MATERNAL INVESTMENT AND THE ONTOGENY OF BEHAVIOUR IN THE ATLANTIC HARBOUR SEAL

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DAVID ALLEN SCOTT ROSEN, B.Sc. (Honours)

MATERNAL INVESTMENT AND THE ONTOGENY OF BEHAVIOUR IN THE ATLANTIC HARBOUR SEAL.

BY

© David Allen Scott Rosen, B.Sc. (Honours)

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partial fulfilment of the requirements for the
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Biopsychology Programme
Department of Psychology
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Abstract

The applicability of differential maternal investment and divergent behavioural ontogeny theories to a marginally dimorphic species, was investigated in the harbour seal. Weight changes of unweaned pups on Miquelon were used to test whether mothers invested more in male than female offspring. Males were found to be heavier at birth than females, but grew at a slower rate prior to weaning. Behavioural observations of mother/pup pairs were used to derive indicators of maternal investment. Nosing behaviour and two indices of nursing and proximity governance appeared to be reasonable predictors of relative investment. In contrast, nursing rejection rates and pup checks were not reasonable measures of investment while the validity of nursing times was inconclusive. The results suggested that, over the course of the nursing period, the pup was increasingly responsible for the level of investment obtained and the maintenance of the pair bond. Unweaned male pups were found to spend less time idle than females during haul outs, and all pups became increasingly more active over the nursing period. Sex difference in behaviour are discussed as an indicator of divergent socio-bioenergetic demands.

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Chapter 1 - Introduction

1.1 Preamble

Pinnipeds (Phocidae - true seals; Otariidae - fur seals and sea lions; Odobenidae - the walrus) display some of the most extreme sexual size dimorphism among mammals. Bartholomew (1970) proposed that these sex differences and concurrent differential investment in offspring were important in the evolution of polygyny in pinnipeds. This sexual dimorphism is often manifested by the time of birth or weaning (see Kovacs & Lavigne, 1986b for review) which, in combination with high prevalence of polygyny, make pinnipeds ideal subjects for the study of parental investment.

Phocids are particularly well suited for the investigation of the energetic aspects of maternal investment (see Appendix A for list) because females fast, or eat relatively little during the brief nursing period, creating a closed energy link between mother and pup in which nutrient flow from the former to the latter can be readily measured (although see Bonner, 1984; Testa, Hill, & Siniff, 1989). The general phocid nursing strategy is to transfer as much energy as possible to the pup over the shortest possible time to limit the overhead costs of the females' own metabolism (Anderson & Fedak, 1987a). An extreme example of this is exhibited by the hooded seal (*Cystophora cristata*) which weans its young after only 4 days of growth, with average weight gains of 7 kg/day (Bowen, Boness, & Oftedal 1985; Bowen, Oftedal, & Boness, 1987). This thesis examines sex differences in pup birth weights and growth rates and associated behavioural indices of differential maternal investment in the western Atlantic harbour seal, *Phoca vitulina concolor.*

The theories of differential parental investment described in the next section have been most strongly supported by studies of species which show substantial adult sexual dimorphism. However, the principles of these theories should apply to any polygynous species with minimal dimorphism. Preferential investment by large females in large male offspring has been suggested for a number of otariids, as well as the northern elephant (*Mirounga angustirostris* ; LeBoeuf & Briggs, 1977; Reiter, Panken, & LeBoeuf, 1978; Reiter, Stinson, & LeBoeuf, 1981) and grey seals (*Halichoerus grypus* ; Anderson & Fedak, 1987a; Kovacs & Lavigne, 1986a), which show the most pronounced dimorphism and polygyny of all phocids. The females of these species also stay ashore during the entire nursing period, living entirely off fat stores.

Though it is agreed that harbour seals are polygynous (a male mates with several females), or at least promiscuous (Boulva & McLaren, 1979), the status of harbour seals as a dimorphic species is unclear. Mature males have almost universally been acknowledged to be larger than females, but whether this difference is significant enough to be the result of intrasexual selection has not yet been determined.

Although male harbour seals in the north Pacific can reach over 140 kg and females 125 kg (Burns & Gol'tsev, 1984), harbour seals in the Atlantic are considerably smaller. King (1983) states that western Atlantic seals are similar to those in the eastern Atlantic (*Phoca vitulina vitulina*) with mature males reaching 1.5-1.8 m while females only 1.2-1.5 m. Boulva and McLaren (1979) noted that harbour seals in the western Atlantic (Sable Island) were smaller than the eastern populations, with males reaching 1.54 m and females 1.43 m. They also stated that the "divergence of weights of the sexes is quite well described by Bertalanffy growth functions", with mature males averaging 90 kg and females 70 kg (Boulva & McLaren, 1979; Mansfield, 1967a). The question, therefore is whether the theories pertaining to differential parental investment are applicable to a species with reduced sexual dimorphism.

The period of maternal investment in harbour seals is relatively well defined since females often pup on sand flats to which they are relatively site tenacious. It is believed that these seals do not nurse their young while the pair is at sea (Peterson, 1968), so that all nursing bouts can be documented while the animals are hauled out on the beach. The female harbour seal's external feeding during lactation (Bowen, Oftedal, & Boness, 1989) resembles that of otariids (Gentry & Kooyman, 1986), and may be an indication that her investment strategy is more strictly regulated than in those phocids which stay ashore fasting during the entire nursing period.

On Miquelon (45'45"N, 59'14"W) there is a breeding population of approximately 700 harbour seals which has been studied for 10 years, and which has become quite tolerant of being observed at close range. These seals haul out on sand bars exposed only during low tide, so that pups must accompany their mothers into the water almost immediately after birth (Klinkhart, 1967; Knudtson, 1974; Lawson & Renouf, 1985; Newby, 1973). This increases energetic costs via thermoregulation and locomotion (Hill, 1987; Miller, Rosenmann, & Morrison, 1976), which tax maternal resources, and creates the need for strong mother-pup ties to ensure the pair are not separated at sea. The structure of this relationship changes over the course of nursing, and its dynamics should reflect differences in maternal investment in male and female offspring. The logistics of studying animals which are absent periodically from the study site place limitations upon the methods available to measure maternal investment (see Appendix B) and stresses the necessity of developing alternate measures, such as behavioural indices of mutual dependency during lactation.

1.2 Parental Investment Theory

Many mammals exhibit distinct sexual dimorphism, with the male member of the species typically being larger than the female by the time of sexual maturity. Only a single pinniped species, the Weddell seal, exhibits female-dominated dimorphism. According to classical Darwinian theory (Darwin, 1871), this size difference is the result of sexual selection.

> There are ... sexual differences quite unconnected with the primary reproductive organs, ... such as the greater size, strength, and pugnacity of the male... Since the males have acquired their present structure not from being better fitted to survive in the struggle for existence, but from having gained an advantage over other males, and from having transmitted this advantage to their male offspring alone, sexual selection must here have come into action ... the advantage which certain individuals have over others of the same sex and species solely in respect to reproduction (p. 275-278).

Darwin recognized that the reproductive success of males was more variable than for females and that intense male intrasexual competition resulted in secondary sexual characteristics (e.g. tail feathers, antlers).

Bateman (1948) also recognized that not all members of the breeding population achieved equal matings, and demonstrated the capacity for natural variation in reproductive success using *Drysophila melanogaster*. In an experiment allowing free mating amongst equal numbers of males and females, he found that only 4 percent of the females failed to mate while 21 percent of males failed to produce offspring. In addition, the most successful males produced three times as many offspring as the most successful females.

Since male reproductive success is directly related to the number of matings he achieves (not so for females as long as a single successful fertilization occurs) this would lead to both intrasexual competition among males, and female mate choice. The end result is that a portion of the males competing in mating systems with little or no paternal investment will be more successful at finding mates than others, even in a population with a 50:50 sex ratio.

Fisher (1930) suggested that natural selection should serve to maintain a 50:50 primary sex ratio at the level of the population. If the birth rate for one sex of offspring in a population ('A') is greater than that for the other ('B') there will be a shift in the population ratio towards the former. This would lead to the development of differential reproductive success, since the 'A' sex will have to compete for available mates; only a portion of those members will successfully mate, while most of the 'B' sex will reproduce. Since the reproductive success of those individuals who are predisposed to produce 'B' offspring is greater than others (since most of their offspring successfully mate), there will be an increase in the representation of those genes in the population, thereby producing more 'B' offspring. And since not all of the "A" offspring will mate, their genetic representation decreases in the population, so that their genetic representation is decreased and, consequently, the sex ratio surpasses unity on the other side ('B'). With this new imbalance the reproductive success of the 'A' offspring is now greater, and the process repeats itself in reverse until, eventually, it results in an equal primary sex ratio converging upon 50:50 at the population level. Fisher also suggested that, over the course of evolution, natural selection would favour the stabilizing effect of those individuals who produced equal numbers of male and female offspring, the end result being a sex ratio fixed at unity at both the population and individual levels. This theory assumes that male and female offspring cost the parents an equal investment (with differences not greater than those resulting from anisogamy), usually most applicable to species where no parental investment occurs past fertilization.

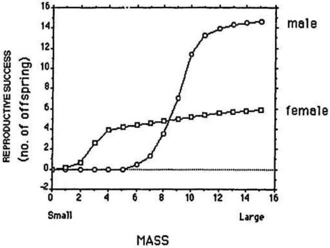
In species with extended parental investment (both pre- and postpartum) male and female offspring do not always obtain equal investment. The circumstances leading to such an inequality arise from sex-associated differences in the variance of reproductive success (as measured by the number of surviving offspring) experienced by members of the same population (Figure 1). In other words, offspring of one sex may be more or less valuable to a parent based upon their offspring's chance of successfully reproducing.

Trivers (1972, 1985) and Trivers and Willard (1973) suggested that individual females do not always produce broods with a 50:50 sex ratio, and that physical condition is a prime determiner of optimal sex ratios for an individual female. One of the pivotal parameters of their theory is the necessity of variance in female condition, most often measured indirectly as gross body weight. As the female's condition deviates from the population mean, the sex ratio of her offspring at conception should concurrently alter from a 50:50 ratio, so that a female in poorer condition would produce more offspring of the sex which is less expensive energetically. In this way, individual deviations will tend to cancel out on a population level, as opposed to Fisher's suggestion that optimal strategies would select for a 50:50 ratio on an individual brood basis.

According to Trivers, large sons have disproportionately greater reproductive success than equally sized daughters, so females who have the resources to pass on above-average condition to their offspring should invest in sons. Otherwise, females should invest in daughters (for details see Section 4.4.1).

The direction of the sex ratio shift is a product of the differences in variance of relative reproductive success demonstrated by the two sexes. In the majority of mating systems with such differences, the male exhibits the greater variance. The

Figure 1: Theoretical reproductive success for male and female members of a population where body size is selected for. Note that, similar to Bateman's (1948) results, males have considerably larger 'variance' (i.e. scope) in reproductive success than females, and the largest males can obtain up to 3 times the reproductive potential of similarly sized females.


16
14
12
10
8
6
4
2
0
-2
0
2
4
6
8
10
12
14
16
REPRODUCTIVE SUCCESS
(no. of offspring)
male
female
Small
Large
MASS

larger the differences in variance of reproductive success the greater the variance in the resulting sex ratios.

There are three postulates upon which the Trivers-Willard theory rests.

1) The condition of the young at the end of the period of parental investment is attributable to the condition of the mother during this phase. Larger females invest proportionately equal resources in offspring as smaller females.

2) Early differences in the size or condition of offspring at the end of parental care endure into adulthood and can not be significantly compensated for by later growth (see Section 4.4.2).

3) Differences in adult size or condition influence the reproductive success of males to a greater degree than females. This assumes that male size and/or condition is the object of sexual selection.

Maynard Smith (1980) expanded and attempted to model certain aspects of this relationship. His premise incorporated not only the differing reproductive success of offspring of a particular sex, but also sex-linked survivorship. From these basics he derived three predictive models.

1) If, for a given parental investment, the probability of survival is greater for one sex of offspring than another, the parent should invest more heavily in the sex with the lesser probability of survival.

2) If survivorship is equal, and one sex has an additional frequency-dependent component of fitness (e.g. offspring of one sex which receive a greater investment have a disproportionately greater resulting fitness) then investment in that sex will be greater.

3) If the sex of an offspring can be recognized after some initial investment (called 'd') then it may be preferable for the parent to invest only in a proportion of the more expensive sex. This will usually only occur if 'd' is relatively very small

and, should it occur prenatally, will conform to Trivers' predictions of unequal sex ratios at birth.

Clutton-Brock, Albon, and Guinness (1985) proposed an alternate explanation for differential growth. In a study of red deer (*Cervus elaphus*) they found that juvenile males had a higher mortality rate than females, and that dominant females produced significantly more male than female offspring (Clutton-Brock, Albon, & Guinness, 1984). In addition, as predicted by Trivers and Willard, male offspring of subordinate (therefore smaller) females suffered higher mortality than female offspring, while there was no sex-linked differences in the mortality of offspring of dominant females. However, mortality among juvenile males increased as resource availability declined. Clutton-Brock *et al.* rejected Trivers' explanation that differential mortality was a result of the postnatal manipulation of the sex ratio by females (i.e. females in inferior physical condition prematurely terminating investment in their male offspring). Instead, they proposed that the pressure of natural selection for greater body size in males has resulted in increased male growth rates with corresponding increases in metabolic rate. In this way, the decreased survival of juvenile males during times of resource restrictions balance the benefits of large adult body size.

1.3 Measurement of Energetic Aspects of Parental Investment

A complete model of parental investment would include costs imposed by changes in metabolism and activity patterns, production of additional primary cells, and numerous external energetic requirements, such as nursing in female mammals (Ralls, 1976). On a long-term scale, parental investment can be viewed as "any behaviour toward offspring that increases the probability of survival of the offspring to the detriment of possible investnent in other offspring" (Lincoln, Boxshall, & Clark, 1982). In mammals, the costs of lactation are the most commonly measured aspect of parental investment. Four general methods have been commonly employed to investigate maternal investment in pinnipeds: behavioural indicators, weight changes, isotope studies of metabolism, and milk transfer quantification. The first two were used in this study, with the development of a set of behavioural indices being of prime concern (descriptions and criticisms of the latter three techniques can be found in Appendix B).

Behavioural indicators can be used as indirect, nonintrusive, versatile, and relatively inexpensive measures of maternal investment. In species, such as the harbour seal, which are skittish by temperament and are therefore difficult to capture more than once, behavioural indices of investment are particularly useful. Because the population at Miquelon has been studied unobtrusively since 1981 it is possible to make close-range behavioural observations during the haul out without causing serious disruptions.

The following behavioural indices of maternal investment were employed in this thesis: suckling time, nursing rejection rates, nosing and checking rates, Hinde coefficient of pair maintenance, and a modified Hinde coefficient for nursing.

If postnatal maternal investment is the primary parameter considered (since it forms the major component of both total and postnatal energetic effort; Fedak & Anderson, 1982; Lavigne, Barchard, Innes, & Øritsland, 1982), then milk input would be a good indicator of energetic flow. One method of estimating the quantity of milk absorbed by the pup may be suckling time. Trillmich (1986), using weight changes over single nursing periods as a comparison, found that suckling time was a good indicator of milk transfer rates in Galapagos fur seals (*Arctocephalus galapagoensis*).

Another aspect of nursing behaviour, rejection rate, may also provide an indication of maternal investment. If an adult is more willing to invest in a particular offspring then its attempts to suckle should be rejected less often. This behaviour could also provide indications of a proximate mechanism of differential investment. If differential investment occurs because of limitations on a pup's ability to process milk, then the pup of the sex into which the adult is investing less should reject more nursing solicitations from its mother. Conversely, if the female actively controls the energy resources available to the pup, then there should be differential rejection rates of the pups' suckling attempts.

It has also been recognized that, if a parent invests differentially in one sex of offspring, its behaviour towards that offspring may vary accordingly (Trivers & Willard, 1973). It may be possible, therefore, to define a set of behaviour patterns which are indicative of the relative reproductive effort invested in that offspring (e.g. Kovacs, 1987; Stewart, 1983). One aspect of behaviour which might reflect these differences are social interactions. Nosing behaviour, which is thought to help establish and maintain the parent/offspring bond, might be more commonly exhibited between mother/son pairs than mother/daughter pairs if male pups receive greater maternal investment. Similarly, a mother may 'check' an offspring into which it has invested more.

The Hinde Coefficient (H_d; Hinde,1969; Hinde & Atkinson, 1970; Hinde & Spencer-Booth, 1971) measures the relative responsibility of the mother and pup in maintaining the pair bond and should provide some indication of the extent of parental investment. Hinde, in a series of primate studies, formulated an equation based on spatial proximity as a reflection of the changing relationship between mother and offspring. This equation utilizes the frequency of distance changes initiated by each member of the pair, and whether those changes increase or decrease intrapair distance (for its calculation see Section 2.4.2.3), suggesting that members which decrease intrapair distances are more responsible for maintaining the pair bond. This index has the advantage over other previous measures (e.g. Hinde, Rowell, & Spencer-Booth, 1964; Jensen, Bobbit, & Gordon, 1968; Kaufman & Rosenblum, 1969) in that it represents the behaviour of both partners so that a change in either partner's behaviour affects the final calculation. It is also independent of changes in the relative or absolute activity levels of the pair (Hinde & Atkinson, 1970).

Lawson (1983; Lawson & Renouf, 1987) utilized a modification of the Hinde coefficient to apply to nursing behaviour (H_n). By recording the relative frequency with which each partner initiated or terminated a nursing bout, he suggested that it was possible to determine which member of the pair was responsible for maintaining a nursing session.

Both the Hinde coefficient and its modification by Lawson may be effective in determining sex-related differences in the weaning process. Lawson and Renouf (1987) reported that harbour seal pups were weaned gradually, with the pup responsible for attempting to maintain the pair bond (although see Finch, 1966; Wilson, 1974), a pattern typical of most mammals. However, these patterns may not be uniform if differential investment in a pup leads to disparate weaning patterns.

1.4 Behavioural Ontogeny

Not only may behavioural differences between offspring be the result of sex-related maternal investment strategies, but they may also be the result of fundamental differences in the course of ontogeny and the development of social and sexual behaviour. Although a growing number of studies have examined reproductive investment in pinnipeds (Appendix A), few have investigated sex differences in behavioural development (e.g. Arnold & Trillmich, 1985; Kovacs, 1986, 1987), and none have examined it in one of the most common phocid species, the harbour seal. The most complete work in these type of early behavioural differences has been on humans (see Maccoby & Jacklin,1974 for review, and Section 4.27).

These early sex differences are thought to have a proximate basis in hormonal makeup (Levine, 1966). This can manifest itself as early as the time of sexual differentiation when testosterone in the bloodstream is thought to cue distinctive episodes of chemical activity within the immature brain (McEwen, 1981). Although many biologists tend to simplify ontogeny so that sexual differences are not addressed until the onset of sexual maturity, it is clear that the early presence or absence of hormones can have a profound effect on early behaviour.

The ultimate basis for such differential behaviour is also sexual. Members of each sex have different roles to fulfill within the established social system and, therefore, their behavioural ontogeny must facilitate their development for these roles. For example, Fagen's (1981) prediction that male offspring will engage in more play episodes than females rests on the assumption that male young, particularly in a sexually dimorphic species, need to hone their competitive abilities more than females for intrasexual mate competitions as adults.

The degree to which differences in early ontogeny develop may be associated with the same selective pressures which determine the extent of sexual dimorphism. This study endeavors to determine the degree to which such behavioural differences manifest themselves in harbour seal pups, particularly in light of their relatively limited dimorphism and undefined breeding system.

Chapter 2 - Methods

2.1 Field Site

The study was undertaken in the summers of 1988 (pilot study) and 1989 on the island of Miquelon. The island lies in the Gulf of St. Lawrence, approximately 19 km off the south coast of Newfoundland. It is one of seven islands comprising the French Territories in the vicinity (Figure 2).

The island is 40.5 km long and 13 km at its widest (total area 215 km^2), and is nearly transected by an inlet at the midway point. This bay, known as the Grand Barachois, covers an area of nearly 9 km^2, and empties into the Gulf through a narrow opening (the Goulet) approximately 150 m wide (Figure 3). Tidal effects within the Barachois are substantial and, for several hours encompassing ebb tide, extensive arrays of sand flats (about 3 km^2) are exposed. It is upon these sand flats that the seals haul out during the breeding season.

Approximately 600 harbour seals and 60 gray seals haul out at the site during the summer months (Davis & Renouf, 1987). The grey seals are entirely non-breeding, and mostly juveniles (Lawson, 1983).

The harbour seal population is composed of a cross section of ages. Approximately 100-150 pups are born every year within the breeding area. Pregnant females do not arrive until just prior to parturition, which in 1989 commenced on May 20, with the last birth observed on June 5.

The seals do not haul out in a single group, but aggregate to some extent according to species, breeding status, and age class (Davis & Renouf, 1987). One group ('the nursery'; Figure 3), which was made up predominantly of females and their pups, was concentrated on the southeastern edge of the the main sand flat, and extended northwards as the size of the herd increased during haul out.

Figure 2: Location of the islands of the French Territories in relation to Newfoundland, and enlargement of the island of Miquelon. The study took place within the Grand Barachois, located at the southern end of Grande Miquelon.

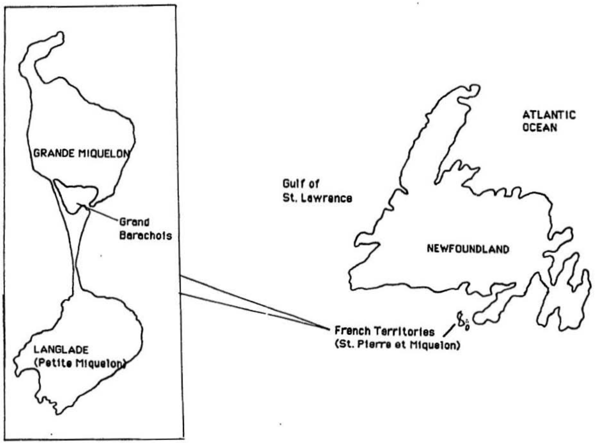
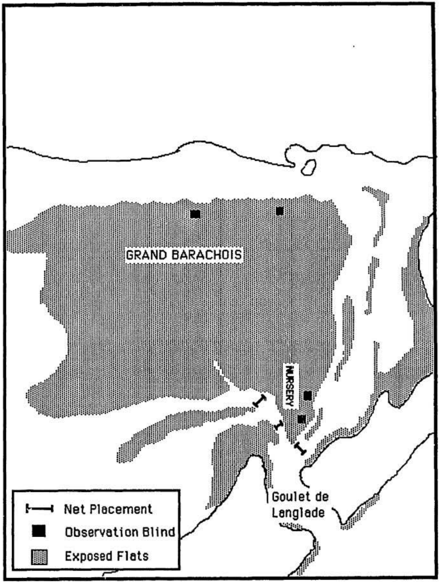

GRANDE MIQUELON
Grand
Barachois
LANGLADE
(Petite Miquelon)
Gulf of
St. Lawrence
ATLANTIC
OCEAN
NEWFOUNDLAND
French Territories
(St. Pierre et Miquelon)

Figure 3: Details of the study site within the Grand Barachois. Shaded areas represent approximate configuration of the sand flats at low tide during the 1989 season. The Barachois connects to the Gulf of St. Lawrence via the Goulet de Langlade. The positions of the observation blinds and capture nets are also indicated.


GRAND BARACHOIS
NURSERY
Goulet de Langlade
Net Placement
Observation Blind
Exposed Flats

The majority of the grey seals present were concentrated at the northeast point of the flat, although as many as 12 would also emerge around the Goulet.

The majority of the non-nursing harbour seals congregated at the north end of the primary sand flat. Approximately 30 mother/pup pairs also occupied this site, and additional mother/pup dyads were sometimes spotted in solitary formations across the whole of the western section of the flat. Several harbour seals occupied some of the smaller sand flats to the north and east of the main flat. Their numbers increased with higher levels of disturbance (e.g. boat, tourists, noise), and their age composition was highly variable, although largely made up of juveniles.

2.2 Data Collection

Two main types of data collection were employed: physical capture and behavioural observation. On most days either observations or animal captures took place, but rarely both. Occasionally the daily tidal cycle facilitated two daylight haul outs, allowing two collection periods, often split between the two methods.

Early in the season emphasis was placed upon capturing animals, pups in particular, both to facilitate identification for subsequent observations and for early pup weights. Capture efforts were intensified again towards the end of the season to obtain data on mother/pup pairs just prior to weaning.

2.3 Physical data

2.3.1 Measurements

Animals were captured on and around the main sand flat using two general methods (see Appendix C for details). One of these relied on ensnaring the animals on the sand flats ('terrestrial capture'), while the other netted them in the water ('aquatic capture').

Pups were weighed while still in small capture nets, using a 220 lb. x 1 lb. Salter spring scale (calibrated for metric conversion; Model #235). The scale was recalibrated for the net after every weighing. On all animals, several other basic morphometric measurements were taken. Axillary girth (measured immediately posterior to the pectoral flippers) and dorsal curvilinear length (nose to tail measurement along the dorsal side) were recorded (American Society of Mammalogists, 1967).

The sex of each animal was determined by both feeling for a penal opening two-thirds down on the ventral surface and by a visual check for the presence of a vaginal opening at the cloaca. While either method is reliable, both were employed for accuracy.

Age was determined in young pups by either the presence of or condition of the umbilicus. This method has been used in studies with a number of other pinniped species, including the Weddell seal (Lindsey, 1937; Thomas & Demaster, 1978), the southern elephant seal (Laws, 1953; Gibney, 1957) and grey seals (Hewer, 1974; Anderson & Fedak, 1987a). Previous studies on harbour seals (Boulva, 1971, 1975; Boulva & McLaren, 1979) provided basic descriptive details of umbilical and lanugo persistance, and checks against known-age pups proved it to be an accurate estimate for harbour seal pups less than 8 days old.

For identification, large cattle roto-tags were attached through the webbing of a pelvic flipper (left for males, right for females). Each tag was emblazoned with a unique identification number and the alternating flipper placement aided in sex determination even when the number itself could not be read. Each year a different tag colour was used.

On subsequent captures of animals, weight and sex was recorded, and tag security rechecked.

2.3.2 Catch Statistics

In 1989, 69 animals were captured and tagged (Appendix D). Of these, 57 were unweaned pups, 33 of a determinable age. Of the remainder, 4 were mothers of identified (tagged) pups, 3 were juveniles, 2 were adult males, 2 were weaned pups, and 1 lone adult female without a pup. Fourteen pups were recaptured at least once prior to weaning, 8 male and 6 female.

2.4 Behavioural data

2.4.1 Observation methods

Although the formation of the sand flats changed to some extent between pupping seasons, the seals proved to be quite site-tenacious, hauling out in formations similar to past years. This greatly facilitated the initial positioning of observation blinds on the sand flats. By further careful adjustment at high tide, the blinds could be placed as close to the seals as necessary to provide optimal visibility.

In 1989 three blinds were rotated among three sites within the Barachois (Figure 3). The blinds were mounted on 1.7 m supports, and were composed of a 1.5 m high rectangular canvas tent (equipped with three observation windows) secured to a 1 m^2 wooden base.

As far as could be determined, the seals were not affected by the sudden appearance or disappearance of the blinds, nor did they seem to be adversely affected by the presence of the observer. As long as the observer did not make undue noise or break the profile of the observation blind (e.g., extend a lens through a window) the animals seemed undisturbed. Also, because of the tidal haul out pattern, observers were able to enter the blind and make any positional readjustments just after high tide, before the seals hauled out.

Behaviour was recorded using a JVC VHS video camera and recorder. Mother/pup pairs were selected for observation in a left to right sweep, and were filmed as close up as possible with the aid of a Pentax 70-210mm telephoto lens adapted for video use. Pretagged individuals were chosen preferentially, and then untagged pairs. A focal pair observation pattern was employed, using observation sessions of 20 min each (Altmann, 1974) which was judged to be sufficiently long to capture any behaviour including entire nursing bouts. To get an unbiased indication of nursing duration, an observation session on a pair already nursing did not commence until that suckling bout had terminated. Likewise, if a focal pair were still nursing after 20 min the observations continued until the termination of that suckling bout (see Section 2.4.3.2 for appropriate definitions). Also, if either member of the nursing pair left the field of view, the observations were either temporarily suspended or terminated.

At the start of each observation session the sex and tag number (if present) of the pup was recorded. Pups were sexed either by tags (flipper placement or number) or individually by sight. The latter was possible at these short working distances with the aid of a spotting scope (Bushnell, 5-30x power), by noting the presence or absence of a penal opening on the ventrum. Often, the validity of this method could be confirmed through subsequent catches of easily recognized individuals and checking against past records. The tag number (if present) and any distinguishing physical characteristics which could aid in subsequent identification were also noted.

2.4.2 Event frequency

2.4.2.1 Analysis of video

Videotapes were viewed by randomly selecting a prenumbered tape (using a random number generator) and then analyzing the next unviewed segment on that tape.

2.4.2.2 Definitions of behaviour

The rate of the following intrapair behaviour (number of actions observed divided by length of observation period) were extracted from the tapes. Except where noted, the initiating and receiving partner was identified.

Check Pup. Visual examination of the pup by the female. While this behaviour could take place during a scan of the general area, the action must have been a distinct focus upon the pup. This behaviour was usually marked by an obvious turning of the female's head to make visual contact with the pup.

Distance Changes. Any change in body position that was not classified as comfort movements. A minimum distance change of half a body length was required to qualify. Both the initiator (female or pup) and the direction of the action (increase or decrease intrapair distance) was noted. These figures were later used in determining Hinde coefficients (see Section 2.4.2.3).

Nosing .

i] Nose to Nose. Each mutual touching of the initiator's nuzzle to the receiver's. Because the action was almost simultaneous the initiator was sometimes difficult to identify even after repeated viewings. Instances (n=3) where the initiator was unclear were deleted from the analysis.

ii] Nose to Body. Each touching of the initiator's nuzzle to any other part of the receiver's torso except the nasal area, included nursing solicitations by the pup onto the female's ventral region.

Nursing.

i] Initiation and termination. Whenever a nursing event occurred the identity of the initiator and the terminator was recorded if such could be clearly determined.

ii] Rejection. Whenever one partner solicited a nursing episode from the other yet no nursing took place the identity of the rejecting partner was recorded.

2.4.2.3 Hinde Conversions

Distance data were analyzed as Hinde coefficients (Hinde, 1969; Hinde & Atkinson, 1970). This transformation reveals which partner of the mother/pup pair was responsible for maintaining contiguity. An individual coefficient was calculated for each mother/pup pair observed each day. This allowed analysis not only of changes over the course of the season, but also on the basis of pup sex.

The formula which was used for the Hinde coefficient was:

$$H_d = \%MD - \%MI,$$

where '%MD' is calculated as the percent of total intrapair distance decreases which were initiated by the mother, and '%MI' are the percent of total intrapair distance increases initiated by the mother.

This formula yields results from +1.0 to -1.0, where a negative number indicates that the pup is the member actively attempting to maintain the pair, while a positive result indicates that the mother is following the movements of her pup. The magnitude of the coefficient is indicative of the difference in effort of either partner in pair maintenance. This is the converse (in sign) to the calculations originally prescribed by Hinde and Atkinson (1970), but are used to facilitate comparisons to Lawson (1983).

Lawson also used a similar calculation to determine which member of the pair was acting to prolong suckling bouts during the nursing period. It was calculated in a similar fashion to the Hinde coefficient:

$$H_n = \%MI - \%MT,$$

where %MI is the percent of total nursing initiations demonstrated by the mother and %MT are the percent of the total terminations of a nursing episode that the mother is responsible for. In a relationship where both members of the mother/pup pair are equally responsible for maintaining the nursing regime, the resulting coefficient (H_n) will equal zero. If the mother is more responsible for maintaining nursing than the pup, the index will range to +1.0, and will decrease to -1.0 as the pup assumes greater responsibility.

2.4.3 Event duration

2.4.3.1 Video analysis

Videotapes were reviewed following the same randomization process for analysis of behaviour durations as determined by the following definitions. A simultaneous keyboard entry computer programme recorded individual behaviour durations, total behaviour durations per observation period, and total observation time to 0.1 sec. Data entry and summarization was performed on an IBM PC.

2.4.3.2 Definitions of behaviour

Pup behaviour was designated as either 'active' or 'idle', according to the following criteria:

Active: exhibiting any movement, either while stationary or ambulatory.

Idle: reflected by an almost complete lack of movement on the part of the pup, while either awake or asleep.

'Active' behaviour could be further broken down into the following behavioural categories:

Alert: animal is scanning a group or is visually fixed upon a single point; usually characterized by an upwardly extended neck.

Comfort: characterized by readjustments of body positioning, scratching, biting of flippers, rolling, or similar activities involving low levels of exertion.

Locomotion: movement across the sand flat or in adjacent shallow waters; did not include deep water swimming.

Nursing: suckling as determined by on-teat time (i.e. not including intranursing intervals- see Section 4.2.2.2.)

Play: including both social and solitary play. The latter was commonly exhibited as strenuous twisting of the body or rolling (differentiated from comfort movements by the perceived degree of exertion), and exploratory behaviour such as nosing the ground or digging in the sand. Social play was rarely exhibited, and was completely restricted to mother/pup interactions prior to weaning.

Social: interactions between mother and pup which did not classify as either nursing or play.

Chapter 3 - Results

3.1 Birth Weights and Growth Rates

For pups that were caught only twice prior to weaning (n=10), growth rates were calculated by dividing the difference in weight between these two captures by the number of days between measurements. For those pups (n=4) where more than two preweaning weights were available, a linear regression was used to estimate growth rates. Birth weights were then extrapolated from the age of first weighing using the calculated growth rates.

The average growth rate for males (mean=0.47 kg/day, SD=0.11) was significantly lower than that for females (mean=0.74 kg/day, SD=0.08) (Student's t-test; t=5.09, df=12, $p<.01$). The average birth weight of males (mean=10.80 kg, SD=1.37) was significantly greater than that of females (mean=9.70 kg, SD=1.71) (t=2.43, df=12, p=.03) (Figure 4). The growth equations for the 4 pups with more than 2 captures were all significantly linear (r^2; Table I).

3.2 Behaviour durations

3.21 General behaviour

A total of 70 observation sessions were analyzed from the video tapes. The overall mean proportion of time spent in a behaviour for male or female pups was calculated as the total amount of time observed in each behaviour summed for all pups of that sex, divided by the total observation time. The percent of total observation time that each seal spent in 'active' or 'idle' behaviour was determined. Female pups spent a greater portion of their haul out time 'idle' (60.42%) than males (44.33%) (t=2.65, df=68, p=.01). Conversely, male pups spent a significantly greater amount of their haul out time 'active' (55.67%) than female pups (39.58%).

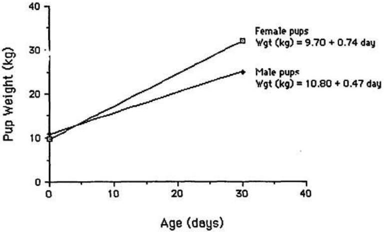
'Active' behaviour was broken down into 6 further categories: alert, comfort, locomotion, nursing, play, and social.

Table I:

Birth weights (kg) and growth rates (kg/d) of harbour seal pups, listing the number of samples (points) used to calculate the growth lines, and the linear component (R-sq) of the regression line for those animals with more than two sample points. See text for details.

Animal #	Sex	Growth (kg/d)	Birth Weight (kg)	Points	R-sq
206	F	0.722	9.82	2	-
207	M	0.267	11.02	3	.89
209	F	0.735	8.80	4	.93
212	F	0.680	10.74	2	-
213	F	0.644	7.76	3	.72
214	M	0.510	10.32	2	-
216	M	0.454	12.25	2	-
220	M	0.624	10.91	2	-
225	F	0.835	8.39	3	.84
230	M	0.499	8.32	2	-
231	M	0.363	12.07	2	-
234	F	0.825	9.82	2	-
238	M	0.544	9.89	2	-
241	M	0.507	11.88	2	-

Figure 4: Birth weights (kg) and growth rates (kg/d) of harbour seal pups. The lines for male and female pups are representative of the calculated average birth weights (y-intercept) and growth rates (slope) for the 14 samples across estimated age in days.


40
30
20
10
0
Pup Weight (kg)
0
10
20
30
40
Age (days)
Female pups
Wgt (kg) = 9.70 + 0.74 day
Male pups
Wgt (kg) = 10.80 + 0.47 day

Male pups spent a significantly greater proportion of haul out time nursing (26.55% vs. 14.55%; t=2.37, df=68, p=.02) and also in social activities (3.08% vs. 1.96%; t=2.66, df=68, p=.01) than female pups. The mean amount of time that male pups spent engaged in alert, comfort, locomotion, and play behaviour was not significantly greater than for females (Table II).

Because the observations were biased towards filming nursing behaviours, it was felt that the removal of this category from the analysis might reveal differences which were previously obscured. Similar to the analysis which included nursing, females spent a greater amount of their haul out time 'idle' than males (70.71% vs. 60.43%; t=2.65, df=68, p=.01). Conversely, male pups spent a significantly greater portion of their haul out time 'active' than females (39.57% vs. 29.29%) (Table III).

When active behaviours were broken down into alert, comfort, locomotion, play, and social behaviour, male pups were found to spend a significantly greater proportion of their haul out in comfort movements than female pups (20.73% vs. 15.89%; t=2.33, df=68, p=.04), as well as social activities (4.20% vs. 2.29%; t=2.14, df=68, p=.05). The differences between the percent of time male and female pups spent in alert, locomotion, and play behaviour all remained statistically insignificant .

Regression analysis on the original data (including nursing time) indicated that, overall, pups showed a significant decrease (negative slope) in the amount of time spent in comfort movements ($F_{[1,69]}$=4.44, p=.04) (Figure 5) and idle ($F_{[1,69]}$=9.77, p=.00) (Figure 6), and a significant increase (positive slope) in the amount of time spent nursing ($F_{[1,69]}$=5.99, p=.02) (Figure 7) across observation days. Alert, locomotion, play, and social behaviour showed no such relationship. A further analysis of the interaction indicated that the slope of the regression lines

Table II.

Results of T-tests on Percent of Time spent in a haul out Behaviour based on sex of the harbour seal pup. Regression analysis of change in Percent of Time across observation day, and a test of the (Day x Sex) Interaction for slope differences. See text for details.

	Percent of Time		t-test (sex)[1]	
Behaviour	Male	Female	t value	Signif
Active[2]	55.67	39.58	2.65	**p=.01**
Idle	44.33	60.42		

	Percent of Time		t-test (sex)[1]		Regression (day)[2]			Interaction	
Behaviour	Male	Female	t-value	Signif	F-test	Signif	R-sq	t-test	Signif
Alert	5.42	4.78	1.07	p=.66	2.01	p=.161	.029	0.22	p=.828
Comfort	15.23	13.48	1.45	p=.15	4.44	p=**.038**	.061	1.08	p=.286
Locomotion	1.79	1.56	1.42	p=.16	2.68	p=.106	.038	0.03	p=.974
Nursing	26.55	14.55	2.37	p=**.02**	5.99	p=**.017**	.081	0.11	p=.912
Play	3.61	3.25	0.03	p=.98	1.81	p=.182	.026	0.19	p=.849
Social	3.08	1.96	2.66	p=**.01**	2.33	p=.131	.033	2.56	p=**.013**
Idle	44.33	60.42	2.65	p=**.01**	9.773	p=**.003**	.126	0.14	p=.891

[1] df=68
[2] df=1,69

Table III.

Results of T-tests on in Percent of Time spent in non-nursing haul out Behaviour based on sex of the harbour seal pup (calculations are similar to Table II. except that all Nursing time has been omitted from total haul out time). See text for details.

	Percent of Time		t-test (sex)[1]	
Behaviour	Male	Female	t value	Signif
Active	39.57	29.29	2.65	**p=.01**
Idle	60.43	70.71		

	Percent of Time		t-test (sex)[1]	
Behaviour	Male	Female	t value	Signif
Alert	7.38	5.60	1.11	p=.27
Comfort	20.73	15.89	2.33	**p=.04**
Locomotion	2.43	1.71	1.52	p=.13
Play	4.80	3.80	0.13	p=.89
Social	4.20	2.29	2.14	**p=.05**
Idle	60.43	70.71	2.65	**p=.01**

[1] df=68

Figure 5: Percent of haul out time spent in Comfort behaviour across day of observation. Mean times for male and female pups are significantly different, but regression slopes are not.

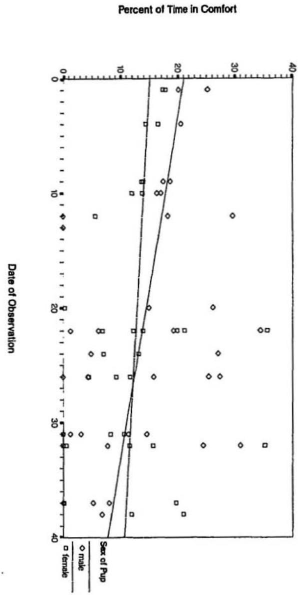

Percent of Time in Comfort
0
10
20
30
40
Date of Observation
0
10
20
30
40
Sex of Pup
◇ male
□ female

Figure 6: Percent of haul out time spent in Idle behaviour across day of observation. Mean times for male and female pups are significantly different, but slopes for regression lines are not.

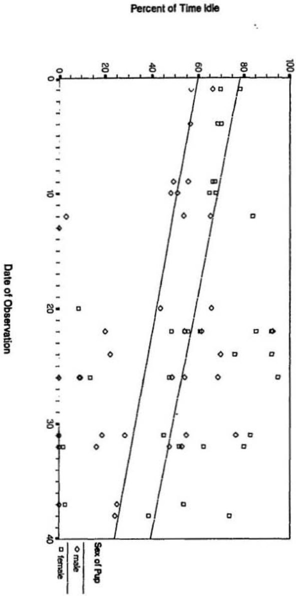

Percent of Time Idle
0
20
40
60
80
100
Date of Observation
0
10
20
30
40
Sex of Pup
◇ male
□ female

Figure 7: Percent of haul out time spent in Nursing behaviour across day of observation. Mean times for male and female pups are significantly different, but slopes of regression lines are not.

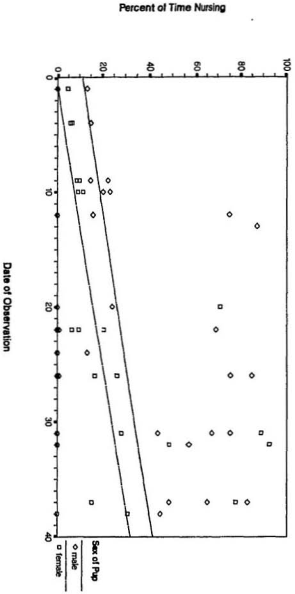

Percent of Time Nursing
0
20
40
60
80
100
Date of Observation
0
10
20
30
40
Sex of Pup
◇ male
□ female

Figure 8: Percent of haul out time spent in Social behaviour across day of observation. Mean times for male and female pups are not significantly different, but slopes of regression lines are.

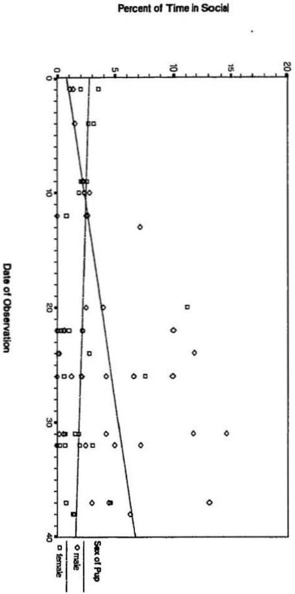

Percent of Time in Social
0
5
10
15
20
Date of Observation
0
10
20
30
40
Sex of Pup
◇ male
□ female

Table IV.

Results of multiple regression of behavioural catagories to predict sex of harbour seal pup, and stepwise regression with forced variables.

Source	DF	F-value	Probabilty
Regression	7	2.57	0.022
Residual	62		
Total	69		

Behaviour	F to enter
Social	2.22
Comfort	1.48
Idle	1.00
Locomotion	0.79
Nursing	0.68
Play	0.47
Alert	0.37

for male and female pups were different only for social behaviour ($t=2.56$, $p=.01$; Figure 8).

A multiple regression was used to approximate a discriminant analysis with two elements (male and female), using the behavioural categories as predictors. However, because the percent of time in all behaviour for each observation equalled 100, the time spent Alert (because it was the least significant) was removed from the total observation percentage to eliminate any pre-imposed mathematical relationships within the data. In the analysis, the remaining six behaviour categories served to predict the sex of the pup ($F_{[7,62]}=2.57$, $p=.02$) (Table IV).

3.2.2 Nursing

Each nursing episode could be composed of a number of suckling segments interspersed by off-teat sequences. These gaps in the suckling bouts could range from several seconds to several minutes in length. For male and female pups combined, the mean length of the on-teat segments was 4.08 minutes, with no statistical difference exhibited between male (mean=3.89 min) and female (mean=4.50 min) pups.

3.3 Behaviour Frequency

3.3.1 Nursing

3.3.1.1 Nursing coefficient

Two modified Hinde coefficients for nursing were calculated for each observation day, one for male pups and one for female, by combining the observed nursing bout initiations and terminations (Table V).

The overall modified nursing coefficient (H_n) for the pups decreased significantly over the observation period (Multiple regression; $t_B=3.56$, $p=<.01$) (Table VI and Figure 9). This reflected a significant decrease in the percent of nursing episodes which the mother initiated ($t_B=3.86$, $p<.01$) (Figure 10), coupled with an increase

Table V.

Percent of nursing bouts terminated (%MT) and initiated (%MI) by harbour seal mothers over the observation period (Day), and their calculated Modified Hinde coefficients (Hn), for male and female seal pups. See text for details.

Male Pups				Female Pups		
%MI	%MT	Hn	Day	Hn	%MT	%MI
1.000	.500	.500	1	.333	.333	.666
.500	.750	-.250	4	-.250	.750	.500
.500	.250	.250	9	.000	.500	.500
1.000	.500	-.500	10	.000	.500	.500
.000	.000	.000	12	.166	.500	.666
.333	1.000	-.666	13	-.250	.500	.250
.600	.750	-.150	20	.000	.333	.333
.333	.666	-.333	22	-.500	.750	.250
.500	.750	-.250	24	.200	.400	.600
.500	.250	.250	26	-.333	.666	.333
.400	1.000	-.600	31	-.250	.750	.500
.000	1.000	-1.000	32	-.400	.800	.400
.000	.500	-.500	37	-.250	.500	.250
.000	1.000	-1.000	38	-.333	.666	.333

Table VI.

Results of multiple regression analysis on the Modified Hinde coefficient and the Percent of nursing bouts Initiated and Terminated by the mother, across observation period (Day) and sex of pup (Sex), including a test of the (Day x Sex) interaction (slope differences by sex). See text for details.

Modified Hinde coefficient (Hn)

Source	DF	F-test	P	R-sq
Regression	2	7.43	.003	.37
Residual	25			
Total	27			

Variable	ß-Coefficient	t-value	Prob.
Day	-.018	3.56	**.002**
Sex	-.17	2.21	**.043**
Day x Sex	-.006	1.20	.242

Percent Mother Initiate (%MI)

Source	DF	F-test	P	R-sq
Regression	2	7.62	.003	.38
Residual	25			
Total	27			

Variable	ß-Coefficient	t-value	Prob.
Day	-.013	3.86	**.001**
Sex	-.047	2.10	**.048**
Day x Sex	-.005	1.40	.175

Percent Mother Terminate (%MT)

Source	DF	F-test	P	R-sq
Regression	2	2.99	.045	.43
Residual	25			
Total	27			

Variable	ß-Coefficient	t-value	Prob.
Day	.008	2.22	**.036**
Sex	.08	0.91	.374
Day x Sex	.002	0.53	.603

Figure 9: Change in the modified Hinde coefficient (Hn) for male and female pups over observation day. The mean value for male and female pups is siginificantly different, but the slopes of the regression lines are not.

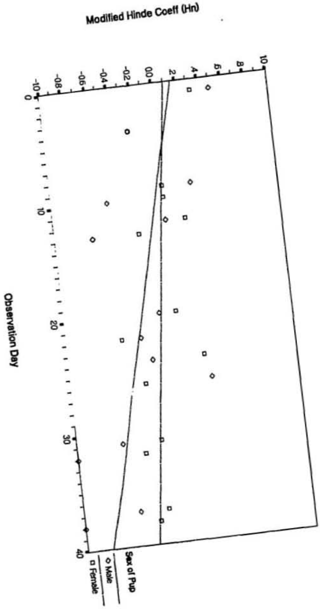

Modified Hinde Coeff (Hn)
-10
-08
-06
-04
-02
00
2
4
6
8
10
Observation Day
0
10
20
30
40
Sex of Pup
◇ Male
□ Female

Figure 10: Change in the percent of nursing bouts initiated by the mother for male and female pups over observation day. The mean value for male and female pups is siginificantly different, but the slopes of the regression lines are not.

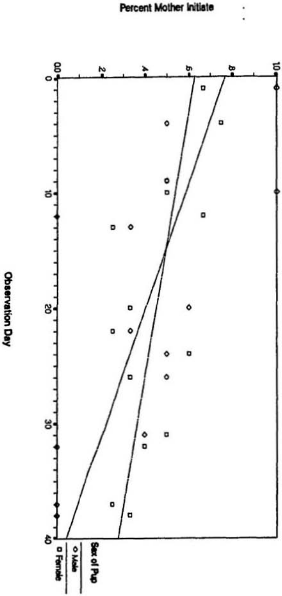
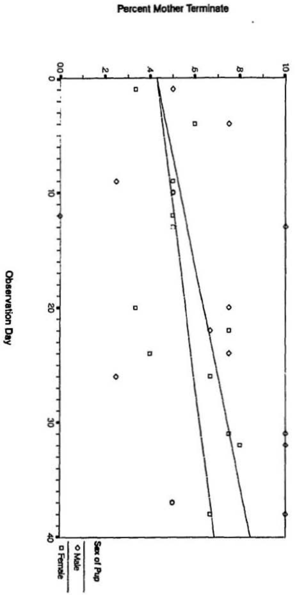

Percent Mother Initiate
1.0
.8
.6
.4
.2
0.0
0
10
20
30
40
Observation Day
Sex of Pup
◇ Male
□ Female

Figure 11: Changes in the percent of nursing bouts terminated by the mother for male and female pups over observation day. The mean value for male and female pups is siginificantly different, but the slopes of the regression lines are not.


Percent Mother Terminate
0.0
.2
.4
.6
.8
1.0
0
10
20
30
40
Observation Day
Sex of Pup
◇ Male
□ Female

in the percent of nursing bouts terminated by the mother (t_{β}=2.22, p=.04) (Figure 11). Pup gender formed a significant component in the regression of H_n and the percent of bouts initiated by the mother, but not in the percent of bouts terminated by the mother. Male pups exhibited a significantly lower overall H_n than female pups (t_{β}=2.21, p=.04), and initiated more nursing bouts throughout the study period (t_{β}=2.10, p=.05).

A test of the interactions indicated that none of the slopes of the regression lines for male and female pups were significantly different.

3.3.1.2 Rejections

A total of 89 nursing supplications were observed, 19 (21%) of which did not lead to nursing episodes. Eight of those rejections were closely followed by similar solicitations that eventually did lead to a nursing bout.

Of the observed 19 rejections, 8 (42%) were the result of unsuccessful presentations by the female. Seven of these occurred prior to observation day 22 (Table VII). The remaining 11 rejections (58%) were unsuccessful attempts by the pup to solicit suckling. All but one of these occurred after observation day 24.

3.3.2 Hinde Coefficients

A Hinde coefficient was calculated for a single pair over each observation period (n=51), discarding those observations where neither the mother nor pup decreased or increased intrapair distance (since the denominator would equal 0). Multiple regressions were used to test the Hinde coefficients on the independent variables of sex of pup and day of observation.

Both the Hinde coefficient (t_{β}=3.45, p=.00) and the two variables, the percent of distance increases (t_{β}=2.77, p=.01) and decreases (t_{β}=2.84, p=.01) initiated by the mother showed significant differences by pup sex. None of these measures exhibited a relationship to date of observation (Table VIII), nor were any

Table VII.

Number of observed rejections of nursing solicitations by harbour seal mothers and pups across observation days, indicating the partner responsible for the rejection and the sex of the pup involved.

		Rejecting Partner	
Day	Sex of Pup	Female	Pup
1	M		2
4	M		1
9	F		1
13	M		1
22	F		2
22	F	1	
26	F		1
26	F	3	
26	M	1	
31	M	1	
32	F	1	
36	M	2	
37	F	2	

Table VIII.

Results of multiple regression on the Hinde coefficient, the Mean Daily Hinge coefficient, and percent of Distance Increases and Decreases by harbour seal mothers, across the observation period (Day) and Sex of the pup, with a test of differences in the regression slopes (Day x Sex).

Hinde coefficient (Hd)

Source	DF	F-test	P	R-sq
Regression	2	6.26	.004	.248
Residual	48			
Total	50			

Variable	ß-Coeff	t-value	Probability
Day	.002	0.32	.754
Sex	-.192	3.45	**.001**
Day x Sex	-.008	1.48	.147

Mean Daily Hinde coeffcient

Source	DF	F-test	P	R-sq
Regression	2	19.15	.0001	.693
Residual	17			
Total	19			

Variable	ß-Coeff	t-value	Probability
Day	-.01	2.78	**.013**
Sex	-.192	5.63	**.0001**
Day x Sex	-.003	0.72	.484

Percent Mother Decreases Distance

Source	DF	F-test	P	R-sq
Regression	2	4.05	.025	.176
Residual	48			
Total	50			

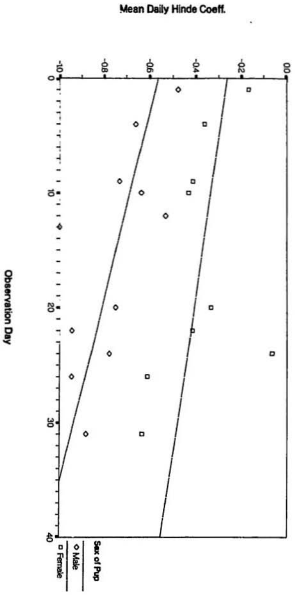
Variable	ß-Coeff	t-value	Probability
Day	-.002	0.49	.630
Sex	-.104	2.84	**.007**
Day x Sex	-.005	1.46	.153

Percent Mother Increases Distance

Source	DF	F-test	P	R-sq
Regression	2	4.95	.012	.207
Residual	48			
Total	50			

Variable	ß-Coeff	t-value	Probability
Day	-.003	1.12	.272
Sex	.088	2.77	**.009**
Day x Sex	.003	0.89	.377

Figure 12: Change in the Mean Daily Hinde coefficient for male and female pups over observation day. The mean value for male and female pups is siginificantly different, but the slopes of the regression lines are not.


Mean Daily Hinde Coeff.
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
Observation Day
0
10
20
30
40
Sex of Pup
◇ Male
□ Female

differences in the slope of the regression lines for male and female pups detected.

When two means (according to the gender of the pup) were calculated for each observation day, a significant relationship was found between the mean daily Hinde coefficient and date of observation, as the Hinde coefficients became increasingly more negative over time ($t_\beta=2.78$, $p=.01$; Figure 12). The mean coefficient for male pups was significantly lower than that of females ($t=5.629$, $p<.01$), but there was no difference in slope of the two regression lines.

3.3.3 Nosing Behaviour

Rate of nosing behaviour was calculated by dividing the number of occurrences by the observation time.

There was no relationship between the frequency of all nosing actions (nasal- and torso-directed combined) initiated by the mother and observation day. Similarly, the day of observation did not show a significant relationship to the rate of total nose to nose behaviour (mother and pup scores combined), the rate of each partner's nose-to-nose behaviour, nor the percentage of nose-to-nose behaviour initiated by either partner (Table IX). Also, the frequency of total nose to body behaviour (mother and pup scores combined) did not significantly relate to observation day.

There was a significant change over time with the percentage of this behaviour that each partner was responsible for (Multiple regression; $t_\beta=2.75$, $p=.01$), though neither the mean score nor line slopes for male and female pups were significantly different. This variable was calculated as the rate of nose-to-body behaviour exhibited by one partner divided by their total rate of display (both partners combined); therefore, one partner's score was inversely related to the other's. The percent of nose to body behaviour exhibited by the pup increased with observation day, while those by the mother decreased.

Table IX.

Results of multiple regression analysis on nosing behaviour between mother and pup harbour seals, across the observation period (Day), between male and female pups (Sex), and examinig the interaction (Day x Sex). Behaviour is classsified by the initiator of the action: the Mother, Pup, either mother or pup (Combined), or as a frequency of the behaviour exhibited by one partner as a fraction of the total frequency of that behaviour (Percent). See text for details.

Behaviour	Partner	Day	Sex	Day x Sex
Nose to Nose:	Combined:	t=0.55 p=0.59	t=0.75 p=0.46	t=0.18 p=0.86
	Mother:	t=0.68 p=0.50	t=0.58 p=0.56	t=0.10 p=0.92
	Pup:	t=0.18 p=0.86	t=0.74 p=0.46	t=0.23 p=0.82
	Percent:	t=0.22 p=0.83	t=0.24 p=0.81	t=1.68 p=0.10
Nose to Body:	Combined:	t=0.88 p=0.38	t=1.56 p=0.13	t=1.23 p=0.23
	Mother:	t=2.24 **p=0.03**	t=0.59 p=0.56	t=0.75 p=.045
	Pup:	t=2.27 **p=0.03**	t=2.10 **p=0.04**	t=1.16 p=0.25
	Percent:	t=2.75 **p=0.01**	t=0.56 p=0.58	t=0.88 p=0.39
Total Maternal Nosing:		t=1.42 p=0.16	t=0.74 p=0.46	t=0.54 p=0.59

This result corresponded with the finding that the rate of nose to body behaviour initiated by the mother decreased with day of observation ($t_\beta=2.24$, $p=.03$). No sex differences were observed. The rate of nose to body behaviours initiated by the pup increased significantly with time ($t_\beta=2.27$, $p=.03$). The rate at which male pups displayed nose to body behaviors was significantly greater than for female pups ($t_\beta=2.07$, $p=.04$), though the slopes of the regression lines were not significantly different.

3.3.4 Pup checks

A multiple regression analysis revealed that the rate at which mothers checked their pups did not change over the study period ($t_\beta=.23$, $p=.81$), nor was there a difference of the rate of checks based upon the sex of the pup ($t_\beta=.58$, $p=.54$), nor was there a difference in the slope of the regression lines for male and female pups.

Chapter 4 - Discussion

The primary aim of this study was to examine sex differences in physical attributes and behaviour that were indicative of differences in maternal investment and/or behavioural ontogeny, and assimilate them into a broader profile of the development of harbour seal pups. An investigation of gender-linked differences linked to maternal investment may help to clarify the mechanisms by which this occurs (see Section 4.4.3). It may also lend support to and discriminate between competing scientific theories of parental investment (see Section 4.4.4).

4.1 Physical Data

In this study, male pups were found to be heavier than female pups at birth. This corresponds to the general finding for dimorphic species, and fits into Kovacs and Lavigne's (1986b) model for early size differences in pinnipeds. It also corresponds to other studies of harbour seals (Table X), although the sex differences are more extreme than previously reported. The implications of such early size differences are discussed later (Section 4.4.2).

Male pups had lower rates of postnatal growth than did females. This result contrasts sharply with the general pinniped pattern (Kovacs & Lavigne, 1986b), previous studies of harbour seals (Table X) and Trivers' and Maynard Smith's theories of reproductive investment within a sexually dimorphic species (for resolution, see Section 4.3).

4.2 Behavioural data

4.2.1 Hinde coefficients (H_d)

The importance of maintaining a mother/pup bond prior to weaning is critical in a species such as the harbour seal. For the pup, all nutritional requirements come from its mother (females only rarely nurse other young; Lawson, 1983), and the female must ensure the survival of her reproductive effort. The present study

Table X.

Past nursing studies of harbour seals, indicating weight changes and length of lactation period.

	Birth Weight (kg)			Length of	Weaning Wgt		
Region	Combined	Male	Female	Lactation	Male	Female	Source
Vancouver	10.2			5-6 wks			Biggs, 1969
Alaska	11.7	11.77	11.59	3+ wks			Bishop, 1968
U.K.	9-11			4-6 wks			Bonner, 1979
Sable Is.	11				24	19.5	Boulva, 1971
Sable Is.^{1971}		9.35	10.59				
Sable Is.^{1972}		9.49	10.40				Boulva, 1975
Sable Is.	9.5	9.53	9.49	30 days			Boulva & Mclaren, 1979[1]
Baltic Sea	9-15			3-4 wks			Curry-Lindahl, 1975
B.C.		9.8	11.77				Fisher, 1952
Alaska		12.77	13.23				Klinkhart, 1968[2]
E. Canada	9						Mansfield, 1967a
Sable Is.				24 days	24.9[3]		Muelbert & Bowen, 1989
Washington	15.27	10.71					Newby, 1973[4]

[1] Boulva & Mclaren give one of the few pre-weaning growth rates: 0.606 kg/d for male pups and 0.565 kg/d for female pups.

[2] Data is quoted originally in Newby, 1973, but lists only Klinkhart, 1967 as a reference.

[3] Muelbert & Bowen analyzed male and female pups separately, but found no significant difference in weaning weights and report only a single figure. they also report a combined total post-weaning weight loss of 9.2% of their initial weaning weight.

[4] Figures calculated from dead newborn pups, including prenatal deaths.

showed that the degree to which the mother and pup was willing or able to maintain the pair bond changed over time.

In this study, mean daily Hinde coefficients became increasingly more negative during the nursing period, indicating that the pups were responsible for maintaining the pair bond throughout and became increasingly so over time. Further analysis revealed that the change in the Hinde coefficient was mostly a result of an increased tendency for the pup to decrease intrapair distance, rather than a decline in the number of spatial increases by the mother.

Finch (1966), in a study of captive harbour seal mother/pup pairs, suggested that harbour seal mothers were primarily responsible for maintaining the pair, and that pups weaned themselves. Wilson (1974) found, with harbour seals in Scotland, that the female was the partner responsible for maintaining contact, a trend which decreased slightly with pup age. Studies by Renouf and Diemand (1984) and Renouf, Lawson, and Gaborko (1983) found that the pup was the member responsible for maintaining spatial proximity, although they detected no change in the relationship and concluded that weaning must have been abrupt.

The results of this study confirm those by Lawson (1983; Lawson & Renouf, 1987), although there is a tendency for the coefficients in this study to be more negative. They suggest that harbour seals conform to the general mammalian pattern, where the young gradually assumes more responsibility for maintaining the pair bond until weaning occurs.

Hinde coefficients can be explored as a possible indicator of maternal investment by investigating differences based on the sex of the pup. The Hinde coefficients of male and female pups show a comparable decrease from birth to weaning. However, the Hinde coefficients associated with male pups are consistently lower than for female pups. At first, this result might seem counterintuitive. If mothers invest greater in male pups than females, they should be more attentive to safeguarding that reproductive investment. But since it is the pup who exhibits the growing responsibility for maintaining proximity, the role of maternal attentiveness is less important.

These results suggest that it is the male pups who are actively seeking greater maternal resources, so that it is physiologically more important for them to maintain the bond to their energy resource than for female pups. Female pups have higher Hinde coefficients, perhaps because they do not seek the same level of maternal resources as male pups (see Section 4.2.3), either because they do not have the same capacity to utilize this extra energy or they do not have the same level of demands to be met (see Section 4.4.3).

4.2.2 Nursing

4.2.2.1 General Nursing Behaviour

Pups usually initiated nursing bouts by nosing the mother in the ventral region. Younger pups often 'searched' for a teat by continuously nosing and mouthing the mother's ventral area for a substantial length of time. Harbour seals pups, although precocious in relation to many other mammals, still suffer from the decreased coordination and observational abilities documented in other infant phocids, such as northern elephant (LeBoeuf, Whiting, & Gantt, 1972) and grey seals (Davies, 1949; Kovacs, 1987). In an extreme case, Bryden (1968) reported that southern elephant seal pups (*Mirounga leonina*) can search for up to an hour for a nipple.

Pups suckled either teat, often switching during a single nursing episode. They were observed to suckle with their heads submerged in the shallow water covering the sand flats just before full ebb tide. While nursing bouts could be interrupted by numerous, short, off-teat sessions, there was no evidence of the distinct primary and secondary nursing bouts reported by Fogden (1971) for grey seals.

Mothers initiated bouts by presenting their nipples towards the pup, a behaviour seen in many phocids (although curiously not in northern elephant seals; LeBoeuf *et al.*, 1972). Frequently, at the onset of nursing, the mother nosed the pup, probably to confirm its identity. If pups are nonselective as to who they nurse from, the onus is on the female to ensure that her pup receives the benefits of her energy expenditure. Nursing bouts were terminated by one of the partners moving away, the pup discontinuing suckling, or the female rolling to cut off access to her teats.

If male pups receive more milk than female pups, differences in suckling patterns would be expected. In this study, mothers spent a significantly greater amount of time nursing male than female pups. This result has also been reported in dimorphic pinniped species such as the grey seal (Kovacs, 1987) and the Galapagos fur seal (Trillmich, 1986). Differences in suckling rates, however, are not necessarily indicative of similar differences in growth rates. Although larger pups have smaller mass-specific metabolic costs, their total costs are greater than for smaller pups. Therefore, for male pups to maintain their greater size from birth, they must receive greater energetic input to achieve similar growth rates as smaller, female pups (for an example, see Appendix E).

Similarly, as the mass of pups of either sex increases over time, they must increase their energetic input to maintain linear growth. In this study, such increasing demands were met by increased nursing durations, a pattern also demonstrated in southern elephant seals (Bryden, 1968). No such increase was found in grey seals (Kovacs, 1987), harp seals (*Phoca groenlandica* ; Stewart, 1987), or Stellar sea lions (*Eumetopias jubatus* ; Higgins, Costa, LeBoeuf, & Huntley, 1988). Lavigne, Stewart, and Fletcher (1982) suggested that increases in nursing time in harp seals may be moderated by increases in milk fat content, while Higgins *et al.*, (1988) suggested that older, larger pups may have an increased suckling efficiency (see Section 4.3). Harbour seals, which have a more prolonged nursing period than harp seals (30 vs. 14 days), may be able to maintain a more constant milk fat content through external feeding during the nursing period (Bowen *et al.*, 1989), thereby replenishing their water resources.

The timing of nursing bouts was closely tied to the local tidal cycle, similar to the pattern reported by both Gardiner (1989) and Newby (1973). Pups were typically nursed within a few minutes of haul out, and again just before the pair left the sand bar, with sporadic feedings in between. The greater total nursing times for male pups was a result of longer nursing bouts which occurred more often. The average length of a nursing bout (4.08 min) was substantially greater than that reported by Newby (72.5 sec, n=6).

4.2.2.2 Validity of Nursing Measures

Suckling time is one of the most readily observable behavioural estimates of energetic input from nursing. The validity of such a measure is questionable, since on-teat time may not an accurate reflection of milk-flow time. Additionally, other physical factors (e.g. pup size, age, sex) may influence the flow rate (ml/sec) of milk from the nipple. For example, suckling efficiency may improve with pup age, increasing the milk flow to suckling time ratio. Also, a changing milk fat content will decrease the relationship among suckling time and energy input (Lavigne, Stewart, & Fletcher, 1982; also see Oftedal, Boness, & Tedman, 1987 for review). Behavioural indicators have been carefully studied in rats (Hall & Williams, 1983) where definite posture changes mark the actual flow of milk from the nipple, but the lack of such indicators for pinnipeds has raised questions as to what proportion of the pup's on-teat time results in milk flow (e.g. LeBoeuf *et al.*, 1972).

Numerous researchers have claimed that, compared to hydrogen isotope studies, suckling time is not a good indicator of the rate of milk ingestion, a statement supported by Mendl and Paul's (1989) studies on cats and mice. Complicating the situation is the observation that the patterns of changes in suckling behaviour differ between phocid species. Nursing time increases with pup age in grey (Boness, in Oftedal *et al.*, 1987) and elephant seals (Bryden, 1968; LeBoeuf *et al.*, 1972), remains constant in harp seals, and decreases in Weddell seals (Tedman & Bryden, 1979).

Oftedal *et al.* (1987) noted that some of the inconsistencies reported may be the result of errors inherent in the definition of suckling that some studies used. Pinnipeds, unlike most mammals (Drewett, 1983; Hall & Williams, 1983), do not spend the entire nursing session attached to the nipple, but transfer between nipples, interspersed with breaks of various lengths. Therefore, if nursing time is calculated from the start to the end of a nursing session it will incorporate a considerable amount of off-teat time (e.g. Tedman & Bryden, 1979); but if only on-teat time is considered, a more reliable measure may be obtained. For example, Trillmich (1986), using weight changes over single nursing periods as a comparison, found that on-teat suckling time was a good indicator of milk transfer rates in the Galapagos fur seal. Therefore, this study discounted inter-teat intervals to gather a more accurate estimate of milk input.

4.2.2.3 Modified Hinde Coefficient (H_n)

In most mammals it is agreed that weaning is a gradual process (see Section 4.2.2.4). It is characterized by an increase in the number of nursing rejections suffered by the pup, and an increase in the proportion of nursing initiations solicited by the pup. This general pattern also seems to be true of both phocids (Christenson & LeBoeuf, 1978; Fogden, 1971; LeBoeuf & Briggs, 1977; Reiter *et al.*, 1978; Ronald & Dougan, 1982; although see Kovacs, 1987) and otariids (Bartholomew, 1959; Sandegren, 1970). Earlier studies of harbour seals indicated the contrary, suggesting that either weaning was sudden (Renouf &

Diemand, 1984; Renouf *et al.*, 1983) or that the mother was responsible for maintaining nursing and the pup weaned itself (Finch, 1966; Wilson, 1974). The results of this study, however, support Lawson's (1983, Lawson & Renouf, 1987) suggestion that harbour seals follow the same strategy exhibited by phocids and other mammals.

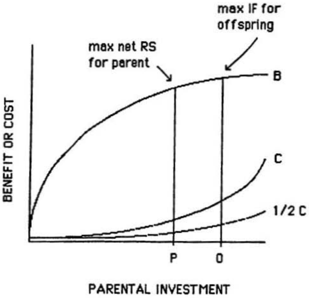
Although more specific in its application, interpretation of the modified Hinde coefficient (H_n) is similar to that for Hinde's original measure (H_d). In the current study, the pups became increasingly more responsible for maintaining nursing, as indicated by a general decline in H_n. These results are supported by the change in the pattern of nursing rejections. Initially, the majority of rejections were by pups failing to act upon nursing solicitations by the mother, while the pattern reversed itself later in the season.

Over the course of the nursing season the pups initiated a greater proportion of the nursing bouts. According to Trivers (1974) the pups' growing demand became greater than the maternal ability (or desire) to produce, resulting in parent-offspring conflict (Figure 13). This is supported by the increase in both the number of nursing sessions terminated by the mother and the number of times she rejected solicitations by her pup later in the season. As with grey seals (Kovacs, 1987), the proportion of nursing bouts initiated by the mother presenting also decreased over time.

Parent-offspring conflict theory suggests that, as the pup's energetic demands increased with age (since $SMR = M_w^{0.75}$; Kleiber, 1975), the level of conflict similarly increased. Even if maternal resources remained constant, her inclination to tax those resources would decrease with pup age. However, the pup's demands would concurrently increase, creating a widening difference between the pup's demands and the maternal inclination or ability to fulfill them. Therefore, the pup would be forced to assume more of the responsibility to solicit feeding.

Figure 13: Triver's Parent/Offspring Conflict model.

This figure shows the changing cost/benefit of investment plotted against level of parental investment. The optimal strategy for the parent is to maximize the difference between B and C, i.e. investing 'P' amount. The offspring is selected to maximize B - 1/2C, when it is half as related to future offspring as itself, and should seek investment up to 'O'. The period between 'P' and 'O' should be the time of greatest conflict over the acquisition of maternal resources (from Trivers, 1974).


max IF for offspring
max net RS for parent
B
C
1/2 C
BENEFIT OR COST
P
O
PARENTAL INVESTMENT

Eventually, the demands of the pup outstrip the limits of the mother and weaning would occur. In a species such as the harbour seal the conflict is magnified since, even with external feeding, available maternal resources decline over the nursing season, accelerating the rate of parent-offspring conflict.

The H_n for male pups was consistently more negative than for female pups. This can be interpreted in two ways: either the mother placed less importance on maintaining nursing with male pups than female, or male pups were more active than females in soliciting suckling, or both. Examination of the differences in nursing rates reveals that males achieved greater total suckling times and this increased with age. If this were achieved through mothers 'allowing' male pups to suckle longer, mothers should have terminated the nursing episodes of female pups more frequently than for male pups, which was not observed. Rather, male pups initiated a greater portion of their nursing bouts than female pups. This indicates that the mother does not react partially to a pup of one sex or another. Rather, the increased nutritional input achieved by male pups may be a result of their actions to extend the nursing relationship (see Section 4.4.3).

4.2.2.4 Weaning

Weaning has been defined as "the breaking of an offspring's dependence on its mother or parents, especially with regard to feeding" (Immelmann & Beer, 1989). The relationship between mother and pup is composed of several separate factors, not all of which follow the same pattern of changes as the pup ages. The weaning process can be analyzed in terms of the switch from nursing to exogenous feeding by the pup, the end of pup attendance by the mother, or the changes in responsibility for maintaining the nursing relationship (i.e. H_n). Failure to clarify which aspect is being reported can lead to difficulties or errors in interpreting and comparing studies .

For example, in this study, as demonstrated by the change in H_n, there is a continual shift in the partner responsible for maintaining the nursing relationship, with the pup becoming more liable. In this way, weaning would be classified as gradual.

But other studies may examine alternate aspects of the weaning process. Harbour seals are nursed regularly until about 30 days of age (Table X). At Miquelon, weaning may occur by the mother simply leaving the sand flat without the pup, facilitating the severance of the bond by either returning to another section of the haul out grounds during the next tide or leaving the general area. In this way, the weaning process would be classified as abrupt.

There is also some question as to whether the change from nursing to exogenous feeding is gradual. Pups on Miquelon, unlike other groups of harbour seals and phocid species, accompany their mother into the water shortly after birth. There is evidence that mothers feed during the nursing period while accompanied by their pup (Bowen *et al.*, 1989). This supplemental feeding may be the result of the higher energetic demands linked to the harbour seal's relatively high percent of birth weight and weaning weight of maternal body mass (12.8% and 30% respectively; Bowen, 1990). Pups initially feed on crustaceans (Bigg, 1973) and it would not be surprising if the pups began to feed while still nursing, or that critical prey-catching 'learning' episodes with the mother might occur. If this were happening, then the weaning process would again be classified as gradual.

Many postpartum investment studies investigate the amount of energy expended by the mother from nursing up to weaning. A newly emerging observation, however, has cast doubt upon many of these birth-to-weaning studies. In pinniped species where maternal attendance is constant or regular, weaning was defined by an abrupt abandonment of the young. Recently, however, evidence has arisen that mothers may return several times to their young for additional nursing after 'weaning' has supposedly occurred, resulting in a decreased estimate of maternal costs.

4.2.3 Relationship Between H_n and H_d.

It is not surprising that the two measures of intrapair dependence exhibit similar changes over the course of nursing.

Although harbour seal pups are relatively precocious at birth (in comparison to other pinnipeds) they are still dependent upon their mothers for factors such as nutrition, protection, and, possibly learning to exploit prey.

The rapid physical changes which occur in the environment due to tidal effects necessitate that the following response of the pup must be in place soon after birth. In the aquatic environment it is extremely important that the pup develop a following response so that the pair do not become separated. As the pup becomes more coordinated and mobile, and as its chances of survival upon separation increase, the onus becomes increasingly more on the pup to maintain the pair. And because the primary function of the pair is to ensure nursing, changes in H_n will closely resemble those in H_d. as the pup attempts to receive the maximum available energy by delaying weaning or abandonment (see Section 4.2.2.3). It is important for the pup to maintain the relationship since harbour seal females have rarely been observed nursing alien pups (Lawson, 1983), and pups which become prematurely separated have decreased chances of survival. In northern elephant seals, only 30% of pups separated from their mother survived to weaning age (LeBoeuf *et al.*, 1972).

The relationship between H_n and H_d is sometimes confounded however, partially because nursing was not the sole reason for pair maintenance. Circumstances where nursing was not the primary reason for pair maintenance may have resulted in these differences. For example, pups spend very little time 'alert', rarely scanning their environment, and were therefore less aware of external threats, either by humans or other seals. When the pair became separated the pup was typically the one who searched out the mother for feeding, sometimes (particularly when younger) attempting to suckle from any adult female (and even the occasional male). The mother rarely made efforts to locate the pup for the purposes of nursing. However, during disturbances, the mother would seek out the pup who rarely fled the perceived danger on its own. More typically, it was the mother who located the pup and first entered the water either followed by the pup (sometimes resorting to nursing presentations to attract it) or physically dragging it in. A similar differentiation of maternal responses to separation during nursing and disturbances has also been noted in northern elephant seals (LeBoeuf *et al.*, 1972).

4.2.4 Nosing Behaviour

Nosing behaviour, alternately called nuzzling, is the most common mother/pup social contact next to nursing (Sergeant, 1965). It is highly stereotyped across pinniped species, and is thought to serve several independent functions.

In harbour seals, as with many phocids, nosing can be broken down into two general types: 'nose to nose' and 'nose to body' contact. Although mothers and pups perform both actions, their individual functions apparently differ.

Nose to nose behaviour may be extremely important in establishing and maintaining the mother/young bond, through tactile and olfactory stimulation (Terhune, Terhune, & Ronald, 1979). Maternal nose to nose behaviour is performed more frequently by mothers with younger pups (e.g. Kovacs, 1987). Typically, the mother can be seen sniffing the pup (nostrils open, whiskers erect, often with accompanying vocalizations), although the offspring do not seem to be obtaining olfactory cues from the mother and may perform mutual muzzling for tactile stimulation. Perhaps, though the mother may initiate a proportion of the nose to nose behaviours, the head is targeted only because it is the closest part of the pup to sniff, coupled with the pup's inclination to make mutual muzzle contact. If true, then this behaviour would serve the same purpose as maternal nose to body behaviour, the difference being only a matter of pup orientation.

Maternal nuzzling occurred throughout the haul out period, but most frequently during nursing bouts, when reestablishing contact with a separated pup, and when awakening, most likely to determine the identity of the pup. Mothers were rarely seen to preferentially nuzzle one part of the pup when another was more accessible.

While nose to nose behaviour may serve a long-term function (i.e. pair maintenance), the pup's nose to body behaviour seemed target a specific area of the mother. Almost all of these actions initiated by the pup were directed towards the mother's mid-ventral region. This was interpreted as attempts to solicit suckling.

The results of this study reaffirm the disparate functions of nosing behaviour. The number of nose to nose behaviours initiated by the mother did not change over the course of the nursing period nor were there any observable sex differences, possibly indicating the continued need of the mother to ensure the identity of the pup attempting to suckle, regardless of its gender.

The rate of nose to body behaviour initiated by the mother decreased during the nursing period (both measured separately and as a percentage of total observed nose to body actions), consistent with an increasing responsibility of the pup to maintain the pair bond. The increase in pup nose to body actions reflected the changing relationship in H_n as well, as the pup increased the number of attempts to solicit feedings while the mother gradually weaned her young. A possible increase in the number of nursing bouts (since average bout time did not change but total nursing time increased) may have also contributed to an increase in these actions. Therefore, the sex differences seen in the intrapair relationships and nursing times seem to be reflected in similar differences in nose to body behaviour, indicating that this behaviour may serve as a useful indicator of the dynamics of the mother/pup relationship.

4.2.5 Pup Checks

Initially, it was proposed that the number of times a mother checked its young would be correlated with her investment in that offspring. Mothers should be more vigilant towards pups in which it has invested more reproductive effort. Kovacs (1987) found that younger grey seal pups were checked more often, but that male pups were monitored more closely on only one of three study sites, possibly due to higher attendance patterns.

In this study, pup checks seemed to be more indicative of external factors. Mothers usually checked their offspring when there was disturbance on the flat, or upon waking. Assuming mothers of both male and female pups were subject to the same levels of disturbance, no differences would be observed in check frequency if this behaviour were primarily triggered by external factors. Although checking behaviour may be a valid index of maternal investment, any differences due to pup sex may be constantly overshadowed by the level of disturbance at the study site.

4.2.6 Duration data

One of the most provocative results of this study is that male and female harbour seal pups exhibit different behavioural patterns. While the pups' behavioural repertoire closely mirrored those demonstrated by other species (Table XI), the gender-specific differences indicate that divergent behavioural ontogenies can be evident early in development.

Like most mammalian young, harbour seals spent the majority of their time idle when hauled out (Kovacs, 1987; Stewart, 1987). This would be expected, since

Table XI.

Comparison of this study with harp and grey seals, showing the mean percent of time spent in a behaviour during haul out (Percent), and the changes (Trend) in the amount of time spent in a behaviour over the course of nursing (inc=increase, dec=decrease, none=no change). Figure adapted from Bowen, 1990.

(data for harp and grey seals from Kovacs 1986, 1987).

Species:	Harbour seal		Grey seal		Grey seal		Grey seal		Harp seal	
Site:	Miquelon		Pilgrim's Haven		Rona Beach		Rona Rocks		St. Lawrence	
Behaviour	Percent	Trend	Percent	Trend	Percent	Trend	Percent	Trend	Percent	Trend
Alert	5.1	none	0.4	none	3.0	inc	2.5	inc	1.0	none
Comfort	14.36	dec	15.0	none	15.0	none	13.0	none	15.0	dec
Idle	52.38	dec	70.0	none	70.0	dec	75.0	dec	72.5	inc
Locomotion	1.68	none	7.0	dec	6.3	none	5.8	none	5.8	none
Nursing	20.55	inc	3.0	none	3.3	none	2.0	none	3.6	none
Play	3.4	none	0.0	none	0.5	inc	0.5	inc	0.1	none
Social	2.6	inc	0.9	inc	0.5	none	0.5	none	1.8	dec

time spent in the aquatic environment is energetically costly due to increased demands from locomotion and thermoregulation, particularly when young . Haul outs provide an opportunity to lower energetic costs, and therefore to maximize energy utilization. Kovacs (1987) suggested that grey seal pups' immobility also functioned to facilitate female relocation of pups. While this may be somewhat true of harbour seals, their pair bond (including relocation and recognition abilities) is probably stronger, since it must function in the aquatic environment as well.

Male pups spent less time idle than females, and most of this difference in the first part of the season could be attributed to the increased time that male pups spent in comfort movements. Comfort movements were composed primarily of stretching and curling the flippers, scratching of the torso with the foreflippers, rubbing on the sand, or similar low energy-level behaviour. While male pups frequently exhibited such behaviour, females were more often completely immobile.

The activity levels of both male and female pups changed with age, with more time spent in more energetically demanding activities and less performing idle or comfort behaviours. Similar results were found for grey seals (Kovacs, 1987). During the same period nursing times increased, probably to maintain growth in the face of increased activity budgets and metabolic demands.

Fagen (1981) suggested that male young of dimorphic species should play more than female young, and Gentry (1974) suggested that there were early sex differences apparent in the motor components of play in Steller's (northern) sea lion. Human males are more active than females (Eaton & Keats, 1982; Phillips, King, & Dubois, 1978), more willing to take risks (Ginsburg & Miller, 1982), more likely to take part in physical, nonaggressive play (DiPietro, 1981), and are more physically and verbally aggressive (Maccoby & Jacklin, 1974). Although male harbour seal pups did show a tendency to play more often than female pups, the difference was not statistically significant. However, Fagen's prediction referred primarily to social play. On land, harbour seal pups primarily displayed solitary play behaviour that was object or self directed. These included exploratory actions such as furrowing in the sand with the snout, and tossing seaweed, driftwood, or man made objects (for a review see Renouf & Lawson, 1987). Only rarely was social play observed, although its occurrence in the aquatic environment could not be monitored and may be substantial. It is also interesting to note that, when hauled out, harbour seal pups are surprisingly sedentary for a young mammal not under threat of predation (Gardiner,1989).

4.2.7 Ultimate Basis of Activity Levels

The proximate basis of early behavioural differences has been shown to be based on early hormonal differences, and their effect upon the brain (Erhardt & Meyer-Bahlburg, 1981; MacLusky & Naftolin, 1981; Rubin, Reinisch, & Haskett, 1981). Differences in parental treatment of offspring may also be related to early behavioural differences between the sexes. The ultimate causes of behavioural differences between males and females are thought to be linked to the divergent social roles fulfilled by the animals. Because males and females must perform distinct social functions at maturity, their early behaviour should both reflect and prepare them for these activities.

These activities have an energetic cost, and the benefits derived from such activities must be sufficient to maintain them (on an evolutionary scale) despite these expenses. Such evolutionary pressures are evident in other pinniped species. Differences in activity levels have been noted in Galapagos fur seals (Arnold & Trillmich, 1985), and the energetic effects of these differences was evident as male pups showed increasing weight loss with increasing activity levels, while female pups demonstrated the opposite trend. Even greater sex differences were reported in Stellers sea lions (Gentry, 1974), possibly an ultimate result of greater sexual dimorphism.

If increased activity levels decrease the energy available for physical growth then the benefit must be greater for male pups than females (since males would experience higher energetic costs via higher activity levels). Even small differences in the percent of time spent in a behaviour may be energetically significant if the activity as energetically demanding as play (Coelho, 1974). This assumes that milk does not provide 'excess' energy to the pup that could not be otherwise directed towards growth (both muscle and blubber). Besides direct energetic losses, an additional cost of higher activity levels in pups may be the tendency to increase the chance of separation from its mother.

Some of the suggested direct physical benefits of increased activities include increased stamina, coordination, and muscle bulk. Even increased time spent scanning or alert may help develop the information processing systems of pups, although this activity was largely performed by older members of the haul out group. Male pups may also benefit from the development of fighting tactics important later in mate competition, or increased activities may serve to establish a site specific dominance hierarchy (Arnold & Trillmich, 1985).

4.3 Reconciling Nursing and Growth Rates

The fact that male and female harbour seals can be differentiated on the basis of gross behavioural categories is interesting in its own right. However, the data also re[illegible] two paradoxes.

First there is the problem of Maynard Smith's prediction that mothers should preferentially invest in male offspring in a polygynous or sexually dimorphic species. The physical measurements in the present study, when taken on their own, seem to indicate that female pups are at least as large as males at the time of weaning. Not only is this contrary to the general phocid pattern, but it also raises the question of how males can be significantly larger at sexual maturity.

The second paradox is far more complex. Although the data from the physical measurements indicate that female pups grow at least as quickly as male pups, male pups spend a greater amount of their haul out time nursing. Five nonexclusive hypotheses are suggested in an attempt to resolve these paradoxes. These hypotheses may individually or collectively account for the findings.

1) Behavioural differences.

As was demonstrated by an examination of the general behavioural data, male pups are more active than females during the haul out period. This would suggest that males partition more of their available energy toward physical activity rather than growth, what Coelho (1974) referred to as socio-bioenergetics. The degree to which even marginally higher levels of activity might affect the pup's energy budget (i.e. time spent in comfort vs idle states) has never been quantified.

Kleiber (1975) recognized the importance of acquiescence on metabolic rates, stipulating it as one of the fundamental conditions for measuring basal metabolic rates. Lavigne, Barchard, Innes, and Øritsland (1982) suggested that the disregard for this criterion was partially responsible for Irving's (1972) conclusion that marine mammals have significantly greater metabolic rates than terrestrial ones.

The degree to which higher activity levels during haul out affect growth is difficult to determine, and it is questionable if such differences in activity budgets could be solely responsible for the reversal of predicted growth rates. It may be that the actual energetic cost of this activity is negligable compared to the amount devoted to growth, or that it utilizes energy that can not be directed towards growth regardless. Although the degree to which this higher activity level in male pups affects their overall energy budget might seem insubstantial, recent research by the U.S. National Institute of Health indicates that humans who 'fidget' can burn up to an additional 800 calories per day (Ravussin, 1987). The behavioural differences exhibited by the pups during the haul out period may also be indicative of an overall differential energy allocation strategy, since only a portion of their daily activity patterns can be observed.

2) Metabolic differences.

Male pups may be devoting less of their available energy to growth because they must fulfill a greater metabolic demand. This may be due to an overall higher standard metabolic rate for males (SMR - an equivalent of basal metabolic rate for growing animals). However, high SMR's are often associated with greater growth rates, which runs counter to our hypothesis.

Another explanation might be that male pups suffer a greater thermoregulatory demand. This would come about either through more time spent in the water or less thermoregulatory ability due to decreased insulation. If male pups are either born with or develop less blubber insulation (directing more effort to somatic growth) they would experience a greater thermoregulatory demand, particularly in the water (thermal conductivity is 20 times greater in water than air; Hart & Fisher, 1964). However, this would necessitate that the beneficiary of this diverted energy has a greater value to future reproduction than the increased costs associated with decreased thermoregulatory capabilities. As Blix and Steen (1979) showed, the thermoregulatory costs imposed on marine mammal young (particularly newborns) are already expensive, and any further costs would probably be prohibitive. Therefore, increases in standard metabolic rates which facilitate greater thermoregulatory abilities (including a broader thermoneutral zone) might be evolutionarily more stable, as suggested by Miller, Rosenmann, & Morrison (1976).

It is also possible the male harbour seals have greater total daily metabolic costs, even if their thermoregulatory capabilities or SMR's do not differ from females'. For example, if males spend a greater portion of their time in the water than females, their total daily costs would be greater, even if their physiological parameters were identical. Hill (1987) found that growth rates were negatively correlated with the amount of time the pup spent swimming. Such a strategy would be evolutionarily stable if such time was spent enhancing muscle strength and coordination, learning from its mother (e.g. catching prey), socializing, perfecting swimming or diving skills, or in some other behaviour which increased its fitness.

3) Energy Utilization Efficiency.

It is possible that, although males ingest a greater amount of milk, the resulting available energy is less than that available to female pups from a smaller volume of milk. This could result from a less efficient energy extraction system, a character seen in other mammalian infants, particularly humans. The proximate cause of such a 'deficiency' is often a less-developed alimentary tract in one sex. Again, there is the question of why such a 'disability' would not have been selected against since, clearly, there is a selective advantage to being an efficient energy converter. There must be some associated character which increases fitness to counterbalance its disadvantages. For example, if male pups are born earlier in the season they may be less physically developed, but may reap the benefits of extended parental care. However, no changes in the sex ratio of newborn pups over the course of the pupping season have been reported for harbour seals.

4) Nursing Efficiency.

While energy utilization efficiency refers to the ability of a pup to extract the available energy from a set volume of milk, nursing efficiency refers to the ability of a pup to obtain milk over a set suckling time (given absence of resource limitations). If males are less efficient sucklers (more likely than the mothers of male pups being less efficient lactators) they would have a lower potential energetic input to suckling time ratio. Again, the source of this may be developmental, and the same arguments *vis a vis* natural selection apply to this possibility. The paradox would thus be solved by the fact that nursing times did not correspond to milk input levels.

5) Catch Statistics.

While working on Miquelon it was easy to identify a class of pups which seemed significantly smaller than average. Results of subsequent catching and observations revealed that most of these pups were male. I suggest that there is greater variability in male pup size, and that this may be the result of a bimodal size distribution. This is significant in that the catch statistics for male pups in this study may be heavily biased towards the smaller end of this distribution.

If the premise is correct that male pups are more expensive to raise than females (given their increased suckling demands and energetic budgets) it is possible that two generalized postpartum maternal investment strategies have developed. The first would be, for females which can tolerate this extended cost, to invest fully in male offspring. This would mean a greater energetic investment for male than for female pups, since the former suckle longer. The increased investment would allow male and female pups similar growth rates, despite higher metabolic costs (Appendix E), consistent with the reported results for harbour seals (Table X) and and a number of other phocids (Kovacs & Lavigne, 1986b).

The second strategy is a derivative of Maynard Smith's preferential abandonment theory. If females can/will not endure the extra costs associated with raising a male pup, they should still invest in it, but to a lesser degree. These females have already invested energy in the pup prenatally and have incurred the costs of initial milk processing and storage. The latter is energy already spent, and it would cost the female little to transfer it to her male pup. However, the mother may be less willing to incur additional expenses by continuing nursing through its normal term. She may choose to shorten the nursing period or, alternately, shorten the individual nursing bouts. The decision to continue nursing to a minimum level rather than early abandonment may be influenced by evidence that nursing increases the chances of successful mating (Bigg & Fisher, 1974).

These two strategies would, theoretically, result in two male pup size classes: 'normal' and 'runt'. Initial results from work on northern elephant seals indicate that the majority of runts at the end of the nursing season are males (LeBoeuf *et al.*, 1972).

At the start of the pupping season both of these size classes would be equally likely to be caught. But these 'runts' may be easier to catch in the latter half of the field season. This would lead to the calculated lower growth rate being a biased catch statistic. Since observations were on all available nursing pairs they did not suffer from this bias, and the higher nursing rates of male pups with high levels of investment would overshadow the low nursing rates of the 'runts'. This possible explanation leads to another set of questions on female nursing strategies, their abilities to limit their resources, and the possible mechanisms of differential maternal investment.

There may, in fact, be an entire set of 'decision rules' which the female is subject to over the course of fetal development and offspring growth. Distilling investment strategies to a single 'all-or-nothing' decision based on offspring sex may result in a simpler, but not necessarily more accurate, model. It seems that a series of choices, similar to that outlined by Stewart (1983; Figure 14) but incorporating the sex of the pup, may be more practical. Such a strategy would allow the female to adjust her reproductive effort according to current condition, rather than making a single, irreversible decision based on forecasts of future resources It also may account for a portion of the observed variability in offspring length and weights, similar to those predicted by Stewart.

4.4 Evaluation of Investment Theory

4.4.1 Maternal Condition

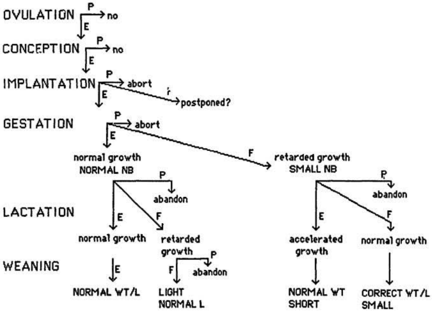
One of the base assumptions of the Trivers-Willard and Maynard Smith investment theories is that larger females should produce more male offspring, because they can invest more energy in pups, giving them a size advantage for later mate competition. Trivers and Willard (1974) felt that this probably was more true of smaller litter sizes than larger ones, since the impact of maternal body condition would be more clearly emphasized in the former.

This suggests that the offspring of larger females should be larger at birth and grow faster and that pup size should correlate to maternal size and/or condition (although condition is a more reliable indicator of available investment energy, mass is more often used). This theory is especially relevant to harbour seals, since newly born pups are the largest percentage of maternal weight (13.6%) for any reported phocid (Bowen, 1990).

The mechanics of Triver's theory can be best understood in the following example. He assumes that a female in poor physical condition is free to produce either a male or a female offspring, and that it inherits its maternal physical condition. A female offspring will have a below average reproductive success, while a male offspring will possibly experience no reproductive success at all. In

Figure 14: Stewart's model for investment decisions.

Schematic of a possible array of choices presented to a female over the course of investment. Note that the decision criteria are present condition (p=poor, f=fair, e=excellent) rather than predictions of future events. Also, notice the absence of the Trivers-Willard "all-or-nothing" investment decision (from Stewart, 1983).


OVULATION
P
no
E
CONCEPTION
P
no
E
IMPLANTATION
P
abort
E
postponed?
GESTATION
P
abort
E
F
normal growth
NORMAL NB
retarded growth
SMALL NB
P
abandon
P
abandon
LACTATION
E
F
E
F
normal growth
retarded growth
accelerated growth
normal growth
P
WEANING
E
F
abandon
NORMAL WT/L
LIGHT
NORMAL L
NORMAL WT
SHORT
CORRECT WT/L
SMALL

the opposite scenario, the female offspring of a female in above average condition will also have greater than average reproductive success. But a male offspring will have a disproportionately higher reproductive success.

Although the effect of female condition is not directly addressed by Maynard Smith, its effects can still be extrapolated. Disregarding the effects of maternal condition, a female should invest more heavily in male offspring because a greater investment will yield a disproportionately greater reproductive success (thereby increasing the female's fitness). However, given differential maternal selection facilitated by early recognition, the female should only invest in a portion of the more expensive sex so that the total investment in offspring of either sex is equal. Factoring in the effects of maternal condition, if the female's resources are limited then she should invest in a smaller proportion of male offspring by prenatal selection so that, in extreme cases, only female offspring are produced. If a female is of above-average condition then she should invest in as many male offspring as possible. In cases where offspring numbers are small this will result in all-male broods.

The relationship among mammals, however, between birth weight and maternal mass is still unclear (Calder, 1984). The available pinniped data do not concur with the Trivers-Willard theory. Although Anderson and Fedak (1987a) found that mothers of male grey seal pups tended to be heavier at parturition, the difference was not statistically significant. They also found that above-average weight females produced slightly more male pups (13m:9f) than below-average weight females (9m:14f) (Anderson & Fedak, 1987b).

Additionally, no differences were found between mothers of male or female pups in southern elephant seals (McCann, Fedak, & Harwood, 1989) or Antarctic fur seals (Boyd & McCann, 1989; Costa, Trillmich, & Croxall, 1988) in either maternal length, condition, mass, or even date of parturition. McCann *et al.* (1989)

found that birth weight was positively correlated to maternal weight for female southern elephant seal pups. However, there was no significant relationship between male pup birth mass and maternal postpartum mass, mainly due to the fact that smaller females also gave birth to male pups. Similarly, in Antarctic fur seals, the relationship between maternal mass and birth weight for male pups was barely significant, while that for female pups was extremely strong (Costa *et al.*, 1988). This is contrary to Boyd and McCann (1989) who found that much of the variation in the birth weight of male Antarctic fur seal pups could be accounted for by maternal condition or mass, whereas no such relationship was evident for female pups.

Shaughnessy (1987) found that South African fur seals (*Arctocephalus pusillus*) produced an overall skewed birth ratio of 1.32. However, This seems to be the exception rather than the rule. Equal sex ratios at birth have been reported for a number of pinniped species, including harbour seals (Bigg, 1969; Boulva, 1971; Boulva & McLaren, 1979), Antarctic fur seals (*Arctocephalus gazella* ; Boyd & McCann, 1989; Costa *et al.*, 1988), ringed seals (*Phoca hispida* ; McLaren, 1958), harp seals (Sergeant, 1973), hooded seals (Øritsland, 1964) and northern elephant seals (LeBoeuf, Condit, & Reiter, 1989). This seems to support suggestions by Maynard Smith (1978) and Clutton-Brock and Albon (1982) that there is little empirical evidence to support prepartum adjustment of the sex ratios in mammals.

Data detailing postpartum maternal investment are also nonsupportive of the Trivers-Willard theory. Fedak and Anderson (1982) found that larger grey seal mothers did not confer greater growth rates upon their offspring. Although male pups had significantly greater growth rates than female pups, there was no significant increase in their growth rates with increasing maternal size (Anderson & Fedak, 1987a). Female grey seal pups did demonstrate increasing growth rates with greater maternal size, but only 16% of the variance in female pup growth rates could be accounted for by maternal size (Anderson & Fedak 1987b). In Antarctic fur seals, male pups average 14.6% of maternal weight, while females averaged only 12.3% (Costa *et al.*, 1988).

These patterns in birth weights and growth rates suggest that maternal size is not the prime determinant of sex differences in pups' physical size. Females appear to produce sons at birth which are as large as possible, given the ultimate constraints imposed upon her by physical size and energetic stores. It seems that, where differential investment is evident, females of all sizes expend a greater reproductive effort upon male offspring than female.

This suggests that male pups make higher energetic demands on their mothers than females (both pre- and postpartum), regardless of maternal size. This pattern runs counter to current theory regarding the change in reproductive strategies with age. If females invest according to their remaining reproductive potential, then older females should produce offspring which make greater demands upon their future reproductive success (i.e. males). Theory states that older females should be more willing to take reproductive risks, since they have 'less left to lose' (Fagen, 1972). Conversely, younger females should produce offspring which minimally jeopardize their future reproductive success. However, no such differentiation of offspring sex with maternal age occurs. And since male offspring make higher energetic demands regardless of female condition, larger, older females are actually expending less relative reproductive effort than younger, smaller females.

The strategy of leaving the nursing grounds with superfluous milk would not seem to be a stable strategy if females could control the sex of their offspring, as is suggested by both Trivers and Maynard Smith. However, it does make sense if females are unable to exert such control, and if the controlling mechanism of differential investment lies with the pup and not with the mother.

4.4.2 The Importance of Early Size Differences

One of the central tenants of Trivers' and Maynard Smith's theories of maternal investment is that early size differences, due to differential prenatal or postnatal investment, will directly manifest themselves as equal levels of dimorphism at the time of sexual maturity. As a corollary, such differences in adult size can not be attributable to post-weaning growth.

This was contrary to findings from Laws' (1959) study of prenatal parental investment in two highly dimorphic pinniped species (southern elephant seal and northern fur seal, *Callorhinus ursinus*) which concluded that "the sexual disparity in mature size in the polygynous species is not reflected in the size of the sexes at birth". Both he and Bryden (1972) independently concluded that there was little evidence that either birth weight or weaning weight were related to adult size. Rather, they suggested that adult sexual dimorphism is largely the result of differential growth just prior to or after the onset of sexual maturity. In their model the growth curves of male and female offspring would be identical until around puberty, when males would demonstrate a second cycle of accelerated growth.

Kovacs and Lavigne (1986b), in a more complete review of the available data, concluded that dimorphism of body size, both at birth and at weaning, varied in the direction demonstrated in the adult forms. However, the magnitude of the differences seen in the early stages did not correlate to the absolute mass differences exhibited at sexual maturity. More importantly, their study also demonstrated that, although the direction of size difference was similar in species with early sexual dimorphism, early size differences were not a necessary prerequisite for adult size differences. For example, Bowen *et al.* (1985) found no differences in the initial weights of male and female hooded seal pups, yet the species is highly dimorphic.

In examples of differential maternal investment the elephant seal is often presented as a 'classic' example, since adult males are 4 times larger than mature females. However, although McCann *et al.* (1989) did find that male southern elephant seal pups (*Mirounga leonina*) were significantly heavier at birth, these weight differences were not significant at weaning.

4.4.3 Maternal vs Pup Control

The emphasis of the Trivers-Willard argument suggests that investment in male offspring should only be made if there is a reasonable probability of yielding a reproductively competitive offspring. Therefore, females which are able to invest greater resources in an offspring should produce more sons than daughters.

The genetic mechanism forwarded by Trivers is quite precise. If the target of natural selection were a gene (or genes) predisposing a certain fixed sex ratio (as suggested by Fisher (9130)), then females in poor condition would tend to accumulate the gene for producing female-biased sex ratios, while females in good condition (relative to the population average) would accumulate complimentary genes that produced male-biased sex ratios. But since mothers in better condition outproduce others, the gene for female offspring would become negligible in the population.

Instead, argued Trivers, natural selection should work upon a genome that facilitates the manipulation of the sex ratio based upon maternal condition at the time of parental investment. In that way, females which produce offspring in the sex ratio best suited to their current condition would have a higher reproductive success than those which produce offspring in a fixed ratio.

The details of how the genome might manipulate the sex ratio are unclear. Trivers maintains that some type of differential mortality of offspring of one sex is necessary for the female to maximize her lifetime reproductive success. It is possible that this occurs early in development, perhaps through a combination of differential sperm selection (James, 1989), differential mortality due to deleterious alleles associated with the X chromosome (Myers, 1978; Page *et al.*, 1987), or biochemical changes (e.g. vaginal pH) related to the timing of ovulation resulting in differential mortality of X and Y sperm. Another suggested mechanism has been differential abortion rates early in prenatal development (i.e. differential mortality in utero), or selective mortality during postpartum maternal investment, consistent with Maynard Smith's (1980) predictions if the event occurred before a substantial investment of 'd'.

It is unlikely that differential abortion rates is a stable evolutionary strategy. Since mothers can pup every year it seems unlikely that the cost of nursing 'the wrong' offspring impinges a greater cost to reproductive success than raising no offspring at all. For larger females which produce female foetuses, it is likely more beneficial to underutilize its reproductive potential by not aborting it than to realize none at all. Similarly, investment in male pups may also increase the reproductive success of smaller females, even if their offspring's chance for reproductive competition is low. Among pinnipeds, a number of alternate mating strategies (e.g., "sneaker males") confer reproductive success to small males far in excess of that predicted for their size by Trivers. There is also some evidence that partum is conductive to the timing of estrous and soliciting matings (Bigg & Fisher, 1974). This would agree with Boulva and McLaren's (1979) finding that 85-92% of mature females produced a young each year.

Similar arguments cast doubts upon the concept of differential abandonment. If sex ratios at implantation are fixed at unity, females which give birth to pups of the 'suboptimal' sex and then prematurely abandon them would be eliminating all reproductive success for that year (see Figure 14). Surely, a minimal investment in pups of any sex, even if reduced, would be a more beneficial strategy than abandonment prior to ensuring a reasonable probability of survival.

The mechanics of Maynard Smith's theory are dependent on two assumptions: that the primary sex ratio is fixed at unity (reviewed by Maynard Smith,1978; although see Weir, 1962), and that parents can recognize the sex of their offspring and invest differentially in them so as to affect the offsprings' fitness. Postpartum recognition is probably quite feasible through sex-linked chemical cues. Actual energy input can be controlled easily enough by physically limiting the degree of nursing available. The theory also suggests that females must somehow monitor the amount of energy received by a pup or that still available to invest, (perhaps through biochemical cues such as hormone levels) and make decisions regarding further investment based upon this knowledge. However, monitoring is not necessary if the mechanism of control shifts from the female to the pup.

Predictions by Clutton-Brock *et al.* differ from the Trivers-Willard and Maynard Smith theories in that they remove the active role of the female from the mechanism of differential growth and survival. In their model, differential mortality should occur beyond the initial life stages of maternal investment (after Maynard Smith's 'd' has become quite substantial), and would be expected throughout the entire period of differential growth. This differential mortality should be the result of increased energetic demands on available maternal resources by male offspring, as opposed to inadequate maternal investment.

Not only is this solution more parsimonious, but it also accounts for certain observations that do not fit into alternate explanations. Larger females have been seen leaving the nursing grounds with substantial fat stores still available (Fedak, Boyd, Arnbom, & McCann, 1989; McCann *et al.*, 1989). If the maternal strategy was to invest as heavily as possible in her offspring, then this surplus should not exist. However, if pup demands regulate investment, then the pup may not be able to acquire all maternal resources prior to weaning.

It has also been suggested that, even if pups are limited by the amount of nutrition they can process, maternal investment could still be increased by extending the nursing period. The data, however, do not support this hypothesis. Although larger females exhibit a tendency to give birth earlier in grey seals (Anderson & Fedak, 1987a,1987b) and Antarctic fur seals (Boyd & McCann, 1989), no such pattern was observed for the southern elephant seal (Little, Lyden, & Barnes, 1987). Further, although more male grey seal pups may have been born earlier in the season (Anderson & Fedak, 1987a), this did not translate into greater growth rates or extended nursing periods (Anderson & Fedak, 1987b).

If male pups have the physiological ability to process larger quantities of energy than female pups, their birth weight should be greater and less highly correlated to maternal condition, since they will also be geared to maximizing prepartum maternal investment. Such results are clearly seen in the pinniped literature (Kovacs & Lavigne, 1986b). Similarly, male pups should be able to process greater quantities of milk over shorter periods of time, regardless of scaling. Whether this results in greater growth rates may depend on their specific socio-bioenergetic demands and energy allocation strategy. This increased energy input may be acquired through greater total nursing times and/or increased suckling efficiency. The biochemical constraints imposed on pup assimilation capacities can be quite significant. Anderson & Fedak (1987b) have calculated that grey seal pups must digest, transport, and store the equivalent of 3 kg of butter each day, while hooded seal pups may be consuming over 8 kg of 50% fat milk each day.

The question arises, however, as to why female pups do not attempt to utilize maternal resources to an equal extent as male pups. While the proximate cause of differential investment might be the ability of pups to suckle and process milk, the ultimate cause could lie in evolutionary pressures which might select for higher metabolic rates in male pups. Clutton-Brock *et al.* (1985) suggested that, due to greater differential reproductive success, there is greater selective pressure for males to grow larger and faster, resulting in higher metabolisms. But the limit to which this can be selected for is delineated, not only by biochemical laws, but by the effects of lower food availability. Because of their higher maintenance costs, male pups will suffer increased mortality during times of environmental stress. Trillmich (1986) found that male Galapagos fur seal pups suffered increased mortality the year following an El Nino event, when maternal resources would be lower. In addition, harbour seals exhibit differential mortality later in life. Although the primary sex ratio is equal from birth to about 5 years, males die at a higher rate thereafter until females outnumber males at about 10 years (Bigg, 1969; Stirling, 1975).

If this is an effect of higher metabolic rates (as suggested by Clutton-Brock), male pups must (in an evolutionary sense) balance the benefits of larger body size with the higher maintenance costs. Females would be under less selective pressure for large body size, since it is less correlated to reproductive success and would, therefore, have lower metabolic costs resulting in higher survival during environmental stress.

So how would differences in adult size occur if size at birth, weaning, or growth rates do not adequately reflect size differences at maturity? Even in the most polygynous and sexually dimorphic pinniped species, the northern elephant seal, recent studies have indicated that neither maternal investment nor pup growth are greater for one sex than another (Kretzmann, Costa, & LeBoeuf, 1989).

Most probably, dimorphism is partially attained through differential rates of sexual maturity, as is exhibited in other mammals. Although male harbour seals may not be larger than females at the time of weaning, they do not mature until 6 years of age, while females mature at about 3-4 years (Boulva & McLaren, 1979). This gives the males more time to invest in somatic growth by delaying the costs associated with sexual maturity, perhaps resulting in a second period of accelerated growth as originally postulated by Laws (1959).

4.4.4 Trivers vs Maynard Smith vs Clutton-Brock

It is difficult to design a study that conclusively differentiates between competing investment theories (Ono & Rice, 1989); the Trivers-Willard theory of differential investment does not appear to be supported by this study, nor by much of the available pinniped literature. Although prepartum investment may reflect trends in sexual dimorphism, this does not appear to be a precondition for it. Differences in prepartum investment may also disappear by the end of maternal investment, suggesting that pup size is not directly regulated by maternal condition.

Maynard Smith's theories are also questioned. The suggestion that maternal recognition and control of resources is necessary to regulate differential investment does not concur with the data obtained in this study for Hinde coefficients, modified nursing coefficients and nosing behaviour. This study suggests that male pups are responsible for increased investment by soliciting more nursing and retaining more of the responsibility for maintaining the pair bond and the nursing relationship. Perhaps, maternal control might be a more feasible mechanism with animals of a litter size greater than one, where active decisions could be made between current offspring of different sex.

The behavioural data is also indicative of Clutton-Brock's hypothesis that male pups obtain greater investment to compensate for greater metabolic rates. This study suggests that, not only may male pups have a greater SMR necessary to facilitate greater growth rates later in development, but they may also be bound by higher activity budgets. This would decrease the effectiveness of postpartum growth as a measure of maternal investment.

The results suggest that the pups regulate investment up until the point of maternal-initiated weaning, within the ultimate bounds placed by maternal resources. Clutton-Brock has suggested that the food processing abilities of the pups are further constrained by the evolutionary limits placed on their metabolic rates by natural selection. Regardless of the ultimate cause, the results of this study suggest that the proximate cause of differential investment seems to be the ability of the pup to obtain and process maternal resources. In this sense, the process may be more clearly understood as 'differential procurement of maternal resources' rather than 'differential maternal investment'.

4.5 Future Research

Harbour seals are one of the most widely distributed phocid species in Canada yet, surprisingly, little work has been done on basic life history patterns. Estimates of birth weights, weaning weights, growth rates, and lactation period are scarce and vary wildly. Reliable population data have only recently started to be accumulated, and the problems of differences between breeding groups has barely been addressed.

Future studies should not only examine the 'averages', but should attempt to account for observed variance. Until recently, sex differences were not examined, resulting in both less significant statistics and an incomplete picture. Further selective factors should be explored which may lead to greater understanding of ultimate and proximate basis of behavioural differences.

Sex-linked differences in phocid behaviour has been examined in a small number of species, but only rarely has early ontogeny been studied (but see

Kovacs, 1987 and Stewart, 1983). The importance of studies which examine pups as future breeding members of a particular sex and not as androgynous growth capsules will help to reveal the proximate mechanisms and ultimate causes of differential behavioural ontogeny.

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Appendix A - Past Maternal Investment Studies

The following is a partial list of studies published since 1980 which have examined some aspect of parental investment in pinnipeds. They note which ones examined some aspect of differences based on the pup's sex (Sex Diff), and whether the investment studied was pre- or postpartum (invest: Pre/Post). The technique used to measure the investment is also listed as weight changes in the female or her pup (Weight: Fem/Pup), stable isotope techniques (Isot), behavioural indicators (Behav) and/or milk sampling (Milk).

Species	Sex Diff	Invest Pre	Invest Post	Weight Fem	Weight Pup	Isot	Behav	Milk	Source
Arctocephalus galapagoensis	X	X	X		X		X		30
Arctocephalus gazella	X		X		X		X		2
		X	X		X	X			6
		X	X		X				9
Cystophora cristata	X	X	X		X				4
	?	X	X	X	X				5
Eumetopias jubatus	?		X		X	X	X		11
Halichoerus grypus	X	X	X	X	X				1
			X				X		3
			X	X	X				10
	X		X				X		12
Leptonychotes weddelli		X	X		X				7
			X	X	X	X			28
				X	X	X	X		29
Lobodon carcinophagus			X	X	X			X	23
Mirounga angustirostris			X	X	X				8
	X	X	X		X				15
		X	X		X	X			21
Mirounga leonina	?	X	X		X				16
			X				X		18
	X	X	X	X	X			X	19

	Sex	Invest		Weight					
Species	Diff	Pre	Post	Fem	Pup	Isot	Behav	Milk	Source
Phoca groenlandica	?	?	X		X				13
		X	X		X				26
			X	X	X				27
			X	X	X				24
			X				X		25
		X	X		X				31
Phoca vitulina			X				X		14
			X		X				17
			X				X		22
Zalophus californianus	X		X			X	X		20

SOURCES

1. Anderson & Fedak, 1987a
2. Arnold & Trillmich, 1985
3. Boness et al., 1982
4. Bowen et al., 1985
5. Bowen et al., 1987
6. Boyd & McCann, 1989
7. Bryden et al., 1984
8. Costa et al., 1986
9. Doidge et al., 1984
10. Fedak & Anderson, 1982
11. Higgins et al., 1988
12. Kovacs 1986, 1987
13. Kovacs & Lavigne, 1985
14. Lawson & renouf, 1987
15. LeBoeuf et al., 1989
16. Little et al., 1987
17. Markussen et al., 1989
18. McCann, 1983
19. McCann et al., 1989
20. Ono et al., 1987
21. Ortiz et al., 1984
22. Renouf et al., 1983
23. Shaughnessy & Kerry, 1989
24. Stewart, 1986
25. Stewart, 1987
26. Stewart & Lavigne, 1980
27. Stewart & Lavigne, 1984
28. Tedman & Green ,1987
29. Testa et al., 1989
30. Trillmich, 1986
31. Worthy & Lavigne, 1983

Appendix B - Methods To Determine Parental Investment.

The components which make up an individual's investment in an offspring are varied and complex. No study can realistically expect to measure all aspects of investment, so various indicators of relative investment are used instead. Typically, the energetic component is explored and, since the methods employed are numerous and varied, a single standard is yet to emerge. This, no doubt, is a result of both the diversity of subjects and the questions being investigated. The three most common techniques used for pinnipeds are isotope, milk sampling, and test weighing. The following is a description of these methods and the problems in utilizing them with harbour seals.

Isotope Methods

In nursing studies the pup is injected with a known concentration of a biological tracer, usually water containing one of the rare hydrogen isotopes, either deuterium (^2H, administered as deuterium oxide ^2H_2O) or tritium (^3H, administered as tritiated water ^3HOH) (see Sawby, 1973 and Costa, 1987 for review). The labeled water mixes with the body fluids and the labeled isotopes exchange with the hydrogen atoms in the water. Isotope concentration at initial equilibrium allows for computation of total dilution space (or 'pool size'), assumed to be total free body water (Stansell & Mojica, 1968). Changes in agent concentrations are used to extrapolate the amount of water being absorbed by the animal. With knowledge of milk composition, total milk intake can then be calculated (see Oftedal and Iverson, 1987 for details).

This study method has become increasingly popular in determining both metabolic turnover rates and nursing energetics. However, the applicability of the method are severely restricted by both its techniques, criteria, and assumptions.

Among pinniped studies, this technique has been employed primarily with otariids, where the periodic absence of mothers for long periods facilitates constant handling of the pup. One of the few species of phocids that this technique has been routinely applied to are elephant seals (*Mirounga* sp.), where the lactation period is extended and females are unusually sessile. However, this method is very difficult to employ on such a species as harbour seals, particularly on a population with tidal haul outs.

The intrusiveness of this technique can be prohibitive. When animals are initially injected the isotopes must equilibrate over a period of time, typically about 3-4 hours. During that time the pup must be kept physically isolated from its mother so that it can not nurse. Past observations have indicated that pups can be removed from their mothers for no longer than 20 minutes before a high chance of abandonment occurs. In addition, pups must have their stomachs evacuated so as to avoid increases in pool space by previously ingested milk. These same techniques are again necessary at the end of the study when the animal is reinjected to determine final pool size.

Repeated samples are necessary to establish the linearity of the isotope decline and because small sample errors can lead to large errors in estimates. They are also particularly important in species such as *Phoca vitulina* where the water turnover rate may change over the course of the study, due to changes in milk composition over lactation (Oftedal *et al.*, 1987). Even if repeated, extended, captures are possible, disturbance levels would still be extreme.

This technique rests on several basic assumptions which are often untested. Accuracy requires that maternal milk be the only source of water input to the pup. Pups which nurse from additional mothers violate this assumption, as do species where external feeding or drinking prior to weaning may occur (Depocas *et al.*, 1971; Scott & Renouf, 1989). Various parallel tracer methods (e.g. Holleman *et* *al.*, 1975; Tedman and Green, 1987) have been employed to try to separate these water sources, but none have been completely successful and, since they require additional captures of both mother and pup, they are unlikely to be useful on wild populations.

Another assumption of the original model is that pool size is constant. Unfortunately, pool size is not constant in a growing animal, so that changes in the isotope concentration are due to both isotope loss and dilution by increased pool size. This, if uncorrected, can lead to significant errors (e.g. Dove and Freer, 1979).

Another critical factor of this method is that it measures not only water intake from preformed water in milk, but also the metabolic water which results from the catabolism of milk constituents and/or body nutrient stores. The error that results from this assumption that all milk constituents are catabolized is probably small in otariids, but may be quite significant in phocids where a larger proportion of milk fat is utilized in a blubber layer and not catabolized (Oftedal, 1984). Therefore, a separate measure of metabolic water is essential. This can involve either the application of an additional tracer such as ^{18}O or the measuring of resting metabolic rates in pups (e.g. Thompson *et al.*, 1987; Higgins *et al.*, 1988). The first method is expensive and requires additional handling due to ^{18}O's higher turnover rate (Mullen,1973 for review), while the second lacks in external validity since further assumptions must be made about daily metabolic and thermoregulatory demands.

Additionally, hydrogen isotope methods require substances which may be difficult to obtain and/or transport. Parallel radioactive tracers are often also needed (such as ^{18}O), and blood samples must be kept frozen at all times to avoid decay, an often impossible task under field conditions.

Milk Sampling

Using this technique the volume of milk passed from mother to pup is estimated by removing the sample from the animal. Estimates of milk volume can be made from the pup by evacuating its stomach immediately following a nursing bout, by either removing the stomach from a euthenized subject or gastric intubation. Alternately, milk volume can be estimated from the female by removing the milk just prior to nursing, either on live animals with the aid of an injection of oxytocin, or by surgical removal from sacrificed subjects.

However, this latter method relies on the assumption that complete mammary evacuation takes place during a nursing session, so that mammary volume equals transfer volume. This supposition has never been demonstrated in pinnipeds (see Oftedal, 1984) and may, therefore, result in overestimates of energy transfer. Milk volumes removed from the pup also tend towards overestimates if there is leftover milk from a previous nursing, or underestimates of absorption takes place during the suckling bout. Additionally, harbour seals are difficult to anaesthetize for any complex physical manipulations.

Serial Weighings

This technique attempts to measure the transfer of milk by changes in weight of the female and/or pup.

These repeated measures can take place over two general time frames; either across one nursing period or over a large portion of the entire period of parental investment. The former attempts to measure weight changes that result directly from milk transfer, while the latter measures long-term weight changes in body mass from mass transfer. While single nursing bout measurements may be an acceptable method to determine milk mass transfer in trained or domestic animals, it is far too disruptive to utilize with wild subjects (Oftedal, 1984).

Long term maternal weight loss measures have the advantage of reflecting total energy expenditures. However, its usefulness as a measure of maternal investment is decreased if normal weight patterns (i.e. for similar individuals without offspring) are not known, since it is necessary to determine what portion of the lost energy is directly attributable to the offspring. Differences in weight loss may be complicated by covariates such as external feeding or age-specific metabolic changes. For example, older females may have a predisposition towards producing a particular sex of young, and concurrent age-dependent physiological changes may be misinterpreted as offspring-specific factors.

Another method is to measure offspring weight gain. This has the advantage of pups generally being easier to handle, and is a clearer indicator of the energy which is directly absorbed by the offspring. It is, however, an indirect measure of maternal investment since pup energy assimilation, and not maternal energy output, is being considered. Direct calculations of KJ input/output based on pup mass gain suffer from the assumption that offspring expend only enough energy for basal or standard metabolism, and that their activity levels, absorption efficiencies, and metabolic rates are uniform across the comparison level. It also assumes no external feeding by the young prior to weaning. Pup mass at birth has been used to approximate the gestation costs of the foetus, but the values used (e.g. Brody, 1945; Rahn, 1982) are generally extrapolated from other animals.

The two measures, pup and maternal mass change, are often combined in a ratio of maternal weight loss to offspring gain as a measure of transfer efficiency. Testa *et al.*'s (1989) study of transfer efficiency in Weddell seals reported an unexpectedly high variability in transfer efficiency. This led them to conclude that weight transfer measurements may not be an accurate measure of postpartum maternal energetic investment, perhaps due to variance in maternal and pup metabolism, or extra nursing episodes either from other females or while at sea.

A paradox arises when determining the methodology for measuring weight changes in seals. In cross-sectional studies (e.g. Stewart & Lavigne, 1984), where single mass measures are taken and then fitted to a population model, estimates of growth rates may be inaccurate if the date of pupping are related to female size (Anderson & Fedak, 1987b). The alternative, frequent serial weighings, often creates unacceptable levels of disturbance, particularly if the nursing period is short.

Appendix C - Capture Techniques

Details of animal captures are rarely given in scientific papers due to space constraints. However, they can be of great benefit to other researchers and are necessary in evaluating the results of the study. In this case, two basic techniques were employed.

Terrestrial Capture

This method relied on surreptitiously approaching the animals with nets while they were hauled out. Two types of nets were utilized, the primary ones composed of a 1 inch mesh netting slung between two 1.5 m long aluminum poles, secured at one end to form a 'V'. The net was placed on the hauled out individuals before they could reach the safety of the water. Approach was made primarily over the sand flats from land (as the water is preferentially watched by the seals) or, secondarily, by snorkel approach from the water. Catches were most effective either when sunny weather seemed to make the animals more passive, or when fog decreased visual acuity.

Alternatively, on a few occasions, a larger net (see Aquatic Capture) was employed by placing it on the sand flats prior to haul out, and then throwing it over a portion of the group later in the haul out. Captures were attempted directly from the blinds at the end of an observation session. However, although capture success was high, there was trepidation as to the degree of disruption caused and of having the seals associate the otherwise 'inert' observation blinds with capture, so that these episodes were discontinued.

Terrestrial captures had two distinct advantages. It required only 2 or 3 people and it caught primarily pups. These pups were largely either very young (under 5 days) who were to weak or uncoordinated to quickly reach the water, or older pups who had grown fatter, less alert, and less mobile. However, this also proved to be its greatest disadvantage. It was nearly impossible to catch any age classes other than pups, and there may have been a catch preferential for smaller pups at the end of the season (see Discussion section 4.3)

Aquatic Capture

With this method, one or two long sealing nets (40 feet long, and 1 foot mesh) were strung out perpendicular to the main sand flat from the southeastern point (Mussel spit) and held in position by several colleagues. On most occasions the nets were laid to the east of the point, though they were also drawn across the channel to the west several times. During the outgoing tide, the currents within the Barachois can be quite strong so that, in either position, the currents bowed the nets into a U-shaped trap (figure 3).

In the former position the seals, when flushed from the flats (either by people approaching overland or by boat), followed two lines of escape: either east towards the larger open channel, or south along the channel parallel to the sand flat. The seals that followed this latter route were herded into the net, dragged to shore, and placed in the smaller catch nets where they could be handled safely. Care was taken that animals did not become entangled and drown in the net. Mother/pup pairs were caught preferentially over single seals (particularly juveniles) by trying to dissuade the latter from the net area by splashing and yelling.

This method was much more labour intensive than terrestrial captures, requiring a number of assistants and, therefore, could only be used during part of the season due to logistical constraints. It was also, perhaps, more disruptive. It had the distinct advantage, however, of catching a greater variety of animals than terrestrial captures.

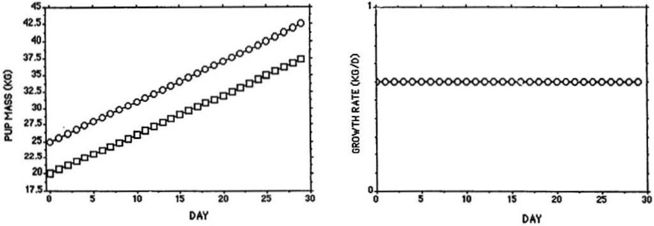
Appendix D - Tagged Seals, Miquelon 1989

Record of harbour seal captures giving the applied tag number (new tags only), the animal's sex, its approximate age (P=nursing pup of the year, W= weaned pup, J=juvenile, and A=adult), and the tag number of its pup if known. Ten previously tagged individuals were recaptured, including two territorial males which were not retagged.

Tag#	Sex	Age	Pup#
202	M	P	
203	M	P	
206	F	P	
207	M	P	
208	F	P	
209	F	P	
210	F	P	
211	F	P	
212	F	P	
213	F	P	
214	M	P	
215	M	P	
216	M	P	
217	F	P	
218	F	P	
219	F	P	
220	M	P	
221	M	P	
222	M	P	
223	M	P	
225	F	P	
226	F	P	
227	F	P	
228	M	P	
229	M	P	
230	M	P	
231	M	P	
232	M	P	
233	F	P	
234	F	P	
235	M	P	
236	F	P	
238	M	P	
239	F	P	
241	M	P	
242	F	P	
243	F	P	
244	F	A	246
245	M	P	
246	F	P	
247	M	J	
248	M	P	
249	M	P	
250	F	A	249
252	F	A	238
253	M	P	
255	M	W	
258	F	A	
259	F	J	
260	F	P	
261	F	W	
262	F	J	
263	F	A	216 or 229
264	M	P	
265	M	P	
266	F	P	
267	F	P	

Appendix E - Theoretical growth curves of harbour seal pups.

These figures illustrate the effects of metabolic rates and different energy inputs on growth rates. For simplification, all graphs assume equal energy utilization efficiencies for male and female pups.



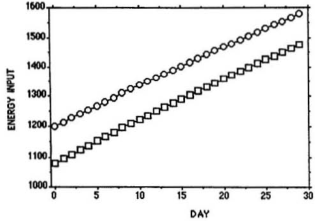


Figure E(1): Constant growth

In order to maintain a constant growth rate (0.6 kd/d) to yield a linear growth curve, the energy input must also increase linearly to compensate for increasing metabolic demands. Also, to maintain its initial size advantage, male pups (O) must maintain greater levels of energy input over female pups (□).

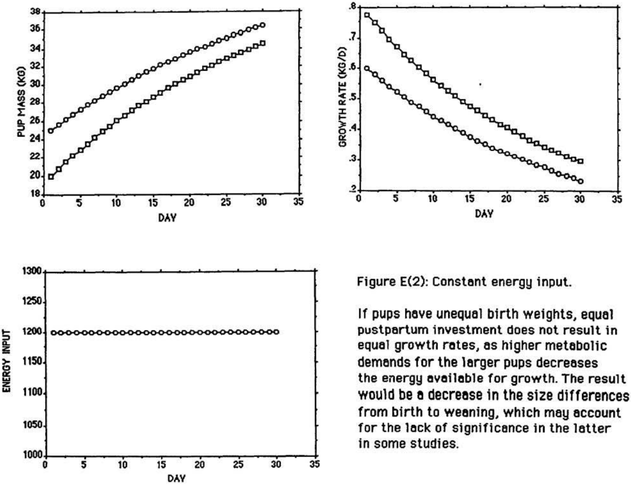
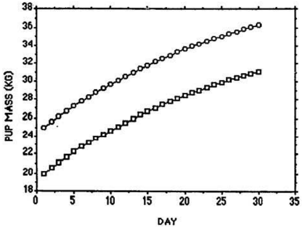
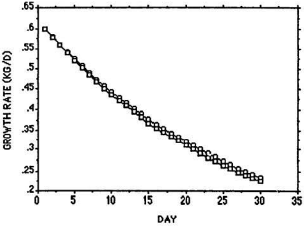


Figure E(2): Constant energy input.

If pups have unequal birth weights, equal pustpartum investment does not result in equal growth rates, as higher metabolic demands for the larger pups decreases the energy available for growth. The result would be a decrease in the size differences from birth to weaning, which may account for the lack of significance in the latter in some studies.





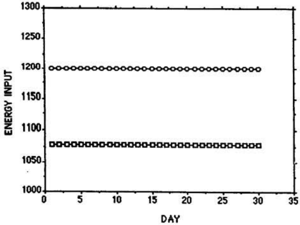


Figure E(3): Unequal investment.

Given unequal birth weights, even when investment levels are set at a level that would be sufficient to maintain equal growth (0.6 kg/d) given their initial birth weights, increasing metabolic rates preclude linear growth. Also, the higher metabolic costs experienced by larger pups causes them to have lower growth rates than smaller pups.