigated was the role of tactual communication during these bouts of aquatic social play. However, because harbour seals have highly developed mystacial vibrissae (Miller, 1991), any incidence of seemingly deliberate nosing contact may involve both olfactory and tactual communication.

Further investigation by Wilson and Kleiman (1974) revealed that to the human nose, both the neck and jaw regions of seals emanated strong odours, and that the odours from these two regions were qualitatively different. Skin samples were then taken from the different odoriferous body regions (e.g., neck, jaw, muzzle, trunk etc.) to estimate the amounts of sebaceous gland material surrounding hair follicles. A number of differences in the amount of glandular material present in the different regions, combined with the perceived differences in odour quality, led Wilson and Kleiman (1974) to hypothesize that the skin of the muzzle and neck regions is particularly odoriferous and that odour perception plays an important role in muzzle-to-muzzle contact. They concluded that the high degree of nose-to-body contact in seals may serve as an opportunity for the long-term learning of the olfactory characteristics of conspecifics which will subsequently "be important in the development and maintenance of the subgroups which seem to exist within the herd" (p.362). This notion is in agreement with studies of other animals which have indicated the importance of odour communication for social cohesion (Brown & Macdonald, 1985; Colgan, 1983).

<u>The Tactual Senses in Pinnipeds</u>. The tactual senses in pinnipeds are not much better understood than the chemical senses. Both forms of communication have received inadequate attention by way of empirical investigation so that most of what is known is derived from anecdotal or general descriptions. Nonetheless, Miller (1991) has distinguished between two forms of tactual communication – those that are not

evolutionarily specialized as displays and those that are more elaborately structured, evolutionarily specialized displays. Miller emphasized that a continuum exists between these unritualized and highly ritualized forms of tactual signals. Incidental body contact that sometimes occurs in resting harbour seals is an example of an unspecialized signal, while dyadic social play (i.e., rolling) is considered by Miller (1991) to be evolutionarily specialized display. However, Miller did not speculate on the display value of rolling behaviour; that is, the question of what is communicated during a bout of dyadic rolling was not addressed. Miller (1991) also considered nuzzling to be an example of formalized tactual communication in harbour seals, but again did not consider signal function. However, Poole (1985) suggested that, apart from biting, most tactile signals are associated with affiliation.

Implications for the Present Study. The above evidence, derived from anecdotal reports and empirical investigations, indicates that olfactory and tactual communication are important to a number of social behaviours in pinnipeds. These include: (i) mother-pup recognition; (ii) adult greeting; (iii) pre-copulatory behaviour; (iv) territorial defense; (v) sexual signaling; (vi) detection of humans/predators; and (vii) social cohesion/tolerance. Of these social behaviours, social cohesion has perhaps been the most inadequately studied. This oversight may be the result of the tendency for researchers to focus on the conspicuous behaviours associated with fighting, mating, and mother-pup interaction, which are not, generally, all that frequent or which occur only within particular contexts during specific seasons. Not enough is known about either the quantity or quality of the affiliative behaviours that likely determine many aspects of pinniped social organization. Of particular interest are the patterns of affiliative interaction that exist in a captive situation where social cohesion or tolerance is essential to the well-being of the seals.

In summary, despite the fact that neither olfactory nor tactual communication have received much attention in pinnipeds, these sensory modalities may be more important to their general social behaviour than is currently realized. In particular, olfactory and tactile sensation may play a significant role in behaviours relating to social cohesion. Some affiliative behaviours that have been shown to promote group cohesion in other species have also been observed in both captive and free-ranging harbour seals. These behaviours include social play, social nosing, and nuzzling – all of which very likely involve olfactory and tactual information.

Objectives

The main objective of the present study is to investigate the role of nosing in the social behaviour of captive harbour seals. This interest stems in large part from the relatively impoverished nature of the O.S.C. harbour seal enclosure; that is, nosing may be especially important to these captive seals because such behaviours will enhance sensory stimulation in an otherwise boring environment. Both chemical and tactual stimulation may be achieved through nuzzling, social nosing and social play, so these behaviours will be examined in particular detail. Furthermore, because odours are borderless, chemical stimulation may also be realized through frequent environmental sampling; thus, nosing of the air and of objects will also be examined. I will also attempt to show that some of these behaviours that provide chemical and tactual stimulation, particularly, nuzzling, social nosing, and social play, also serve as affiliative behaviours that promote social cohesion or tolerance. Thus, social cohesion is used as the interpretive context of this study. Note, however, that social cohesion is *not* thought to cause nosing, *nor* is nosing thought to directly lead to social cohesion.

In order to accomplish these aims, the O.S.C. seals were observed regularly (i.e., twice per day, 3 days per week) over a study period of 43 weeks. During this period, active, quiescent, and display behaviours were quantified in order to determine the timing of the breeding season and to establish the behavioural context during which nosing acts were most likely to occur. All occurrences of nosing behaviour, including nose-to-tail rolling, were collated and analyzed according to the individual seal/dyad, week, season, location, apparent attention, and wind direction. Dyadic patterns were also quantified with respect to the initiator and recipient of the interaction, and in terms of preferred partners. Finally, the relative position and movement of the nares and vibrissae were examined to ascertain whether nosing acts involved olfactory and tactual senses.

Chapter Two: Methods

Study Animals and Facility

At the start of the study, six captive Atlantic harbour seals ranging in age from 5 to 24 years were kept in an outdoor enclosure at the Ocean Sciences Centre (O.S.C.) at Logy Bay, Newfoundland. Three seals were captured as weanling pups on Sable Island, Nova Scotia, and have remained in captivity since then. Oscar, the oldest seal was captured in 1972. Kevina (the only female harbour seal) and Clarence were both captured in 1978. Kevina has since given birth to 12 pups, one of which was born during my investigation (on June 23, 1996), and three of which formed the remainder of the study group: Julius (born in 1985), Caesar (1986) and Darby (1991).

The seals were housed in an outdoor enclosure, as represented in Figure 1, which consisted of three above-ground seawater tanks surrounded by 100 m^2 of decking for hauling out. Tanks were supplied with a continuous supply of fresh seawater from Logy Bay. The largest circular tank (7.5 m in diameter and 1.6 m deep) held 60,000 l of sea water, flowing through at 200 l/min. This main tank (MT) was bridged by a viewing platform 1.3 metres above the water surface. Seals normally entered and exited this main tank from the surrounding deck by means of wooden steps, or via a smaller circular satellite tank (ST) connected to the main tank by a ramp. However, seals could also enter and exit the main tank without using the steps or ramp, provided the tank was about one third full of water. The ST was 2 m in diameter and 1 m deep and held 2500 l of ambient

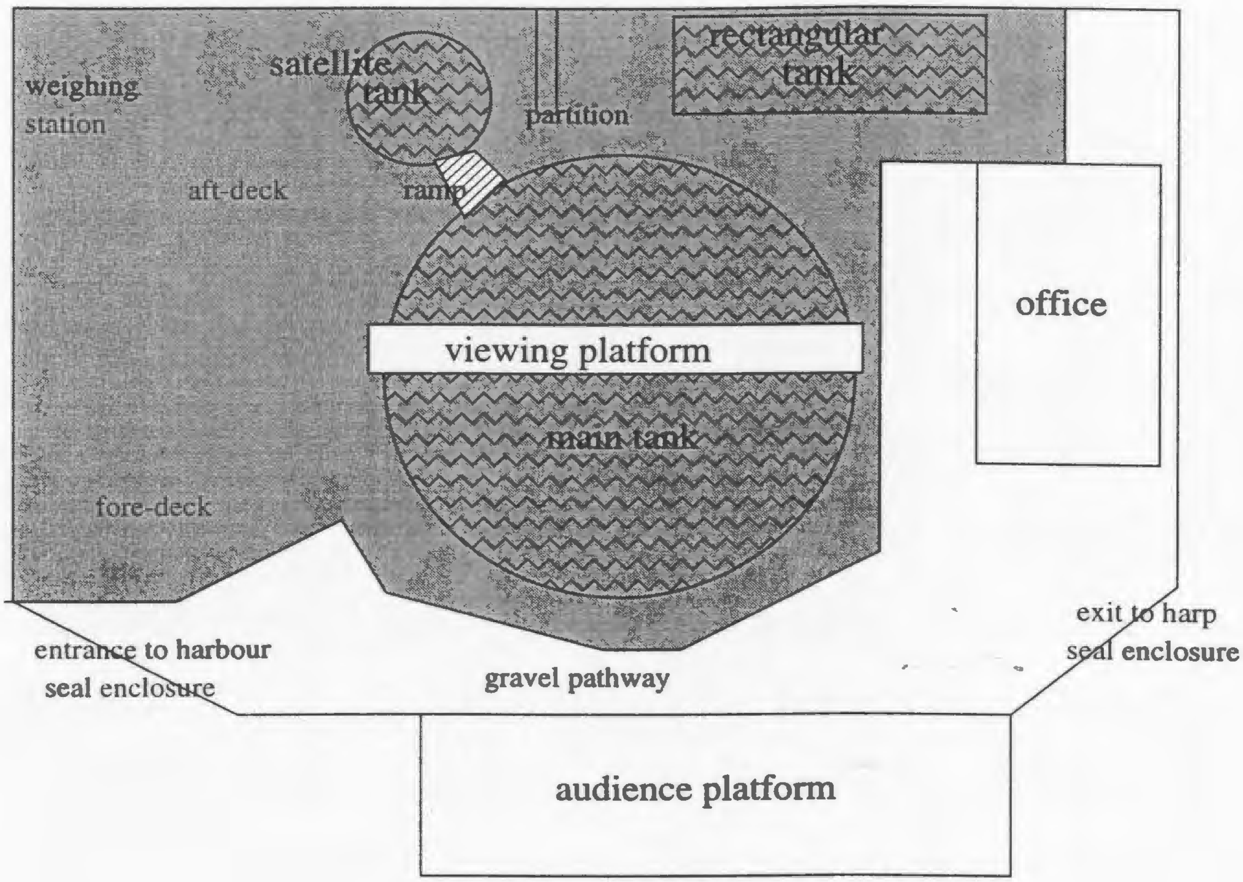

Figure 1: Schematic representation of the harbour seal enclosure at the Ocean Sciences Centre at Logy Bay, Newfoundland.

seawater. The rectangular satellite tank (RT) was 1 m wide, 3 m long and 1 m in depth. Both smaller tanks could easily be entered and exited by seals directly from the deck. Access to the rectangular tank could be blocked by a movable partition on the adjacent deck area.

All seals were fed herring (*Clupea harengus*) ad libitum in one daily meal and each meal was supplemented with vitamins ("Seatabs"). As well, each seal received a cysteine tablet twice a week. On most days, feeding occurred in the morning and lasted at least one half hour. On days when the main tank was drained for cleaning (generally weekly), feeding took place in the afternoon. When tanks were being cleaned, seals were weighed in a corner of the seal enclosure (Figure 1).

Collection of Data

Preliminary observations of the seals were carried out for approximately three months (from October to December 1995) to ensure accurate identification of individuals and determine behavioural categories. In addition, this period of time served to habituate the seals to my presence in the compound, particularly on the viewing platform over the main tank. During this preliminary observation period, a coding scheme was developed (Appendix A). In brief, this scheme contained codes for all motor behaviours other than swimming (swimming was recorded only in the context of a nosing act), all nosing behaviours, location of seals within their enclosure, and contextual information, such as whether or not the seals had been fed, estimates of wind direction and strength, temperature, cloud cover, the arrival/departure of a human audience (on a viewing deck adjacent to the seal enclosure), and technician activity around the enclosure. Individual seals were coded according to the first letter of their names, except for Clarence; hence, from oldest to youngest, individuals were denoted as O (Oscar), L (Clarence), K (Kevina), J (Julius), C (Caesar), D (Darby) and E (Eddy, the pup).

For every occurrence of a nosing behaviour, the behavioural context and other important contextual information (e.g., weather conditions, audience presence), and the duration of the act itself (when possible), the action of the nares (open/closed/not visible), and the position of the vibrissae (protracted/retracted/not visible) were recorded. Also recorded was whether an individual appeared to be attending to another seal or to a person (myself, technicians, or audience members); attention was judged to occur if a seal was visually focused on a seal or human, or if the seal's behaviour was judged to occur in response to either subject. When the nosing behaviour was dyadic, the following information was also recorded: (i) who was involved in the interaction, including, if possible, who was the initiator and who was the recipient; (ii) which body part was nosed; and (iii) the response of both the initiator and recipient or if the nosing act was mutual, the action of each participant immediately following the nosing act.

Observation sessions were 30 minutes in duration and usually occurred twice per day, once before feeding and once after feeding, three times per week. Sessions held *before* the seals' daily feeding occurred, on average, 1333 minutes (range: 983 to 1731 minutes) after the previous day's feeding, while observations held *after* the daily feeding occurred on average 53 minutes (range: 1 to 318 minutes) after feeding. Delays after feeding were usually due to the cleaning of the deck of the enclosure, inclement weather or other uncontrollable factors. Data used in this study came from a total of 245 observation sessions beginning January 8 and ending October 30, 1996. The timing of observation sessions was selected to coincide with times when the seals were likely to be active and hence, when the probability of social interaction was high [i.e., Almon, (1987) found circadian activity rhythms for the O.S.C. seals wherein most activity occurred during the day.]

During each 30 minute session, the seals were observed collectively. All occurrences of the behaviours outlined in Appendix A were recorded for each seal. In keeping with Martin and Bateson's (1993) recommendations, observation sessions included continuous recording of each occurrence of the behaviour patterns, together with the time (and whenever possible, the duration) of occurrence. In this way, frequencies of the observed behaviours per observation session (os) were obtained. Most behaviours were analysed in terms of frequency rather than duration since the latter was difficult to measure accurately for some of the short-lived or rapid behaviours (e.g., pop-ups). Duration measures were more often obtained for those behaviours, such as lying on the tank floor or deck and nose-to-tail rolling, in which both a start and finish time could be easily recorded. All timing was recorded by means of a hand-held stopwatch. Because observations were intentionally conducted during high-activity periods of the day, frequency was expressed *per observation session* rather than *per time unit*; this was done

sessions. For each quarter (7.5 min) of a 30 minute os in which a seal was non-visible, I subtracted a quarter of an observation session from their total number of sessions.

Table 1: Number of observations sessions (os) used to calculate each seal's rate of behaviour for activity and nosing behaviours[4]. Presented here are the number of os in which a seal was present in the enclosure, and in a non-visible area of the enclosure. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina, E=Eddy)

Seal	Number of Observation Sessions			
	present	non-visible	activity rate	nosing rate
O	245	0.00	245.00	233.00
L	245	0.75	244.25	232.25
J	245	5.00	240.00	228.00
C	245	10.25	234.75	222.75
D	245	12.00	233.00	221.00
K	194	8.75	185.25	185.25
E	56	20.75	35.25	35.25

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[4] Because nosing behaviour was not recorded during weeks 31 and 32, a maximum of 233 os included nosing data compared to a maximum of 245 os which included general activity. Thus, different number of os were used to calculate the rates of activity and the rates of nosing; however this is not the case for the K and E since they were removed from the enclosure from week 29 to 37.

Structuring of Data

Behaviours were considered in terms of discrete acts or events. For instance, if a seal performed five consecutive pop-ups in the same location, this was considered to be five discrete acts rather than a bout or sequence of pop-outs. A bout[5] of nose-to-tail rolling, regardless of duration, was also considered a discrete. All discrete behavioural acts or events were considered 'solo' if the act itself involved only one seal; thus, if each seal performed a pop-out at the same time and location, each pop-out was recorded as solo even if the seals were attending to one another. An act was considered dyadic if it involved two seals; for instance, nuzzling and nose-to-tail rolling were dyadic.

Certain behaviours were divided into one of two categories (see Appendix A): (i) 'active behaviours' or 'action', including pop-outs, pop-ins, pop-ups, porpoising, pirouettes, and movement into or out of either the ST or MT, required high energy expenditure relative to the seals' usual swimming patterns; and (ii) 'quiescent behaviours', including bobbing quietly, lying on the deck/tank floor, surface floating, underwater suspension, draping, and headstands, were low-energy or resting behaviours. This categorization was performed conservatively so that some high- or low-energy behaviours were not included if they occurred only during certain weeks of the study period (e.g. piggy-backs occurred almost exclusively during the breeding season), or

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[5] For the purposes of this study, a 'bout' was defined as a relatively prolonged behaviour pattern which occurred continuously for a period of time (Martin & Bateson,1993). For example, a bout of nose-to-tail rolling was the complete nose-to-tail rolling event, measured from onset until the two seals stopped rolling for a measurable time period.

when the behaviour itself could fit into either category (e.g., lying on the ramp sometimes occurred for long durations in which case the seal was probably resting, or this behaviour may have occurred when a seal was quite active, moving from one tank to another, and was lying on the ramp only long enough to observe the activities of other seals). Flipper-slapping and bubble-blowing were analyzed together as display behaviours, in accordance with general practice (Sullivan, 1981; Venables & Venables, 1957); thus, these behaviours were not included in the active behaviour category despite their apparent vigour. The active and quiescent behaviour indices, as well as the display behaviours, were analyzed to determine the overall activity patterns which provided contextual information for the examination of nosing behaviour. That is, nosing behaviours were examined with respect to seasonal and individual variation in active and quiescent behaviour.

All solo and dyadic behaviours were examined with respect to the presence of nosing; this is distinct from the analyses of solo and dyadic *nosing* behaviours. Solo and dyadic acts with nosing were examined to establish whether there were particular behaviours in which nosing was more likely to occur, and whether there were individual or seasonal differences with respect to this question. In contrast, the analyses of solo and dyadic nosing behaviours dealt specifically with the types of nosing outlined in Appendix A. To illustrate this distinction, if C popped-out at the ramp location of the MT and nosed D's hind region while D was lying on the ramp, then the pop-out itself would be considered a *solo act with nosing,* while the nose-to-body act would be considered a *dyadic nosing act*; however, if C popped-out in the same location but simply nosed the ramp itself, then the pop-out would remain a *solo act with nosing*, but the nosing act would be a *solo nosing act*.

Nosing behaviours were divided into solo and dyadic acts based on the number of seals involved in the act itself. Because Wilson (1974a) suggested that nose-to-tail rolling involves the exchange of olfactory and tactile stimulation, this behaviour will be considered here as a unique form of dyadic nosing. In fact, although it was always dyadic, nose-to-tail rolling is a fairly fluid locomotor-rotational behavioural interaction, characterized most often as social play or courtship (Renouf, 1993; Sullivan, 1981; Wilson, 1974b), during which many nosing acts are usually interspersed. Nose-to-nose and nuzzling acts were considered here as one category of behaviour; nuzzling simply consisted of a nose-to-nose act of prolonged duration. No distinction was made between nose-to-head and nose-to-neck acts due to difficulties in determining an unambiguous and appropriate head-neck boundary.

Because wind direction is thought to influence seal behaviour (Evans & Bastian, 1969; Lowell & Flanigan, 1980), the wind direction from each observation session was classified into functional wind direction categories according to the following scheme: (i) harp enclosure and dump (i.e., south and south-west winds); (ii) offshore (i.e., north and north-east); (iii) uninhabited land (i.e., east and south-east) and (iv) inhabited/residential land (i.e., west and north-west).

The behavioural patterns of each seal were examined separately in order to discern individual differences. Males were also, where appropriate, examined collectively to determine if a 'typical' male pattern existed. Kevina was usually analyzed independently, due to her unique circumstance (i.e., not only was she the only female, but she was either pregnant or nursing during much of the study period), and her lengthy (9.5 week) absence from the study site. Due to the fact that the pup, Eddy, was born late in the study period and was, therefore present during less than a quarter of all observation sessions, his behaviour was rarely included in the analyses. For instance, data from the pup were excluded from the analyses of active, quiescent and display behaviours as his behavioural repertoire was developing throughout the study period and, thus, did not lend itself to analyses comparable to that of the other seals. However, for the examination of solo and dyadic acts with nosing, data from Eddy were included in the calculation of means. For the detailed examination of nosing patterns, Eddy's data was usually included with the following exceptions: analyses over weeks, most analyses between the breeding and non-breeding seasons, and the analysis of patterns of interactions. Eddy's individual nosing scores are, however, made available in Table 5 and Appendix C.

Analyses of Data

All behavioural data were transcribed into PARADOX 3.5 (Borland International, Scott's Valley, CA, USA), a relational database management program, using the behaviour codes detailed in Appendix A. Frequency and duration scores were then extracted from PARADOX. As noted above, duration could not be recorded for all acts so that mean durations were calculated from a smaller data pool than were mean frequency measures (see Tables 2 and 3). From these data, mean durations were calculated despite the bias towards long acts. Thus, frequency per os per seal was the preferred measure for descriptive and comparative purposes. Regardless of whether duration was recorded for an observed behavioural act, *all acts* contributed to the calculation of frequency.

Frequency values per week were calculated as the total weekly count divided by the number of observation sessions per week, which was usually six. Weekly behavioural patterns over the entire study period could, therefore, be assessed with respect to previous research with the O.S.C. harbour seals, in particular, Almon (1987), Renouf (1993) and Rosen (1995). Overall mean frequency values were calculated in one of two ways: (i) by adding the mean frequency from each week and dividing by the appropriate number of weeks; or (ii) by dividing the total score from the entire study period by the appropriate number of observation sessions. The former method introduced some amount of error due to rounding but allowed for a measure of variability (e.g., standard deviation or standard error of the mean) to be calculated; thus, when this method was implemented, both the overall mean value and its variability are reported in the results (i.e., in Tables and Figures). When the second method was used, no rounding error was incorporated into the overall mean value; however, no measure of variability could be reported.

Exploratory data analyses were performed, first, to provide a picture of the general activity patterns, and possible weekly and seasonal[5] influences. Second, behavioural patterns were examined with respect to the presence or absence of nosing. Third, the types of nosing were examined – overall and at the level of the individual seal. Fourth, the patterns of solo and dyadic nosing behaviour were considered with respect to the type of nosing and the individual seal. Fifth, seasonal effects were added to the analyses of patterns of nosing behaviour. Sixth, the patterns of interaction, in terms of the initiator and recipient of dyadic nosing acts, were investigated. Last, the involvement of the nares and vibrissae in the various nosing behaviours was considered.

With respect to statistical testing, the required assumptions of many of the usual tests meant that some 'creativity' was necessary to analyze for individual differences. That is, some measure of independent error was required to test for individual differences, but because behaviour from the same seal was measured each week and weeks are a systematic component of the time of year and season, weeks *could not* be considered independent of each other; thus, weeks were not an appropriate source of error by which to evaluate variance among seals (Hays, 1994; Keppel, 1991; Winer, Brown & Michels, 1991). In order to generate an independent estimate of variability within each seal, by which to assess possible individual differences, three estimates of rate per seal were calculated in the following way: each of the six observation sessions per seal per week were randomly assigned to one of the three estimates, balancing before and after feeding

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[5] The study period was divided into a non-breeding and a breeding season based on active and quiescent behaviour patterns. The rationale for determining these two seasons is provided in chapter three (pp.77).

sessions; then, the frequency of each of the three estimates was calculated for each seal (i.e., by dividing the total number of behaviours in each estimate by the number of observation sessions contributing to that estimate). This method was used to calculate three estimates of a behavioural rate per seal for both the breeding and non-breeding seasons. Hence, an analysis of variance could then be performed that would test for differences between seasons, between seals, and for season by seal interaction effects.

Another way in which individual differences were quantified involved the calculation of overall mean frequencies and standard deviations for each behaviour (or behavioural category). Individual means (*M*) could then be compared to a 'high' (*H*), the overall mean plus one standard deviation, and a 'low' (*L*), the overall mean minus one standard deviation.

Prior to the onset of this study, no specific predictions were made regarding the various types of nosing or regarding each individual's pattern of nosing behaviour. However, both seasonal and individual differences were expected; these differences were tested for statistical significance by means of analysis of variance (within-subjects design) and paired t-tests. When statistical tests were performed, Minitab (Minitab Statistical Software, State College, PA, USA) and SPSS (SPSS Inc., McGraw-Hill, New York) were used.

Chapter Three: Results and Discussion

This chapter presents the results of detailed exploratory data analyses, as well as statistical analyses where warranted. First, the general activity patterns are explored to provide contextual information for the detailed analyses of nosing behavioural patterns. General activity is examined in terms of active and quiescent behavioural patterns, and in terms of display behaviour. The types of behaviour in which nosing occurred are then presented. This is followed by analyses of the patterns of nosing behaviour across weeks and between seasons. Group and individual patterns are also examined; males are initially considered collectively to establish whether a 'typical' male pattern exists, and then the female and her pup are included in the analyses. The next section deals with patterns of interaction among the individual seals. Finally, the involvement of the nares and vibrissae during nosing acts is examined.

Description of Study Period Events

The data discussed below are derived from observations made during the 43-week study period, from January 8 to October 30, 1996. Several specific events occurred during this period that most likely affected the observed behavioural patterns. The only female subject was pregnant during the first 25 weeks of the study. The composition of the study group was not the same throughout the entire study period. From week 1 to 24, observations were conducted on the five adult males and one adult female, described in the methods. However, the birth of a pup on June 23 meant that from week 25 to 28, the pup was present and interacting exclusively with his mother (at least during the observation sessions). The sole female, Kevina, and her pup were then removed from the seal enclosure before mating could take place, so that from weeks 29 to 37, only the five males were observed. From week 38 to week 43, the study group consisted of all seven seals, the five adult males plus Kevina and her pup. The physical signs of the moult were apparent from week 34 to 36 for the males, but Kevina's moult occurred later (week 38 onwards) and followed an atypical pattern, most likely as a result of a bout of actinomyces (a bacterial skin infection) from August 18 to mid-September. No observations were made in week 33, and no nosing data were collected from week 31 to 33 (see Methods).

Active and Quiescent Behaviour

Overall Patterns: Frequency. The mean rate of active behaviour (17.94 acts/os/seal), as measured by the frequency of pop-outs, pop-ins, pop-ups, porpoising, pirouettes, and movement into or out of either the ST or LT, was almost four times the mean rate of quiescent behaviour (4.80 acts/os/seal; $t=6.86$, $df=5$, $p<.001$), as measured by the frequency of quiescent bobbing, lying on the deck/tank floor, surface floating, underwater suspension, draping and headstands (see Table 2).

Table 2: Mean and total frequency of active and quiescent behaviour for each seal. Mean frequency per observation session (os) [+ standard deviation (Std. Dev.)] was calculated as the mean of each seal's weekly rate (the total number of acts per week divided by the number of os that the seal was present and visible during that week). (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

Seal	Mean Frequency per os		Total Number of Acts	
	Active	Quiescent	Active	Quiescent
O	21.12 (11.102)	6.87 (4.215)	5186.00	1694.00
L	14.89 (7.974)	2.64 (1.524)	3642.00	646.00
J	11.27 (5.863)	5.41 (3.282)	2685.00	1326.00
C	20.29 (7.766)	1.94 (1.692)	4797.00	443.00
D	16.15 (5.674)	5.71 (3.879)	3823.00	1349.00
K	23.89 (13.941)	6.20 (3.889)	4443.00	1134.00
Mean	17.94	4.80	4096.00	1098.67
Std. Dev.	4.648	2.015	902.383	470.069
N	6	6	6	6
Total	--	--	24576.00	6592.00

Individual Patterns: Frequency. As shown in Table 2, the rate of active behaviour differed across individuals. The sole female had the highest frequency [23.89 acts/os, compared to the high of 22.59 acts/os (*H*=mean + 1standard deviation)] and J exhibited the lowest [11.27 acts/os, compared to the low of 13.29 acts/os (*L*=mean - 1 standard deviation)]. Mean quiescence levels also showed individual variation with the oldest seal, O, having the highest level (6.87 acts/os vs. *H*=6.82acts/os) while C showed the lowest (1.94 acts/os vs. *L*=2.79 acts/os). Although all seals showed a higher mean rate for active than for quiescent behaviours, the magnitude of the difference varied greatly depending on the individual seal. For instance, C showed a 10:1 ratio of active to quiescent acts while J exhibited a 2:1 ratio. These individual differences in overall action and quiescence levels were consistent with the hypothesis that the behavioural patterns of each seal would vary considerably so that it would be important to analyze behaviour on an individual as well as a group basis.

Overall Patterns: Duration. Although the mean rates of active behaviour were higher than those of quiescent behaviour, mean duration showed the opposite pattern (Table 3). On average, quiescent behaviours were over four times longer than active behaviours (130 vs. 30 seconds, respectively; t=-6.81, df=5, p<.001). This result indicates that the high-energy behaviours included in the activity index tended to be short relative to the low-energy behaviours contributing to the quiescence index. The active behaviours were likely to be even more short, relative to quiescence behaviours, than is evident here due to the fact that duration was rarely recorded for very brief actions such as pop-ups; thus, the durations contributing to the action index were biased towards the longer active behaviours such as extended pop-outs. This bias is evident when one considers that less than 6% (N=1715 acts) of the total number of acts contributing to the active behaviour frequency (N=24576 acts), are included in the calculation of the total active behaviour duration (Tables 2 and 3). In contrast, almost 72% of the total number of quiescent acts contributed to the calculation of the total duration of quiescent behaviour.

Table 3: Mean and total duration of active and quiescent behaviour per seal. Mean duration was calculated by dividing the total duration of active or quiescent behaviour by the total number of active or quiescent behavioural acts. Duration (in seconds) was recorded to the nearest second, so that the decimal place in this table is shown only for comparative purposes. The totals* in the columns for mean duration of active and quiescent behaviour represent the number of acts for which duration was recorded for each behaviour type. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

	Mean Duration (in seconds)		Total Duration (in seconds)	
Seal	Active	Quiescent	Active	Quiescent
O	28.4	124.7	4204	149903
L	44.5	153.0	11608	60108
J	41.1	137.8	16943	130603
C	23.0	188.1	5056	57354
D	21.1	89.9	10905	98951
K	20.4	86.1	3198	66813
Mean	29.7	129.9	8652	93955
SD	10.55	38.79	5385	39294
N	6	6	6	6
Total	1715*	4725*	51914	563732

Individual Patterns: Duration. Individual differences were also evident for the mean duration of active and quiescent behaviours. K, who showed the highest mean frequency for active behaviours, had the shortest mean durations for both active and quiescence behaviours (20 and 86 seconds, respectively); this is not surprising given that sampling periods were fixed. The two seals who showed the lowest mean active behaviour rates, J and L, had the highest mean durations for active behaviour (41 and 44 seconds, respectively). Although C's mean frequency of quiescent behaviours was lower than all other seals, his mean duration for quiescent acts was the longest at 188 seconds. The ratio of quiescent to active mean durations was largest for C, at over 8:1, while all other seals showed a ratio of between 3:1 and 4:1.

Patterns in Relation to Feeding. A comparison of active and quiescent behaviour before and after feeding revealed that the behaviour of all individuals was influenced by the feeding event (Figure 2a and 2b). The mean frequency of active behaviour was higher prior to feeding (M_b=12.04 acts/os/seal) compared to post-feeding (M_a=5.98 acts/os/seal; t=5.75, df=5, $p<.05$), while the reverse pattern was true for quiescent behaviour (i.e., before: M_b=1.33 acts/os/seal vs. after: M_a= 3.48 acts/os/seal; t=-3.24, df=5, $p<.05$), although this pattern was not as pronounced for C and L.

The mean duration for active behaviour tended to be shorter before feeding (M_b = 27 sec) than afterwards (M_a=37 sec); however, only three of six seals fit the overall pattern so that this pre/post-feeding difference was not significant (Figure 3a). The reverse pattern was true for quiescence levels (Figure 3b); that is quiescent acts lasted longer before feeding (M_b=183 sec vs. M_a=106 sec), and this duration pattern was

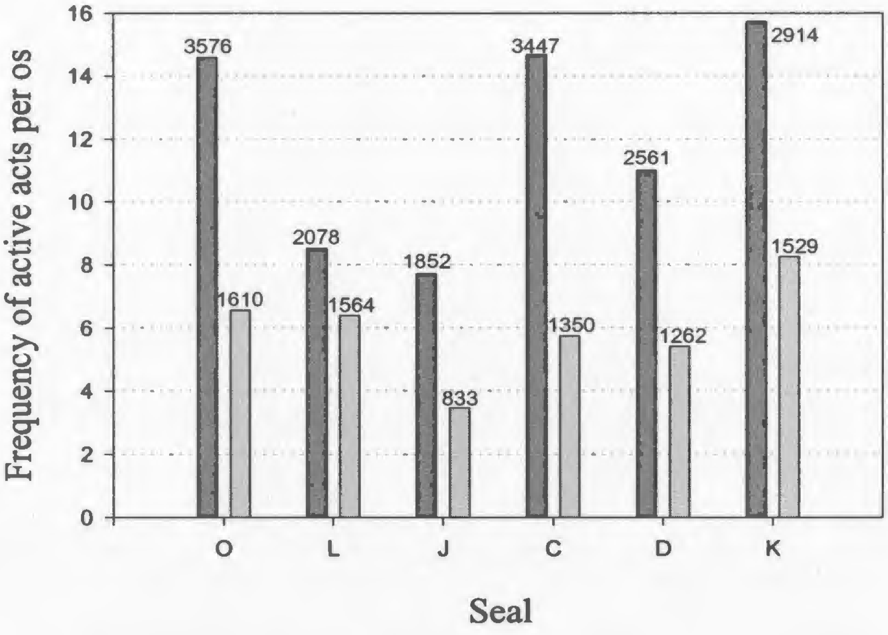


Figure 2a: Frequency of active behaviour per observation session (os) before and after feeding for each seal. Frequency was calculated by dividing the total frequency by the number of os appropriate for each seal (see Table 1). Total sample size per seal is indicated at the top of each bar. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

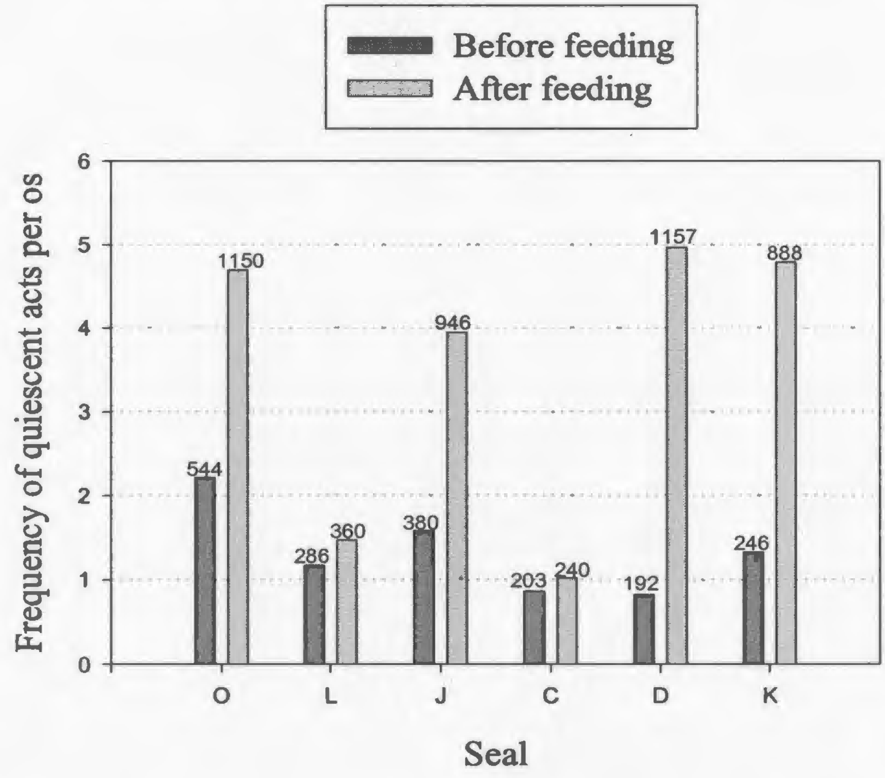


Figure 2b: Frequency of quiescent behaviour per observation session (os) before and after feeding for each seal. Frequency was calculated as above. Total sample size per seal is indicated above each bar. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

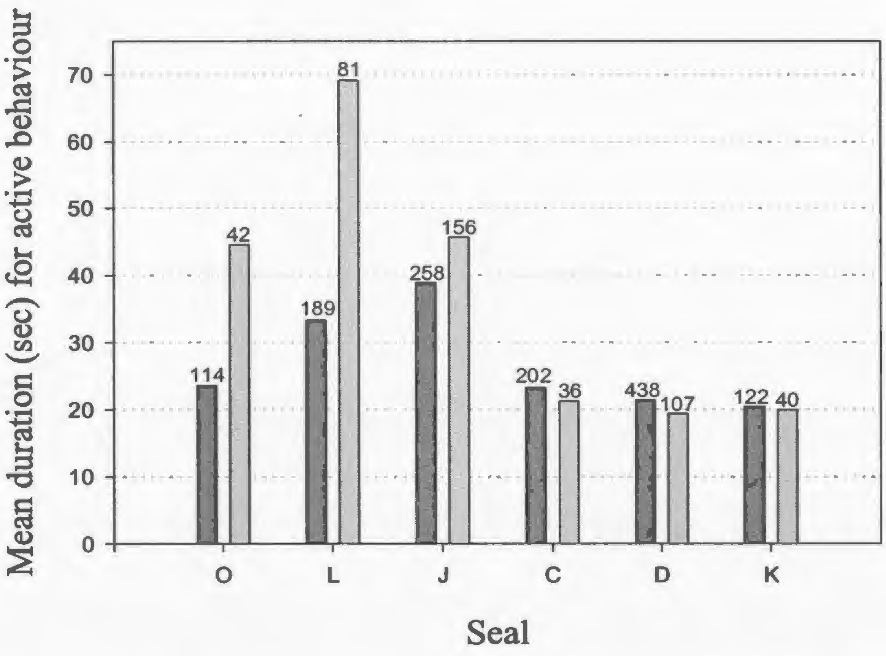


Figure 3a: Mean duration (seconds) for active behaviour before and after feeding for each seal. Mean duration was calculated by dividing the total duration by the number of acts contributing to that total. Total sample size per seal is indicated above each bar. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

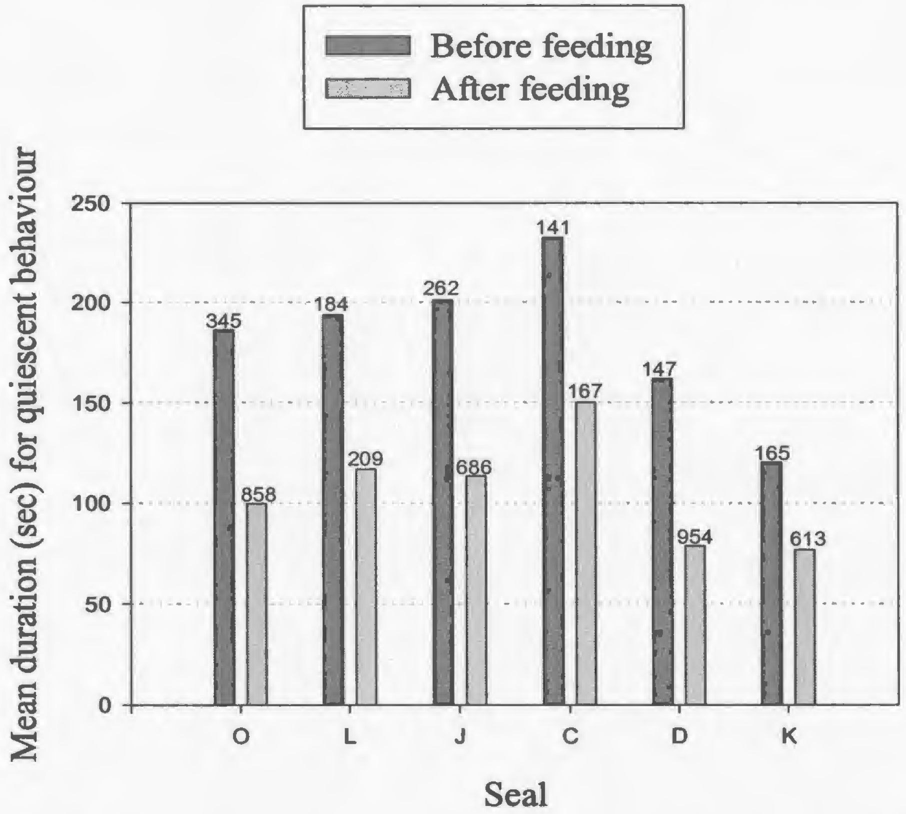


Figure 3b: Mean duration (seconds) for quiescent behaviour before and after feeding for each seal. Mean duration was calculated as above. Total sample size per seal is indicated above each bar. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

consistent across seals for quiescent behaviour (t=11.22, df=5 p<.001).

These patterns suggest that prior to feeding, activities such as pop-outs/ups/ins were performed more often and more rapidly, probably reflecting the seals' tendency to monitor the area surrounding the enclosure in the expectation of the arrival of food. However, after feeding, these same behaviours may have served a different purpose; for example, the seals may have popped-out for longer to monitor a seal in another area of the enclosure. Location and attention measures support this notion – before feeding 73% of pop-outs/ups/ins occurred at the gate/fence region of the MT which was the best vantage point from which to monitor the arrival of technicians; after feeding, however, only 36% of pop-outs/ups/ins were at this location. Furthermore, when the seals' apparent attention was considered, the results showed that before feeding, only 20 % of pop-outs/up/ins were judged to involve attention towards other seals, while after feeding, this percentage doubled.

The longer duration of pre-feeding quiescent behaviour is, however, counter-intuitive to what one would normally expect (i.e., that the seals' quiescent activities would be longer *after* feeding because the seals would be full and, therefore, less active). However, further analyses revealed that quiescent acts were longer before feeding primarily because of differences in the duration of seals lying on deck; before feeding, this activity averaged 559 seconds compared to an after feeding average of 464 seconds. In addition, before feeding, 34.5% of occurrences of seals lying on deck were in the foredeck area where arriving technicians could easily be viewed, while after feeding, only 24.7% of lying on deck acts were located in the foredeck area. When seals were lying in the foredeck area, the before feeding duration (foredeck: M_b=640 sec) was substantially longer than both the after feeding duration (foredeck: M_a=455 sec), and the before feeding duration in areas where arriving food could not be viewed easily (aftdeck: M_b=506 sec); no such difference in duration was evident for deck area after feeding (cf. foredeck: M_a=455 vs. aftdeck: M_a=466 sec). Altogether these findings strongly suggest that the difference in the mean duration of quiescent acts before and after feeding resulted, at least partially, from behavioural patterns that reflected the anticipation of arriving food.

Patterns Across Weeks. The mean frequency of activity and quiescence scores was calculated across the five adult males to examine the overall male pattern across the study period (Figure 4). There was a gradual increase in active behaviour during the first 20 weeks of the study period, followed by a sharp decrease during the four weeks prior to the pup's birth (i.e., from weeks 21 to 24). After the birth, active behaviour levels increased and remained relatively high throughout the rest of the study period. Rosen (1995) also found an increase in locomotor activity levels for adult males following parturition, during the breeding season and during the early part of the moult. Renouf (1993) also detected increased activity for all adult seals during the combined breeding/moulting season (June 9 to October 5) relative to the rest of the calendar year.

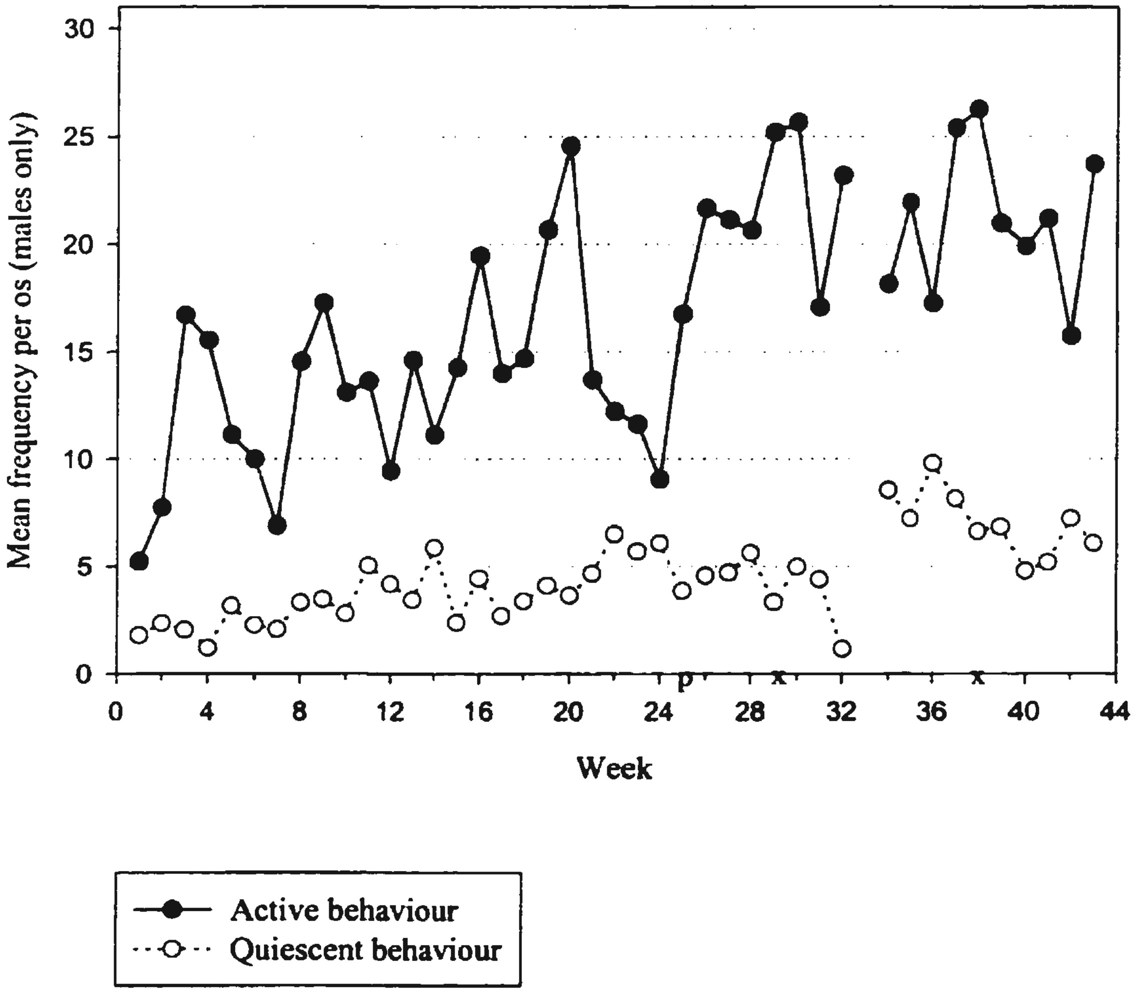


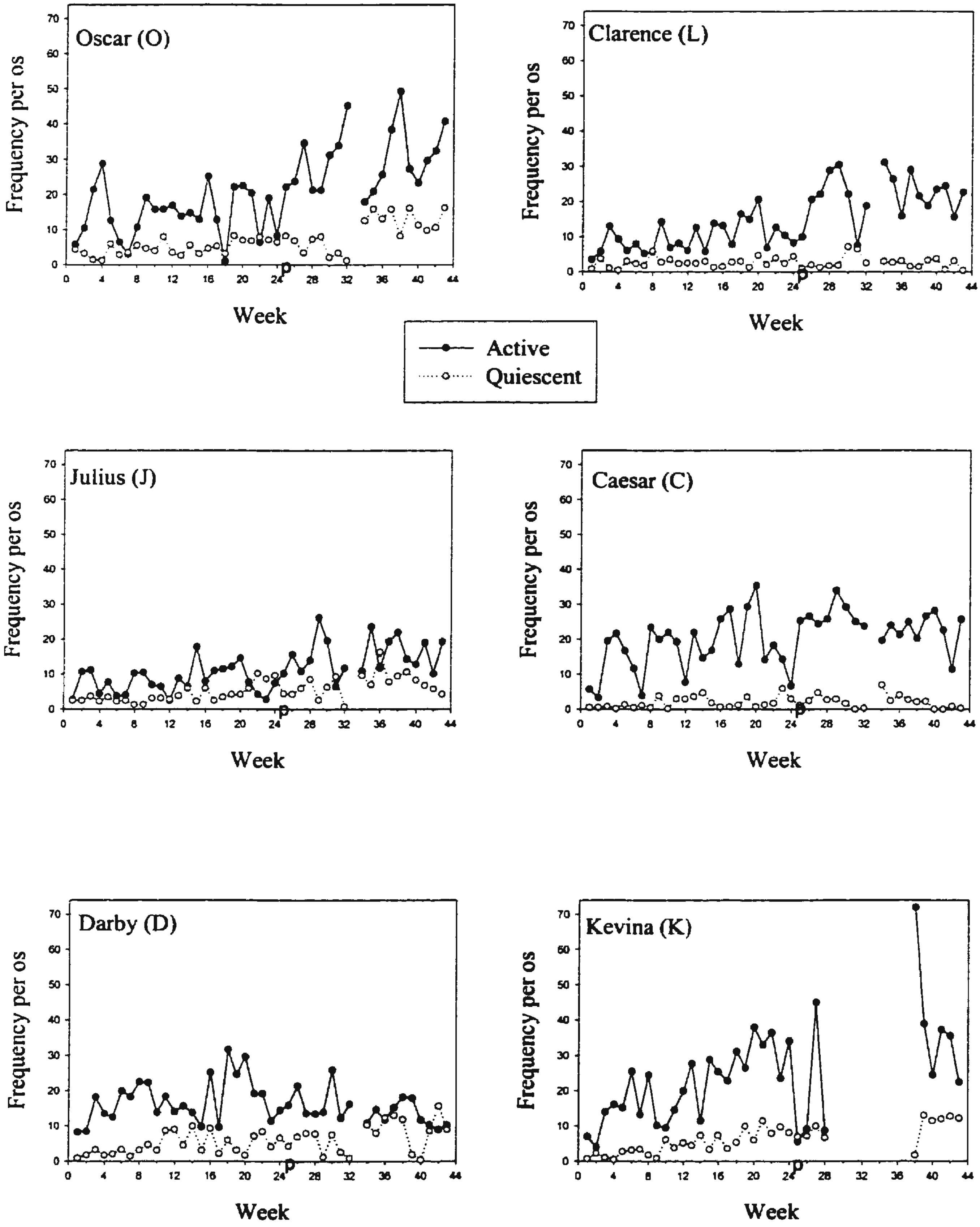
Figure 4: Mean frequency per observation session of active and quiescent behaviour across weeks for males. Parturition is denoted by a 'p' on the week axis. The period during which Kevina and her pup were not present is indicated by the two 'x's on the week axis.

Mean quiescence levels remained at low levels throughout the first 20 weeks before increasing, by 80%, (i.e., from a mean of 3.18 acts/os in the first 20 weeks to a mean of 5.74 acts/os from weeks 21 to 24) during the four weeks prior to the pup's birth; this increase corresponded with the pre-birth decrease in activity. Quiescence levels again showed an increase from weeks 34 to 37 which corresponded with the male moult, followed by a decrease in week 38 (when the female and her pup were reintroduced to the enclosure). Despite this drop in mean quiescence levels following the return of K and the pup, quiescence was higher from week 38 to the end of the study period than during the first 20 weeks of the study period.

Individual Patterns Across Weeks. The activity of each seal showed considerable variation over the 43 weeks of the study period (Figure 5). Four of the five males (C, D, J, L), showed a pattern consistent with the overall male pattern whereby there was a decrease in active behaviour four weeks prior to the pup's birth on June 23 (i.e., from weeks 21 to 24). Only the youngest seal, D, did not show the increase in active behaviour at week 25 that was typical of the overall male pattern. Although O did show this increase, he was unusual in that his activity levels continued to increase after week 29 (i.e., when K and the pup were no longer present), while the active behaviour levels of L, J and C all decreased at this time.

Quiescent behaviour appeared to be at relatively low levels for all seals during the

Figure 5: Frequency per observation session (os) of active and quiescent behaviour across weeks for each seal. The week of parturition is indicated with a ‘p’ on the week axis.


Oscar (O)
Clarence (L)
Julius (J)
Caesar (C)
Darby (D)
Kevina (K)
Frequency per os
Week
0
10
20
30
40
50
60
70
0
4
8
12
16
20
24
28
32
36
40
44
P
Active
Quiescent

early part of the study period (i.e., 8 weeks for D and C, 13 weeks for J, 9 weeks for K etc.; Figure 5). O, J, C and D all showed a slight increase in quiescence prior to the pup's birth (corresponding with the decrease in activity level). In week 25, the first week of the pup's life, all males except O showed a drop in quiescent behaviour (again corresponding with increased activity). For L, J and D, there was an increase in quiescence after the removal of the female and her pup.

O showed a noticeable decrease in the frequency of active behaviour, and a corresponding increase in quiescence during weeks 34 to 36, the period during which the physical signs of moulting were apparent for all of the male seals. Quiescence levels appeared to increase somewhat for J and D during the moult, but not for L or C. Thus, these results are not fully consistent with other research showing decreased activity levels during the moulting season (Rosen, 1995). The finding that not all males substantially decreased active behaviour, or increased quiescent behaviour, during the moult may be a reflection of the disruption in normal mating activities; that is, seals may have remained more active throughout the moult because no mating had taken place. However, without comparable behavioural data (i.e., obtained from the same measures used in this study) from years in which the female was *not* removed prior to the mating season, it is not possible to ascertain how the removal of the only female influenced the males' behaviour patterns.

As for the sole female, K showed a gradual increase in quiescent behaviours throughout the study period, although there was a levelling-off both immediately before and after parturition. In addition, K's quiescence levels were consistently high during her moult (i.e., during her moult, K averaged 10.6 quiescent acts/os compared to her high, across all weeks, of 6.8 acts/os), except for the first week of her reintroduction to the male population (i.e., week 38) during which her activity rate peaked to the highest level for any seal. Although K showed extremely low activity rates immediately after pupping, her activity then increased dramatically at week 27. A more detailed analysis of this pattern revealed that K's high active behaviour rate in week 27 was due to her vigilance (e.g., regular pop-outs/ups with attention directed towards other seals). Prior to week 27, much of K's time was spent on deck attending to the pup, so that active behaviour rates remained low. Unfortunately, the use of frequency rather than duration in this situation means that K's tendency to remain on deck during weeks 25 and 26 was not reflected in a corresponding increase in quiescent behaviour.

Conclusions. Despite a high level of individual variation over time, all males except O showed a gradual increase in activity levels over the first 20 weeks, from the beginning of winter into the spring, followed by decreased activity during the four weeks before pupping (i.e., during the early part of the reproductive season). After parturition, active behaviour rates rose again for all males except the youngest, D; this increase coincided with what is normally the pre-mating and mating seasons. O was again atypical of the males in that his active behaviour continued to increase even after the removal of the female and her pup. K also showed increasing activity rates during the first 20 weeks, then her activity leveled off before dropping to a lower level around the time of parturition. Although the overall male patterns of quiescent and active behaviour corresponded well with one another, the quiescence patterns of each individual were more difficult to interpret; however, for three of the males and for K, quiescence levels increased during the moult, as expected. The fact that the mean active and quiescent behaviour rates were consistent with most predictions regarding pre- and post-feeding activity levels, as well as some of the biologically significant events of the study period (e.g., removal of the sole female during what would normally be the mating season) suggests that the behavioural measures were well chosen. Regarding this point, other researchers (Almon, 1987; Renouf, Almon & Noseworthy, 1988; Rosen, 1995) used grid crossing (i.e., the number of times per 5 minute sample period in which a swimming seal crossed from quadrant into another in the MT) as an activity measure. Grid crossing scores also resulted in variable activity levels per individual which is consistent with the active behaviour scores presented here. However, grid crossing scores cannot yield a quiescence index with which to compare the activity index; such a comparison may provide a more complete picture of general behaviour patterns. In an effort to determine the relationship among the various activity indices, it might be worthwhile to look for a correlation between measures based on observable activity, such as those used by myself and Rosen (1995) and more mechanical measures obtained from time-depth recorders modified as activity recorders that record the rotational behaviour of an individual animal (Moulton, 1997).

Display Behaviour

Flipper-slapping and bubble-blowing are generally considered male display behaviours in that they are thought to signal physical or reproductive quality to potential mates (Beier & Wartzok, 1979; Perry, 1993; Renouf, 1993; Sullivan, 1981; Venables & Venables, 1957). However, these behaviours have also, albeit more rarely, been discussed as a form of play (Bishop, 1967; Renouf, 1986; 1993), as threat signals to exclude other males from aquatic territories (Perry, 1993), or as defensive acts (Wilson, Miller, Hursey, Frantz & Gorte, 1985). To investigate whether display behaviours were associated with the breeding season, as determined by active and quiescent behaviour patterns, all occurrences of bubble-blowing and flipper-slapping acts were examined in relation to breeding and non-breeding seasons, and with respect to both overall and individual patterns.

Determination of Seasons. Although researchers often refer to breeding, mating, or reproductive seasons, the basis for determining the season's onset or duration is not always clear. The scientific literature indicates that the breeding season for harbour seals should normally be about 8 to 10 weeks in duration (Boulva & McLaren, 1979); however, there is also evidence that estrus is prolonged for captive unmated females (Bigg & Fisher, 1974). In addition, it is known that males remain potent for at least four months (Boulva & McLaren, 1979).

For the purposes of this study, the onset of the breeding season was estimated to occur at the start of week 21, four weeks prior to the birth of the pup, in accordance with Boulva &McLaren (1979), and in agreement with the changes in the seals' active and quiescent behavioural patterns, examined in the previous section. The end of the breeding period was estimated to occur at the end of week 32 to allow for the possibility that the breeding season may have been prolonged due to the disruption of normal mating patterns caused by the removal of the sole female. Thus, the breeding season was twelve weeks in duration. The remaining 30 weeks of observations were considered to be the non-breeding season.

Overall Patterns. Almost all bubble-blowing (98.9%) and most of the foreflipper-slaps against the water surface (80.2%) occurred in the main tank. While 14.7% and 4.1% of flipper-slaps took place in the ST and RT respectively, the remaining 1.1% of the total bubble-blowing events all occurred in the ST. The mean frequency of bubble-blowing, across males and weeks, was 0.50 acts/os/seal, while flipper-slapping occurred over four times as often (M_{ffx}=2.10 acts/os/seal) (Table 4). Bubble-blowing occurred over 16 times as frequently during the breeding season as it did during the non-breeding season; however, this difference was statistically non-significant, probably due to the small number of seals. Nonetheless, for four of the five males, there was a large increase in bubble-blowing during the breeding season. There was no significant difference between the mean frequency of flipper-slapping acts during the breeding season (2.14 acts/os/seal) and the non-breeding season (2.08 acts/os/seal). There was a significant correlation between flipper-slapping and bubble-blowing rates during the breeding season ($r=0.98$, $df=3$, $p<0.05$), but not during the non-breeding season ($r=0.63$, $df=3$, $p=0.25$).

Table 4: Mean frequency of bubble-blowing and flipper-slapping per male by season. Frequency per observation session (os) is presented for the non-breeding season, the breeding season, and over the entire study period. The overall male mean frequency and standard deviation (SD) are also presented. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby)

Seal	Mean bubble-blowing frequency/os.			Mean flipper-slapping frequency/os.		
	Non-breeding	Breeding	Overall	Non-breeding	Breeding	Overall
O	0.01	1.63	0.47	0.68	3.03	1.35
L	0.02	1.86	0.55	0.03	0.07	0.05
J	0.01	0.03	0.09	0.08	0.01	0.06
C	0.10	3.76	1.15	1.43	4.99	2.45
D	0.28	0.06	0.22	8.16	2.61	6.58
Mean	0.08	1.47	0.50	2.08	2.14	2.10
SD	0.116	1.540	0.410	3.448	2.119	2.70

Individual Patterns. The two youngest males accounted for the greatest proportion of the total number of bubble-blowing events, and of the total number of flipper-slapping acts (Figure 6). Caesar accounted for 46.4% of bubble-blowing and 23.3% of flipper-slaps, while Darby accounted for 62.8% of flipper-slapping but only 8.8% of bubble-blowing. The two oldest males accounted for similar proportions of the total bubble-blowing (L: 22.1%, O: 19.1%), but only O made a sizable contribution to the total number of flipper-slaps (12.9%); J's contribution to both totals was negligible. In addition, the oldest male (O) accounted for all instances of flipper-slapping against the body (n=21), all of which occurred while O was lying on deck. Thus, there did not appear to be a direct relationship between the amount of bubble-blowing and flipper-slapping that each seal performed overall; that is, a seal who flipper-slapped frequently did not necessarily bubble-blow frequently. J performed both behaviours at a low rate and this may reflect his spatial separation from other males (i.e., since most flipper-slapping and bubble-blowing occurred in the MT rather than the ST where J spent the great proportion of his time).

Of particular interest was the observation that the female performed three flipper-slapping acts in which both the hind- and fore-flippers were simultaneously slapped against the water surface. These three double flipper-slaps occurred consecutively while K was in the MT, following one occurrence of K nosing the tank wall. After her flipper-slapping sequence she popped-out at the spot she had previously nosed, and she did not appear to be attending to either seals or people (no technicians or audience were present

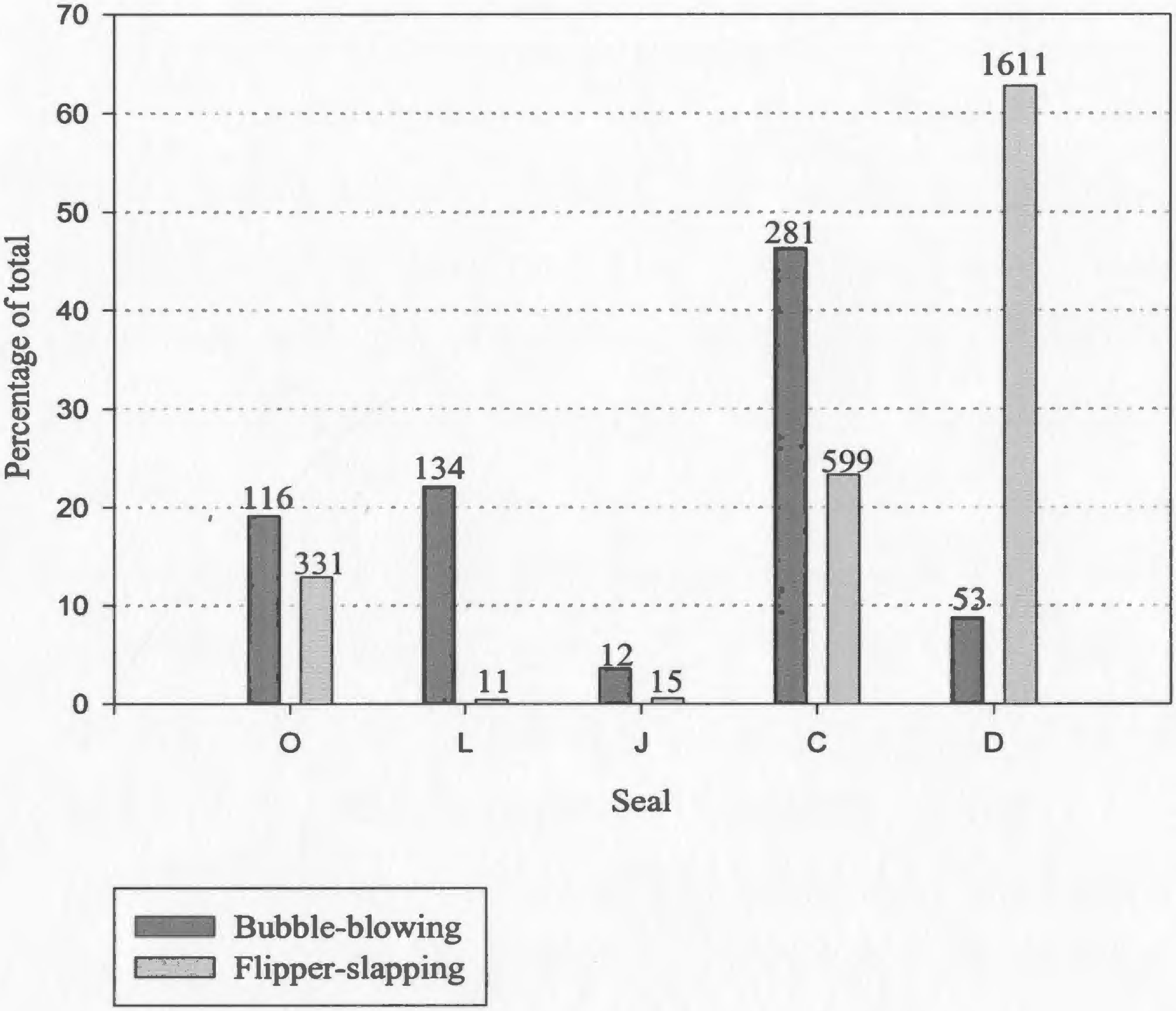


Figure 6: Percentage of the total number of bubble-blowing and flipper-slapping acts accounted for by each male (all types of flipper-slapping included). Total sample size for each seal indicated above bar. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby)

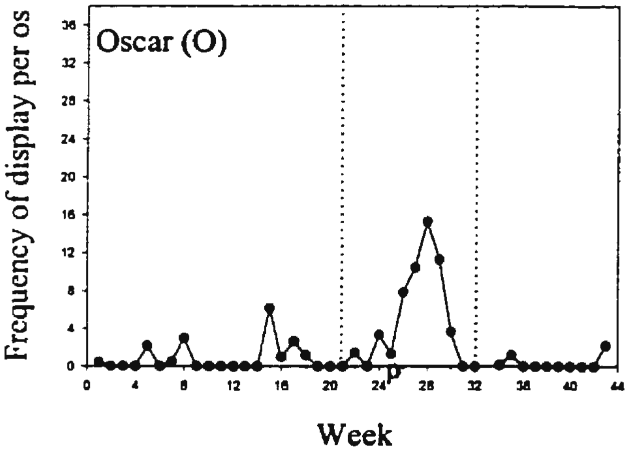
at the time). Given the context of this flipper-slapping bout, it is difficult to speculate on its function; however, given her sex, it is even more difficult to consider this behaviour to have a 'display' function, as is normally done when it is performed by males.

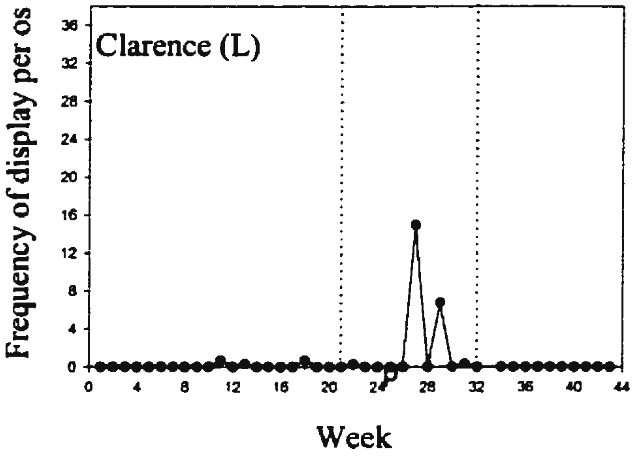
Individual Patterns Between Seasons. Analyses at the level of the individual revealed that all males, except D, performed bubble-blowing more often during the breeding than during the non-breeding season. The ratio of breeding to non-breeding bubble-blowing acts/os ranged widely from 3:1 for J to 163:1 for O (Table 4); C showed a breeding season rate that was greater than the high (M_b=3.76 acts/os vs. H_b=3.01 acts/os). For D, bubble-blowing was almost 5 times as frequent in the non-breeding season than in the breeding season. In fact, D was the only seal to show a mean bubble-blowing rate in the non-breeding season that was above the high (M_{nb}=0.28 acts/os vs. H_{nb}=0.20 acts/os),. When D is excluded from the calculation of the mean number of bubble-blowing acts, then this behaviour was over 50 times as frequent during the breeding season than during the non-breeding season (i.e., M_b=1.82 acts/os/seal vs. M_{nb}=0.035 acts/os/seal).

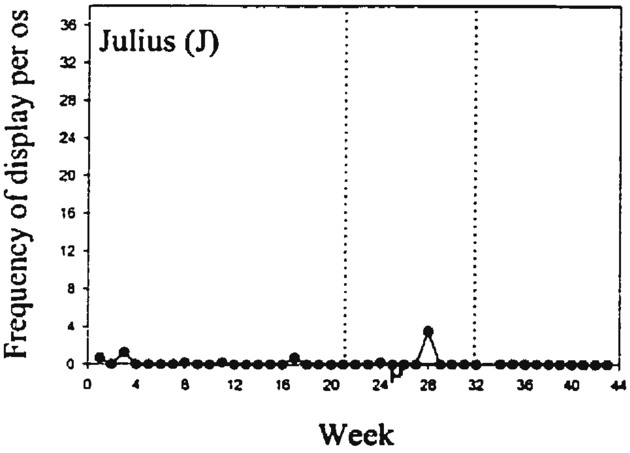
Flipper-slapping did not seem to be as specific to the breeding season as was bubble-blowing. For the three males (C, L and O) who showed a higher mean flipper-slapping frequency in the breeding versus the non-breeding season, this ratio ranged from approximately 2:1 (L) to over 4:1 (O). In contrast, D flipper-slapped over 3 times as often in the non-breeding season than in the breeding season; again D was the only male to show a flipper-slapping rate during the non-breeding season that was greater than the high (M_{nb}=8.16 acts/os vs. H_{nb}=5.53 acts/os), while C was the only male to show a higher breeding season rate (M_b=4.99 acts/os vs. H_b=4.26 acts/os). It should be noted that the only seal other than D to show a higher flipper-slapping frequency in the non-breeding than in the breeding season was J who also had the smallest ratio of breeding to non-breeding season *bubble-blowing* rates (i.e., 3:1). The finding that the display patterns for D and J were not always consistent with the overall male patterns suggests that, although a display function is likely during the breeding season, this may only constitute a partial explanation. In particular, given the high frequency of flipper-slaps in the non-breeding season, this behaviour is likely to serve functions other than display.

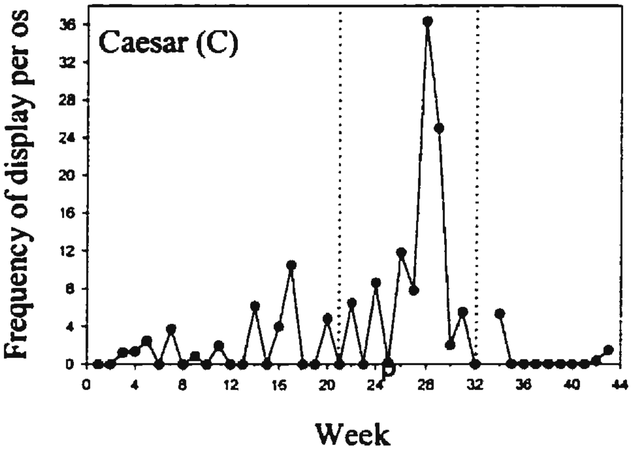
Individual Patterns Across Weeks. To examine the display function in more detail, the combined frequencies of bubble-blowing and flipper-slapping were analyzed by individual over weeks. For the four oldest males, O, L, J and C, there was an increase in flipper-slapping and bubble-blowing after the birth of the pup, which occurred just before the start of week 25 (Figure 7). For J, the frequency of display behaviours increased slightly and only four weeks after the pup's birth which would approximate the typical timing of weaning if the seals were free-living; this display was short-lived for J as it stopped in week 29 when the female and her pup were removed. As already noted, J's low display frequency could reflect his spatial preference, or perhaps J was more selective about the timing of display behaviours (i.e., maybe an increase would have been evident

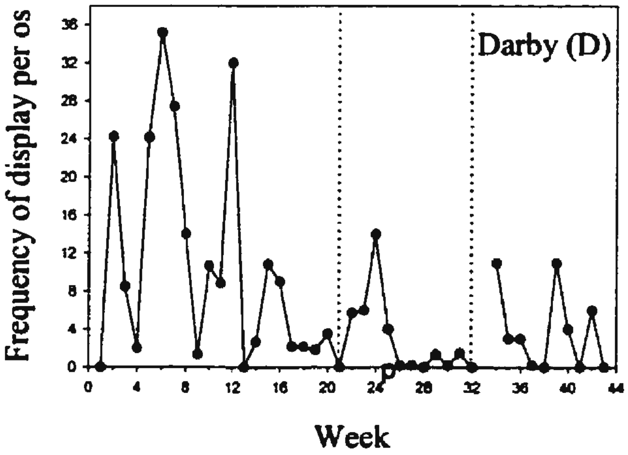
Figure 7: Frequency of display behaviour (flipper-slapping and bubble-blowing) across weeks for each male. The weeks between the dotted lines represent the breeding season. The week of parturition is indicated by a 'p' on the week axis.


Oscar (O)
Frequency of display per os
0
4
8
12
16
20
24
28
32
36
p
0
4
8
12
16
20
24
28
32
36
40
44
Week


Clarence (L)
Frequency of display per os
0
4
8
12
16
20
24
28
32
36
p
0
4
8
12
16
20
24
28
32
36
40
44
Week


Julius (J)
Frequency of display per os
0
4
8
12
16
20
24
28
32
36
p
0
4
8
12
16
20
24
28
32
36
40
44
Week


Caesar (C)
Frequency of display per os
0
4
8
12
16
20
24
28
32
36
p
0
4
8
12
16
20
24
28
32
36
40
44
Week


Darby (D)
Frequency of display per os
0
4
8
12
16
20
24
28
32
36
p
0
4
8
12
16
20
24
28
32
36
40
44
Week

if K had remained in the enclosure throughout estrus.). Nonetheless, despite the finding that two of the mature males (L and J) rarely displayed, when they did, they did so at the appropriate time given the presumed function of display behaviours. L is known to be father of two seals, C and D (Perry & Amos, 1998); thus he has shown reproductive success despite low overall display frequency relative to C, D, and O (Table 4). Unfortunately, it is not known who sired J, E, or any of the other pups born at the O.S.C.

Conclusions. Frequency of display behaviours was more variable across the study period for the two youngest and presumably, the most sexually inexperienced, males. Although harbour seal males are considered sexually mature between age 5 and 6, based on sperm production (Boulva & McLaren, 1979), younger males may not actively engage in sexually relevant behaviours in a captive environment with only one female and several senior males. It would be interesting to compare these findings with a captive breeding colony of the opposite sex ratio; perhaps younger males would display at earlier ages or with more seasonal precision. It is also possible that the display pattern for C and D is the normal pattern in the wild; that is, despite being sexually mature, perhaps young inexperienced males practice flipper-slapping and bubble-blowing outside of the breeding season when they are safe from retaliation from competing males. D's display pattern lends some support to this notion in that the frequency of his display behaviours was at its lowest when the other males displayed at the highest frequency.

In summary, the patterns of flipper-slapping and bubble-blowing were consistent with predictions based on what is known about display behaviour in male harbour seals; that is, despite variable rates, the four oldest males displayed at the highest frequency during the breeding season. Only the youngest male displayed more often in the non-breeding season. This conformity between the display rates and seasonal predictions indicated that the determination of the breeding and the non-breeding seasons, based on the patterns of active and quiescent behaviour (i.e., as was done in this study), was appropriate; thus, this seasonal distinction[6] was used for following analyses.

Although bubble-blowing and flipper-slapping did occur most frequently during the breeding season, however defined, three males (O, C, D) also displayed often outside of the mating season. That 'display' behaviours occurred during the non-breeding season, plus the fact that the female flipper-slapped in her own unique context, suggests that flipper-slapping and bubble-blowing, behaviours normally categorized as 'male displays' may serve other functions. In particular, it is possible that 'display' behaviours which occur outside of the breeding season may be a form of play, or perhaps, a communication of well-being (Fagan, 1992). Often, when a seal started to flipper-slap or bubble-blow, another seal would promptly join him and also start performing a 'display' behaviour; that these interactions were often prolonged and did not appear to culminate in an agonistic

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[6] Breeding season was *not* determined solely on information associated with birth, as is commonly done, because both captivity and the removal of the female *prior* to mating were thought to likely alter the onset and duration of breeding.

event is not consistent with the suggestion (Wilson et al., 1985) that display behaviours may be defensive acts. Other questions arise from the observation of K's flipper-slapping bout; in particular, is flipper-slapping by a female a form of play or does it serve a function akin to 'male display'? Lastly, the possibility exists that flipper-slapping and bubble-blowing events during the non-breeding season, and performed by K, simply reflect the unique behavioural patterns of a captive group of animals with time and energy to spare.

Solo and Dyadic Acts With Nosing

Overall Patterns. In terms of frequency (acts/os), most behaviour consisted of solo acts (97.9%) as opposed to dyadic acts (2.1%). In contrast to Wilson (1974), no group activities were observed, although dyadic activities were frequently observed by other seals who may then have responded to them in some manner. Nosing was present in over half (56.7%) of the total number of dyadic activities nosing (Figure 8). In contrast, nosing was *not* present during 84.8% of the total number of occurrences of solo activity. During one third of dyadic activities, the presence or absence of nosing was impossible to observe, usually because the interaction itself prevented observation.

Solo acts in which nosing occurred included the following: pop-outs/ins/ups, representing 28.2% of the total, bobbing-alert (22.4%), swimming (14.4%), bobbing-quiet (13.6%), lying on deck (10.0%), lying on ramp/step (4.2%), moving on deck (3.7%),

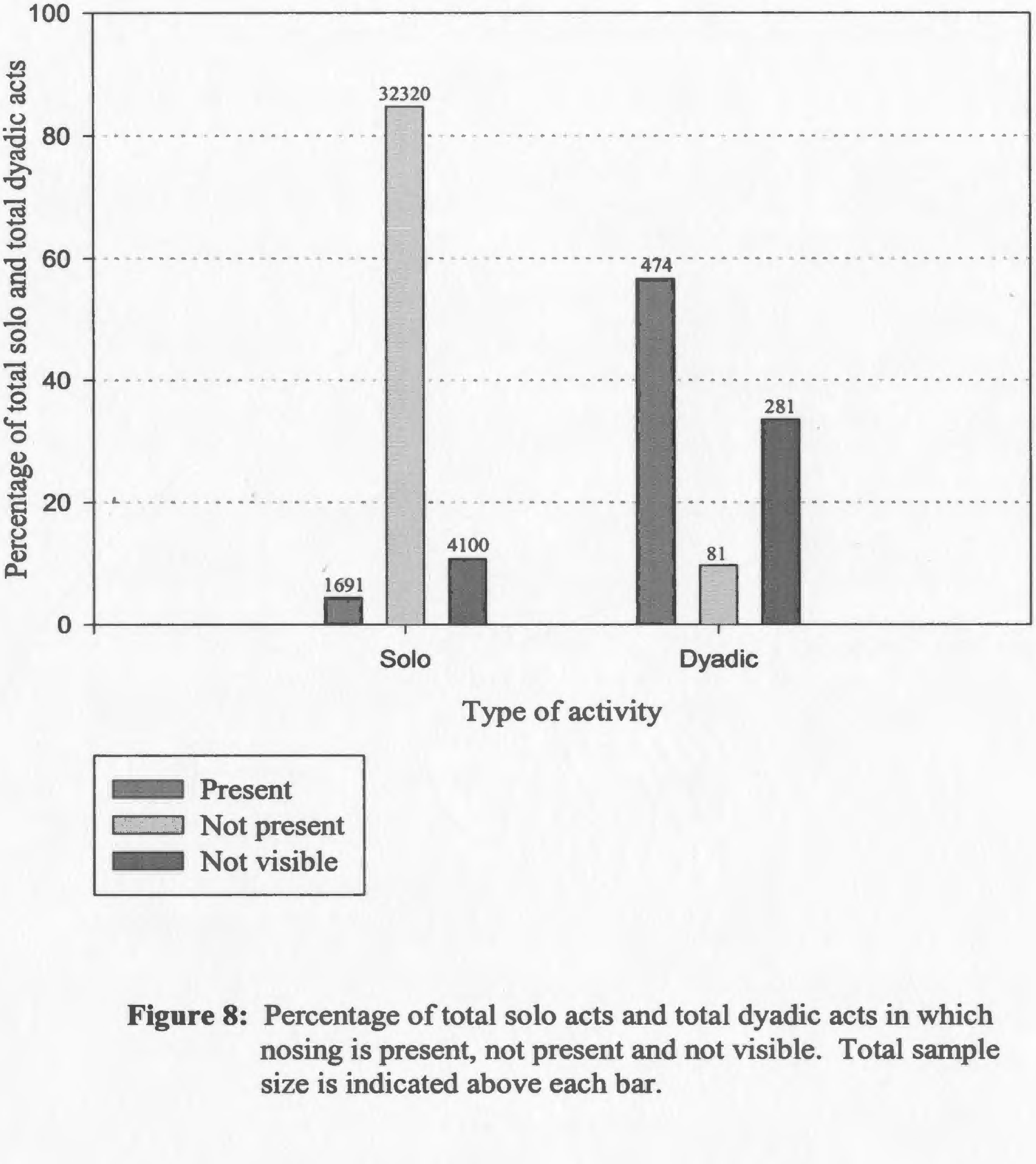


Figure 8: Percentage of total solo acts and total dyadic acts in which nosing is present, not present and not visible. Total sample size is indicated above each bar.

surface floating (2.3%) and other activities (e.g., draping, movement in/out of tanks) which accounted for the remaining 1.5% of the total (Figure 9a). Most of these solo acts with nosing present occurred in either the MT (46.7%) or the ST (35.3%), with the remainder taking place on deck (13.7%), on the ramp and steps leading to the tanks (4.0%), or on the ground (0.3%).

The most common type of dyadic act in which nosing occurred was nose-to-tail rolling (i.e., social play); this activity represented 49.6% of the total number of dyadic acts with nosing present (Figure 9b). Almost all (98.7%) rolling took place in the MT, with the remainder occurring in the ST. Another sizeable percentage of the total dyadic activity with nosing consisted of a uni-directional swimming approach ('app-swim') toward another seal (33.8%), while a mutual swimming approach ('mutual-swim') accounted for 13.7% of the total. Together, 84.0% of swimming approaches occurred in the large tank with the other 16.0% in the ST. Only 3.0 % of the total dyadic activity with nosing consisted of behaviours other than rolling or swimming; this included chases, hugs, piggybacks and head-thrusts.

The mean frequency of solo acts with nosing present (1.36 acts/os/seal) was over twice as high as the mean frequency of dyadic acts with nosing (0.61 acts/os/seal; $t=2.01$, $df=5$, $p<.05$). When all adult seals were considered, there was a slightly higher rate of solo acts with nosing during the non-breeding season than during the breeding season ($M_{nb}=1.28$ acts/os vs. $M_{b}=1.19$ acts/os), but this seasonal difference approached

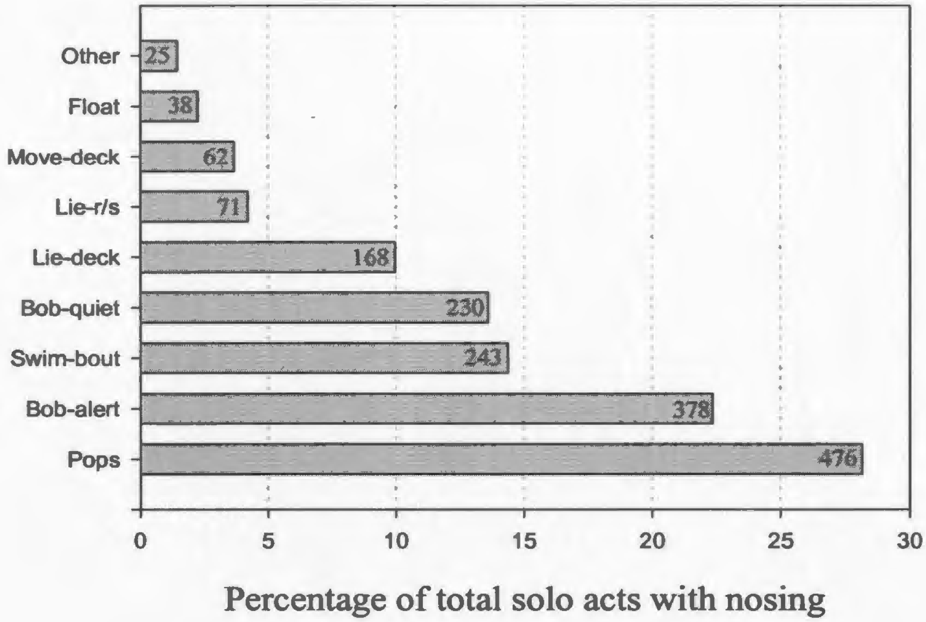


Figure 9a: Per cent of the total number of solo acts with nosing by activity type. Total sample size is indicated within each bar. ('Pops'=pop-outs/ins/ups, 'Lie-deck'=lying on deck, 'Lie-r/s'=lying on ramp/step, 'Move-deck'= movement on deck,'Other'=draping, movement into and out of tanks; see Appendix A)

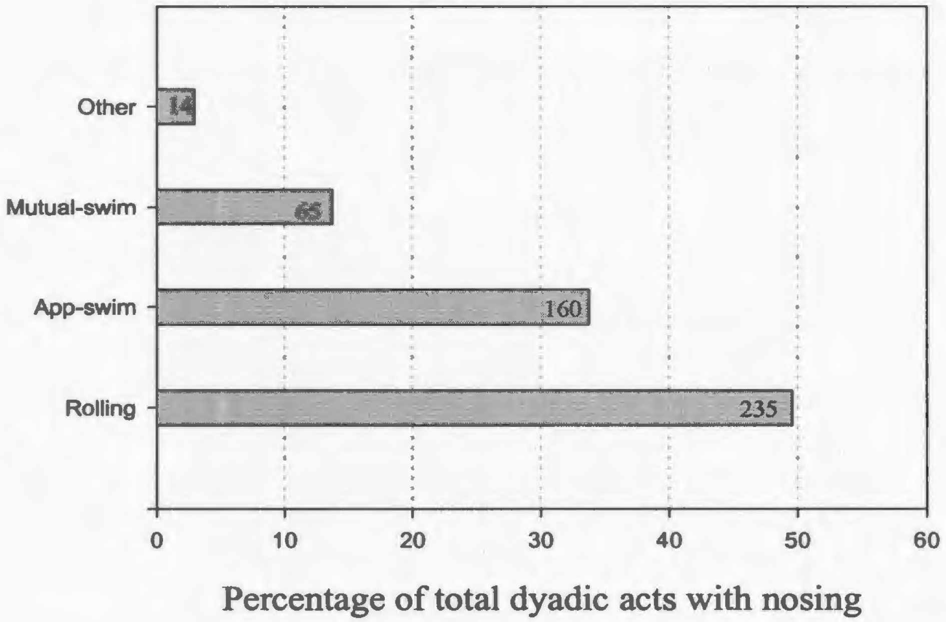


Figure 9b: Per cent of the total number of dyadic acts with nosing by activity type. Total sample size is indicated within each bar. ('Rolling'=nose-to-tail rolling, "App-swim'=swimming approach by a single seal, "Mutual-swim'= swimming approach by two seals towards one another, 'Other'=chases, hugs, piggybacks, headthrusts; see Appendix A)

significance only when K's data were removed (M_{nb}=1.43 acts/os vs. M_b=1.05 acts/os; t=2.67, df=4, p=.06). With respect to dyadic acts with nosing, slightly more acts occurred during the breeding season than during the non-breeding season (all adults: M_b=0.70 acts/os vs. M_{nb}=0.58 acts/os).

Individual Patterns. For five of the six seals, solo acts with nosing were more frequent than dyadic acts with nosing (Figure 10). The ratio of solo acts with nosing to dyadic acts with nosing varied from 12.2 for J, 3.9 for K, 2.4 for O and L, 1.5 for C, and 0.77 for D. J showed the highest mean frequency of solo acts with nosing (2.20 acts/os vs. H=1.76acts/os/seal), and also had the lowest mean rate of dyadic acts with nosing (0.18 acts/os; vs. L=0.22 acts/os/seal). Only D displayed a higher rate of dyadic acts with nosing (1.51 acts/os; vs. H=1.00 acts/os/seal) than of solo acts with nosing (1.16 acts/os).

Individual Patterns Across Weeks. When solo acts with nosing were examined across weeks for each individual, much individual variation was apparent (Figure 11). Both L's and K's rates were low throughout the study period; L's frequency never was higher than 1.83 acts/os while K only exceeded a rate of 1.50 acts/os in the three weeks immediately following the birth of her pup. While 27.3% of K's nosing during this 3-week period (weeks 25, 26 and 27) involved nosing objects and 10.9% involved nosing the air, half involved *direct* nosing of the pup which occurred while K was engaged in a *solo* act, such

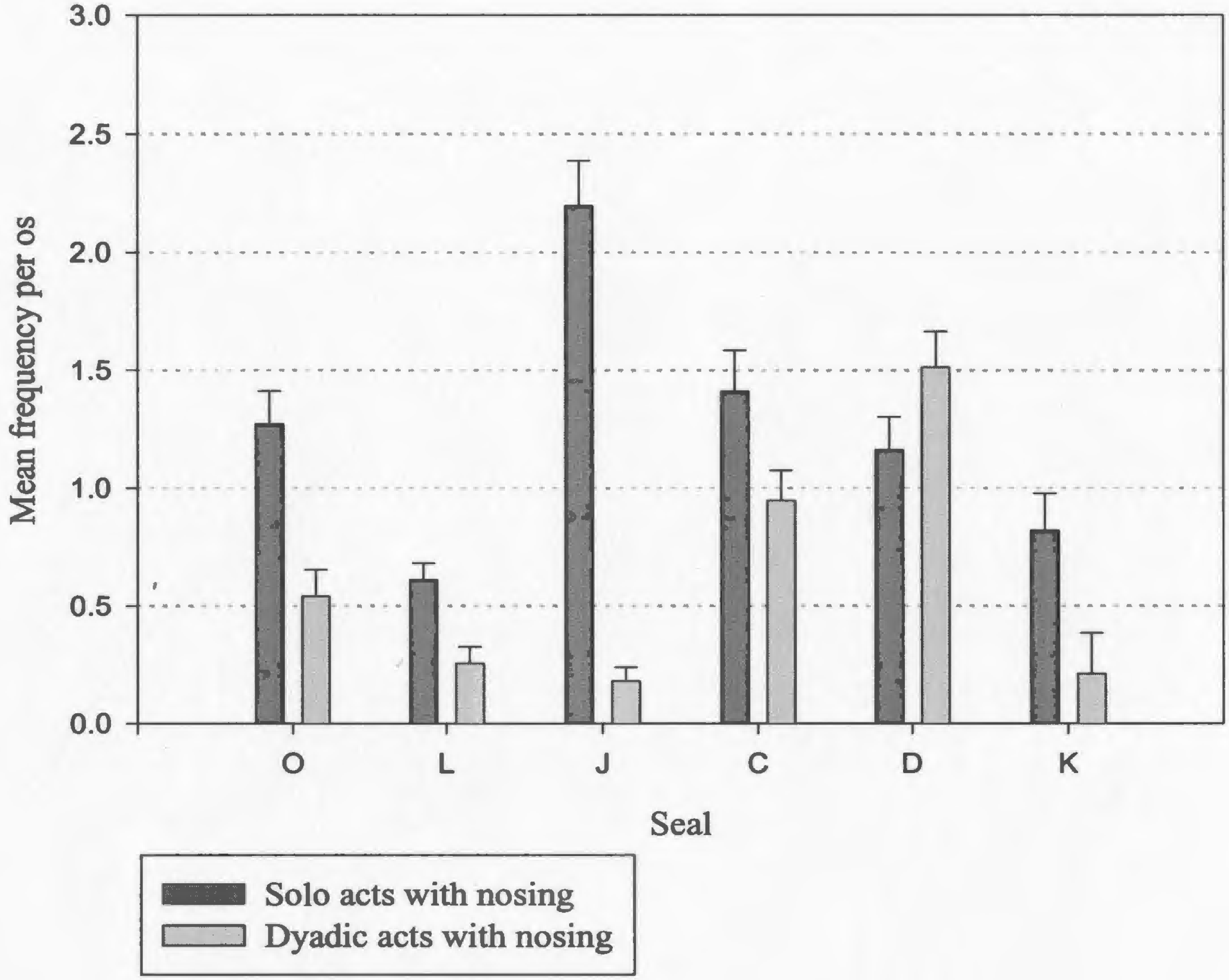
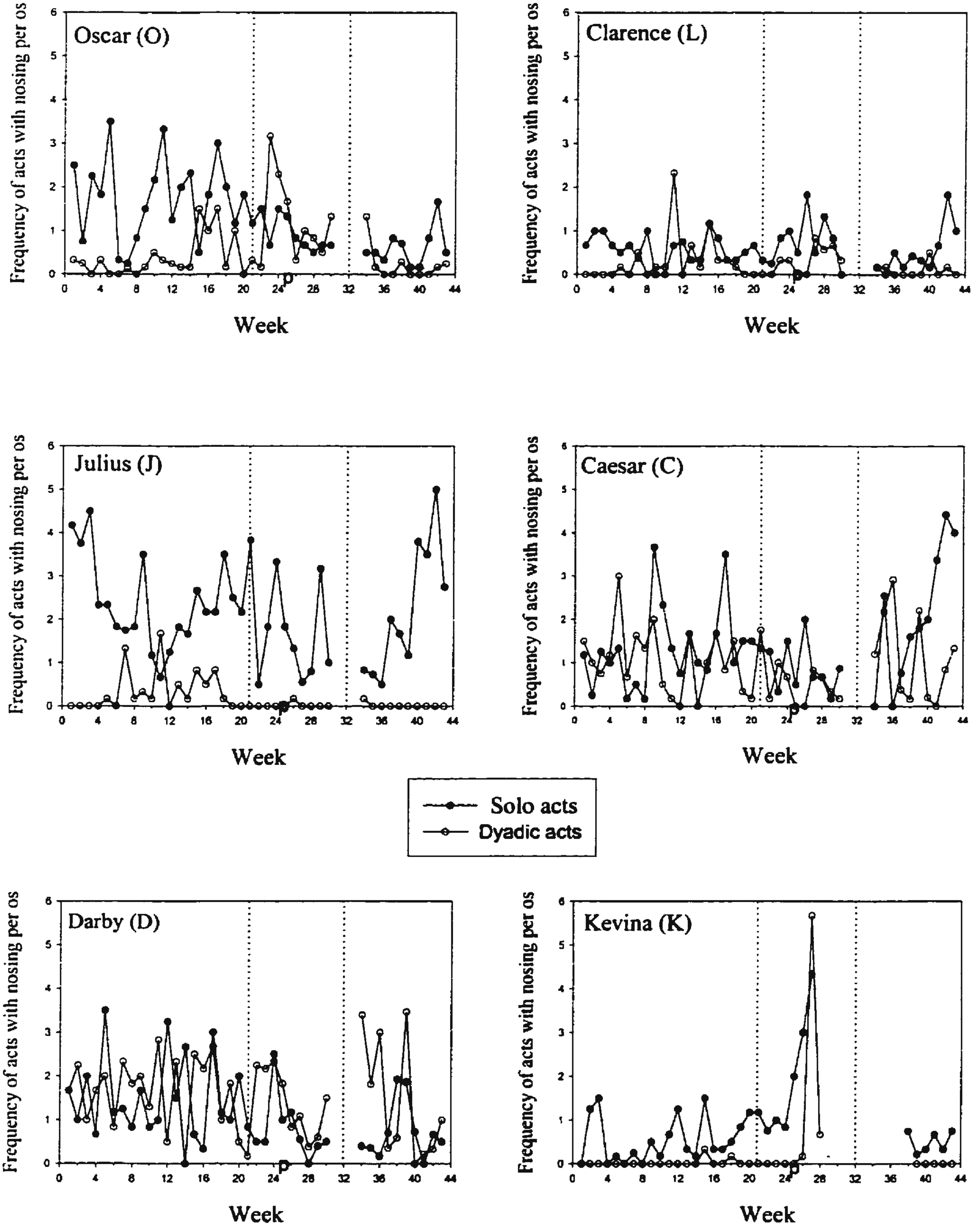


Figure 10: Mean frequency (+ std error) per observation session (os) of solo and dyadic acts with nosing by seal. Total sample sizes per seal (**solo** in bold-face, *dyadic* in italics) are as follows: Oscar(O), **296**, *126*; Clarence(L), **142**, *60*; Julius(J), **502**, *41*; Caesar(C), **314**, *212*; Darby(D), **256**, *334*; Kevina(K), **152**, *39*; and Eddy (not shown), **29**, *68*.

Figure 11: Frequency per observation session (os) of solo acts with nosing and dyadic acts with nosing across weeks for each seal. The weeks between the dotted lines represent the breeding season. The week of parturition is indicated with a 'p' on the week axis.


Oscar (O)
Clarence (L)
Julius (J)
Caesar (C)
Darby (D)
Kevina (K)
Frequency of acts with nosing per os
Week
0
1
2
3
4
5
6
0
4
8
12
16
20
24
28
32
36
40
44
P
Solo acts
Dyadic acts

as, lying on the deck. L also showed an increase in solo acts with nosing after the pup's birth but D, J and O all decreased solo acts with nosing at this time; however, as soon as K and E were removed (after week 28), J returned to his prior level. Finally, both C and J showed an increase after the return of K and E to the enclosure (week 39).

As for dyadic acts with nosing, again no particular pattern was apparent across weeks and individual patterns were highly variable, especially for C and D. Once more, only K revealed a sizable increase in acts with nosing after the pup was born. O and D both exhibited a decrease after the pup's arrival, followed by an increase after the pup and K were removed from the enclosure.

Conclusions. Nosing acts occurred frequently and in a variety of behavioural contexts. Although nosing occurred during a greater proportion of dyadic acts than during solo acts, the frequency of solo acts with nosing was over twice that of dyadic acts with nosing. With respect to solo acts, nosing was most likely to take place during pop-outs/ins/ups and alert-bobbing. Nose-to-tail rolling, or social play, was the most frequent dyadic context during which nosing occurred. That nosing was found to occur in over *half* of dyadic interactions among the harbour seals highlights the possibility that nosing is an important behavioural component of harbour seal social behaviour, especially when one considers that, among the highly social and cohesive collared peccaries, nosing was present in only 20% of social acts (Byers, 1985). In addition, if harbour seal nosing behaviours do in fact involve olfaction, then these results bring into question the assertions found in the scientific literature that the seals are 'micronosmic' (Fobes & Smock, 1981; Lowell & Flanigan, 1980).

More specifically, the results indicate that the seals had distinct individual behavioural patterns with respect to the context in which they performed a nosing action. In particular, these data suggest that the two youngest seals, C and D, were most likely to nose in a social context and hence, perform some form of directly observable social nosing. This view would suggest that J would be least likely to nose in a social context. However, it does not follow that nosing actions performed in a solitary manner are necessarily non-social in nature. For example, the solo acts of nosing the air or an object may be inherently social in that odours from another seal may be detected by means of these behaviours. Further information regarding patterns of nosing behaviour must be discovered via direct analyses of the nosing data.

Types of Nosing Behaviour

Solo and dyadic nosing accounted for 80.0% and 20.0%, respectively, of the total frequency of nosing that occurred throughout the study period. Solo nosing consisted of nosing the air (NTA), nosing objects (NTO), nosing one's own foreflipper (NFS) and one occurrence of a seal nosing his own body (NTB-self). The types of dyadic nosing included nose-to-nose or nuzzling (NTN), nose-to-tail rolling (NTR), nose-to-head

(NTH), nose-to-body (NTB), nose-to-tail/hindflipper (NTT) and nose-to-foreflipper (NFD) (Table 5).

<u>Nose-to-Air[7].</u> Nosing the air (NTA) accounted for almost half (48.8%) of all nosing observed throughout the study period (Table 5). This high frequency of nose-to-air acts is particularly interesting because this type of nosing may either be social or non-social in nature. For example, nosing the air may indicate that seals were sampling the air for interesting or changing environmental odours (e.g., odours from the nearby harp seal enclosure), or that seals were 'sniffing' the air to keep track of events in their own enclosure. If, in fact, nosing the air indicate sampling of social or environmental cues, then wind direction might be expected to affect the frequency of this behaviour. Indeed, it appears that nosing the air occurred twice as often during offshore wind conditions (i.e., north and northeast; M_o=8.93 acts/os) than during wind directed over uninhabited land (i.e., east and southeast; M_u=4.44 acts/os; t=2.26, df=5, p<.05)). Observations held at times when the wind came from the direction of the harp seal enclosure and the city dump (i.e., south and south-west) also showed a higher frequency of nose-to-air ($M_{h/d}$=7.88 acts/os) than when winds came from uninhabited lands (M_u=4.44 acts/os), although this

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[7] When bobbing at the surface of the water, seals sometimes point their nose upwards. However, this is not considered here to be a nosing behaviour; rather, this bobbing posture can be distinguished from nose-to-air acts in that the latter involve an extended neck.

Table 5: Total number of all solo and dyadic nosing acts collapsed across seals and weeks. The percentage of the sub-total and the overall total number of nosing acts accounted for by each type of nosing are also presented. The number in parentheses represents the total number of solo nosing acts performed by the pup and the total number of dyadic acts involving the pup either as an initiator, recipient or mutual participant. Totals for each seal are presented in Appendix C. [NTA=Nose-to-air, NTO=Nose-to-object, NFS=Nose-to-foreflipper(self), NTB-self=Nose-to-body(self), NTN=Nose-to-nose, NTR=Nose-to-tail rolling, NTH=Nose-to-head, NTB=Nose-to-body, NTT=nose-to-tail, NFD=Nose-to-foreflipper(dyadic)]

Type	Nosing Action	Number of Acts	% of Sub-total	% of Total
Solo	NTA	1781 (13)	61.0	48.8
	NTO	997 (28)	34.2	27.3
	NFS	140 (8)	4.8	3.8
	NTB-self	1 (0)	0.0	0.0
Sub-total	All solo	2919 (49)	100.0	80.0
Dyadic	NTN	277 (30)	38.0	7.6
	NTR	238 (0)	32.7	6.5
	NTH	97 (30)	13.3	2.7
	NTB	63 (21)	8.6	1.7
	NTT	46 (14)	6.3	1.3
	NFD	8 (0)	1.1	0.2
Sub-total	All dyadic	729 (95)	100.00	20.0
Total	all types	3648 (144)	--	100.0

difference was not statistically significant.

Nose-to-Object. The fact that the second most common type of nosing (Table 5), nosing objects (NTO) within the enclosure accounted for over one quarter (27.3%) of all nosing, also supports the notion that seals did indeed monitor their own environment closely, especially given that objects within the enclosure were generally familiar (i.e., new objects were almost never introduced). Objects in areas of high 'traffic' in the enclosure were nosed a high percentage of the time. For example, the ramp adjoining the two tanks accounted for 18.7% of the total number of nose-to-object acts while the steps leading into the MT and ST accounted for a combined 12.8% of the total. Other objects frequently nosed included deck areas (39.0%), and the walls of both the main tank (10.3% of the total) and the satellite tank (17.9%); these nose-to-object acts were often directed to the area where seals performed pop-outs/ups in the MT and ST.

Nose-to-Foreflipper (self). The type of nosing least frequently observed was the nosing of one's own foreflipper (NFS, 3.8%), a behaviour not previously discussed in the literature but of interest despite its relatively low frequency (Table 5). In particular, it would be interesting to know whether the foreflipper region in harbour seals has a large amount of sebaceous material relative to other body regions, and what function nosing this area might serve. Ling's (1965) study showed that phocids have large and abundant sweat glands in both the fore- and hind-flippers, and that the lipid-secreting sebaceous glands were larger in sparsely haired phocids. Wilson and Kleiman's (1974) preliminary estimate indicated that the region *between* the foreflippers contained a lot of sebaceous material, relative to other body areas, and that this region was nosed by other seals primarily in non-play contexts. However, the function of nosing one's own foreflipper remains unclear. One difficulty in determining the functional significance of nosing one's own foreflipper is that this behaviour may be difficult to distinguish from grooming. In addition, because the nosing of one's own foreflipper usually obstructs the view of the nares and vibrissae, it is difficult to speculate on the role of olfactory or tactile senses.

Nose-to Nose. Nose-to-nose or nuzzling (NTN) occurred more frequently than any other type of dyadic nosing (Table 5). Nosing another seal's nose or muzzle region (7.6%) was more frequent than nosing all other body regions combined (including head, body, fore-flippers, and tail/hind-flippers; 5.9%) supports the notion that the muzzle is an especially salient source of sensory (i.e., chemical or tactile) information.

Other Types of Dyadic Nosing (Nose-to-Head, Body, Foreflipper, and Tail). Nosing of the head and neck region accounted for 2.7% of the total number of nosing acts; thus, these combined areas were more frequently nosed than any region aside from the nose and muzzle region (Table 5), a finding that is consistent with Wilson and Kleiman (1974). Nose-to-body acts represented only 1.7 % of the total which suggests that a seal's torso offers limited olfactory or tactile stimulation. Again, this low frequency of nose-to body acts is consistent with Wilson and Kleiman's (1974) study in which she suggested that one reason that the body is nosed infrequently during harbour seal play is because the skin of this region has less sebaceous material and, hence, less odour. The foreflippers were very rarely (0.2%) the target of a dyadic nosing act, which is interesting since the amount of odoriferous sebaceous material in the foreflipper area is thought to be high (Wilson, 1978); however, this region seems to elicit more interest when it is directed to a seal's own foreflipper region. The tail/hind-flipper region also received little attention in the way of nosing, accounting for 1.3% of the total – again this is in agreement with Wilson and Kleiman's (1974) study. However, in another study by Wilson (1978), individual seals who hauled out close to neighbours were sometimes observed to approach a neighbour and initiate a nose-to-nose contact or sniff its hindflipper region; this may suggest that the tail/hindflipper region would receive more nosing attention in a free-living population situation where unfamiliar seals may meet one another.

Nose-to-Tail Rolling (Social Play). Nose-to-tail rolling (NTR) accounted for 6.5% of all nosing acts. However, the nature of this behaviour is different from all other types of nosing in that it is not a discrete act. Rather it is a continuous social behaviour composed of somersaulting, rolling, and twisting during which many discrete nosing acts are usually interspersed. These nosing acts typically include nosing of the body and tail/hindflipper region while the seals are rolling in the direction of their longitudinal axes in a nose-to-tail manner, which is the principal mode during a rolling event. Frequent nuzzling and nose-to-head acts were also common when seals were oriented in a head-to-head fashion. However, because seals are underwater or obscured by splashing during much of a typical rolling bout, it was virtually impossible to determine the frequency and types of dyadic nosing which occurred during a bout. Thus, discussing nose-to-tail rolling in terms of frequency will inevitably result in an underestimate of dyadic nosing frequency. Nose-to-tail rolling would be best examined in detail by means of video analyses. Such a future analysis would likely enable an accurate representation of the amount and type of nosing involved, and would also hopefully reveal the specific involvement of the seal's nares and vibrissae.

Individual Differences. If each seal had contributed equally to the total number of solo and dyadic nosing acts, then each seal would account for 14.3% of each type of nosing; however, individual differences were evident. Three of the seven seals, J, L and K, were involved in a greater proportion of the total number of solo nosing acts than the total number of dyadic nosing acts, while the reverse pattern was true for the oldest seal, O, and for the three youngest seals, C, D, and E (Table 6). Overall J accounted for a very low percentage (6.9%) of the total number of dyadic nosing acts, but 40.8% of all solo nosing (cf. H_{sn}=26.9%). In contrast D performed 37.0% (cf. H_{dn}=26.2%) of all dyadic nosing observed but only a moderate 13.4% of the total solo nosing. O and C both represented more moderate amounts of the solo and dyadic nosing totals, while L and K accounted for low amounts of both the solo and dyadic nosing total frequencies. The pup, Eddy, accounted for 3.8% of the total dyadic nosing acts which is not much less than the percentage accounted for by K, L or J; this

Table 6: Mean percentage of the total solo nosing (SN) and the total dyadic nosing (DN) accounted for by each seal. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina, E=Eddy)

Seal	Mean Percentage of SN	Mean Percentage of DN
O	11.5	18.4
L	8.3	7.9
J	40.8	6.9
C	15.4	20.5
D	14.3	37.0
K	8.1	5.6
E	1.7	3.8
Mean	14.3	14.3
Std. Dev.	12.56	11.9
N	7	7

is surprising given that Eddy was present during only 15% of the 233 observation sessions in which nosing was recorded. However, this result serves to emphasize the impact of a new individual on a group of highly familiar captive seals; that is, the pup was both the source of curiosity for the other seals, and highly curious himself. In brief, these results reveal considerable individual differences with respect to the broad categories of solo and dyadic nosing. Although, as already noted, solo nosing may be either social or non-social, dyadic nosing is clearly a social behaviour – and one in which the oldest and two youngest adult males appeared to participate more frequently than the other seals.

With respect to solo nosing, one of the most striking individual differences involved J who nosed the air between 2.5 and 6 times as often as any other seal, and nosed objects at least twice as frequently as any other seal (Figure 12a). C, L and K each nosed the air about twice as often as they nosed objects, while D performed both equally often. The only seals that nosed objects more often than the air were O and E. The frequency of nose-to-foreflipper (self) was negligible for all seals.

A different pattern emerged with respect to dyadic nosing rates. D performed nose-to-nose, nose-to-tail rolling and all other types of dyadic nosing combined (dn-other) more frequently than any other seal, except E, whose high dyadic nosing rates can be largely attributed to interactions with his mother. J and L both showed very low rates of nose-to-tail rolling and other types of dyadic nosing, and although their nose-to-nose rates

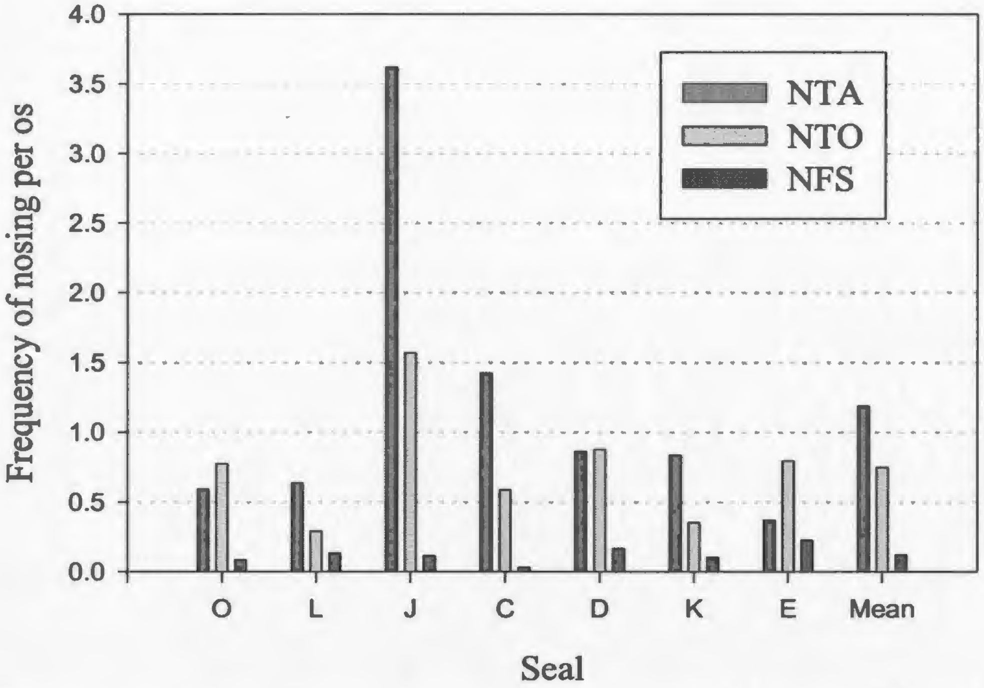

Figure 12a: Mean frequency per observation session (os) of Nose-to-air (NTA), Nose-to-object (NTO) and Nose-to-foreflipper-self (NFS) acts for each seal. Frequency was calculated as the total number of nosing acts divided by the number of os appropriate for each seal. For sample size, see Appendix C. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina, E=Eddy).

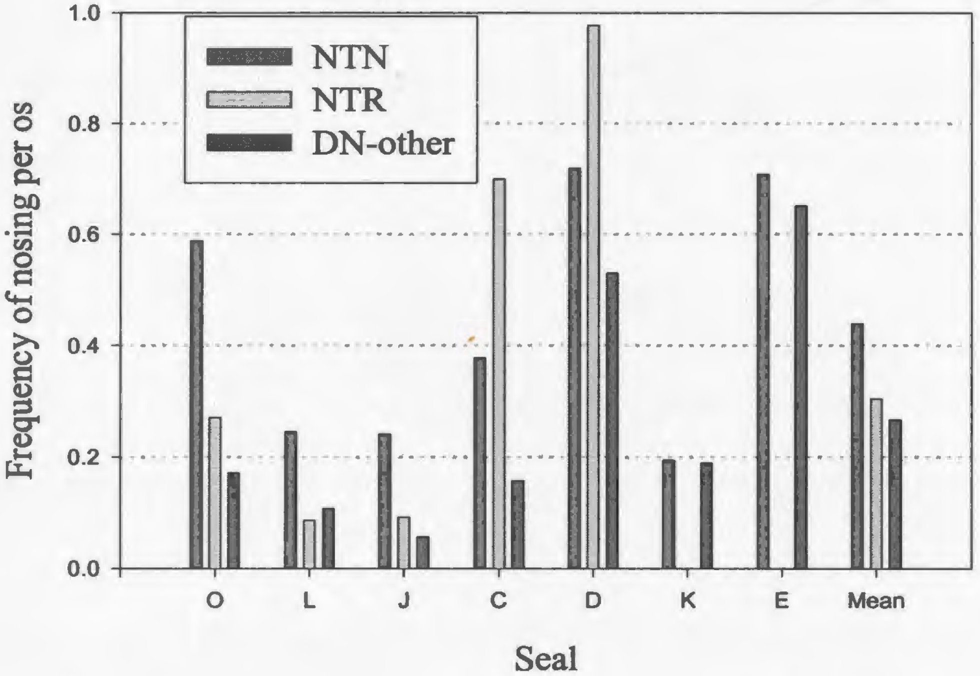

Figure 12b: Mean frequency per observation session (os) of Nose-to-nose (NTN), Nose-to-tail rolling (NTR) and other types of dyadic nosing [DN-other (NTH, NTB, NTT, NFD)] per seal. Frequency was calculated as above. For sample size, see Appendix C. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina, E=Eddy)

were greater, they were still substantially lower than that of the other adult males (Figure 12b).

As to the question of whether a particular solo nosing act is social in nature, the apparent attention of an individual during the act revealed some differences between nosing the air and nosing objects. Both the vast majority of the total nose-to-air acts (91.4%) and the total nose-to-objects (96.6%) appeared *not* to involve attention to either another seal or a human in the immediate vicinity. However, when a seal did attend to seals or people or both, it was more likely to occur during nosing of the air rather than during nosing of an object. For example, another seal was attended to during 4.1% of nose-to-air acts versus 2.5% nose-to-object acts, while a human was attended to in 3.6% of nose-to-air acts but only 0.5% of nose-to-object acts. Both a seal and human were simultaneously attended to during only a minute fraction of all nose-to-air acts (0.9%) and all nose-to-object acts (0.4%). Thus, there appeared to be a greater tendency for nosing of the air to involve immediate monitoring of social events in and around the seals' enclosure. The possibility that nosing of the air can be a form of social nosing (e.g. sniffing the air to detect another seal's odour) may help explain J's particularly high rate of nose-to air acts. That is, J generally favoured the ST where he was often alone, and this is where the majority of his nose-to-air acts occurred. For example, J nosed the air almost 42 times as frequently in the ST as in the MT, while he nosed objects less than four times as often in the ST as the MT. In contrast, dyadic nosing acts were performed more than twice as often in the MT as the ST.

Conclusions. Nosing of the air was the single most common type of nosing for four of seven seals with D, O and E being the exceptions. Thus, if this behaviour does involve social or environmental sampling of some kind (i.e., smelling the air), then the results indicate that this group of captive seals were actively monitoring their surroundings via nosing behaviours. Because some forms of nosing the air activity may not be associated with olfaction (e.g., perhaps a nose-in-the-air action might serve as a visual signal in some circumstances), it will be important to determine which types of nose-to-air acts produce activity in the brain regions associated with olfaction and which do not (D. J. Bonness, personal communication, 1998). The fact that nosing objects was the most frequently occurring type of nosing for both O and E, and the second most frequent for all other seals, also supports the notion that these seals closely monitor their environment.

The finding that C, D and E[8] participated frequently in the various types of dyadic nosing might suggest that these highly social behaviours are age-related (i.e., since C, D and E were the three youngest seals); however, this idea is inconsistent with the finding that the oldest seal also showed relatively high rates of dyadic nosing, particularly nose-to-nose acts. That nose-to-nose acts were performed more frequently than any other type

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[8] Although Eddy accounted for less than 4% of the overall total number of dyadic nosing acts, he showed high *rates* (i.e., number of acts/number of observation sessions present) of dyadic nosing (other than nose-to-tail rolling).

of dyadic nosing suggests that this type of interaction plays an important role in social behaviour. Interestingly, the three seals, O, D and E, who did *not* perform nose-to-air acts more frequently than any other nosing behaviour, showed high rates of dyadic nosing; this suggests that individuals who often engaged in direct social contacts were less dependent on the more indirect nose-to-air act to monitor their social environment. Overall, the sole female participated infrequently in nose-to-nose and other types of dyadic nosing, and neither she nor the pup were ever involved in nose-to-tail rolling. Furthermore, most (69.9%) of K's dyadic nosing acts involved her pup. Unfortunately, because the study group contained only one female, it is unwise to speculate on possible sex differences. Thus, while the results indicate that individual behavioural differences exist, no consistent differences emerged with respect to sex or age.

Patterns of Solo and Dyadic Nosing Behaviour

For each seal, three estimates of solo nosing rates [as measured by nose-to-air, nose-to-object, nose-to-foreflipper(self), and nose-to-body(self) acts] and dyadic nosing rates [as measured by nose-to-nose, nose-to-tail rolling, nose-to-head, nose-to-body, nose-to-tail, and nose-to-foreflipper(dyadic) acts] were entered into an analysis of variance for repeated measures where the factors were: type of nosing (solo and dyadic), season (breeding and non-breeding), and seal (O, L, J, C, D and K; see Methods for details). Two analyses were performed, one for males only and one for all adults (see Tables I and

II, respectively, in Appendix F). The results of these analyses are presented in two sections: the first section will focus on the effect of the type of nosing, on individual differences between seals, and will include an examination of weekly patterns; the second section will focus on the effect of season as a main effect and in interaction with the other factors (i.e., type of nosing and seal).

Regarding the examination of weekly nosing patterns, although these patterns may be directly related to seasonal differences, it is also possible that some patterns may simply reflect temporal changes (i.e., time of year effects). Additionally, since the breeding season consisted of weeks during which the sole female was pregnant (weeks 21 to 24), was nursing her pup (weeks 25 to 28), and was absent from the enclosure (weeks 29 to 32), and the non-breeding season contained weeks during which the female was present in the enclosure (weeks 1 to 20), absent (weeks 33 to 37), and present along with her pup (weeks 38 to 43), the examination of the weeks within the seasons may reveal some insights into the seals' behaviour which would not be discovered via a seasonal analysis.

Effects of Type and Seal (Males Only). The mean frequency of solo nosing for male seals was over twice as high as the mean frequency for male dyadic nosing (M_{sn}=2.34 vs. M_{dn}=0.99, Table 7; F(1,40)=112.29, p<.001, Appendix F). The examination of solo and dyadic nosing rates across weeks revealed the following pattern: solo decreased over the first 25 weeks of the study period, then leveled off at a low rate after the pup's birth, remained low during the moult, before rising thereafter (Figure 13). Dyadic nosing remained at relatively low levels, compared to the solo nosing rate, throughout the study period; however, there appeared to be a slight increase in dyadic nosing just before and after parturition.

Table 7: Mean frequency (+ Std. Dev.) of solo and dyadic nosing for each seal. Mean frequency per observation session (os), collapsed across weeks, is presented for males only and when all seals are included. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina, E=Eddy)

Seal	Mean Frequency (+Std. Dev.) (Males Only)		Mean Frequency (+Std. Dev.) (All Seals)	
	Solo Nosing	Dyadic Nosing	Solo Nosing	Dyadic Nosing
O	1.48 (1.517)	0.97 (0.996)	no change	0.99 (0.998)
L	1.10 (1.252)	0.40 (0.616)	no change	0.41 (0.619)
J	5.00 (3.374)	0.36 (0.496)	no change	0.37 (0.492)
C	2.23 (2.162)	1.15 (0.738)	no change	1.20 (0.745)
D	1.87 (1.871)	2.05 (1.139)	no change	2.13 (1.168)
K	--	--	1.25 (1.507)	0.48 (1.607)
E	--	--	1.31 (0.916)	1.46 (1.736)
Mean	2.34	0.99	2.03	1.01
Std. Dev.	1.548	0.688	1.365	0.651
N	5	5	7	7

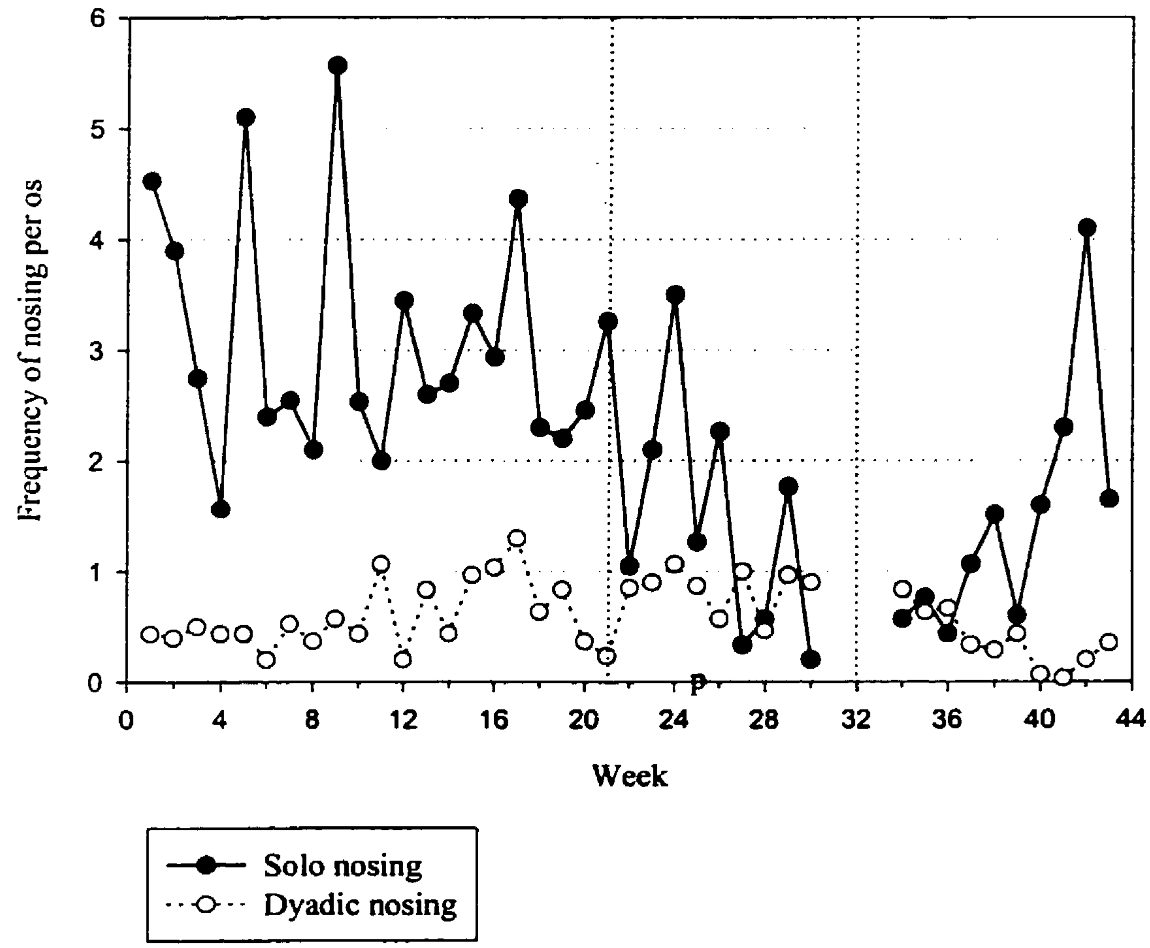
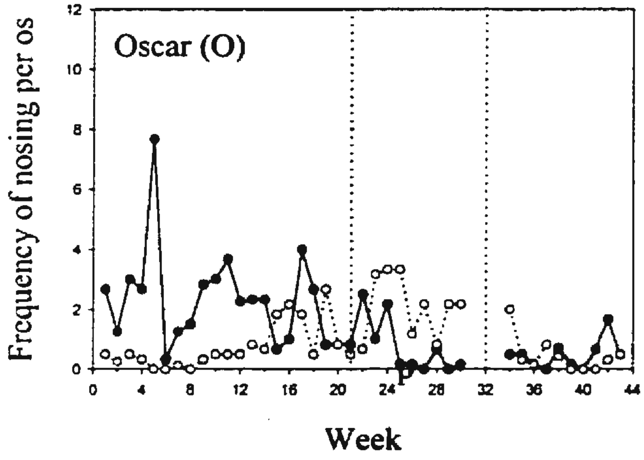


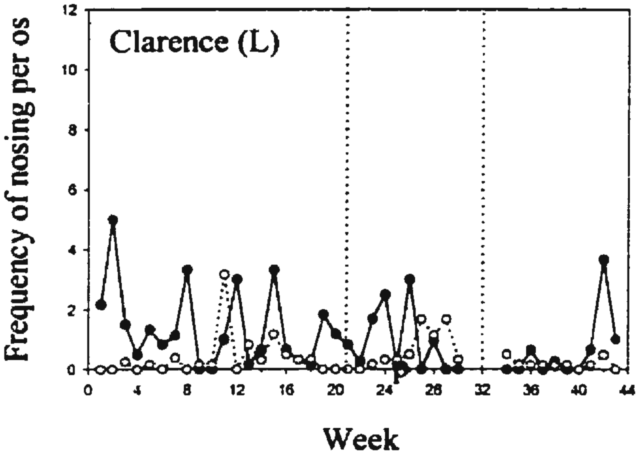
Figure 13: Frequency of solo and dyadic nosing per observation session (os) per male seal across weeks. Dotted lines indicate breeding season and 'p' indicates parturition.

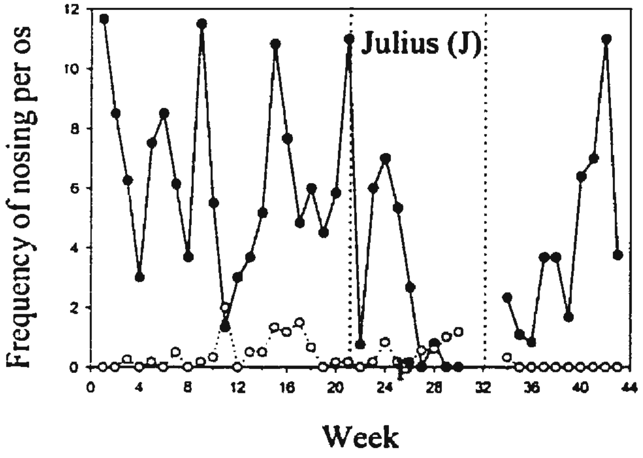
The finding of statistically significant individual differences between males [F(4,40)=47.12, p<.001] was qualified by the significant interaction between the type of nosing and the seal [F(4,40]=92.98, p<.001; see Appendix F, Table I]. This interaction is made evident in Table 7 ; J performed solo nosing acts almost 14 times as often as dyadic nosing acts, while the solo nosing rate for O, C and L was only 1.5 to 2.75 as high as the dyadic rate, and D actually had a higher rate of dyadic than solo nosing acts.

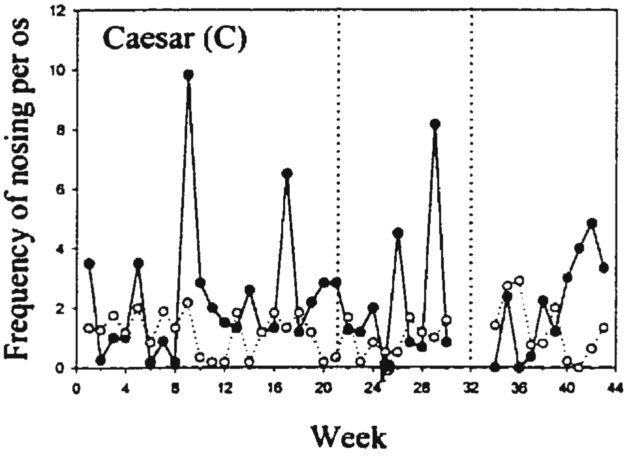
Although each male showed highly variable rates for solo and dyadic nosing across weeks, the significant interaction of type and seal remained evident (Figure 14). For instance, while both D and C showed much overlap between their solo and dyadic nosing rates across weeks, J's rate of solo nosing was substantially greater than that of dyadic nosing throughout most of the study period (this may reflect his spatial preference since J was often alone in the ST). L also showed a higher rate of solo than dyadic nosing for most of the study. For both L and J, dyadic nosing was very low throughout except around weeks 11 and 15 (for L) and weeks 11 and 15 to 18 (for J), and then again for a few weeks following the pup's birth. In contrast, O showed consistently lower rates of dyadic nosing than solo nosing only during the first 14 weeks, followed by a conspicuous increase in dyadic nosing rates around the time of parturition (weeks 23, 24 and 25). Thus, it appears that only the two oldest males, O and L, showed both solo and dyadic nosing patterns consistent with the overall male mean rates across weeks. J's solo nosing rates were also fairly consistent with the mean male pattern. However, in general, the

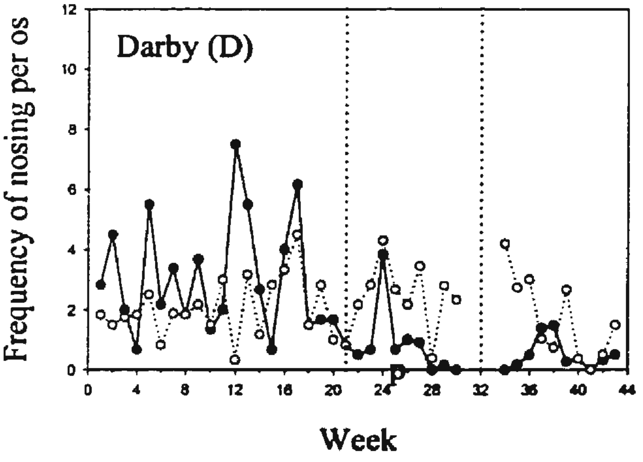
Figure 14: Frequency per observation session (os) of solo and dyadic nosing across weeks for each male. Dyadic nosing rates do not include interactions with K or E. The weeks between the dotted lines represent the breeding season. The week of parturition is indicated with a 'p' on the week axis.











—●— Solo nosing
····○···· Dyadic nosing

high degree of individual variability precluded the notion that a 'typical' male pattern existed across weeks.

Effects of Type and Seal (All Seals). The results of this analysis, in which dyadic nosing rates *included* interactions involving Kevina and the pup, were virtually identical to the analysis of males only. Type of nosing [F(1,48)=138.19, p<.001], seal [F(5,48)=41.37, p<.001] and the interaction of type and seal [F(5,48)=81.86, p<.001] were all statistically significant (see Table II, Appendix F). In fact, the only apparent difference in outcome when K and E were included was a slight increase in the dyadic nosing rate following the pup's birth at week 25; this difference can be attributed to K's high rate of interaction with her pup during the weeks following her pup's birth until their removal (i.e., from week 25 to 28, 92% of dyadic acts with K involved her pup).

Comparing the individual male patterns for the male-only graphs (Figure 14) to the individual male patterns when K and E were included in the calculation of dyadic nosing (see Appendix E), reveals that the small increase in dyadic nosing for the overall pattern was due to the high frequency of dyadic nosing interactions between K and her pup. In fact, a detailed look at the dyadic nosing interactions from week 25 to 28, showed that all but three occurrences of K's dyadic nosing involved the pup. However, this finding does not necessarily mean that the pup's birth did not influence the behaviour of individual males.

Another way to examine the interaction between type of nosing and seal is to look at the proportion of each seal's total nosing that is dyadic (i.e., each seal's rate of dyadic nosing divided by his/her total nosing rate); Figure 15 shows each seal's mean proportion, while Figure 16 shows the weekly pattern of this proportion. On average, a very low proportion of J's (0.08) total nosing frequency was dyadic (cf. *L*=0.19), compared to O's (0.42), D's (0.53) and E's (0.50) proportions (cf. *H*=0.51), and the more moderate proportion of between 0.23 and 0.38 shown by the K, L and C (cf. *M*=0.35; Figure 15). Although the two youngest seals were the only two individuals to show a proportion of dyadic nosing that was at least one standard deviation above the group mean, the oldest seal showed the next largest proportion. Thus, no age trend was apparent.

The proportion of each seal's total nosing that is dyadic, as a function of weeks, serves to emphasize the impact of the pup's birth on the males' behaviour patterns – all males increased their proportion of dyadic nosing in the weeks immediately following the pup's birth (Figure 16). In addition, there were distinct individual patterns across time. The three oldest males, O, L and J, showed very low dyadic nosing proportions early in the study period (i.e., for the first 8 to 14 weeks); for O and L, this was followed by variable but relatively high levels thereafter (except for almost nil levels for L from week 19 to 24) just prior to parturition. J also showed a reduced proportion of dyadic nosing in the weeks prior to the pup's arrival, although his levels were relatively low throughout most of the study period. Both C and D showed variable proportions of dyadic nosing

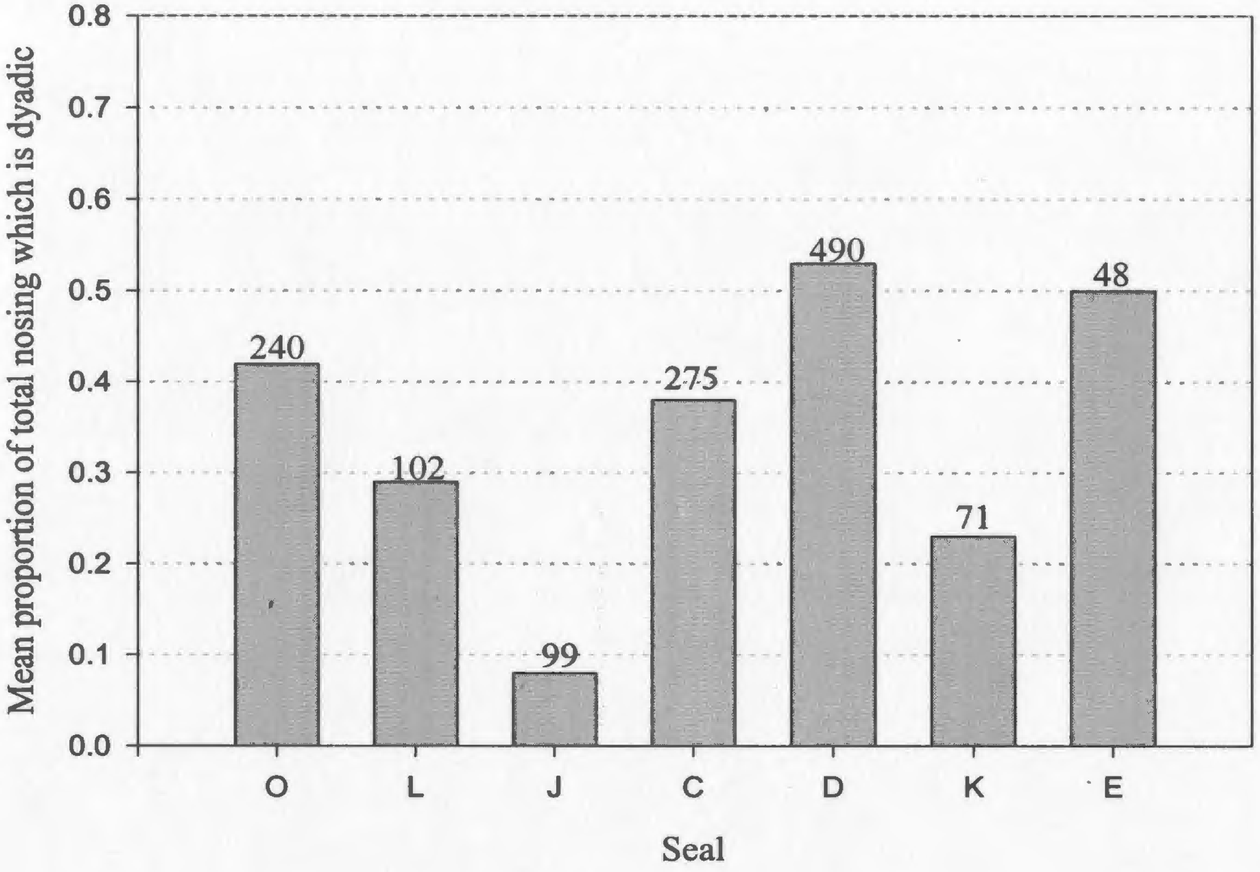
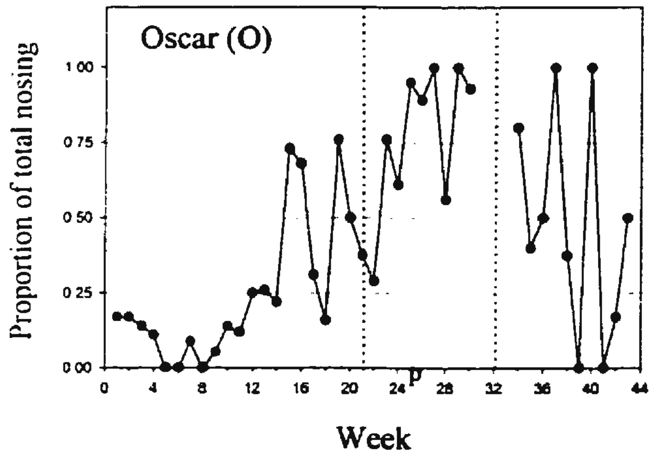
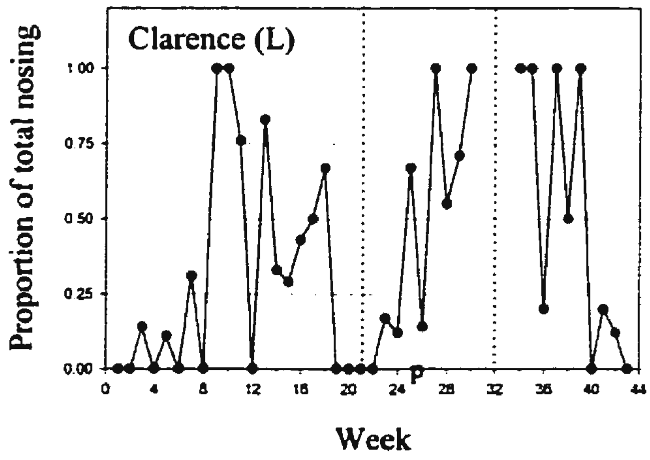
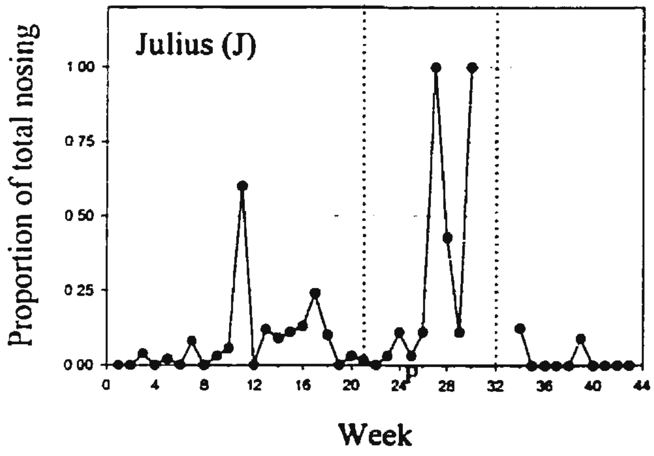


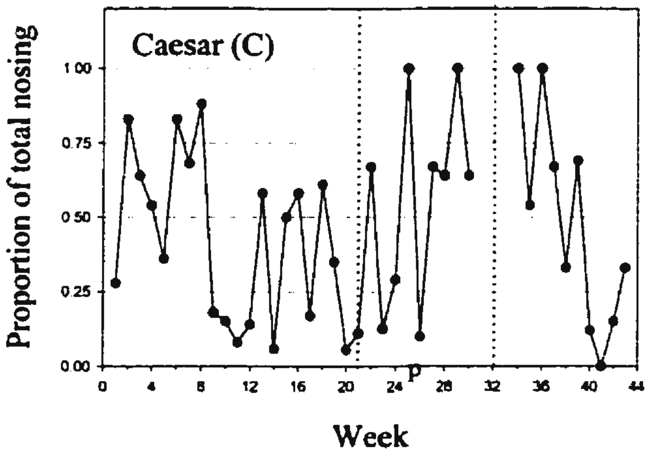
Figure 15: Mean proportion of each seal's total nosing which is dyadic. Total number of dyadic interactions in which the seal was an initiator or mutual participant is indicated above each bar. (Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina, E=Eddy)

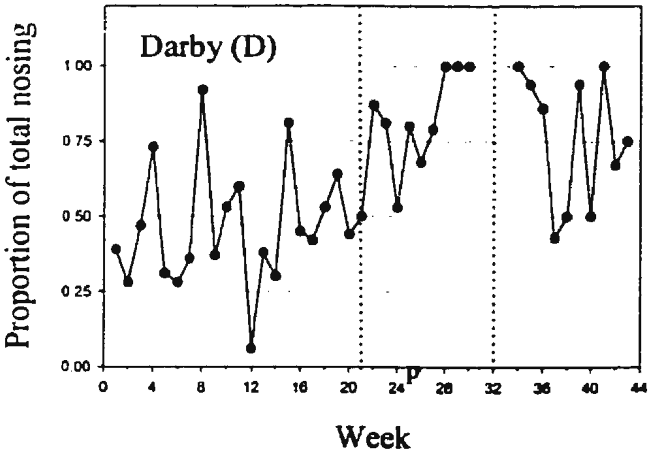
Figure 16: Proportion of each seal's total nosing that is dyadic, as a function of weeks. The dotted lines indicate the breeding season and parturition is indicated with a 'p' on the week axis.

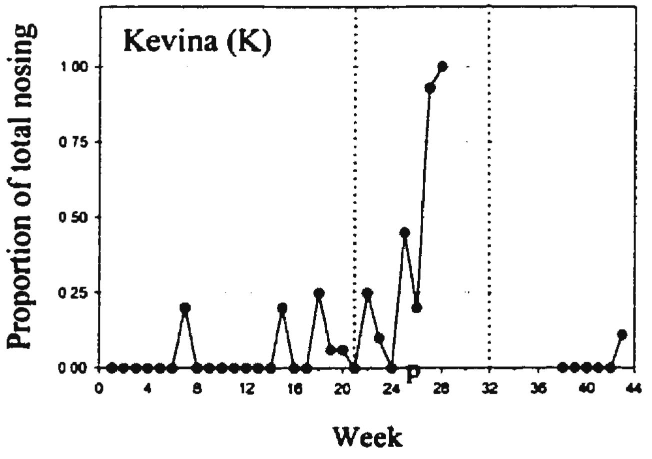

Oscar (O)
Proportion of total nosing
1.00
0.75
0.50
0.25
0.00
0
4
8
12
16
20
24
P
28
32
36
40
44
Week


Clarence (L)
Proportion of total nosing
1.00
0.75
0.50
0.25
0.00
0
4
8
12
16
20
24
P
28
32
36
40
44
Week


Julius (J)
Proportion of total nosing
1.00
0.75
0.50
0.25
0.00
0
4
8
12
16
20
24
P
28
32
36
40
44
Week


Caesar (C)
Proportion of total nosing
1.00
0.75
0.50
0.25
0.00
0
4
8
12
16
20
24
P
28
32
36
40
44
Week

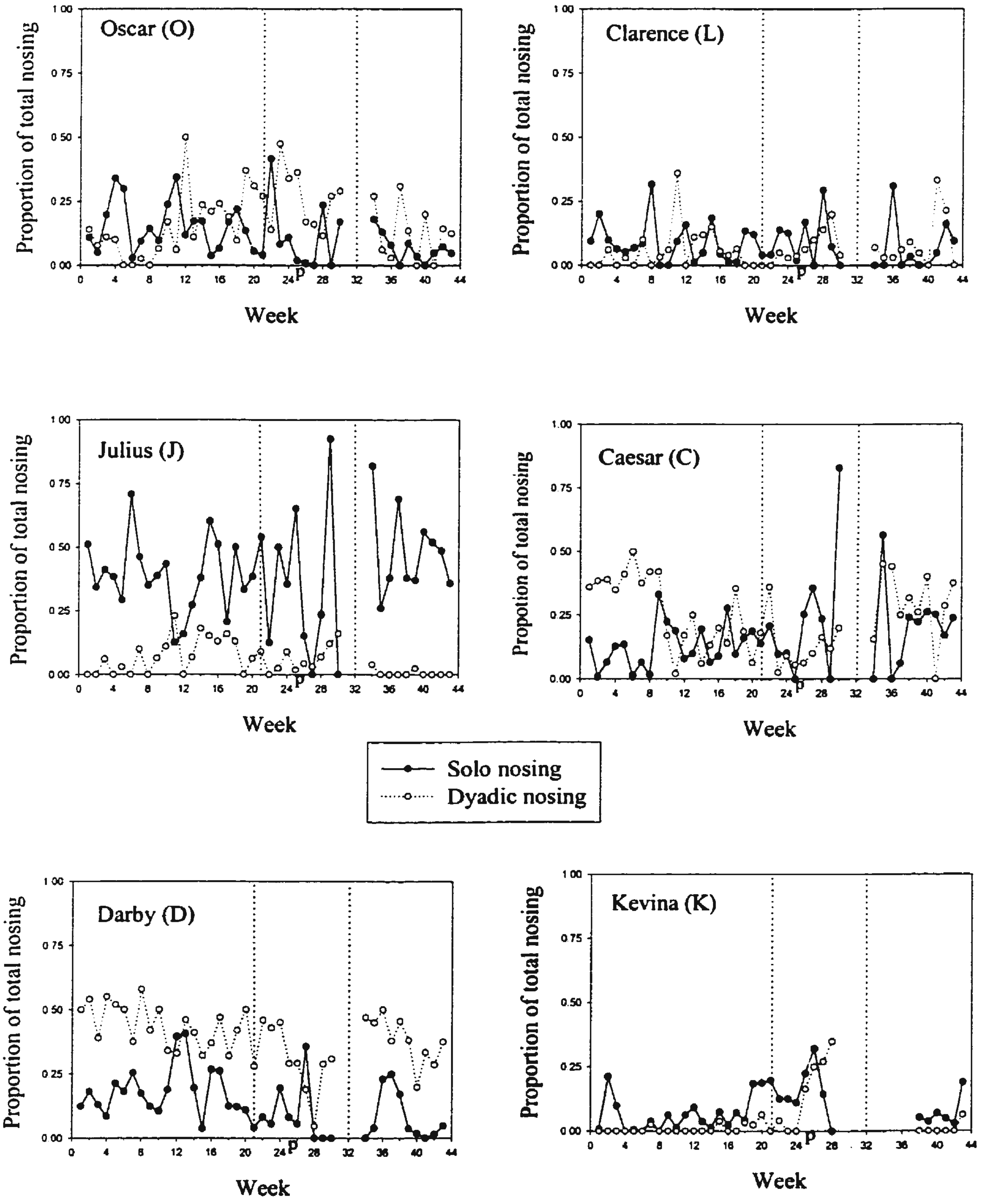

Darby (D)
Proportion of total nosing
1.00
0.75
0.50
0.25
0.00
0
4
8
12
16
20
24
P
28
32
36
40
44
Week


Kevina (K)
Proportion of total nosing
1.00
0.75
0.50
0.25
0.00
0
4
8
12
16
20
24
P
28
32
36
40
44
Week

across weeks, yet levels did appear to increase around the time of parturition. Kevina also had a negligible proportion of nosing which was dyadic, except for the four weeks (25 to 28) prior to her removal, during which time she was nursing her pup; all but three of her dyadic nosing acts during this time involved the pup.

One final way to illustrate the individual differences in nosing patterns is as a proportion of both the overall total solo nosing rate and the overall total dyadic nosing rate accounted for by each seal, across weeks (Figure 17). When compared to each seal's weekly rate of solo and dyadic nosing (see Figure 14 and Appendix E), Figure 17 emphasizes the distinct individual differences with respect to each seal's preferred mode of nosing (i.e., solo or dyadic), and how this changed over time. That is, because the rate of dyadic nosing was less than that of solo nosing for all seals other than D, changes in dyadic nosing *rates* over weeks were not readily apparent; however, changes in dyadic nosing *proportions* were more clear. For instance, for the first four weeks of the pup's life (from weeks 25 to 28), D showed a substantial decrease in the proportion of dyadic nosing that he accounted for, while K and L both showed increases. Also following the pup's birth (weeks 26, 27, 28), C's proportion of the total solo nosing increased, while J and O both showed a decreases. The removal of Kevina and her pup following week 28 also appeared to affect the male nosing patterns; the proportion of the total dyadic nosing accounted for by D increased, while the proportion of the total solo nosing accounted for by both J and C showed a dramatic rise at this time. As for the sole female, K

Figure 17: Proportion of the total number of solo nosing acts and the total number of dyadic nosing acts accounted for by each seal across weeks. Dotted lines represent the breeding season and parturition is indicated by a 'p' on the week axis.


Oscar (O)
Clarence (L)
Julius (J)
Caesar (C)
Darby (D)
Kevina (K)
Proportion of total nosing
Propotion of total nosing
0.00
0.25
0.50
0.75
1.00
0
4
8
12
16
20
24
28
32
36
40
44
P
Week
Solo nosing
Dyadic nosing

only claimed more than quarter of the total solo or dyadic nosing for the few weeks around the time of parturition

Conclusions. Overall, the solo nosing rate was over twice as high as the dyadic nosing rate, whether or not the dyadic nosing rates included interactions involving K and her pup. Only D (and the pup, Eddy) showed a higher rate of dyadic nosing than solo nosing. Of each seal's total nosing frequency, the two youngest seals (D and E) and the oldest seal (O) showed the greatest proportion of dyadic nosing; thus, no age trend was apparent.

Although the solo and dyadic nosing rates of all male seals appeared to be affected by the birth of the pup and the subsequent removal of Kevina and her pup, no universal pattern emerged across weeks. Interestingly, the two males with the highest overall proportions of solo and dyadic nosing, J and D respectively, both showed decreases in these nosing actions immediately after parturition. This may be indicative of individually distinct behavioural responses to such important events; for example, attempts by D to initiate a dyadic nosing action may have been unwelcome (hence, his decrease in nose-to-tail rolling), and the normally high rate of solo nosing shown by J may have diminished due to being 'ejected' from his favoured ST. Thus, the examination of nosing patterns across weeks was beneficial inasmuch as it uncovered behaviour changes *within* the breeding season which would not be revealed by seasonal analyses alone.

Effects of Season, Type and Seal. Although season was not significant as a main effect, it did interact significantly with the type of nosing [F(1,48)=25.49, p<.001] and with seal [F(5,48)=16.54, p<.001; see Table I, Appendix F]. The triple interaction of type by season by seal was also significant [F(5,48)=6.35, p<.001]. With respect to the interaction of type of nosing by season, dyadic nosing rates increased in the breeding season, while solo nosing rates declined. This interaction is illustrated by the following: the ratio of solo to dyadic nosing during the non-breeding season was almost 3 to 1 (M_{sn}=2.30 vs. M_{dn}=0.78), while during the breeding season this ratio decreased to only 1.2:1 (M_{sn}=1.72 vs. M_{dn}=1.39).

Other seasonal differences, beyond those considered in the analysis of variance, were evident by examining the various types of nosing behaviours that constitute solo and dyadic nosing (Figure 18). Almost twice as many nose-to-object acts and solo nose-to-foreflipper acts occurred in the non-breeding season than in the breeding season; however, these differences were not significantly different. Two types of dyadic nosing were more frequent in the breeding season; nose-to-nose acts occurred almost three times more often (t=-3.77, df=5, p<.05), while nose-to-body acts occurred almost twice as often. Nose-to-air, nose-to-head, nose-to-tail acts, and nose-to-tail rolling did not show any sizable differences between seasons. Dyadic nose-to-foreflipper acts never occurred in the breeding season, but this may simply reflect the overall low frequency of this behaviour (i.e., a total of 8 acts in the entire study period). Thus, some forms of directly

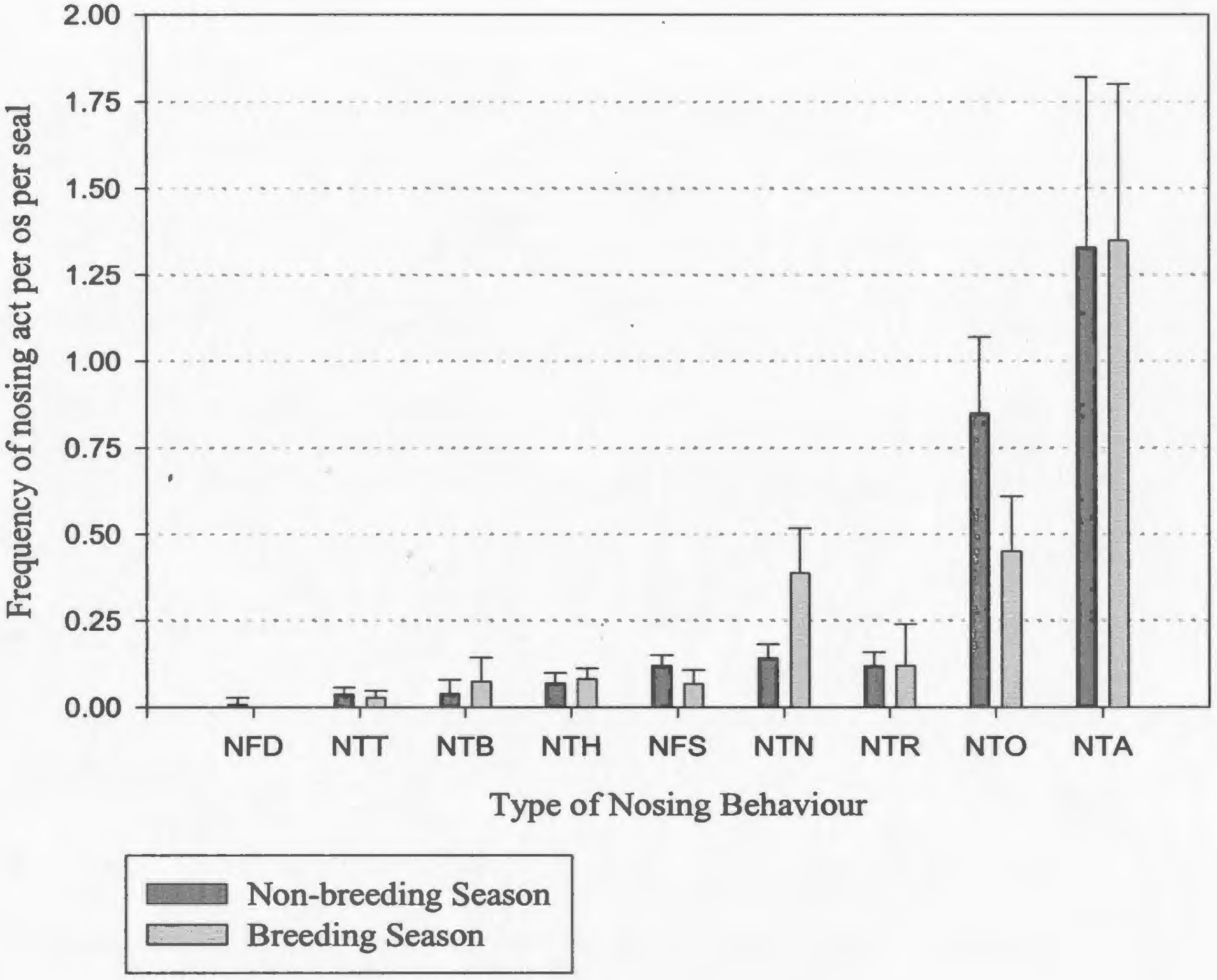


Figure 18: Mean frequency per os per seal of each type of nosing behaviour in the non-breeding and the breeding season. For total sample size, see Appendix D. [NTA=nose-to-air, NTO=nose-to-object, NTR=nose-to-tail rolling, NTN=nose-to-nose, NFS=nose-to-foreflipper(self), NTH=nose-to-head, NTB=nose-to-body, NTT=nose-to-body, NTT=nose-to-tail, NFD=nose-to-foreflipper(dyadic)]

observable social nosing were more common in the breeding season. Because this analysis *did not* include nosing acts which involved the pup, the increased breeding season rates of nose-to-nose and nose-to-body acts *cannot* be attributed to mother-pup interactions.

With respect to the significant triple interaction between type, seal and season, some seals (O, J, D and K) showed strong seasonal differences in solo nosing rates while others (L and C) did not (Figure 19a). Large seasonal differences in dyadic nosing rates were also apparent, for O and K, while the other seals showed smaller seasonal influences (Figure 19b). This three-way interaction is consistent with conclusions drawn from the examination of nosing across weeks that each seal has distinctive patterns of nosing behaviour – it is evident that the O.S.C. seals are individually distinct with respect to nosing type and seasonal influences.

When mean rates for each seal during the non-breeding and breeding season were compared, it was apparent that C was unusual; while most other males decreased their solo nosing rates in the breeding season, C showed no change, and while all other males increased their dyadic nosing rate in the breeding season, C showed a decrease. D, J and O all showed sizable decreases in solo nosing acts in the breeding season, and O showed the largest increase in dyadic nosing during the breeding season. The decline in J's solo nosing rate during the breeding season may be explainable by the fact that during much of this period, he was no longer alone in his favoured ST because, following parturition, this

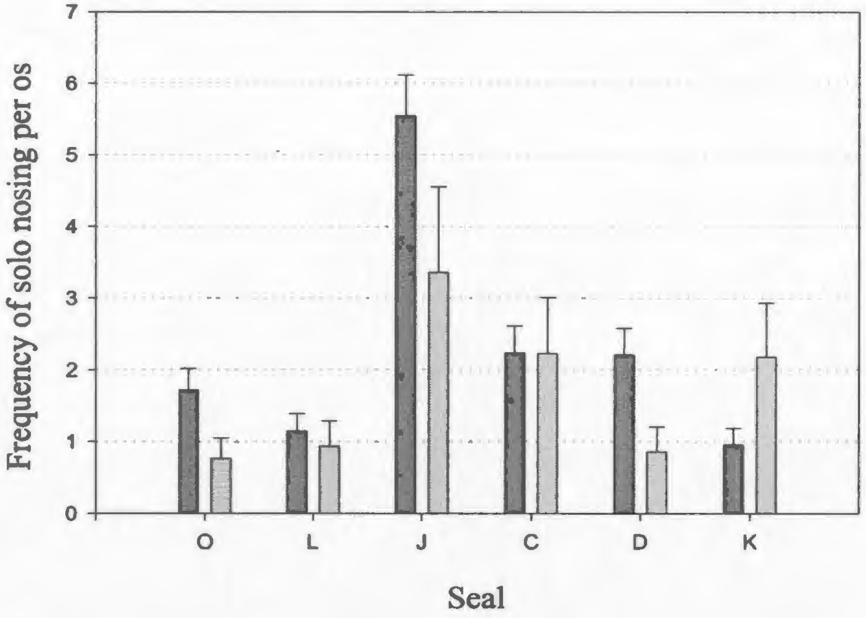


Figure 19a: Mean frequency of solo nosing per observation session (os) in the non-breeding (NB) and the breeding (B) season. Total sample sizes (NB in bold-face, B in italics) are as follows: Oscar(O), **298**, *41*; Clarence(L), **188**, *59*; Julius(J), **961**, *248*; Caesar(C), **374**, *82*; Darby(D), **374**, *49*; Kevina(K), **139**, *101*; and Eddy(not shown), **33**, *16*.

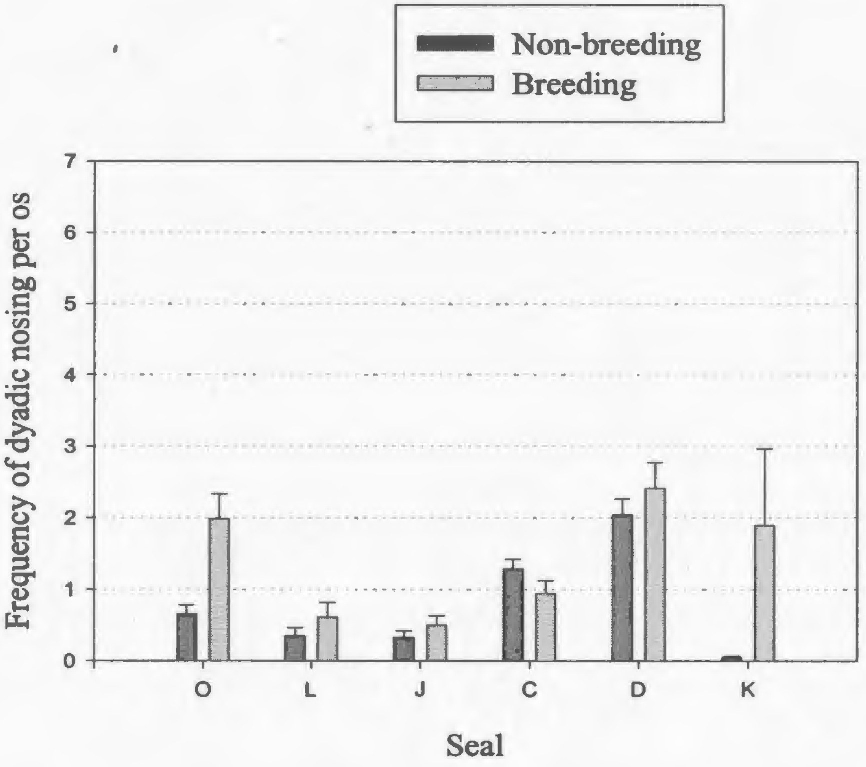
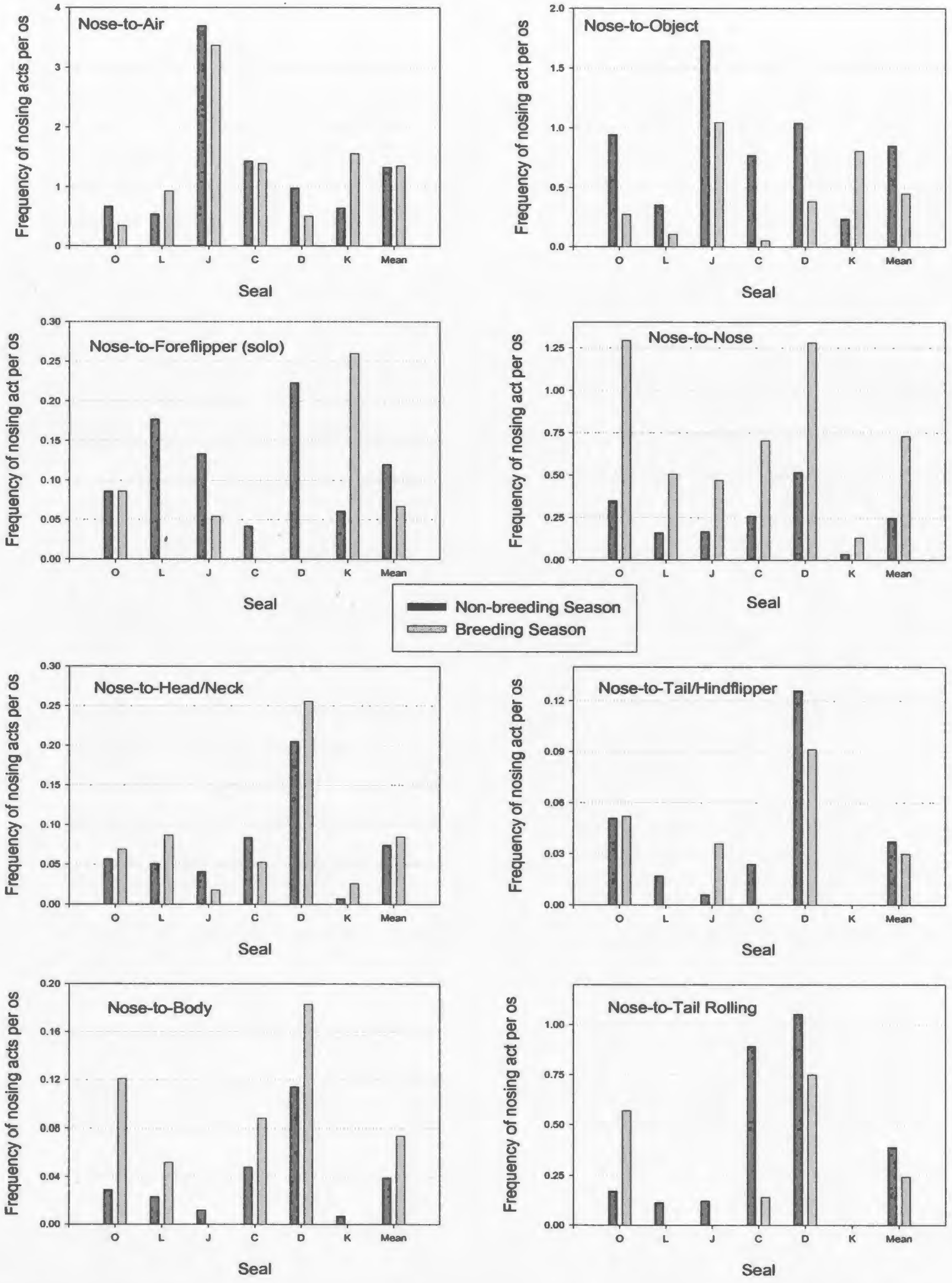


Figure 19b: Mean frequency of dyadic nosing per observation session (os) in the non-breeding (NB) and the breeding (B) season. Total sample sizes (NB in bold-face, B in italics) are as follows: Oscar(O), **117**, *123*; Clarence(L), **64**, *37*; Julius(J), **60**, *29*; Caesar(C), **216**, *56*; Darby(D), **338**, *140*; Kevina(K), **7**, *64*; and Eddy(not shown), **16**, *32*.

tank was dominated by K and her pup. However, the breeding season decreases in solo nosing rates for the other males are more difficult to explain. Perhaps, their energies were simply invested on other activities, or perhaps the air was so saturated with interesting odours that the distinctive nose-to-air act was not necessary to detect social odours. The influence of the pup's birth on K's behaviour is reflected in the large differences in her nosing rates between the breeding and non-breeding seasons; solo nosing was over twice as high, and dyadic nosing was 38 times higher in the breeding season. Further insight into seasonal influences will be achieved through examination of the particular types of nosing behaviour.

Although the female seal did not participate in all types of nosing (e.g., nose-to-tail acts, dyadic nose-to-foreflipper acts, or nose-to-tail rolling), for five of the six nosing behaviours in which K did participate, she showed a higher rate in the breeding than in the non-breeding season (Figure 20); the exception was nose-to-body acts, which K never performed during the breeding season. No individual male showed such an obvious tendency for a rate increase during the breeding season; however, all males performed nose-to-nose acts at a significantly higher rate during the breeding season (males only: $t=-4.47$, $df=4$, $p<.01$). The ratio of breeding to non-breeding season nose-to-nose acts for all seals ranged from C's low of 2.5:1, to K's high of 3.8:1. That K's rate of nose-to-nose acts was higher in the breeding season even when acts involving her pup were excluded illustrates the influence of season on her interactions with the males.

Figure 20: The mean frequency per observation session (os) of each type of nosing for each seal in the non-breeding and the breeding season. For total sample size for each seal, see Appendix C. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina).


Nose-to-Air
Frequency of nosing acts per os
0
1
2
3
4
O
L
J
C
D
K
Mean
Seal
Nose-to-Object
Frequency of nosing act per os
0.0
0.5
1.0
1.5
2.0
O
L
J
C
D
K
Mean
Seal
Nose-to-Foreflipper (solo)
Frequency of nosing act per os
0.00
0.05
0.10
0.15
0.20
0.25
0.30
O
L
J
C
D
K
Mean
Seal
Nose-to-Nose
Frequency of nosing act per os
0.00
0.25
0.50
0.75
1.00
1.25
O
L
J
C
D
K
Mean
Seal
Non-breeding Season
Breeding Season
Nose-to-Head/Neck
Frequency of nosing acts per os
0.00
0.05
0.10
0.15
0.20
0.25
0.30
O
L
J
C
D
K
Mean
Seal
Nose-to-Tail/Hindflipper
Frequency of nosing act per os
0.00
0.03
0.06
0.09
0.12
O
L
J
C
D
K
Mean
Seal
Nose-to-Body
Frequency of nosing acts per os
0.00
0.04
0.08
0.12
0.16
0.20
O
L
J
C
D
K
Mean
Seal
Nose-to-Tail Rolling
Frequency of nosing act per os
0.00
0.25
0.50
0.75
1.00
O
L
J
C
D
K
Mean
Seal

The males did not exhibit any seasonal pattern for nose-to-air rates. Three of five male seals showed a higher breeding season rate for nose-to-head acts, while four of five seals showed a higher breeding season rate for nose-to-body acts (t=-2.46, df=4, p<.05). The males showed a more consistent pattern with respect to nose-to-object acts in that they all had a much higher rate during the non-breeding than during the breeding season (t=6.83, df=4, p<.001). Four of the five males also had a higher rate of nose-to-foreflipper(self) during the non-breeding season (t=2.50, df=4, p<.05). K's opposite seasonal pattern for nose-to-object acts may have been due to the pup's influence. That is, although dyadic nosing acts which involved E were not included in this seasonal analyses, the pup's presence most likely affected both nose-to-air and nose-to-object acts, especially for K who was usually in close proximity to the pup. Indeed, 38.7% of K's nose-to-air acts and 47.0% of her nose-to-object acts occurred in the breeding season, despite the fact that this season accounted for only 20.8% of K's total number of observations. Interestingly, during the breeding season itself, 80.0% of the nose-to-air acts performed by K occurred *prior* to her pup's birth which may indicate enhanced sensitivity to environmental and social odours in the weeks leading up to parturition. In contrast, 96.8% of nose-to-object acts performed by K during the breeding season occurred *after* the pup's birth, and of this 96.8%, almost all acts involved nosing of the deck, step or ramp - all areas frequented by the pup. These results further support the idea that this behaviour may also represent social sampling. All in all, although K performed almost 2.5 times as many nose-to-air acts during the breeding season, four of the five males performed *fewer* nose-to-air acts during this season.

Conclusions. In general, solo nosing rates decreased and dyadic nosing rates increased during the breeding season; however, very little of the dyadic nosing increase could be attributed to increased male attention towards the sole female, as would normally be expected. Unfortunately, the removal of K prior to her weaning the pup meant that some behaviour patterns related to mating, including an anticipated increase in nosing of the female, were unrealized.

Individuals showed distinctive nosing patterns with respect to seasons. Overall, both J and K showed very low rates of dyadic nosing, while D and E showed much higher rates than average. All males, except C, decreased solo nosing and increased dyadic nosing rates during the breeding season, while K substantially increased both solo and dyadic nosing rates during the breeding season. Both of K's solo and dyadic nosing increases could be largely attributed to behavioural changes in response to parturition; for instance, 90% of K's nose-to-nose and nose-to-head/neck acts during the breeding season involved her pup, and both nose-to-air and nose-to-object acts appeared to be pup-related. Hence, these findings further support the contention that many solo nosing acts may be inherently social. The frequency of nose-to-nose acts was substantially higher in the breeding season for all males which suggests that this behaviour may have a functional significance distinct from that of other types of dyadic nosing. In contrast, nose-to-object acts were much less frequent during the breeding season among males; this may reflect the tendency for the males to show more direct attention, in terms of dyadic nosing acts, towards one another during the breeding season. Thus, despite finding highly individual nosing patterns across weeks in previous analyses, the results of this section show that consistent seasonal patterns exist among the males.

Patterns of Dyadic Interaction

Individual Patterns. When dyadic nosing was examined in terms of the initiator and recipient of each interaction, the most striking feature was the high percentage (*M*=56.6%) of events which appeared to be mutually initiated. Mutually initiated dyadic nosing acts accounted for more than half of each individual's total dyadic nosing except for the female (32.3%). Other individual differences were also evident (Figure 21). For instance, the youngest male, D, was the initiator of a dyadic nosing interaction over twice as often as he was the recipient, while for males C, J and L the reverse pattern was true – these three seals were almost twice as likely to be the recipient as they were the initiator of a dyadic nosing act. The sole female was six times more likely to be the recipient of a dyadic nosing act than she was to be an initiator, which suggests that the males were far more interested in her than she was in them, or that she smelled stronger. Only O was equally likely to be the initiator and recipient of dyadic nosing. While it must be

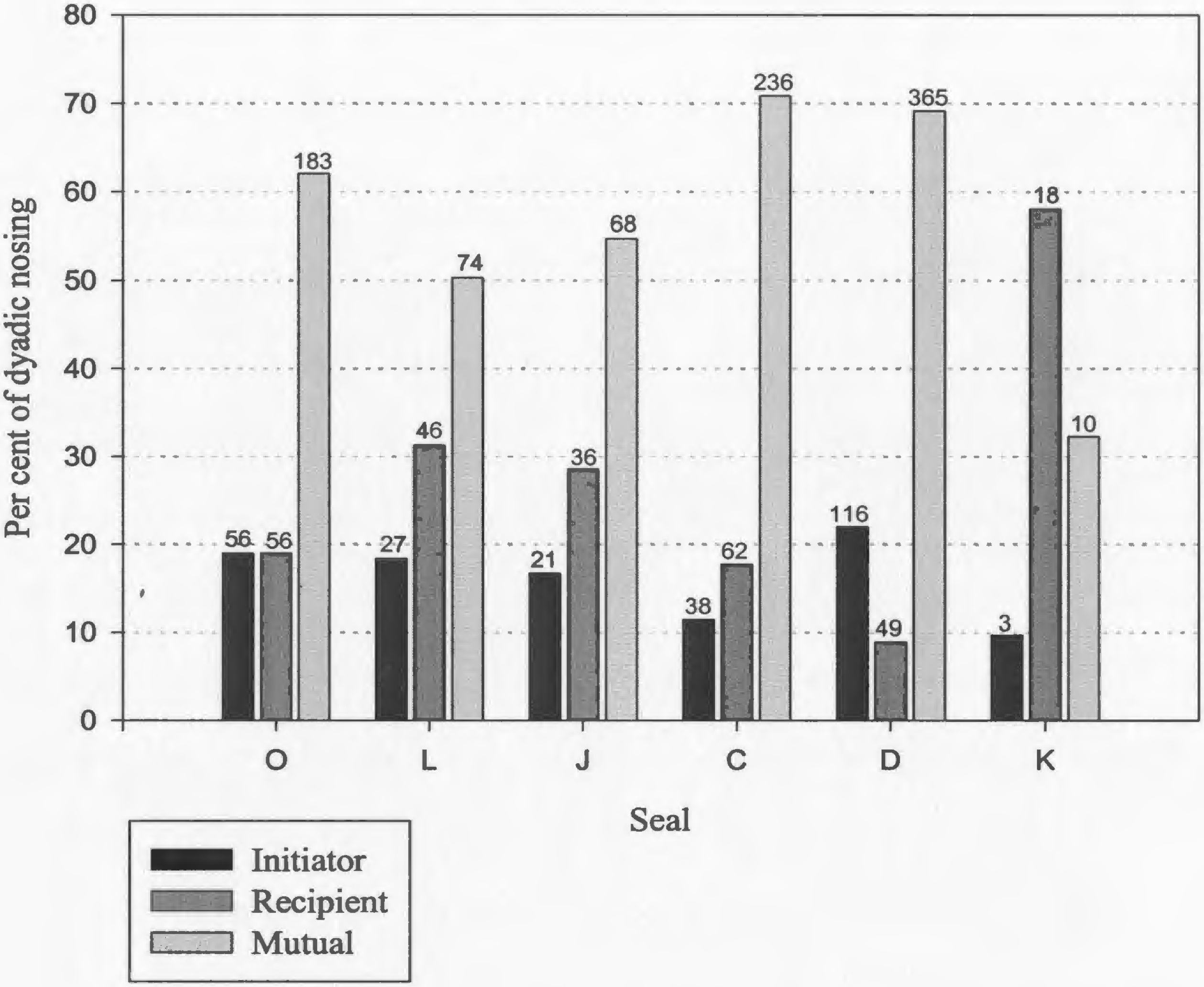


Figure 21: Percentage of each seal's total dyadic nosing as initiator, recipient or mutual. Total sample size indicated above bar. Interactions with the pup are not included. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

acknowledged that individuals may have used cues to initiate a nosing interaction that were too subtle for my detection, the likelihood exists that the mutual participation required by nose-to-tail rolling, nose-to-nose and nuzzling behaviours, by their very nature, has as its corollary mutual initiation.

Individual Patterns Between Seasons. On average, approximately the same proportion of dyadic nosing acts were initiated in both the non-breeding season (M_{nb}=17.5%) and the breeding season (M_b=15.1%). K and L were slightly more likely to initiate during the breeding than during the non-breeding season, while O, J and D showed the opposite pattern, and C showed no seasonal difference (Figure 22a). Overall, a greater proportion of dyadic nosing acts showed a recipient during the non-breeding season (M_{nb}=30.7%) than during the breeding season (M_b=26.1%). Four (O, L, J and K) of the six seals were consistent with this seasonal pattern, but C was the recipient of a dyadic nosing act three times more often in the breeding than in the non-breeding season (Figure 22b). Although not statistically significant, there was a greater proportion of mutually initiated dyadic nosing acts in the breeding season than in the non-breeding season (M_b=64.0% vs. M_{nb}=51.9%), and this was true for all seals except C and L (Figure 22c). K was almost three times more likely to be involved in a mutually initiated nosing act during the breeding season than during the non-breeding season.

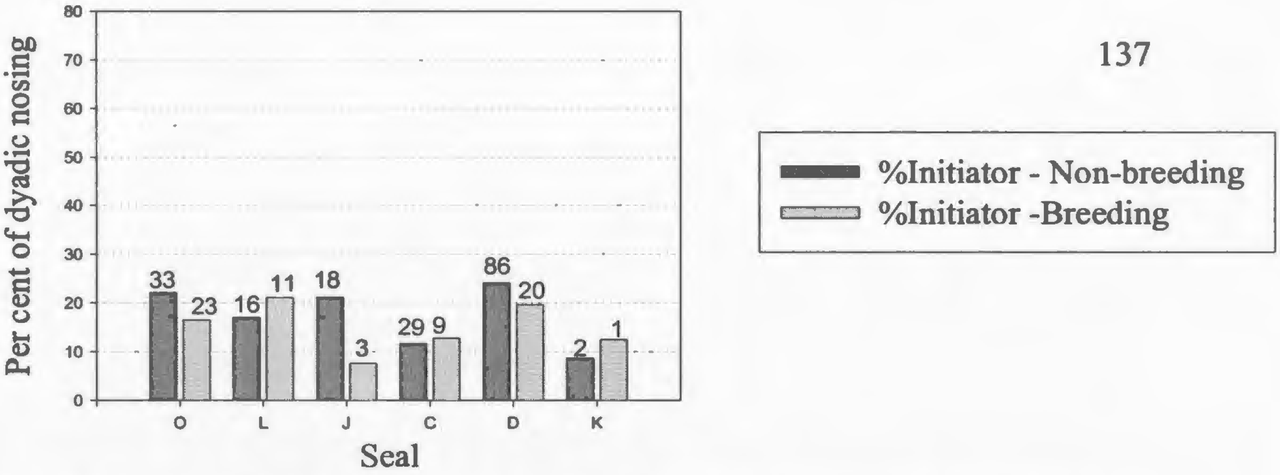


Figure 22a: Percentage of each seal's total number of dyadic nosing acts as initiator in the non-breeding and the breeding season. Sample size above bar. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

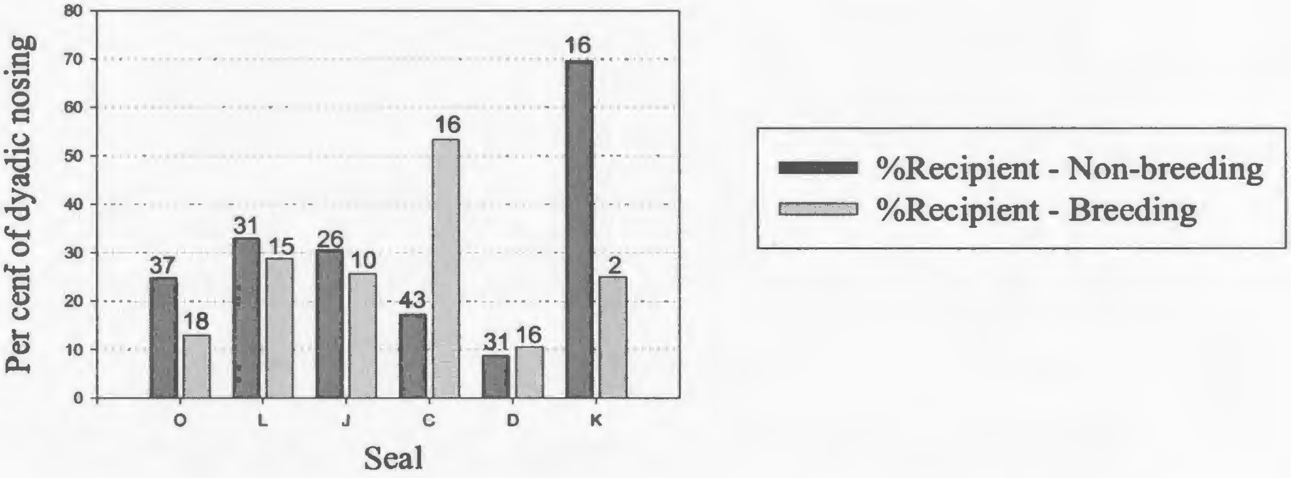


Figure 22b: Percentage of each seal's total number of dyadic nosing acts as recipient in the non-breeding and the breeding season. Sample size above bar. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

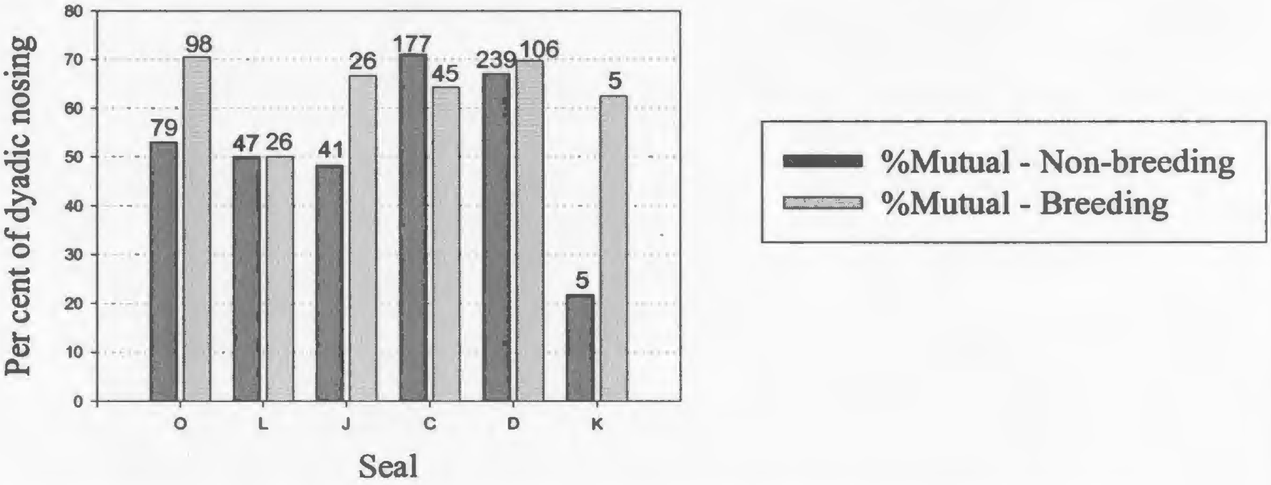


Figure 22c: Percentage of each seal's total dyadic nosing acts that are mutually initiated in the non-breeding and the breeding season. Sample size above bar. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

Overall, 87.7% of nose-to nose acts were mutually initiated in the breeding season, compared to 70.2% in the non-breeding season ($t=-4.75$, $df=5$, $p<.01$). It was evident that *all* of K's mutual nosing events during the breeding season were nose-to-nose acts (Figure 23a and 23b). All other seals also showed a higher percentage of mutually initiated nose-to-nose acts in the breeding versus the non-breeding season; the ratio of which ranged from 1.1:1 for D, to 1.5:1 for J (Figure 23a).

With respect to all other types of dyadic nosing (i.e., nose-to-head, -body, -tail, and -foreflipper; nose-to-tail rolling is excluded here as it always appeared to be mutually initiated), the percentage of mutually initiated acts was slightly higher in the non-breeding than in the breeding season (M_{nb}=5.0% vs. M_{b}=3.3%). However, only D and J showed greater proportion of mutual acts during the non-breeding, while C showed the same proportion in both seasons. Notably, O, L and K were never involved in any mutually initiated nosing acts of this type during the breeding season (see Figure 23b).

Individual Partner Preferences. Other individual differences in dyadic nosing patterns were apparent when each seal's partner preferences were examined. For instance, although each seal performed nose-to-nose acts with every other individual, the oldest (O) and the youngest seal (D) performed the greatest number of these acts and were often partners (Table 8). Overall, D initiated or mutually-initiated 69.9% of his total

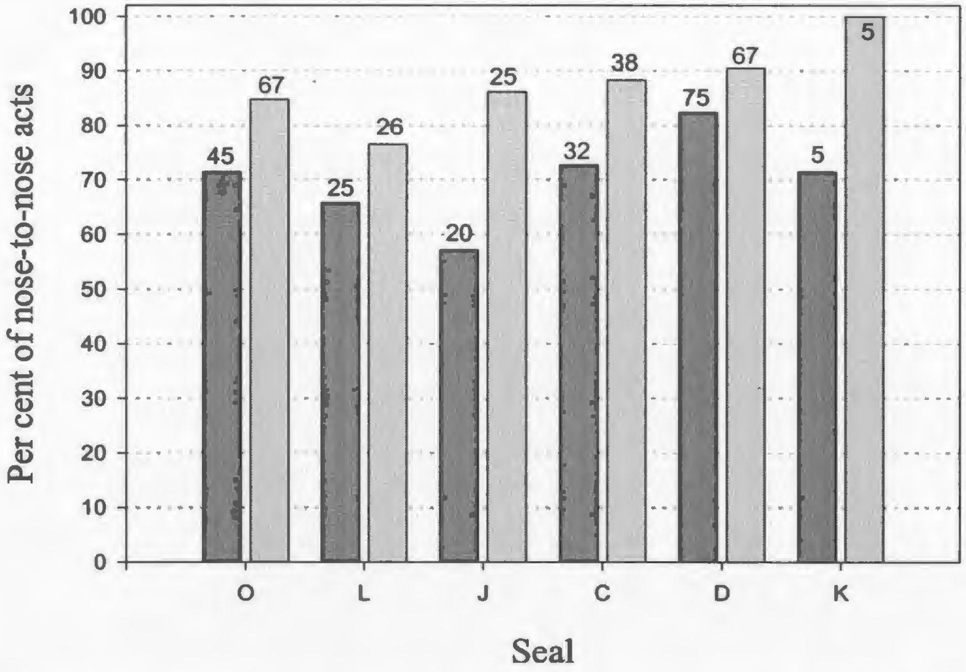


Figure 23a: Percentage of each seal's total nose-to-nose acts that are mutually initiated in the non-breeding and the breeding season. Sample size above bar. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

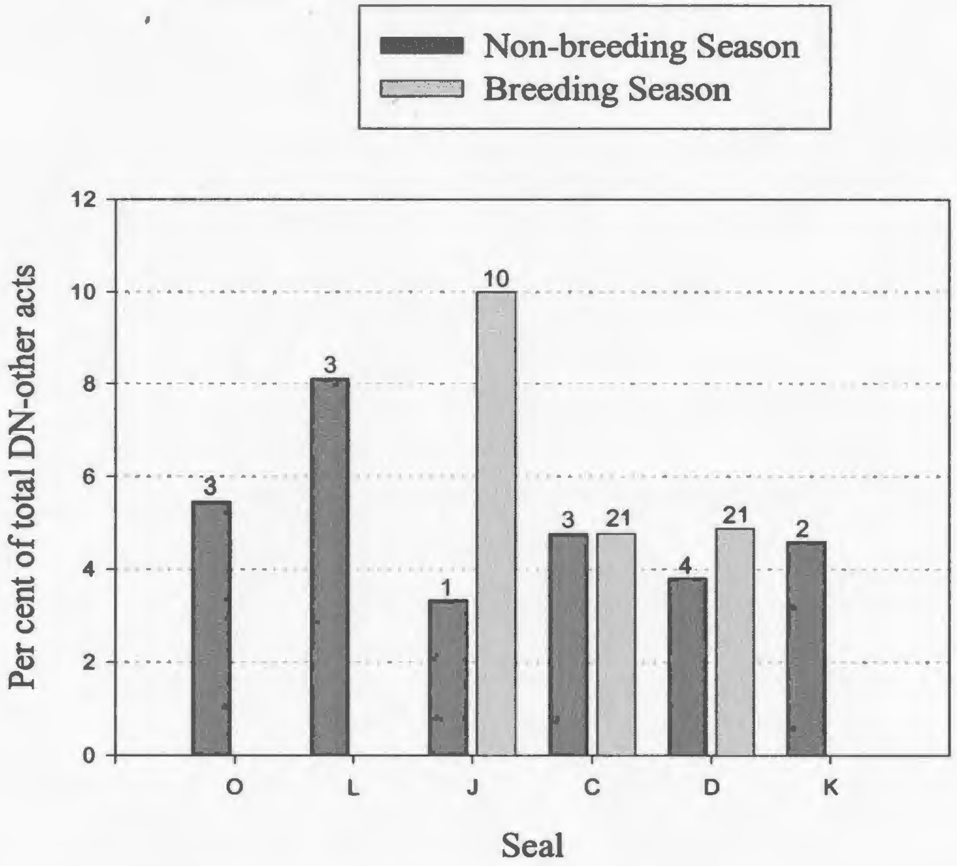


Figure 23b: Percentage of each seal's total of other dyadic nosing types combined [DN-other (nose-to-head, -body, -foreflipper, -tail)] that are mutually initiated in the non-breeding and the breeding season. Sample size above bar. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

Table 8: Total number of nose-to-nose (NTN) interactions with each partner. The number in bold indicates the total number of mutual interactions and interactions initiated by the focal seal (column one); the smaller italicized number below represents the number of the total acts that were mutual. Totals for each column represent the total number of times the seal was a recipient or mutual participant. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

	Total Number of NTN Interactions with Focal Seal						
Focal	O	L	J	C	D	K	Total NTN as Focal
O	—	**18** *12*	**15** *12*	**31** *24*	**69** *65*	**4** *4*	**137** *117*
L	**16** *12*	—	**11** *11*	**5** *5*	**23** *21*	**2** *2*	**57** *51*
J	**14** *12*	**15** *11*	—	**7** *6*	**17** *15*	**2** *1*	**55** *45*
C	**26** *24*	**6** *5*	**7** *6*	—	**42** *30*	**2** *1*	**83** *66*
D	**67** *65*	**25** *21*	**20** *15*	**42** *30*	—	**2** *2*	**156** *133*
K	**4** *4*	**2** *2*	**1** *1*	**1** *1*	**2** *2*	—	**10** *10*
Total NTN	**127** *117*	**66** *51*	**54** *45*	**86** *66*	**153** *133*	**12** *10*	**498** *422*

number of nose-to-nose acts with O and C, and D was, by far, the most popular partner choice for both C and O. Despite very low rates for all types of dyadic nosing, K participated in *mutual* nose-to-nose acts with all males; however, O was her most frequent partner for this nosing behaviour.

With respect to nose-to-tail rolling, again D was the most popular partner choice for O and C (Table 9), while L and J chose each other almost exclusively for rolling partners. Of interest is the finding that the female was never observed to participate in nose-to-tail rolling; this is consistent with other research showing a low incidence of nose-to-tail rolling in females (Renouf, 1986; Wilson, 1974b).

Table 9: Total number of nose-to-tail rolling (NTR) interactions with each partner. All NTR interactions are considered to be mutually initiated. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina)

	Total Number of NTR Interactions with Focal Seal						
Focal	O	L	J	C	D	K	Total NTR
O	—	0	0	1	62	0	63
L	0	—	20	0	0	0	20
J	0	20	—	1	0	0	21
C	1	0	1	—	154	0	156
D	62	0	0	154	—	0	216
K	0	0	0	0	0	—	0
Total NTR	63	20	21	156	216	0	476

Although L and J preferred one another for nose-to- tail rolling, they participated in the other types of dyadic nosing interactions (e.g., nose-to-head, -body, -foreflippers and -tail) with *all* other individuals (Table 10). However, K never initiated other types of dyadic nosing with O or L. Again, D chose O and C most often for these other types of dyadic nosing and, in turn, was often the recipient of acts initiated by O and C.

Conclusions. The finding that over one half of all nosing interactions were mutually initiated, as well as the finding that distinct partner preferences existed, indicates that nosing behaviours served a function other than random investigation. That is, if seals were simply randomly nosing one another in order to identify each other in passing, for example, then such strong individual preferences would not be evident, nor would mutual initiation be so common. It is interesting that the sole female was not the recipient of dyadic nosing acts more often in the breeding season; in fact, K was almost three times as likely to be the recipient in the non-breeding as in the breeding season. This result may reflect K's propensity for mutually initiated nosing acts during the breeding season and of her very low involvement in other types of dyadic nosing with the adult males. Regardless, in both seasons, K was more likely to be the recipient than the initiator of a dyadic nosing act.

The finding that almost 80% of nose-to-nose acts were mutually initiated supports the notion that this behaviour serves as an affiliative act. That all seals participated in more mutually initiated nose-to-nose acts in the breeding season than in the non-breeding

Table 10: Total number of all other types of dyadic nosing (DNO) interactions with each partner. DNO includes nose-to-head/neck, nose-to-body, nose-to-foreflippers and nose-to-tail acts. The number in bold in each column indicates the total number of mutual interactions and interactions initiated by the focal seal (column one); the smaller italicized number below represents the number of the total acts that were mutual. Totals for each column represent the total number of times the seal was a recipient or mutual participant. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina).

	Total Number of DNO Interactions with Focal Seal						
Focal	O	L	J	C	D	K	Total DNO as Focal
O	—	**13** *2*	**3**	**4**	**19** *1*	**0**	**39** *3*
L	**8** *2*	—	**3** *1*	**5**	**6**	**2**	**24** *3*
J	**1**	**5** *1*	—	2	**4** *1*	**1**	**13** *2*
C	**10**	**3**	**3**	—	**13** *4*	**6**	**35** *4*
D	**29** *1*	**13**	19 *1*	**41** *4*	—	**7**	**109** *6*
K	**0**	**0**	**1**	**1**	**1**	—	**3**
Total DNO	**48** *3*	**34** *3*	**29** *2*	**53** *4*	**43** *6*	**16**	**223** *18*

season, and that this pattern did not exist for the other types of dyadic nosing, suggests that nose-to-nose or nuzzling acts serve a special role in regulating social behaviour during the breeding season. However, the question remains as to whether nosing involves the olfactory or tactile senses. The literature suggests that nares dilation may be indicative of olfaction, while vibrissae protraction reflects some tactile sensation (Renouf, 1991; Rosen, 1991); thus, the involvement of the nares and vibrissae during each nosing act is examined next.

Involvement of Nares and Vibrissae in Nosing

Position of Nares and Vibrissae. Whenever visible, the position of the nares and vibrissae was recorded for each nosing act. Nares were either open, closed or not visible, while vibrissae were either in their normal position (i.e., retracted), projected forward (i.e., protracted), or not visible; thus, there were nine possible nares/vibrissae combinations for each observed nosing act. These combinations were not recorded for nose-to-tail rolling bouts because the splashing made it impossible to view the nares and vibrissae; thus, nose-to-tail rolling acts are not included in this analysis.

Open nares and forward-projected vibrissae accounted for the overwhelming majority of all potential combinations for all types of nosing (82.1%). Neither the nares or vibrissae were visible during 11.8% of all acts, while non-visible nares and forward vibrissae accounted for another 2.7% of the total, and closed nares and normally-positioned vibrissae accounted for a mere 2.3%. The remaining nares/vibrissae configurations each accounted for less than 0.5% of the total number of nosing acts.

Almost all (97.1%) nose-to-air acts and most nose-to-object acts (72.2%) involved open nares and protracted vibrissae (Figure 24). Nose-to-nose and nuzzling acts also usually (i.e., 71.0%) involved open nares and forward vibrissae, however because in a large number (20.9%) of nose-to-nose acts, the nares and vibrissae were not visible, this result may be an underestimate. A moderate 50.0 to 62.2 % of all other types of nosing, except nosing one's own foreflipper, showed open nares and forward vibrissae. In 61.4% of all nose-to-foreflippers (self), the nares and vibrissae were not visible; thus, a mere 27.0% were observed to involve open nares and protracted vibrissae, while 4.7% involved closed nares and retracted vibrissae.

Individual Differences. Few individual differences were evident with respect to open nares and protracted vibrissae being the dominant configuration; all seals, except E, showed this configuration during 71.4 to 90.6 % of all types of nosing (Figure 25). Most of this variation appears to have resulted from individual differences in the occurrence of non-visible nares and vibrissae, which in itself is connected to each seal's predominant nosing behaviour. For example, O, D and E had the highest rates of nose-to-nose or nuzzling behaviours, and also the highest proportion of non-visible nares and vibrissae. Nonetheless, when the proportion of acts with open nares and protracted vibrissae are

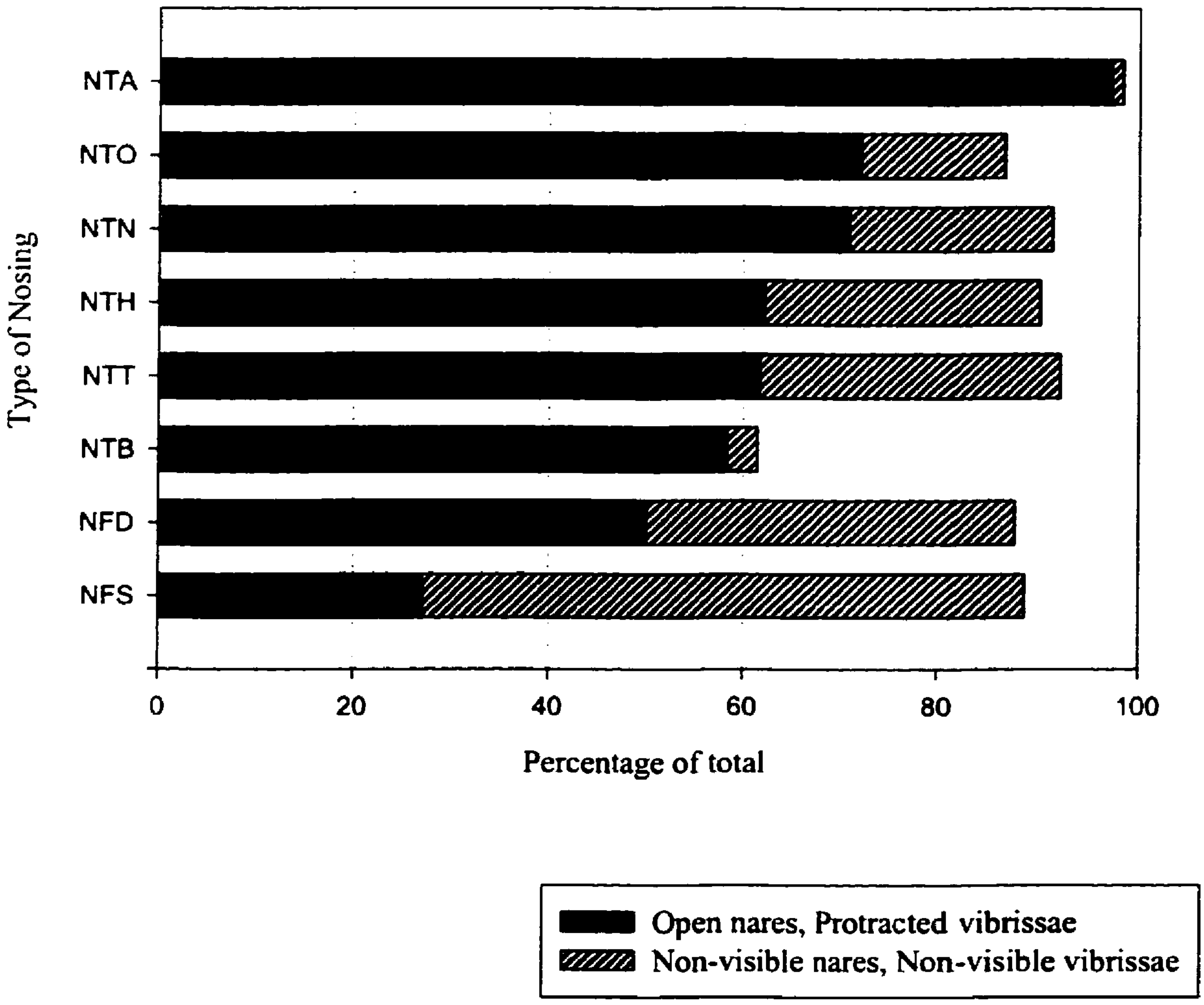


Figure 24: Percentage of each type of nosing with open nares and protracted vibrissae, and non-visible nares and vibrissae. [NTA=nose-to-air, NTO=nose-to-object, NTN=nose-to=nose, NTH=nose-to-head, NTT=nose-to-tail, NTB=nose-to-body, NFD=nose-to-foreflipper (dyadic), NFS=nose-to-foreflipper(self)]

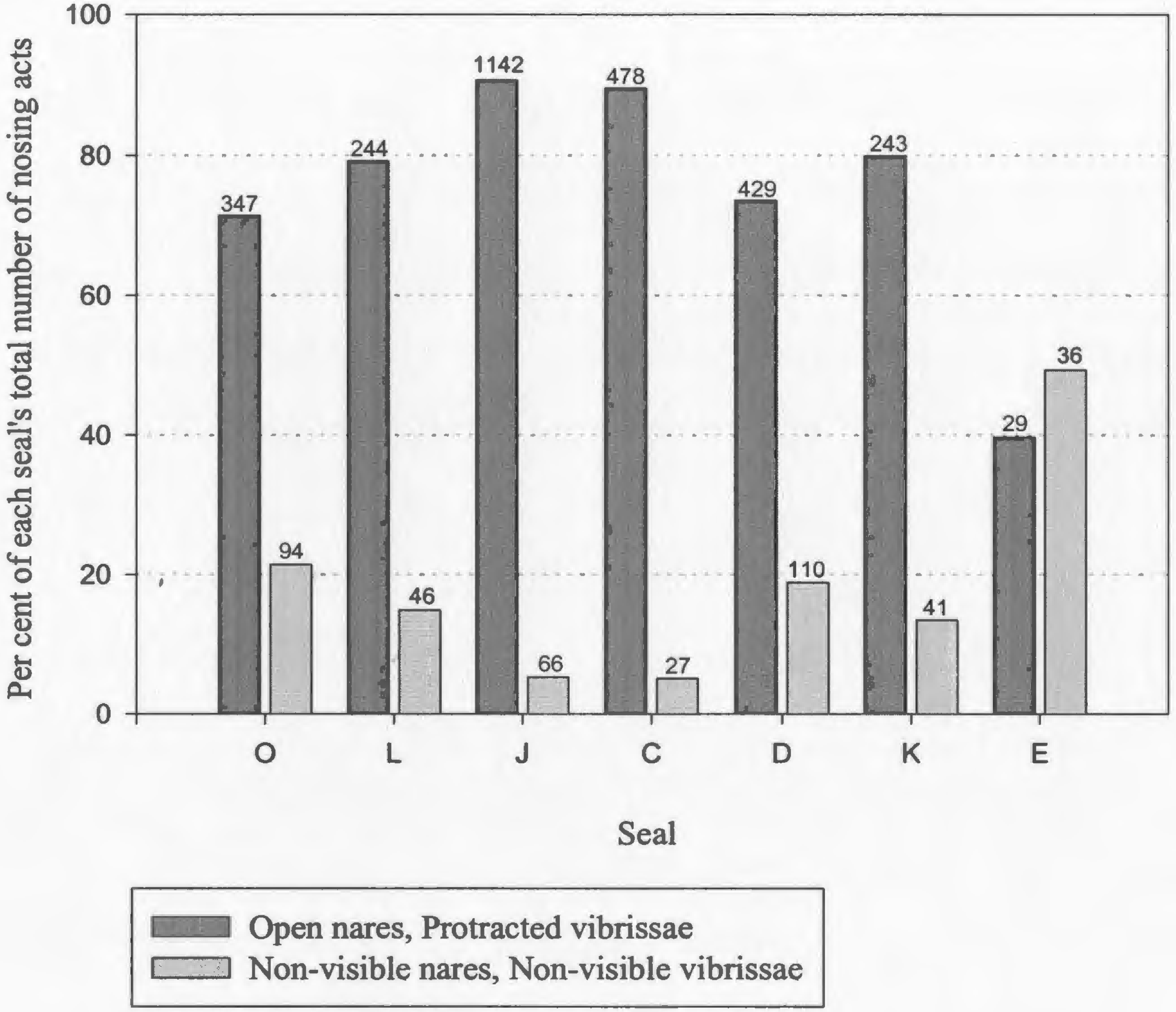


Figure 25: Percentage of each seal's total nosing with open nares and protracted vibrissae versus non-visible nares and vibrissae. Sample size indicated above bar. (O=Oscar, L=Clarence, J=Julius, C=Caesar, D=Darby, K=Kevina, E=Eddy)

added to the non-visible configurations, between 92.8 and 95.9% of each adult seal's total number of nosing acts is accounted for, while for E, 89.1% of his total number of nosing acts are accounted for.

Conclusions. Open nares and protracted vibrissae are a predominant feature of nosing behaviour. These results strongly support the notion that nosing acts to mediate both olfactory and tactile senses. However, it is difficult to imagine what function protracted vibrissae serve during nose-to-air acts; this may indicate that the vibrissae project forward as a consequence of nares dilation. This possibility seems unlikely given harbour seals' control over their highly sensitive vibrissae (Mills & Renouf, 1986; Renouf, 1979). Harbour seal vibrissae are known to be prominently protracted during social encounters (Miller, 1975) – a behaviour that is postulated to be an integral part of social display. Thus, perhaps vibrissae protraction during nose-to-air acts also serves a display function of some kind.

Chapter Four: General Discussion

Although nosing behaviours have long been known to be an important component of many social behaviours in a variety of mammals, nosing has rarely been investigated in any of the marine mammals, except in relation to mother-pup interactions in pinnipeds. However, this study has shown that nosing behaviour occurs frequently, and in a variety of contexts, among all of the O.S.C. harbour seals, as it probably does among free-living pinnipeds. Despite the restrictions of their captive lifestyle, the inclusion of social partners allowed the O.S.C. seals limitless opportunities for social interaction (i.e., 'response contingent stimulation', Carlstead, 1996), in which nosing appeared to play an important role. That significant effects of the type of nosing, season, and individual seal were found indicates that nosing behaviour is not simply performed as a random act of investigation; rather, each seal showed a highly individualized pattern of behaviour both in terms of activity levels and nosing with respect to seasons, major events (e.g., parturition), and each other. In addition, if nares dilation and protracted vibrissae are indicative of olfactory and tactual involvement, respectively, then the observed nosing patterns suggest that these two sensory systems were often involved in mediating harbour seal social behaviour.

The results of this study were consistent with the notion that dyadic nosing acts serve as affiliative behaviour in the O.S.C harbour seals. In particular, the large proportion of mutually initiated nosing acts, plus the existence of distinct partner preferences, are both indicative of affiliation. The high rate of nose-to-nose and nuzzling acts suggest that these behaviours may play an especially important role in regulating social behaviour. That the rate of nose-to-nose acts increased substantially for *all* seals during the breeding season indicates that the need for social regulation may be enhanced during this period. Although this observational study could not examine the sensory basis of dyadic nosing, the high proportion of acts with dilated nares and protracted vibrissae suggests that chemical or tactual stimulation may underlie this behavioural pattern, a finding consistent with Lawson (1983) and Rosen (1990).

Most of the nose-to-nose acts and all of the nose-to-tail rolling acts appeared to be mutually initiated, and the prolonged nature of some nuzzling and most rolling bouts indicated continued mutual participation. More detailed examination, via a frame-by-frame video analyses, of nuzzling and rolling bouts would undoubtedly yield further insight into the behavioural mechanisms which mediate these behaviours. In particular, it would be interesting to know what behavioural cues determine the onset, vigour, and termination of a bout; in addition, questions relating to the role of the visual, acoustic, olfactory or tactual senses in these behavioural cues would be worth pursuing. The other dyadic forms of social nosing (e.g., nosing of the head/neck, body, foreflippers, and tail/hindflippers) may have been mutually initiated infrequently, but the fact that these nosing acts were performed by each seal in almost every possible partner combination suggests that dyadic social nosing may serve as an investigatory behaviour; this possibility merits further research. In particular, it would be interesting to know if recipients of dyadic nosing acts orient themselves to allow nosing to take place, as is often the case in other species (e.g., canids). Intentional orientation to expose a region of the body would indicate that the individual seal trusts that no harm will result. In addition, the finding that nose-to-head and nose-to-body acts occurred, on average, more often during the breeding than during the non-breeding season indicates that these particular behaviours may also relate to the complex of social behaviours that occur during the breeding season.

Bradbury and Vehrencamp (1998) postulated that the affiliative signals that serve to maintain harmonious relationships among group members can be categorized along two dichotomous axes: duration of the benefits of the signal, and symmetry of the sender and receiver. According to this scheme, harbour seal social play and all forms of dyadic nosing would be examples of long-term benefit symmetric partner interactions, the long-term benefit being the maintenance of the group. The fact that nose-to-nose acts occurred at such a high rate and involved all seals suggests that this behaviour may be particularly important in maintaining a relatively amicable atmosphere, and one in which the seals not only coexisted peacefully in a restrictive, static enclosure, but were interdependent for sensory stimulation.

The findings of this study suggest that in order to provide a comprehensive description of the social behaviour of a group of individuals, *both* affiliative and agonistic interactions should be considered; that is, an examination of just one of these classes of social interaction would not enable a complete and accurate depiction of the social life of any species. Unfortunately, as outlined earlier, agonistic behaviours have usually received more scientific attention than affiliative behaviours and, thus, may have disproportionately influenced ideas regarding social structure. However, just as it may be important to quantify *both* active and quiescent acts in order to describe general behaviour patterns completely, then it may be important to quantify *both* affiliative and agonistic acts in order to most precisely portray patterns of social behaviour.

If dyadic nosing acts, including social play behaviour such as nose-to-tail rolling, are recognized as affiliative behaviours that promote a peaceful coexistence among a group of harbour seals, then perhaps researchers will begin to quantify and use these behaviours in an objective manner to describe social interactions and structure, as suggested by Ross (1972). For example, affiliative behaviours could be used in conjunction with, or in comparison to, the long-recognized agonistic behaviours of head-up stare, head-thrusts, foreflipper scratch/wave/erect, and growls (Miller, 1991; Sullivan, 1982), to enable the development of a composite measure by which to quantify dyadic and group interactions. For instance, two individuals who never engage in either affiliative or agonistic interactions might be characterized as a non-interactive dyad; in contrast, two other individuals who engage in both frequent affiliative and agonistic acts might be characterized as a highly interactive pair, while a dyad which interacts frequently in terms of affiliative acts but never engages in agonistic acts might be considered to share a strong positive social bond. Such characterizations could help define the social matrix within which other behaviours, such as reproduction, occur (Carter, Lederhendler & Kirkpatrick, 1987). Furthermore, the lack of agreement surrounding the existence of social organization in harbour seals may be rectified in future investigations if affiliative, as well as agonistic behaviour patterns were taken into account. For example, if two or more seals were found to share a positive social bond, and this bond was found to exist over an extended period of time, then these seals might be characterized as 'cohesive', as suggested by Wilson, (1974a; 1978). In contrast, Sullivan's (1982) idea that harbour seals form dominance hierarchies might find support if behavioural data were comprised of a composite measure of affiliative and agonistic interactions.

Another principal finding of this study was that the concept of social nosing should *not* be limited to acts in which one seal noses another seal; that is, nose-to-air and nose-to-object acts may serve as a way to monitor social or environmental cues. That the nares were open for most nose-to-air and nose-to-object acts suggests that these behaviours were involved in the detection of odours; thus, it is possible that nosing of both air and objects involve the sensation of volatile and non-volatile chemical compounds. In addition, the high rate of protracted vibrissae during nose-to-air and nose-to-object acts implicates tactual involvement, although this finding is difficult to interpret with respect to nose-to-air acts, as discussed previously. Regardless, the high rate of nosing the air and nosing objects by J , a seal who was often alone in the satellite tank, and the female's high rate of nose-to-objects *after* the pup's birth, support the notion that these *solo* nosing behaviours may be a means to sample *social* cues (e.g., the odour of conspecifics). Thus, despite lack of evidence concerning the nature of chemical and tactual involvement in nosing, sufficient evidence exists to consider that some nose-to-air and nose-to-object acts may be a form of social nosing . Whether these behaviours can also be thought of as affiliative behaviours is not clear. Certainly, nose-to-air and nose-to-object acts bear little resemblance to nuzzling, social play and dyadic forms of social nosing, in that they are not performed mutually, nor do they promote contact between individuals, at least not immediate contact. Nonetheless, it is possible that some solo forms of social nosing do ultimately serve as affiliative behaviours in that they may function as a means of monitoring changing physiological states of other individuals, or as a way to keep track of the whereabouts of others within the enclosure. The seasonal differences between the various types of nosing include a lower frequency of nose-to-object acts among males during the breeding season; this may reflect a tendency for the males to perform dyadic nosing acts, specifically those directed at the nose, head/neck and body, in order to monitor one another during the breeding season.

Although the results support the notion that affiliative nosing acts to influence the overall behaviour patterns of the O.S.C. seals, no conclusions can be made regarding the specific role played by nosing behaviours in determining the social structure of the seals. Despite year-round observations of the study population, the existence of a well-defined social organization, in its conventional sense (e.g., harem, pod), in the study animals seems an unlikely proposition. Although the seals revealed distinct patterns with respect to both solo and dyadic behaviour, and clear partner preferences were evident, no specific social structure, such as a dominance hierarchy based on age or sex, could be discerned. Furthermore, despite being a socially interactive and reproductively successful group of captive animals, the degree of social cohesion in this group was unclear. Thus, even in a captive situation in which regular observations of known individuals were possible over a lengthy period, the social structure of harbour seals remained undetermined.

It may be that the inability to categorize the social structure of a group of individuals based on their social dynamics is inconsequential. Instead, the O.S.C. harbour seals may have a fluid social structure and can be characterized as a socially tolerant, if not cohesive, group of individuals who have successfully adapted their behaviour patterns to their own unique circumstances. Consequently, perhaps the most accurate characterization of this group should be at the level of the individual; this is especially appropriate given the extensive individual differences described in the previous chapter. What follows is a profile of each seal, including their basic activity styles, display patterns, nosing behaviour and interaction patterns.

Not surprisingly, the sole female seal showed the most distinctive behavioural profile. Kevina was a highly active, yet non-interactive, individual, whose nosing behaviour was most often related to her role as a mother of a newborn pup. K showed high rates of both active and quiescent acts, and both types of behavioural act were of short duration. Overall, her rates of solo and dyadic nosing were the second and third lowest, respectively, of all individuals. During the breeding season, K's rate of both solo and dyadic nosing increased substantially, largely as a result of involvement with, and proximity to, her pup. When interactions with her pup were excluded, K was least likely of all seals to initiate a dyadic nosing act; however, when she did initiate nosing interactions, it was more likely to occur in the breeding season and to involve a nose-to-nose act with O. Within the breeding season itself, K's pattern of nose-to-air acts suggests that K's sensitivity to environmental and social odours increased prior to parturition; this finding highlights the value of examining nosing behaviour across weeks, as well as between seasons. Because K was the only female present in the study group, it is unknown whether her active, yet non-interactive behaviour patterns reflect a sex difference that is typical of harbour seals, behavioural changes related to her pregnancy or, individual difference. Past research has shown conflicting results regarding sex differences in harbour seal; for instance, Wilson (1974a) found that female juvenile seals in captivity were less likely than male juveniles to engage in social play, while Renouf and Lawson (1987) found a higher incidence of social play forms in free-living females across all age groups. Since population differences are likely to exist with respect to behaviour patterns, and captivity also undoubtedly influences social interactions, perhaps a synthesis of relevant data from the various study groups, both captive and wild, would be the best way to discover whether sex differences are the norm for harbour seals.

Overall, the male patterns showed individually distinctive variations, many of which were consistent with what is known about harbour seal biology. That this conclusion can be drawn from analyses of the nosing data attests to the importance of nosing in harbour seal social behaviour. Of the males, Julius displayed the most distinctive behavioural pattern in that he appeared to be a solitary seal who did not often interact directly with other individuals, but monitored his environment. He appeared to be the least active seal (i.e., he had the lowest rate of active behaviour), and displayed at the lowest rate relative to the other males. However, his pattern of active behaviour, across weeks, was consistent with the overall male pattern, and when he did display, it was at the biologically appropriate time. He showed both the highest rate of solo nosing and the lowest rate of dyadic nosing, yet these rates showed seasonal differences consistent with the other males; that is, solo nosing decreased in the breeding season, while dyadic nosing increased in this season. One of the most notable aspects of J's nosing behaviour was the finding that he had the highest rate of both nose-to-air and nose-to-object acts, and that this was true for both the non-breeding and breeding seasons. Taken together, J's patterns of behaviour appeared to reflect his spatial preference for the satellite tank where he was often alone, and hence, *less* likely to participate in dyadic nosing acts and *more* likely to have to depend on solo nosing acts if he were to monitor both the activities of the other seals and his environment. That his active behaviours were of the longest duration was consistent with his social isolation; that is, because the tank walls of the ST were substantially lower than that of the MT, half and three-quarter pop-outs, which were usually of longer duration than head pop-outs, were necessary to monitor the activities of other seals in the MT. Unfortunately, due to limitations in the design of this study, more detailed analyses of spatial preferences and proximity between individuals were not possible. Future investigations might profitably examine the correlation of the frequency of the various nosing behaviours with spatial preference and proximity scores.

Oscar, the oldest seal in the study group, might aptly be characterized as the 'patriarch' of the O.S.C. seals. This is not meant to imply that he was dominant, in the classical sense, but rather that he interacted with all other seals; for instance, he was twice as likely as any other seal to engage in nose-to-nose acts with the female and he engaged in frequent interactions with the youngest seal, D. Overall, O seemed to show a strong preference for dyadic nosing interactions with D, and this was true for all types of dyadic nosing, especially nose-to-tail rolling. O's preference for interactions with D contrasts to the behaviour of free-living adult males who rarely interact with juveniles; this difference likely reflects the unique constraints and opportunities that captivity has placed on the O.S.C. seals. Despite his advanced age, O's rate of active behaviour was the highest of any male seal; however, his quiescent rate was also the highest. Unlike all other males, his rate of active behaviour did *not* decrease four weeks prior to parturition, and this rate *increased* after the removal of K and her pup; these patterns may suggest that O was not influenced in the same way as the younger males by the events of the breeding season. However, O's display patterns were, perhaps, the most typical of the males; like C, J and L, O displayed more frequently during the breeding than during the non-breeding season, but like C and D he also displayed during the non-breeding season. With respect to solo and dyadic nosing, O showed rates intermediate to those of the other males, although during the breeding season, O's dyadic nosing rate was higher than average. Relative to the other males, some of O's dyadic nosing patterns appeared to be more strongly influenced by season. For example, O was the only male to show a higher breeding than non-breeding season rate for nose-to-tail rolling acts, and he showed a substantially larger increase in his ratio of breeding to non-breeding season nose-to-body acts than the other males (i.e., O showed a 4:1 ratio while the average ratio was 1:1.9). When partner preferences were considered, it was apparent that O's high nose-to-tail rate during the breeding season was due to increased interaction *exclusively* with D. In contrast, O's breeding season increase in nose-to-nose acts could be attributed to increased interaction with *all* seals which supports the idea that this behaviour plays an especially important role in promoting group tolerance.

The second oldest male can, perhaps, be characterized as a 'typical' male of the study group; that is, Clarence's behaviour patterns were the *least* distinctive in that his rates of behaviours were often lower than the group average, but were not often the lowest. L was similar to J in that his pattern of active behaviour across weeks was consistent with the overall male pattern and, despite showing a very low rate of display behaviours, when he did display he did so at the most appropriate time. Also, similar to J, L showed a low rate of dyadic nosing; however, in contrast to J, L exhibited the lowest rate of solo nosing. All of L's nose-to-tail rolling acts occurred during the non-breeding season, and all involved J as his partner. That L only ever engaged in rolling with the one individual least likely to be present in the MT, where most of the social play took place, supports the idea that the seals did indeed exhibit distinct partner preferences. In brief, nothing about L's behaviour or nosing patterns was particularly conspicuous, yet this was the one male in the study group known to have fathered at least two pups (C and D) in past years (Perry & Amos, 1998). Unfortunately, there exists no data regarding the paternity of the other seals born at the O.S.C., including J and E. The results regarding L are especially interesting in view of efforts by some researchers (e.g., Sullivan, 1982) to assume that dominance hierarchies exist in harbour seals; that is, nothing about L's behaviour would implicate him as being a dominant individual despite his past reproductive success.

Caesar was, like L, somewhat difficult to characterize; he appeared to be a highly interactive seal, but also one who decreased his rate of interaction during the breeding season. C exhibited the lowest rate of quiescent behaviour and a higher than average rate of active behaviour. His active behaviours tended to be short-lived while his quiescent behaviours were of the longest duration of all seals. C accounted for the greatest proportion of bubble-blowing and the second largest amount of flipper-slapping. Despite displaying throughout the study period, C rates of display behaviour were higher during the breeding than during the non-breeding season. C showed the second highest rates for both solo and dyadic nosing, yet with respect to seasons, C was atypical of the males in that he showed no change between seasons in his solo nosing rate, and his rate of dyadic nosing decreased in the breeding season. Although his nose-to-air rates did not change with season, nose-to-object and solo nose-to-foreflipper seasonal patterns were consistent with the other males (i.e., they were higher in the non-breeding season). In addition, nose-to-nose and nose-to-body seasonal patterns were similar to those of the other males in that his breeding season rates were higher than his non-breeding season rates. However, with respect to social play the reverse pattern was true for C; he was over six times more likely to engage in social play in the *non-breeding* than in the breeding season. Taken together, these results suggest that C may have compensated for his breeding season decrease in most types dyadic nosing interaction by maintaining his usual rate of nose-to-air acts (i.e., in order to monitor the breeding season social cues). Thus, C's results emphasize the individualistic nature of behavioural responses to seasons.

Darby, the youngest seal, was the most interactive individual in terms of dyadic nosing behaviours. He exhibited average rates of active and quiescent behaviour, and these rates, across weeks, were consistent with those of the overall male pattern, *except* at the time of parturition; whereas all other males increased their active behaviour when the pup was born, D's active rate remained steady. D's display patterns were also influenced by parturition in a manner opposite to that of the other males; that is, his display behaviours almost stopped entirely after the pup's birth and remained at their lowest levels throughout the remainder of the breeding season just when the other males increased their display rates substantially. Thus, despite being 5 years old at the time of the study, an age normally considered 'sexually mature' (Boulva & McLaren, 1979), D's behaviour patterns were not, in fact, consistent with those of individuals known to be sexually mature. Furthermore, the frequent display behaviour shown by D (as well as C) during the non-breeding system suggests that bubble-blowing and flipper-slapping, especially the latter, are likely to serve some function(s) other than reproduction-related display signals. In particular, D's results suggest that flipper-slapping may sometimes be a form of play, at least in captive animals. The most striking aspect of D's behaviour was his high rate of dyadic nosing. Aside from the pup, D performed nose-to-nose, nose-to-tail rolling and all other forms of dyadic nosing at a higher frequency than any other seal, and this was usually true for both seasons, the exception being O's slightly higher rate of nose-to-nose acts during the breeding season. D was more likely to initiate dyadic nosing interactions than any other seal, and other than during social play in which O and C were D's only partners, D interacted with *all* individuals. Thus, despite not being a highly active individual, D appeared to be highly social and involved in frequent nosing. Furthermore, the finding that both D and C engaged in social play more often during the non-breeding than during the breeding season, while O showed the opposite pattern, is reminiscent of the frequency with which D and C flipper-slapped in the non-breeding season. These patterns suggest that both nose-to-tail rolling and flipper-slapping, when performed in the non-breeding season, represent forms of play. During the breeding season, the functional significance of these two behaviours may change. Although this idea is highly speculative, a seasonal distinction regarding the function of nose-to-tail rolling and flipper-slapping may help explain why so many conflicting hypotheses exist regarding the role played by these two behaviours.

In conclusion, this study provides the basis for a new way of thinking about harbour seal social behaviour. Many of the results are consistent with the ideas espoused in the introductory chapter; for example, that the various forms of dyadic social nosing act as affiliative behaviours which promote the maintenance of the group, and that olfactory and tactual senses may help mediate these affiliative behaviours. However, this study has not provided conclusive evidence regarding an affiliative role for harbour seal nosing behaviour or regarding the involvement of chemical and tactual senses in nosing behaviour. The strength of this study rests largely in the generation of many testable hypotheses for future consideration, and of suggestions to improve future investigations.

Future Considerations. Unfortunately researchers often do *not* justify the criteria used to determine the seasonal distinctions upon which they test for differences. For example, Almon (1987) divided her 10-week study period into four seasons, pre-mate, mate-moult, moult and post-moult, while Renouf (1993) divided observations from a four-year period into one of two seasons, breeding-moulting and other; however, neither investigator explained the basis for their seasonal classifications. Unless the basis of the classification is made clear, it is difficult to interpret data across studies in seasons may not be comparable from one study to the next.

In fact, evidence exists that breeding seasons vary in duration and timing between populations, possibly based on ecological constraints (Tempte, 1994; Tempte, Bigg & Wiig, 1991). The duration of male fertility may differ among populations (Boulva & McLaren, 1979), estrus may be prolonged by 3 to 5 weeks in unmated females (Bigg & Fisher, 1974), and lactation may last longer in captivity than in the wild since the mother has no need to forage. In addition, since females may mate with more than one male (Perry & Amos, 1998), observed copulation should not be used to define the close of the breeding season. In this study, flipper-slapping occurred year-round by three males, suggesting that the function of display behaviours may be dependent on context and the individual; thus, display behaviours may not be an accurate indicator of breeding season either. Furthermore, moulting can be defined according to physiological or visually observable changes, and this definition will undoubtedly influence conclusions regarding the behavioural correlates of moulting. Taken together, the above evidence strongly supports the contention that the basis for establishing biologically related seasons should be specified. The present study made use of active and quiescent behaviour patterns over weeks in order to determine the appropriate time limits of a non-breeding and breeding season. Undoubtedly many other behavioural criteria can be utilized; the main point here is that they should be made clear so as to facilitate comparisons between studies and populations.

Another suggestion for future investigations stems from the distinct individual patterns of behaviour found in this study; these individual differences suggest that all interpretations of behaviour patterns should consider the individual or dyad involved. Although many investigators (e.g., Almon, 1987; Renouf, 1993; Rosen, 1995; Wilson, 1974a) have, in fact, analyzed behaviour by individual, often these analyses aim only to determine whether a group pattern exists; that is, no effort has been made to determine how the various behaviour patterns of *one* individual fit together into a cohesive picture. The results of this study indicate that all aspects of individual behavioural patterns (e.g., active, quiescent, display and nosing behaviours) may reflect some underlying behavioural characteristic such as a preference for spatial isolation, a high degree of sociality, or a particular partner preference. For example, individual differences with respect to a preferred mode of interaction might influence a seal like D to monitor his social environment by engaging in frequent and direct social contacts, while another seal, such as J, who showed a preference for physical isolation, might sample social cues in an indirect manner by smelling the air and objects.

Differences in the behaviour patterns between individuals may ultimately help clarify questions relating to the social structure in a group of animals forced to live together in a captive environment. For instance, if spatial preference within the enclosure, proximity to other individuals, affiliative *and* agonistic behaviours are quantified (e.g., see Van den Bos & de Cock Buning, 1994), it may be possible to objectively address the issue of whether any form of social organization exists in captive harbour seals. Although the distinct individual patterns of the O.S.C. seals were discovered largely because of their captive state, it would also be possible to quantify spatial preference, inter-individual proximity, affiliative acts and agonistic acts in an aggregation of hauled-out wild seals, provided they were identifiable in some manner. Thus, perhaps direct comparisons of wild and captive social behaviour would be made possible; such comparisons could lead to a better understanding of the manner in which captivity shapes behaviour patterns. For example, during the breeding season (i.e., when free-living harbour seals are observable), affiliative behaviours might be found to occur more often than agonistic behaviours in a captive population, while agonistic behaviours might occur more frequently in the wild. Such a hypothetical finding would, therefore, suggest that one response to captivity is a reduction in the agonistic acts which could potentially undermine the tolerance needed for group maintenance.

Technological advances (e.g., the use of 'critter-cams', small camcorders attached to an animal) may eventually enable long-range observations of harbour seal social behaviour while they are at sea, which will hopefully provide answers to specific questions related to social structure, such as: (i) do seals form long-term bonds?, (ii) do they forage in groups?, (iii) do seals interact socially at sea and, if so, how frequently?, (iv) what is the pattern of affiliative and agonistic interactions?, and (v) what are the differences in the behavioural repertoire of wild and captive seals? In light of recent evidence, acquired by means of video recordings, that pups accompany their foraging mothers and engage in nose-to-nose interactions with them ***underwater*** (Bowen & Boness, unpublished data, 1996), it would be interesting to discover what other types of nosing occur at sea, both above and below the water surface. In addition, knowledge regarding the duration that pups accompany their mothers to sea may clarify questions of social structure.

Other questions may be more readily addressed in captive animals by means of experimental manipulations. For instance, whether nosing of the air and objects are ways to sample volatile or non-volatile odours could be tested by introducing specific chemical compounds, either presented on objects or directed through a controllable air current, to a captive group and monitoring the behavioural responses of individuals. Video analyses of these responses may help clarify the specific nature of nares and vibrissae involvement in nosing, and may also define the role played by the olfactory and tactual senses. Video analyses of *all forms* of nosing may clarify the distinction between nosing 'with intent' (i.e., for chemical or tactual stimulation) and incidental nosing which may not involve the nares or vibrissae. Furthermore, video analyses of intentional nosing may enable the investigation of the potential role played by the other chemical sensory systems, gustation and the vomeronasal system, during contact nosing. If these other systems are found to function in harbour seals, then ultimately investigators may find that harbour seals use their chemical senses while underwater; such a finding would undoubtedly radically change our view of the world in which harbour seals live.

Summary. This study has suggested that nosing behaviour may be an important component of harbour seal social behaviour, and that some forms of nosing may be indicative of affiliative interaction. Measures of affiliation may ultimately serve as behavioural criteria which, along with agonism and spatial measures, may clarify questions related to the social organization of both captive and wild populations. The behavioural patterns found in the O.S.C. harbour seals strongly support the notion that the type of nosing (solo and dyadic), the season (breeding and non-breeding), and the individual seal all interact in a distinctive manner which may reflect some underlying characteristic of the seal, such as a preference for a particular partner or for an area of the enclosure. Some types of nosing [e.g., nose-to-object, -foreflipper(self), -nose, and -body) showed seasonal effects consistent across males; only nose-to-body and nose-to-nose acts were more frequent in the breeding season for all males. Of the types of nosing performed by the sole female, five of six types were more frequent in the breeding season, including nose-to-nose acts. Nose-to-nose acts and nuzzling may be especially important in the regulation of social behaviour among the O.S.C. seals. The involvement of the nares and vibrissae in the various types of nosing, indicate that the olfactory and tactual senses may mediate some behaviours; this finding highlights the need for further investigation into the sensitivity of these sensory modalities. Without a comprehensive knowledge of the sensory world in which seals exist, our understanding of their behaviour will remain incomplete.

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Appendix A: Coding scheme.

The following scheme contains the codes used to record general behaviour, nosing acts, location, weather and other contextual information. The category titles are not intended to imply a functional classification.

Behaviour	**Code**	**Description of seal's behaviour**
Pops/Vigilance		
head pop-out	po1	head is popped out of water so that 'chin' is resting on edge of tank wall
half pop-out	po2	as above but foreflippers are resting on the edge of tank wall
full pop-out	po3	torso resting on edge so that only ¼ seal (hind region) remains in tank
extended pop-out I	po4	head pop-out moves into half pop-out
extended pop-out II	po5	half pop-out moves into full pop-out
head pop-up	pu1	head is popped up fully above water surface (no break in swimming required)
half pop-up	pu2	extended pop-up in which the foreflippers are at/above/near water surface (break in swimming motion necessary)
full pop-up	pu3	full torso is almost completely out of water (break in swimming necessary)
head pop-in	pi1	on deck with 'chin' resting on edge of tank wall, looking into tank
half pop-in	pi2	on deck with foreflippers resting on tank edge
full pop-in	pi3	on deck with torso resting on edge (tail and hindflippers may be on/off deck)
extended pop-in I	pi4	head pop-in moves into half pop-in
extended pop-in II	pi5	half pop-in moves into full pop-in
Bobbing/Floating		
alert bobbing	bax	bobbing at water surface with eyes open (possibly attending to something/one)
quiescent bobbing	bqx	bobbing at surface with eyes usually closed (appears to be resting)
surface float-up	sfu	floating at water surface, ventral side up
surface float-down	sfd	floating at water surface, dorsal side up
suspension-up	ufu	suspended in water below surface but not touching tank floor, ventral side up
suspension-down	ufd	suspended in water below surface but not touching tank floor, dorsal side up

Behaviour	Code	Description of seal's behaviour
Resting/Lounging		
lying on deck/step/path	lod/s/g	lying on any deck area in enclosure, steps to MT/ST, or gravel pathway
lying on ramp	lor	lying on ramp adjoining MT and ST
lying on tank floor	lof	lying on the floor of either MT or ST
drape	drp	in water but partially draped on edge of ST wall, usually with foreflipper on edge (not seen in MT)
'headstand'	hst	head is resting on tank floor or against lower tank wall and tail and hind-flippers are at or above the water surface (no apparent motion)
Movement		
movement on deck/step/path	mod/s/g	movement on deck(d) in any area of enclosure, on steps(s) of ST or MT, or on gravel pathway(g)
porpoising	por	leaps out of water one or more times while swimming
pirouette	pir	makes 360° spin one or more times in either vertical or horizontal plane
departure from tank	dst/dmt	leaves ST or MT
entrance into tank	est/emt	enters ST or MT
swimming	smx	swimming (only recorded if this is the behaviour during which a nosing act occurs)
Interact/Display/Other		
foreflipper push	ffp	a light push, tap or scratch with the foreflipper towards another seal
head-thrust	hdt	head is thrust rapidly forward in direction off another seal
head-thrust and snort	hdtst	snort-like sound emitted concurrent with head-thrust
ambiguous	ain	ambiguous interaction between two seals (not fully visible or too rapid)
chase	chs	pursuit of another seal in the water
'piggyback'	obk obk*	one seal's ventral surface pressed up against another seal's dorsal surface (*seal on back has erection)
'drown' another seal	das	one seal appears to use foreflipper(s) to push another seal's head underwater
nip at another seal	nip	nip or bite motion at another seal
foreflipper slap,water	ffs	slaps foreflipper against the water surface and produces a loud 'smacking' noise
foreflipper slap,body	fsb	slaps foreflipper against own body and produces a loud noise (can occur while seal is in water or on deck)
foreflipper slap, dual	ffd	slaps fore- and hindflipper simultaneously against the water surface

Behaviour	Code	Description of seal's behaviour
Other (cont.)		
bubble-blowing	bbx	head is partially or fully submerged under water and a stream of air is expelled from seal's mouth
mouth object	mox	manipulates an object in mouth
spit water	swx	water is taken in mouth and then spit out
Nosing Acts - Solo		
nose-to-air	nta	neck is extended so that nose is directed upwards
nose-to-object	nto	nose is directed at some object within enclosure, contact may or may not occur
nose-to foreflipper (self)	nfs	nose is directed at seal's own foreflipper
nose-to-body (self)	ntb-self	nose is directed at seal's own body
Nosing Acts - Dyadic		
nose-to- nose or nuzzling	ntn	nose is directed at another seal's nose or muzzle region either for a brief moment or for an extended period
nose-to-head	nth	nose is directed at another seal's head or neck region
nose-to-body (dorsal/ventral)	ntb (d/v)	nose is directed at another seal's body (x=unspecified region, d=dorsal, v=ventral, m=mid-torso, h=hind)
nose-to-foreflipper	nfd	nose is directed at another seal's foreflipper
nose-to-tail (or hind-flippers)	ntt	nose is directed at another seal's tail or hindflippers
nose-to-tail rolling	ntr	two seals perform fluid somersaulting rolls near the water surface, usually oriented either nose-to-tail or head-to-head
Nares action	o/c/z	nares is open, closed or not visible during the nosing action
Vibrissae position	p/r/z	vibrisssae are extended forward (protracted), are retracted, or are not visible
Attention	yes/no	seal appears to be attending to (i) person(s) or (ii) seal(s)

Contextual Information	Code	Description
Weather		
temperature	#	air temperature recorded prior to observation session
wind speed	l/m/s	light(l) = 0 - 19 km/hr, medium(m) = 20 -34 km/hr, strong(s) = 35+ km/hr

Contextual Information (cont.)	**Code**	**Description**
wind direction	n/s/e/w ne/nw/ se/sw	wind direction during observation session was estimated
cloud cover	f/m/p/n	full, most, partial, or no cloud cover
precipitation	h/m/l/n	heavy, moderate, light or no precipitation
Audience Presence	yes/no	if an audience was present on the viewing platform, the number of persons was recorded
Fed/Not Fed	yes/no	if feeding has occurred, amount eaten was recorded

Appendix B: Total frequency and mean duration for each behavioural category. The total frequency over all observation sessions of each behavioural act for which duration was and was not recorded; when duration was available, the mean duration (in seconds) for that behaviour is shown. For explanation of codes see Appendix A.

Behaviour	No duration recorded	Duration Recorded	
	Total Frequency	Total Frequency	Mean duration (sec.)
Pops			
po1	17656	704	19.45
po2	387	713	33.99
po3	38	94	30.22
po4	47	149	30.49
po5	14	63	29.35
pu1	2898	3	82.33
pu2	458	1	71.00
pu3	2	0	--
pi1	6	15	77.87
pi2	9	22	105.50
pi3	0	6	101.50
pi4	0	3	117.67
pi5	0	2	38.50
Bobbing			
bax	1016	993	26.44
bqx	1194	2030	50.49
sfu	264	78	58.42
sfd	48	733	43.29
ufu	30	101	56.70
ufd	2	17	79.53
Resting			
lod	15	643	514.03
lor	21	253	64.73
los	6	37	323.59
log	0	4	150.25
lof	300	1196	92.00
drp	12	41	123.41
hst	23	29	37.03
Movement			
mod	59	272	32.2
mos	0	9	15.33

Behaviour	No duration recorded	Duration Recorded	
	Total Frequency	Total Frequency	Mean duration (sec.)
Movement			
mog	0	2	87.00
dst	349	1	14.00
dlt	379	1	19.00
est	380	2	5.00
elt	328	3	12.33
por	73	75	59.78
pir	2	0	--
Interact			
ffp	13	2	6
chs	37	58	15.9
nip	4	0	--
hdt	40	2	25
hdtst	93	0	--
agg	26	1	8
ain	23	10	10.30
das	2	1	20.00
obk	15	4	54.00
obk*	0	2	25.50
swx	35	0	--
mox	59	35	75.00
bbx	435	171	13.53
ffs	683	1862	41.83
fsb	10	11	48.50
ffd	4	0	--
Nosing-solo			
nta	1725	69	13.07
nto	960	55	12.10
nfs	103	45	6.67
ntb-self	1	0	--
Nosing-dyad			
ntn	275	32	7.39
ntr	32	206	146.00
nth	126	1	10.00
ntb	84	0	--
nttt	59	1	2.00
nfd	7	1	15.00

Appendix C: **Total frequency of nosing acts between seasons for each seal.**

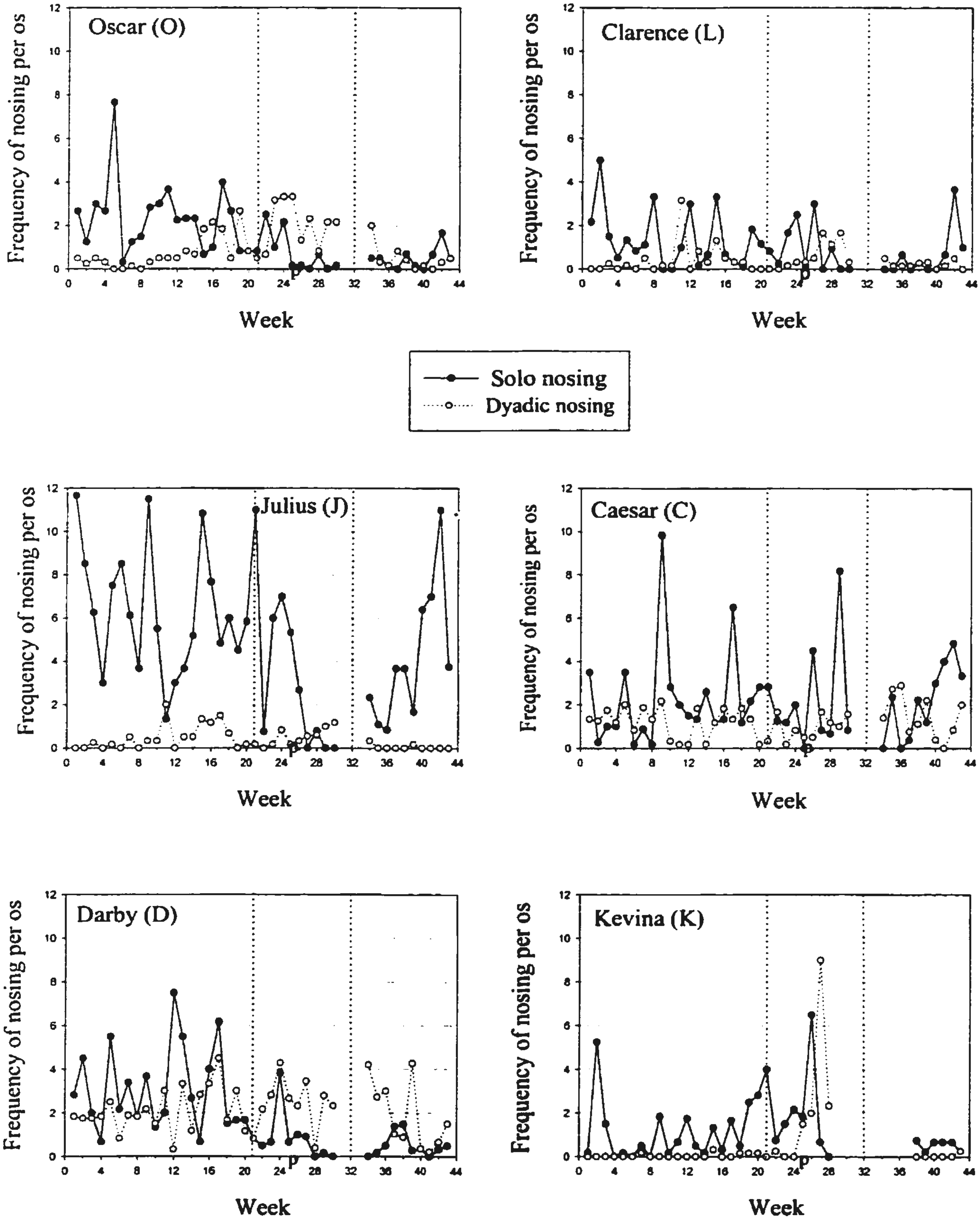
The total number of nosing behaviours in the non-breeding (NB) and breeding (**B**) seasons over all observation sessions (see Appendix A for explanation of nosing codes). Nosing rates were calculated according to the number of observation sessions for which nosing was recorded for each seal (see Table 1). For dyadic nosing types, the large number represents the total number of acts in which the seal was an initiator or a mutual participant; the smaller italicized number represents how many of the total acts were mutual. Overall totals, in which mutual nosing acts were *not* counted twice, for each nosing type are presented in Table 5.

Seal	Oscar		Clarence		Julius		Caesar		Darby		Kevina		Eddy	
Season	NB	B	NB	B	NB	B	NB	B	NB	B	NB	B	NB	B
Type **Solo**														
nta	118	**20**	95	**53**	639	**187**	238	**79**	169	**28**	95	**60**	13	**0**
nto	165	**16**	62	**6**	299	**58**	128	**3**	173	**21**	35	**31**	16	**12**
nfs	15	**5**	31	**0**	23	**3**	7	**0**	37	**0**	9	**10**	4	**4**
ntb-self	0	**0**	0	**0**	0	**0**	0	**0**	1	**0**	0	**0**	0	**0**
Dyadic														
ntn	61 *50*	**76** ***67***	28 *25*	**29** ***26***	39 *20*	**26** ***25***	44 *39*	**40** ***38***	89 *79*	**70** ***67***	5 *5*	**31** ***26***	4 *4*	**21** ***21***
ntr	*30*	***33***	*20*	***0***	*21*	***0***	*148*	***8***	*175*	***41***	*0*	***0***	*0*	***0***
nth	10 *2*	**4**	9 *3*	**5**	7 *1*	**1**	14 *2*	**3** ***1***	37 *2*	**14** ***1***	1	**18**	5	**5**
ntb	6	**7**	4	**3**	2	**0**	8	**5**	23	**10**	1	**10**	2	**3**
ntt	8	**4**	4	**0**	1	**2**	4	**0**	21	**3**	0	**5**	5	**3**
nfd	1	**0**	0	**0**	0	**0**	1	**0**	7 *1*	**0**	0	**0**	0	**0**

Appendix D: Total frequency of nosing acts between season for all adult seals. The total number of nosing behaviours in the non-breeding and breeding seasons over all observation sessions. The numbers in parentheses are the totals for Eddy. For dyadic nosing types, the number in normal font represents the total number of acts while the italicized number in bold represents how many of the total acts were mutual. Overall totals, in which mutual nosing acts were *not* counted twice, for each nosing type are presented in Table 5.

Nosing Behaviour	Non-breeding Season	Breeding Season
Solo Nosing (SN)		
Nose-to-air (NTA)	1354 (13)	427 (0)
Nose-to-object (NTO)	862 (16)	135 (12)
Nose-to-foreflipper(self) (NFS)	122 (4)	18 (4)
Nose-to-body(self) (NTB-self)	1 (0)	0 (0)
SN Sub-total	2339 (33)	580 (16)
Dyadic Nosing (DN)		
Nose-to-nose (NTN)	266 (4) ***218 (4)***	272 (21) ***249(21)***
Nose-to-tail Rolling (NTR)	394 (0)	82 (0)
Nose-to-head (NTH)	78 (5) ***10***	45 (5) ***2***
Nose-to-body (NTB)	44 (2)	35 (3)
Nose-to-tail (NTT)	38 (5)	14 (3)
Nose-to-foreflipper(dyadic) (NFD)	9 (0) ***1***	0 (0)
DN Sub-total	829 (16) ***229(4)***	448 (32) ***251(21)***

Appendix E: Figure showing frequency per observation session (os) of solo and dyadic nosing across weeks for all adult seals. Dyadic nosing rates include interactions with Kevina and Eddy. Dotted lines indicate the breeding season and 'p' indicates parturition.


Oscar (O)
Clarence (L)
Julius (J)
Caesar (C)
Darby (D)
Kevina (K)
Frequency of nosing per os
Week
0
2
4
6
8
10
12
0
4
8
12
16
20
24
28
32
36
40
44
P
Solo nosing
Dyadic nosing

Appendix F: **Analysis of Variance (ANOVA) Summary Tables.**

(Source=source of variance, df=degrees of freedom, SS=sum of squares, MS=mean squares, F=F ratio, p=significance level)

Table I: ANOVA of **type** of nosing behaviour (solo and dyadic) by **season** (breeding and non-breeding) by **male seal** (O, L, J, C and D)). Dyadic nosing rates do not include interactions involving Kevina and Eddy. Three estimates of rate per type per season per seal were included in the analysis (see Methods).

Source	df	SS	MS	F	p
type	1	17.4609	17.4609	112.29	0.000
season	1	0.4665	0.4665	3.00	0.091
seal	4	29.3048	7.3262	47.12	0.000
type*season	1	5.2335	5.2335	33.66	0.000
type*seal	4	57.8339	14.4585	92.98	0.000
season*seal	4	1.3323	0.3331	2.14	0.093
type*season*seal	4	2.5369	0.6342	4.08	0.007
error	40	6.2198	0.1555		
total	59	120.3885			

Table II: ANOVA of **type** of nosing behaviour (solo and dyadic) by **season** (breeding and non-breeding) by **seal** (all adults included). Dyadic nosing rates include interaction involving Kevina and Eddy. Three estimates of rate per type per season per seal were included in the analysis (see Methods).

Source	df	SS	MS	F	p
type	1	20.0156	20.0156	138.19	0.000
season	1	0.5292	0.5292	3.65	0.062
seal	5	29.9628	5.9926	41.37	0.000
type*season	1	3.6920	3.6920	25.49	0.000
type*seal	5	59.2869	11.8574	81.86	0.000
season*seal	5	11.9780	2.3956	16.54	0.000
type*season*seal	5	4.5998	0.9200	6.35	0.000
error	48	6.9524	0.1448		
total	71	137.0167			