Growth and Fasting Strategies of New Zealand fur seal, *Arctocephalus forsteri*, pups at Cape Gantheaume, Kangaroo Island

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ABSTRACT

New Zealand fur seals show pronounced inter-sexual differences in adult body size, and males will potentially mate with many females. Consequently, selection is thought to act differently upon pups during growth. Little is known about how male and female fur seal pups conserve energy, and use milk for growth, especially as they fast for such significant periods. There has been a plethora of studies that have viewed pinnipeds as ideal models for the differential investment theory, but the evidence remains equivocal. This study investigated a species that has shown some support for differential investment in the past, in the form of pup growth and maternal attendance behaviour, and looked at the potential that these intersexual differences are due to differential utilisation of maternal resources (different body compositions) and/ or differential fasting strategies by pups, which may be determined by fasting mass loss rates. This study hopes to encompass both aspects of differential investment, such as maternal attendance, as well as differential fasting strategies of pups by looking at their fasting mass loss rates. This study found that males were larger and longer throughout the lactation period, yet grew at the same rate as females. There was no detectable intersexual difference in the maternal provisioning provided by a mother, in the form of attendance. There was some evidence that males and females have different fasting strategies, in that females, from a subset of pups exhibited significantly higher MSMLR's. This finding should be treated with caution however, as sample size was low, and a cross sectional samples revealed no significant differences. Furthermore, study of the activity rates of the same pups over the duration of the fast, found no significant intersexual differences in activity rates. These results suggest that further studies are needed that encompass both aspects of differential investment theory, as well as differential utilisation by pups.

CHAPTER 1

INTRODUCTION

New Zealand fur seal (NZFS), *Arctocephalus forsteri*, populations are currently rapidly expanding in many parts of South Australia (Shaughnessy and Dennis, 2003). The cessation of sealing in the early 19th century has been an important contributing factor to not only this species recovery, but many other fur seal species as well (Ling, 1999). Ultimately, the rate of this recovery is driven by food availability and its affects on female recruitment and breeding success, and the survival of pups to weaning age and beyond. Between birth and weaning, fur seal pups fast for significant periods, and survival is influenced by their growth rate and mass at weaning (Goldsworthy, 1992). The strategies that pups employ during fasting in order to maximise maternal resources are hence as integral as knowledge on maternal provisioning strategies to understand the factors that ultimately shape weaning success and juvenile survival.

How should a parent allocate resources between male and female offspring in order to maximise its reproductive success? There have been numerous publications over the last few decades that have attempted to answer this question and predict how parents should allocate resources between offspring (Wilson and Pianka, 1963; Trivers and Willard, 1973; Dittus, 1979; Maynard-Smith, 1980; Clutton-Brock, 1991). Most notably, Trivers and Willard (1973) attempted to address differential investment in mammals and birds by producing a conceptual model. They suggested that in polygynous species, a male in good condition at the end of maternal investment is expected to out-reproduce a sister in similar condition. Hence, the Trivers-Willard model (TWM) predicts that in polygynous species, given certain assumptions, mothers with extra resources should bias investment towards sons by differential provisioning of sons and daughters. Importantly, the assumptions that needed to be met are that high quality mothers wean high quality offspring, differences in quality between offspring at the end of maternal investment persist to adulthood and the assumption that polygyny leads to greater variance in reproductive success among males, than among females (Mark Hewison and Gaillard, 1999). Here, 'quality' can be taken as any phenotypic trait that influences reproductive success and is partially transferable from mother to offspring (Mark Hewison and Gaillard, 1999).

However, since the TWM was proposed there has been conflicting evidence for its support among mammals. Trivers and Willard (1973) initially used the reindeer, *Rangifer tarandus*, to illustrate their model. Ungulates were seen as good candidates to test the TWM, as most are sexually dimorphic and are generally polygynous, hence, greater variance in the reproductive success of males was expected (Mark Hewison and Gaillard, 1999). In recent studies on certain ungulates, such as fallow deer, *Dama dama*, red deer, *Cervis elaphus* (Clutton-Brock, 1991), and bighorn sheep, *Ovis canadensis* (Mark Hewison and Gaillard, 1999), results have shown that males weighed more and/ or had higher growth rates than daughters during maternal investment. This had been interpreted as mothers having provided higher levels of parental care to their sons. However, despite equally marked sexual size dimorphism and polygyny in white-tailed deer, *Odocoileus virginianus*, bison, *Bison bison*, (as cited in Mark Hewison and Gaillard, 1999), and reindeer (Kojola, 1993), faster growth rates were exhibited in males from these species which could not be attributed to differential maternal care (Mark Hewison and Gaillard, 1999). Therefore, where ungulates were believed to be ideal mammals to apply the concepts of the TWM, evidence for differential maternal investment remains equivocal.

Generally, applying the TWM to mammalian species has resulted in the assumption that greater maternal expenditure is delivered to sons (Goldsworthy, 1995), although there are some exceptions in social primates, where maternal rank has a stronger effect on female reproductive success (Clutton-Brock, 1991).

1.2. Pinnipeds - Ideal Models for Differential Investment Theory (TWM)

Pinnipeds have been viewed as ideal subjects for applying the concepts of the TWM (Trillmich, 1996). As such, there have been a plethora of studies over the last few decades investigating maternal care and the differential investment theory in pinnipeds (reviewed in Trillmich, 1996). Studies on pinnipeds, namely phocids (earless seals) and otariids (eared seals), as well as mammals in general, have invariably started with the preconceived notion that the individual species being studied will in one way or another support or reject the TWM (Goldsworthy, unpublished data). Consequently, a new line of thinking has recently emerged that has started a paradigm shift away from the predictions of the TWM, to equality of maternal investment, and differential utilization of maternal resources by offspring (Arnould *et al.*, 1996; Ono and Boness, 1996; Lunn and Arnould, 1997; Arnould and Hindell, 2002). Evidence supporting this shift in thinking will be discussed later. It is important to understand why pinnipeds were viewed as ideal subjects in the first place.

Firstly, they have a highly polygynous social structure, where successful males mate with multiple females, thus increasing their reproductive success (Trillmich, 1996; Don Bowen, 2002). Evidence to support this presumed higher reproductive success in males is limited, but has been demonstrated in northern elephant seals, *Mirounga angustirostris*. Le Boeuf and Reiter (1988) at Ano Nuevo, in California, demonstrated that successful males were able to mate with as many as 121 females, whereas successful females were only able to wean ten healthy pups in their lifetime. Therefore, as females are limited to the number of offspring they can produce and successfully rear over their lifetime, they are thought to be the limiting sex (Trivers, 1972). Although most females that survive to adulthood will produce offspring, most males won't, hence, greater variance in the reproductive success in males (Harcourt, 1990).

Secondly, land-breeding pinniped species also typically show extreme sexual size dimorphism, which is thought to be the result of sexual selection for traits that improve an individual males ability to hold and defend resources required by females (e.g., birth and thermoregulatory sites) (Don Bowen, 2002). Intersexual size differences in adults are especially evident in phocids, but are also significant in otariids (fur seals and sea lions). New Zealand fur seals exhibit pronounced sexual size dimorphism (Bradshaw *et al.*, 2003), where males may be up to two and a half to three times the mass of females (Dickie and Dawson, 2003). Pinniped adult males show delayed sexual maturation, where even though they may be able to reproduce, they are unable to compete physically for access to females (Berta, 2002). New Zealand fur seal males for example, are only physically able to defend territories at approximately eleven years of age (Troy *et al*., 1999), whereas adult females may, and usually do, begin giving birth between the ages of four and six (Dickie and Dawson, 2003). Consequently, early growth and subsequent increased body size were presumed to affect the reproductive fitness of males more than females. Therefore, under the concepts of the differential investment theory (TWM), mothers were expected to invest more heavily in sons (Clutton-Brock, 1991).

Finally, female pinnipeds, unlike many other carnivores, are the sole providers of nutritional resources to their young, so any measures of parental effort are effectively maternal effort (Harcourt, 1990; Boness and Bowen, 1996). In light of this, and the fact that one pup is produced in most cases (Boness and Bowen, 1996) means that maternal effort provided to subsequent offspring is thought to be potentially easy to quantify in the short term (Harcourt, 1990). Therefore, intersexual differences in pups, such as differential growth rates of pups or biased maternal attendance may reflect differential maternal investment (TWM).

In order to maximise her own lifetime reproductive success, a mother must successfully rear her offspring, and they must then survive and breed in turn (Harcourt, 1990). Trivers (1972) defined parental investment as, "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success), at the cost of the parents' ability to invest in other offspring." With this in mind, it is important to consider the factors of parental investment that are most likely to illustrate any enhancement of an offspring's reproductive success (Goldsworthy, 1995). Most studies on otariid seals, (sea lions and fur seals), have typically investigated differential maternal investment by focusing on offspring's birth mass, growth rates and differences in the maternal attendance behaviour of mothers (periods on-shore/off-shore). Intersexual differences of these factors are ultimately thought to reflect differential maternal expenditure.

Numerous studies have documented intersexual differences in otariids. The mass of pups at birth in the Galapagos fur seal, *A. galapagoensis* (Trillmich, 1986), northern fur seal (Costa and Gentry, 1986), subantarctic, *A. tropicalis* (Bester and Van Jaarsveld, 1994) as well as numerous studies on Antarctic fur seals, *A. gazella* (Doidge *et al.*, 1984a; Boyd and McCann, 1989; Lunn *et al.*, 1993; Goldsworthy, 1995), all reported male pups to have higher birth masses than female pups. Male pups of the New Zealand (Mattlin, 1981; Goldsworthy, 1992), Galapagos (Trillmich, 1986), Antarctic (Doidge *et al.,* 1984a; Lunn *et al.,* 1993; Goldsworthy, 1995), and subantarctic (Kerley, 1985) fur seal, as well as the California sea lion, *Zalophus californianus* (Ono and Boness, 1996) have also been shown to have significantly higher growth rates than females. In addition, intersexual differences in maternal attendance behaviour were reported for New Zealand fur seals on Kangaroo Island, South Australia (Goldsworthy, 1992). Goldsworthy (1992) found that mothers with sons made significantly longer foraging trips than mothers with daughters. Interestingly, this coincided with male pups having higher growth rates for that season. Goldsworthy (1992) suggested that mothers were foraging for longer in order to off load more energy (milk) to males, thus males were more energy demanding were as a consequence growing faster than females. This suggestion was further supported in Antarctic fur seals at Heard Island, where male pups showed a correlation between increases in their mass, and the duration of the preceding and subsequent foraging trip (Goldsworthy, 1995). However, such a correlation was not evident for female pups.

Importantly, a factor of parental investment that has perhaps not been studied as extensively as birth mass, growth rates and maternal attendance in otariids, is the level of milk consumed by fur seal pups. Quantifying the milk intake of pups is an essential component of estimating maternal investment in mammals, including fur seals (Oftedal and Iverson, 1987; as cited in Lea *et al.*, 2002). Methods that have been used to measure milk intake, include the nursing behaviour (suckling rates) of pups, weighing of pups just before and after nursing bout and using tritium dilution techniques (TDT's). The TDT is a complex procedure, but at its simplest involves injecting a pup with tritiated water (radioactive isotope of hydrogen), and through a series of blood samples follow its decline in the body through time. The amount of milk ingested is calculated from the difference between total water influx (water from milk) and water produced from normal metabolic processes of the body, divided by the known fractional water content of fur seal milk (Costa and Gentry, 1986).

Trillmich (1986) observed nursing behaviour in Galapagos fur seals and found that mothers suckled male pups more often. Goldsworthy (1995) weighed Antarctic fur seal pups at Heard Island directly before and after nursing bouts, and found that male pups were significantly heavier than female pups even when body mass differences were taken into account. Thereby indicating that male pups had consumed more milk during the nursing period. Furthermore, male northern fur seal (Costa and Gentry, 1986), and California sea lion (Oftedal *et al.*, 1987; Ono and Boness, 1996) pups, using the TDT, were found to have significantly greater milk intake than female pups; however both Costa and Gentry (1986) and Ono and Boness (1996) found that this significance disappeared when plotted as a function of body mass.

Such intersexual differences in the birth mass, growth rates, maternal attendance behaviour as well as milk intake have been interpreted as evidence of greater maternal provisioning to sons than daughters (Trillmich, 1986; Lunn *et al.*, 1993; Goldsworthy, 1995), and thereby seen as evidence of differential maternal care and the TWM.

However, there have been a number of studies on otariids that have not found intersexual differences in factors of maternal care. Studies on Australian sea lions, *Neophoca cinerea* (Cappozzo, 1991; Higgins and Gass, 1993), South American, *A. australis* (Harcourt, 1990), Antarctic (Lunn and Arnould, 1997; Guinet *et al.*, 2000) and subantarctic (Guinet and Georges, 2000), fur seals have contradicted the evidence for differential maternal investment in otariids. These studies did not find any sex-biased differences in either the birth mass, growth rates and/ or the maternal attendance behaviour of mothers. This has ultimately resulted in a paradigm shift in the interpretation of such results from differential investment to "equal investment/ differential utilisation of maternal resources.

Perhaps the most significant evidence of equal milk consumption between the sexes has come from a number of recent studies using TDT's. Antarctic fur seal pups at South Georgia (Arnould *et al.*, 1996), Australian, *A. pusillus doriferus*, fur seal pups at Kanowna Island off Wilson's Promontory (Arnould and Hindell, 2002) and northern fur seal pups at St. Paul Island, Alaska (Donohue *et al.*, 2002) all showed no intersexual differences in milk consumption by pups. There was, however, an increase in the per-bout, and per-day, milk consumption rate that increased steadily with age (Arnould *et al.*, 1996; Donohue *et al.*, 2002), thus indicating that pups increasingly consume more milk as they age and get bigger. This produces an interesting paradox- males and females of the same mass consume the same, but as males are typically larger than females of the same age, are they consuming more?

It is important to consider that when measuring the milk consumption of free-ranging pups, the TDT assumes that pups do not drink from external water sources (all preformed water from milk). At Iles Kerguelen there have been frequent reports of Antarctic fur seal pups drinking fresh water (Lea *et al.*, 2002). Lea *et al.* 2002 used the TDT, and found that the MWP of free-ranging pups was substantially overestimated when comparing the two groups, as any additional water from drinking is considered as initial body water. As such, the level of milk consumed may be underestimated. Such biases need to be considered when viewing milk consumption rates reported for free-ranging pinnipeds.

Differential milk intake between male and female pups is becoming increasingly unlikely an explanation for differences in growth rates and other sex biased differences. In fact, previously mentioned studies on Antarctic fur seals have shown that male and female pups may differ in mass and growth rates, despite similar rates of milk consumption, because of intersexual difference in both body composition and fasting mass loss rates (Arnould *et al.*, 1996; Guinet *et al.*, 1999; 2000). These studies have ultimately been responsible for the paradigm shift in the way intersexual differences in growth, attendance, and/ or milk consumption are interpreted.

Arnould *et al.*, (1996) examined the body composition of 191 Antarctic fur seal pups on Bird Island, South Georgia and found significant intersexual differences in body compositions. Females had a higher total body lipid % (TBL %) and therefore had greater adipose stores, whereas males had significantly more lean tissue mass (protein/ muscle). Arnould *et al.* (1996) suggested that male and female pups were following different growth strategies, in that they were receiving equal amounts of milk (energy), but that they were directing it to different uses. Male pups were directing more of their energy resources to the laying down of lean tissue whereas females were directing their energy resources to the laying down of adipose tissue. Lean tissue is denser than adipose tissue, and adipose tissue is more energy dense and therefore requires more energy to assimilate (Arnould *et al.*, in press). Ultimately, this means that in order for female pups to be able to achieve the same body mass as male pups they would need to consume more milk (Arnould *et al.*, 1996). As there is equal milk consumption between pups (Arnould *et al.*, 1996), may explain the apparent mass and growth rate differences between the sexes. Similar body composition differences between male and female pups have also been found by more recent studies on Antarctic fur seals at South Georgia (Arnould *et al.*, 2001b), Australian fur seals at Kanowna Island (Arnould and Hindell, 2002), and subantarctic fur seals at Amsterdam Island (Beauplet *et al.*, 2003). Arnould *et al.* (in press) is the only study that did not find significant body composition differences in Antarctic and subantarctic fur seal pups at Iles Crozet, but this result should be treated with caution, as the sample sizes were low in comparison (n=16 and n=14 respectively). With this exception, it does appear that male and female pups are following different growth strategies.

Furthermore, studies by Guinet *et al.* (1999; 2000) have found that female Antarctic fur seal pups on Macquarie and Kerguelen Islands, respectively, have higher mass-specific mass loss rates during fasting. In other words, when comparing a male and female pup of similar mass during fasting, females would lose more weight, and at a faster rate. Once again, in order for female pups to grow at the same rate as females, they would therefore require greater milk consumption. Guinet *et al.* (1999) suggest that this intersexual difference in the rate of mass loss was be due to differences in the metabolic rate, activity level and/ or body composition of male and female pups. Therefore, the following findings from recent studies on male and female fur seal pups: (1) evidence for equal milk consumption (and/ or other factors of maternal investment) even when there are disparities in birth mass and growth rates, (2) different body compositions and (3) different mass-specific mass loss rates have ultimately resulted in a paradigm shift away from the idea of differential investment (TWM) in fur seals, to equality of investment, and differential utilisation of maternal resources by offspring.

In many earlier studies that investigated differential maternal investment in otariids (and indeed phocids), it was presumed that pups were merely passive vessels into which mothers expend energy (Goldsworthy, 1995). The theory of differential investment assumed that mothers were able to control the level maternal input they allocated to their offspring. The idea of pups undertaking strategies of their own during their pre-weaning growth period in order to maximise the use of the energy they receive, has been largely overlooked. Evidence to support the idea that pups are not merely 'passive vessels', is shown by Arnould *et al.*, (2001a) who observed the effect of provisioning Antarctic fur seal pups who were still nursing with a supplemental supply of milk over a period of time, and compared it to a control group. The pups that received supplemental milk, had higher adipose stores, and their mothers undertook progressively shorter foraging trips than the mothers of the control group. Interestingly, the per-bout milk consumption in treatment pups was lower (approaching significance) than the control group during this period. The fact that the duration of foraging trips declined with the mothers of treated pups, suggests that pups are indeed able to influence the rate of provisioning and amount of energy received. These are important considerations when trying to determine not only how pups receive energy, and also what they do with it.

The spatial and temporal separation of reproduction from aquatic foraging in otariids has meant that pups have had to adapt to long periods without food. Numerous studies have indicated that otariid mothers make increasingly longer foraging trips as lactation progresses (Higgins *et al.*, 1988; Goldsworthy, 1992), and Goldsworthy (1992) has shown that pups fast progressively 80 % of the time between birth and weaning lives. Therefore, in order for pups to maximise the maternal resources they receive, careful consideration should be given as to what strategies pups may employ during fasting, in order to enhance their growth an ultimately to maximise survival and future reproductive success.

To date there has been little investigation into how male and female pups conserve energy and use milk for growth (Guinet *et al.*, 1999). Pups tend to be active while their mothers are absent and therefore those with high activity levels or metabolic rates may use a greater proportion of their reserves between feeding bouts and consequently realize a lower growth rate than less active pups or those with lower metabolic rates (Lunn *et al.*, 1993). For example, due to the higher mass-specific mass loss rates observed in female pups (Guinet *et al.*, 1999; 2000), it was suggested that female pups have higher metabolic rates and/ or activity rates. There has been inconsistent evidence in support of this suggestion. A study using TDT, found that female northern fur seal pups expended up to 25 % more energy than male pups (Costa and Gentry, 1986), whilst another study found that the resting metabolic rate (RMR) of female Californian sea lion pups, using open-flow respirometry, were higher than those of male pups (Ono and Boness, 1996). This could be interpreted to mean that male pups have lower metabolic rates during certain periods, which would aid in conserving more of their energy stores, thereby being more energy efficient during fasting. However, such inter-sexual differences in the metabolic rate of seals are limited to these few studies. Female Antarctic fur seal pups at South Georgia had no significant difference in RMR, using open flow respirometry, compared to males, but they did have a higher mass-specific RMR throughout the fasting period (Arnould *et al.*, 2001). The evidence to support higher activity in females is, however, mostly limited to these few studies. In fact a study by Donohue *et al.*, (2000) also using open-flow respirometry, found no significant difference in the RMR's of male and female northern fur seal pups. Therefore the evidence of intersexual differences in metabolic rate is inconclusive, and more investigation is needed. In terms of the activity rates of pups, various behavioural studies have found conflicting evidence of inter-sexual differences in pup activity as well (Arnold and Trillmich, 1985; Harcourt, 1990, Ono and Boness, 1996). Hence, more investigation of behavioural, fasting mass-loss and metabolic rates are needed to gain insight into what strategies pups are undertaking.

1.2 Study Aims

The broader aims of this thesis are to develop a more comprehensive understanding of how male and female fur seal pups receive, conserve and use energy. Ultimately, this project is significant in that it will advance our understanding of the various strategies that male and female New Zealand fur seal pups, and indeed pinnipeds in general, adopt, in order to enhance their future survival and reproductive success.

The main aim of this thesis is to:

- investigate a species that has shown some evidence of differential investment in the form of maternal attendance and growth, and look at the potential that these intersexual differences in maternal attendance and growth are due to differential fasting strategies, such as differential fasting mass loss rates of pups.

CHAPTER 2

MATERIAL AND METHODS

2.1 STUDY SITE

The study was undertaken at Cape Gantheaume (36°04'S, 137°28'E), the southern most point of Kangaroo Island, in South Australia (Figure 2.1.), where New Zealand fur seals breed on broken rock platforms (Goldsworthy and Shaughnessy, 1994). This site is part of the Cape Gantheaume Conservation Park, a wilderness area on the south-east coast of Kangaroo Island. The main study area was an approximately 150 m long stretch of rocky habitat, known as the Beach sector (BS). The BS lies west from the cape, varying in its terrain from large boulders to flat open areas, and has a steep slope that runs above the colony (approximately 20-40 meters above sea level) (Figure 2.2). The remainder of the colony extends from directly east of the cape, and continues east for approximately 1.5 km, in a northeasterly direction (Figure 2.2).

In order to provide information on the growth strategies of fur seal pups, this study focused on pre-weaned New Zealand fur seal pups, investigating aspects thought to have significant influences on their growth and future reproductive success. These aspects are detailed in the four major sections of this chapter.

In January 2003, entire colony pup production for New Zealand fur seals at Cape Gantheaume was estimated to be 2163, and the BS is presently the second largest part

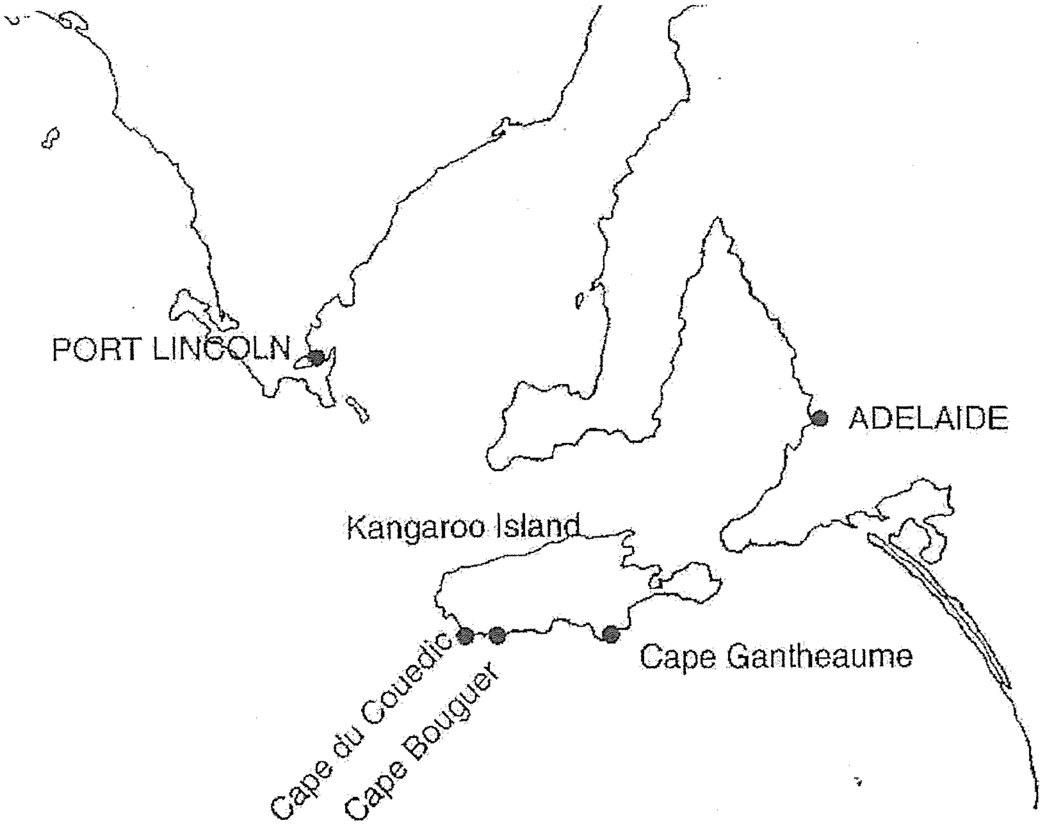

Figure 2.1 Southern part of South Australia showing Kangaroo Island, and Cape Gantheaume (Source: Shaughnessy and Dennis, 2003)

part of the colony in terms of the number of pups born (± 618 pups) Shaughnessy & Dennis, 2003). Pup production for this population has been rapidly increasing at a rate of 16% per annum over the last decade, but appears to have stabilised over the last few years (Shaughnessy & Dennis, 2003). Fieldwork was conducted between late January and late July 2003.

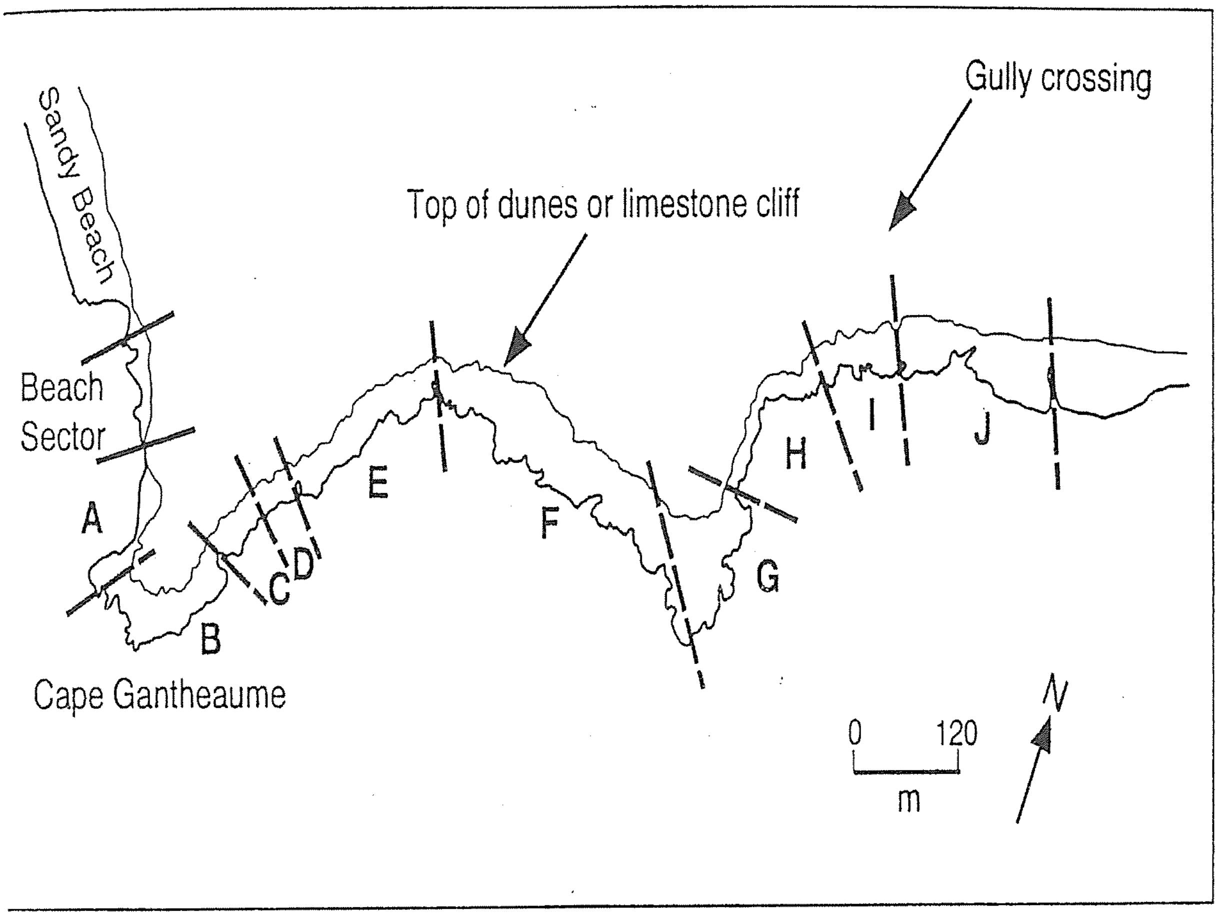

Figure 2.2 Cape Gantheaume colony of New Zealand fur seals showing boundaries between sectors, and the Beach sector (Source: Goldsworthy and Shaughnessy, 1994)

2.2. FIELD METHODS

2.2.1. Pup Growth

Otariid pup growth can be measured using two methods, namely the serial weighing of individually marked pups (Lunn *et al.*, 1993; Lea and Hindell, 1997; Boltnev, 1998; Guinet and Georges, 2000) and the cross-sectional weighing of randomly caught pups (Goldsworthy, 1992; Bester and Van Jaarsveld, 1994; Kirkman *et al.*, 2002; Reid, 2002). This study used the latter method where each independent sample of pups represented a sub-sample of the total pup population for that time period (Kirkman *et al.*, 2002). Growth was monitored four times during the lactation period in order to obtain a growth curve for male and female pups, summarised Table 2.2. During capture pups were sexed, weighed and standard length (STDL) measurements were recorded. Mass was recorded by suspending pups in a canvas bag, from a 25 kg x 100g Salter™ hanging balance (Salter Weigh-Tronix Australia, Blackburn, Victoria). STDL was measured from the straight-line distance from the tip of the nose to the tip of the tail flesh with the head and vertebral column in a straight line, measured to the nearest 0.1 cm (Bester and Van Jaarsveld, 1994). Capture was primarily by hand, but hoop nets were also used as pups became increasingly mobile and more difficult to handle.

Over the study period (January- July), a total of 207 pups were randomly sampled from eleven of the seventeen sectors of the colony (Table 2.2; Figure 2.2). Groups always moved in a forward direction through the colony, and once pups had been measured they were released directly back into the area from where they were sampled, so as to prevent re-sampling. The potential for recapturing the same pup in each successive cross-sectional sample was found to be low. It was calculated from total pup production estimates for each sector in January 2003 (Shaughnessy and Dennis, 2003) that each random sample accounted for about 5-13% of the total pup production for the sectors that they were sampled in.

Table 2.1 Summarised timetable for measurement of growth in 2003

Date sampled	Age[a]	Number of pups sampled Male	Female	Total	Sector sampled
24 January	35 days	41	38	79[b]	BS1/BS2
5 March	75 days	20	20	40	C/D/E
3 April	104 days	20	20	40	J1/H/I
10 July	202 days	24	25	49	BS/F/G/H/I

a Days since mean birth date- ~20 December 2002 (Goldsworthy and Shaughnessy, 1994; Shaughnessy and Dennis, 2003)

b Same pups tagged for maternal attendance observations

As the birth date of randomly caught pups was unknown, growth rates were estimated for each sex from least-squares linear regression analysis of mean mass and STDL (between January and July) against days since the median birth date (MBD) (Guinet *et al.*, 1999; Goldsworthy, in press). Ninety percent of pups at Cape Gantheaume are born within a forty-to-fifty day period between November 2002 and January 2003 (McKenzie, pers. comm.), with the 20 December 2002 the MBD (Goldsworthy and Shaughnessy, 1994; Shaughnessy and Dennis, 2003). As pup birth mass was not obtained, birth mass is not included in the calculation of the growth curves. The MBD for male and female pups was considered to be the same as no difference has been detected in closely related species (Lunn, 1993; Goldsworthy, unpublished data).

2.2.2 Maternal Attendance (pup utilization of maternal presence)

Seventy-nine pups from the BS were randomly caught by hand on the 24 January, about five weeks after their mean date of birth (Shaughnessy & Dennis, 2003). Each pup was tagged with a pair of uniquely numbered three digit orange Dalton^{TM} super tags (Dalton Supplies, Woolgoolga, NSW) on the trailing edge of each fore flipper. At the same time of capture, pups were sexed, weighed, and standard length measurements were recorded (described in section 2.2.1). Observations were conducted twice daily and during two field trips, summarised in Table 2.1. Each observation period lasted 2-3 hours, binoculars (10 x 28) and a Geoma 80A field spotting scope were used to identify tagged pups from the slope above the colony. Six and nine pups from the fasting mass-loss (FML) experiments (March; July) were used to increase the sample size for maternal observations.

Maternal attendance was monitored with the recording of all tagged pups. If an individual pup was present 'with an adult female' or 'nursing', it was recorded as such. If a pup was alone, or with pups, it was recorded as 'other'. The presence/ absence of tagged pup/ mother pairs were used to determine the attendance and foraging trip bouts of lactating females (maternal attendance). A few tagged pups had mothers with identifiable scars, or tags from previous studies, but to ensure continuity of the data, only the presence of a tagged pup with its mother was used as an indication of a mother being ashore. Pup/ mother pairs could be reliably identified because females of this species only tolerate their own pups, and behave antagonistically to non-filial pups that venture too close, or attempt to steal milk (Stirling, 1970; Goldsworthy, 1992; Lea and Hindell, 1997). They also show nursing site fidelity, in that they return to the same area to nurse their pups (Stirling, 1971). Mother-pup pairs were only considered to be present if there was definite physical contact, such as nursing or lying against each other, and they were not seen in an area that was considered to be too far from their normal nursing area. This removed the potential of mistaking pups that were near adult females as mother-pup pairs.

Table 2.1 Summary for maternal attendance observations during 2003

Field-trip	Duration	Number of mother/ pup pairs observed	Daily observation period began
8 March – 4 April	28 days	85	0830; 1730 hours
7 July – 30 July	23 days	75	0900; 1530 hours

The mid-point between successive observation periods was used to estimate female arrival and departure times and, from these, the duration of attendance bouts. A maternal foraging trip (off-shore bout) was calculated from the duration (days) between successive attendance bouts (days absent). The mean of all attendance and foraging bouts for each individual mother-pup pair was used for analysis. The proportion of time a mother stayed on shore/ off-shore was also calculated, which was the total number of days a mother and pup were sighted on-shore/ off-shore, divided by the duration of the entire field trip. The duration of long foraging trips often exceeded the length of each field trip, and was under represented compared to more regularly observed shorter foraging trips. Results had the potential to be biased towards shorter foraging trips. To account for this potential, a formula was used as described first in Goldsworthy (1992), and later by Lea and Hindell (1997), to estimate the mean length (f, in days) of foraging trips for individual females,

$$f = (A \times S) / (1 - S),$$

where A = mean attendance duration (days), and S = proportion of time spent at sea over the entire observation period. This formula is strongly dependent on the duration of attendance bouts, which were less variable in their duration and recorded in their entirety more often then foraging trips. It treats each field trip as a window in time during which females spend a proportion of time at sea. This formula underestimates mean foraging trip length, but is a more reliable estimate than only using the mean length of observed foraging trips (Goldsworthy, 1992; Goldsworthy, unpublished data).

New Zealand fur seal mothers have been observed leaving their nursing area for brief periods in order to swim in rock pools or along the shore-line (Goldsworthy, 1992). There is a potential of recording highly unlikely 'short breaks' between two observed mother-pup attendance bouts, thereby classifying these 'short breaks' as foraging trips, when the mother had actually been on-shore. Results had the potential to be biased towards shorter attendance and foraging bouts. To remove some of this bias, if there were two or less absences between confirmed observations of a mother-pup pair together, it was assumed that the mother had been present on-shore the whole time. If a mother-pup pair was absent for three or more observations since the last observation, it was assumed that the mother had gone out to sea to forage.

2.2.3 Fasting mass-loss rate

Ten male and ten female pups were randomly captured in the BS and carried with large pet packs to an enclosure a short distance from the colony, where human disturbance would not disturb the rest of the colony. To further minimise disturbance, attempts were made to capture pups during two distinct sessions (am/pm), however this was not possible in July. Attempts were made to select pups that had not been fed recently. This was checked as best as possible by laying the pup flat (dorso-ventrally) and both observing and physically feeling the stomach area. There was no way to determine how long a pup had been nursing from obtaining a cross-sectional sample of pups. In March, plotting the daily mass loss revealed that some pups had residual milk in their stomachs. These pups were used to determine the inflection point, the point at which milk had been emptied from their stomach, and from this comparisons of pups with known fasting duration could be made. The enclosure was 6m x 4m in diameter and constructed from evenly spaced star-pickets with a double layer of chicken wire (1.6m high) secured to the star-pickets with fencing wire. Shade cloth was secured with cable ties to the inner surface of the pen to prevent pups from grazing their noses, and pushing directly against the wire. In order for pups to be able to thermo-regulate as they would in the colony, a small pool filled with sea-water was created and shade cloth covered half the enclosure.

Pups were held in the pen for four days and weighed twice daily (0830; 2030 hours) during two field trips (4-8 March; 5-9 July). For identification purposes the pups in March had a unique marking cut into their fur, by removing a small amount of their top layer of fur (guard hairs), whilst the pups in July were tagged (described section 2.2). Pups were weighed using a 30 kg x 50 g portable electronic platform scale (Wedderburn, Melbourne, Australia). Similar experiments have been undertaken on

Antarctic fur seal pups without any adverse effects (Lea *et al.*, 2002), therefore holding pups for a period of 4 days was not considered to adversely affect the pups. Notably, previous studies on maternal attendance at Cape Gantheaume found that the average duration of maternal foraging trip was 7.7 days, (mean = 5.9 to 9.8 days throughout lactation.

Daily mass loss (DML, kg day^{-1}) was calculated during the fasting period as described in Guinet *et al.*, (1999):

$$\text{DML} = (m1 - m2) / \Delta \text{d}$$

where $m1$ is the mass (kg) of the pup measured after calculating the inflection point indicating complete gastric emptying of milk, $m2$ is the subsequent mass (kg) measurement taken during the fasting period, and Δd is the number of days (d) between $m1$ and $m2$.

The mass-specific rate of mass loss (MSML, kg/d/ initial mass-kg) was calculated according to the relationship:

$$\text{MSML} = M_i - \text{M}_f / \Delta t / Mi$$

where M_i is the initial mass, M_f is final mass, and t is time expressed in days.

2.2.4 Activity (enclosure)

Pup behaviour was monitored during the fasting mass loss experiments to compare the activity levels of male and female pups while they were fasting in the enclosure. Behaviour was grouped into two major categories, namely active and resting. "Active" behaviours included both, what was termed 'low active' and 'high active' behaviour (Ono and Boness, 1996). 'Low active' behaviour was when a pup was sitting upright in one place, and moving some part of the body (grooming or looking around etc). 'High active' behaviour involved the pup moving around the enclosure, squabbling with pups, walking or playing etc. Any other behaviour was classed as "resting". Behaviour was monitored daily by focal observations of uniquely marked pups. Observations were conducted directly after pups were weighed for the morning mass-loss study, and continued until darkness (~2000 hours in March; ~1730 hours in July). An observer would sit next to the pen and out of sight of pups, and every five minutes would scan the pen and record all the pups that were active; all other pups were recorded as resting. The proportion of the whole observation period that each individual male and female pup spent on each activity was calculated.

2.3 Data Analysis

The Statview (version 5.0, SAS Institute Inc., USA)) and SYSTAT statistical packages (SYSTAT, 10.0 statistics, SPSS, Inc.,USA) were used for all statistical analysis.

Independent samples t-test was used to compare means for growth. Analysis of variance (ANOVA) was used to test changes in measurements with time. Growth data (age vs mass/STDL) were logged to linearise growth curves, the slopes and intercepts of which were statistically compared using analysis of covariance (ANCOVA).

Independent samples t-test was used to compare means for attendance. Repeated measures ANOVA was used to compare data between two field trips. Percentage that mother-pup pairs were on-shore and off-shore was converted to a proportion, which was than arcsin (inverse sin or $\sin^{-1}$) transformed (Dytham, 2003). The arcsin transformed data was then averaged and means for males and females were statistically compared as other data.

Sex differences in mass loss were analysed using an ANCOVA with initial mass as a covariate, and repeated measures ANOVA for daily comparisons.

Proportions were arcsin (inverse sin or $\sin^{-1}$) transformed (Dytham, 2003). The arcsin transformed data was then averaged and means for males and females were statistically compared across days, using repeated measures ANOVA.

CHAPTER 3

RESULTS

3.1 PUP GROWTH

The growth rates for mass and length are shown in Figures 3.1 and 3.2 and growth data with pair-wise comparisons of mean mass and length for each sex are summarised in Tables 3.2 and 3.3.

As can be seen in Table 3.1, there was no significant relationship between sex and age verses mass, therefore indicating that slopes were homogeneous and that male and female pups had the same rate of growth in mass. Age verses mass was significant, indicating a significant relationship between age and mass and that this relationship was the same for males and females, however males were significantly heavier throughout the study period (Figure 3.1). Results for length were similar, there was no significant relationship between sex and age verses length, indicating that slopes were homogeneous and that males and females had the same rate of growth in length. There was a significant relationship between age verses length and this relationship was the same for male and females, as slopes are homogeneous. Males were significantly longer throughout the study period (Figure 3.2). In summary, male and female pups were growing at the same rate, in mass and length, despite males being heavier and larger compared to females of the same age.

Table 3.1 ANCOVA table for mass and standard length (DF = degrees of freedom, F = F-value, P = statistical significance - P<0.05)

	MASS			LENGTH		
	DF	F	P	DF	F	P
Sex	1	6.61	0.01	1	6.83	0.01
Age	1	759.57	<0.0001	1	600.57	<0.0001
Sex x Age	1	0.16	0.69	1	0.48	0.49
Residual	204			204		

Table 3.2. Comparison of mean mass (kg) of male and female New Zealand fur seal pups during 2003, Cape Gantheaume, Kangaroo Island.

Independent samples t-test was used to test differences between male and female mass (sd = standard deviation, n = sample size, P = statistical significance).

Date	Age (days)[a]	Sex	Mean Mass	sd	n	P
24 January	35	M	7.6	1.16	41	0.008
		F	6.9	1	38	
5 March	75	M	10	2.1	20	0.054
		F	8.8	1.67	20	
3 April	104	M	12	1.72	20	0.01
		F	10.7	1.28	20	
10 July	202	M	16.8	2.73	24	n.s.
		F	15.7	2.29	25	

a Days since mean birth date ~ 20 December 2002 (Shaughnessy and Dennis, 2003)

Table 3.3. Comparison of mean length (kg) of male and female New Zealand fur seal pups during 2003, Cape Gantheaume, Kangaroo Island.

Independent samples t-test was used to test differences between male and female length (sd = standard deviation, n = sample size, P = statistical significance).

a Days since mean birth date ~ 20 December 2002 (Shaughnessy and Dennis, 2003)

Date	Age (days)[a]	Sex	mean length	sd	n	P
24 January	35	M	74.5	2.82	41	0.012
		F	72.8	3.31	38	
5 March	75	M	82.3	4.86	20	0.036
		F	79.3	3.99	20	
3 April	104	M	84.9	3.86	20	0.025
		F	82.4	2.82	20	
10 July	202	M	91.1	4.16	24	n.s.
		F	90	4.12	25	

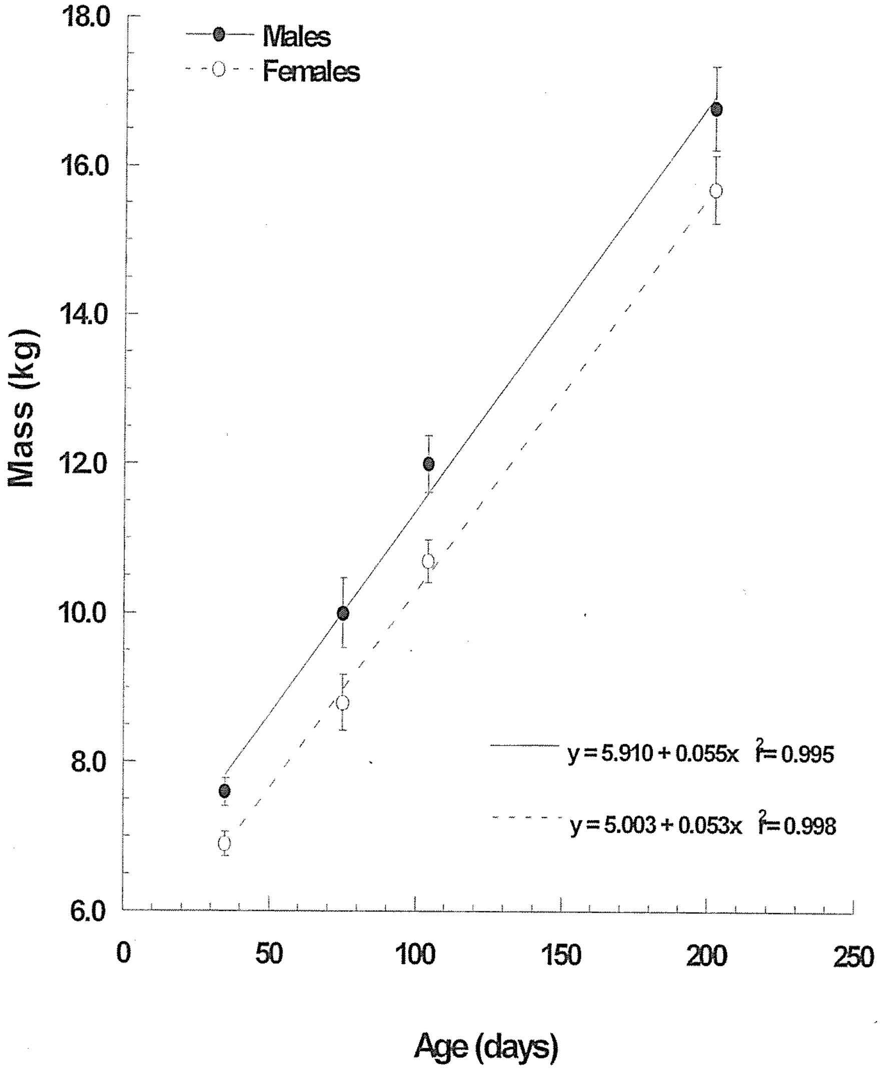

Figure 3.1: Comparing growth in mean mass of both male and female New Zealand fur seal pups during 2003, Cape Gantheaume, Kangaroo Island. Day 0 is 20 December 2002 (~Mean birth date Cape Gantheaume) and error bars are standard error.

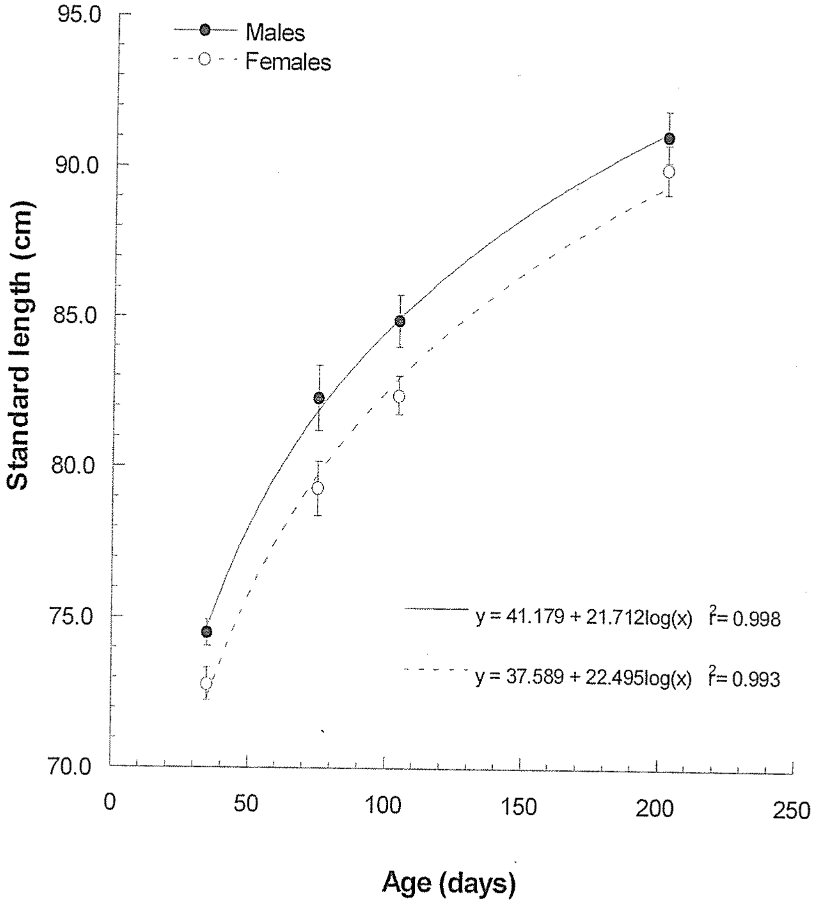

Figure 3.2: Comparing growth in mean length of both male and female New Zealand fur seal pups during 2003, Cape Gantheaume, Kangaroo Island. Day 0 is 20 December 2002 (~Mean birth date Cape Gantheaume) and error bars are standard error.

3.2 MATERNAL ATTENDANCE

There were no intersexual differences in any of the attendance measures during both observation periods. The difference between mothers with sons and mothers with daughters, for all of the attendance measures, were non-significant. Maternal attendance behaviour as a function of offspring sex, including all statistical comparisons, are summarised in Table 3.4. Figure 3.3 shows that mothers' with sons came ashore, on average, a similar duration as mothers' with daughters did, in both March and July. Similarly, there were no significant intersexual differences in the foraging trip measures of mothers' with sons, or daughters.

Between 8 March and 4 April 2003 the grouped mean duration of maternal attendance bouts was 1.4 ± 0.6 days ($n = 85$ mother-pup pairs), while the mean duration of maternal foraging trips was 5.3 ± 1.5 days ($n = 85$). Foraging trips ranged in duration from 2.6 to 8.5 days. This was considerably more variable than attendance bouts, which varied from 0.6 to 3.4 days. Between 7 July and 30 July 2003 the mean duration of attendance bouts decreased to 1.2 ± 0.4 days ($n = 75$), while the mean duration of foraging trips increased to 7.1 ± 2.2 days ($n = 75$). Foraging trips during July were again considerably more variable than attendance bouts, ranging in duration from 3.4 to 11.3 days, with attendance bouts varying from 0.5 to 2.5 days during this period. The actual duration of 290 foraging trips were recorded over the 28 days in March/ April ($n = 85$), which equated to approximately 3 trips per female. During July 156 observed foraging trips were recorded ($n = 75$) over the 23 days, approximately 2 trips per female. The mean of the observed foraging trips (5.0 ± 1.9

days) differed significantly to the mean of the estimated foraging trips (5.3 ± 1.5 days) in March/ April (Paired Samples T-test: n=85, $t<0.001$, $p=0.01$). There was no significant difference between the observed (7.2 ± 3.0 days) and estimated (7.1 ± 2.2 days) foraging trips in July (Paired Samples T-Test: n=75, $t=0.506$, $p=0.61$). There was an increase in the duration of foraging trips over the lactation period (Table 3.4 and Figure 3.3). Mothers spent, on average, 21.2% ashore and 78.8% at sea during March/ April (Table 3.4). The duration that mothers' spent ashore decreased considerably to 14.5% in July.

New Zealand fur seals mothers have been observed moving for brief periods from their nursing spots in order to cool off in rock pools or swim along the shore line (Goldsworthy, 1992). The presence of some mother-pup pairs during daily attendance observations may go undetected even though the mother was still ashore. As such, there was the potential for recording overly long foraging trips. Any outliers, potentially from such a bias, were included in analysis as removing them did not change the statistical significance for any of the attendance measures.

Table 3.4 Differences in the maternal attendance behaviour of New Zealand fur seals during 2003, as a function of offspring sex. Independent sample t-test was used to test differences between the means for male and female pups. Statistically significant difference $p<0.05$, $^{\bullet}$ arcsine transformed data.

	Pup Sex							
	Male			Female			Statistical significance	
	Mean	sd	n	Mean	Sd	n	F	P
Attendance bout duration (days)								
Mar/Apr	**1.4**	0.55	45	**1.4**	0.59	40	0.001	0.847
July	**1.1**	0.45	39	**1.2**	0.44	36	0.795	0.376
% Time ashore								
Mar/ Apr	**21.2**	0.08	45	**21.1**	0.08	39	0.02	0.889$^{\bullet}$
July	**14.8**	0.05	39	**14.3**	0.06	36	0.203	0.654$^{\bullet}$
Foraging trip duration (days)								
Mar/ Apr	**5.4**	1.6	45	**5.3**	1.35	40	0.019	0.892
July	**6.7**	2.22	39	**7.5**	2.18	36	3.009	0.087
% Time at sea								
Mar/ Apr	**78.8**	0.08	45	**78.9**	0.08	39	0.02	0.889$^{\bullet}$
July	**85.2**	0.05	39	**85.7**	0.06	36	0.203	0.654$^{\bullet}$

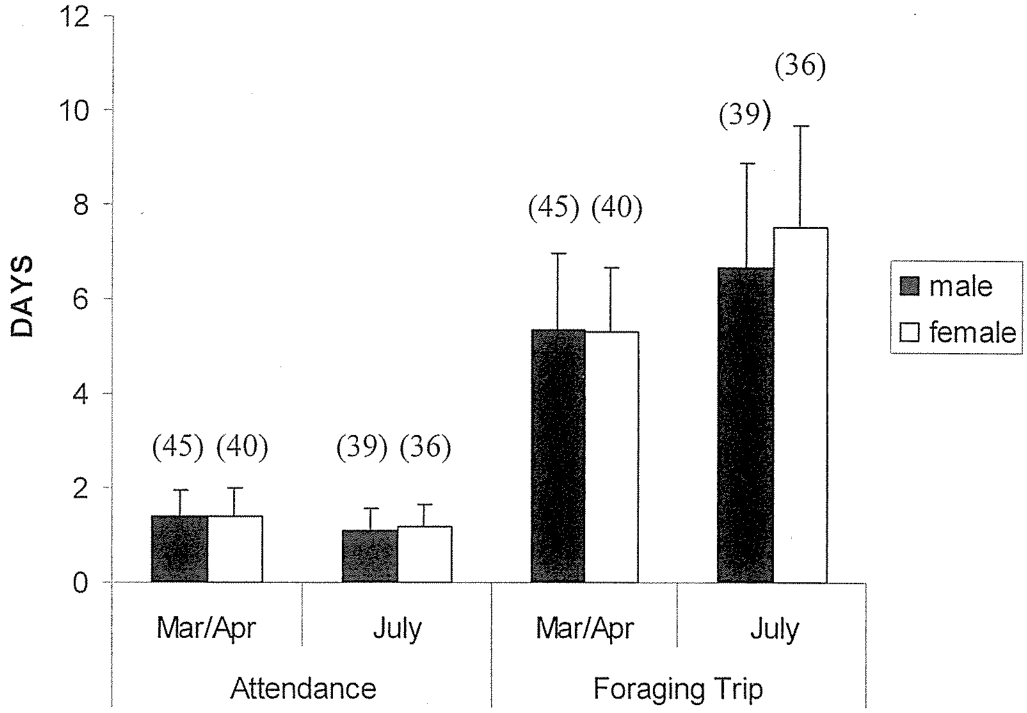

Figure 3.3: Comparison of changes in mean duration of shore bouts and foraging trips of New Zealand fur seal mothers with sons, and mothers with daughters, at Cape Gantheaume, Kangaroo Island in 2003. Error bars are standard deviation; numbers in brackets above are sample sizes.

3.3 FASTING MASS LOSS RATES

The measure of fasting MSMLR, is the rate of mass (kg) lost per day during fasting periods, by pups of the same mass. MSMLR was the main focus for this study, but the mean DML was also calculated and is simply the absolute mass lost (kg) by all pups of varying mass per day.

3.3.1: MASS LOSS OF PUPS OF UNKNOWN FASTING DURATION

Daily mass loss (DML)

Table 3.5 ANCOVA table for DML for March and July 2003 (DF = degrees of freedom, F = F-value, P = statistical significance - $P<0.05$).

	MARCH			JULY		
	DF	F	P	DF	F	P
Sex	1	1.248	0.28	1	0.05	0.83
Initial Mass	1	15.03	0.001	1	7.26	0.02
Sex x Initial Mass	1	0.836	0.37	1	0.004	0.95
Residual	16			16		

When comparing the mean DML of male and female pups, for all four days in March (males, n=10, females, n=10) and July (males, n=10, females, n=10), males were found to have a higher mean DML than females for both periods (March: males, 0.255 kg/day, sd=0.049, females, 0.230 kg/day, sd=0.03; July: males, 0.265 kg/day, sd=0.059, females, 0.254 kg/day, sd=0.038), but as can be seen in Table 3.5, this difference was not significant in either month. Males and females in July had a higher mean DML rate than males and females in March (between March and July), but this difference was not significant ($F_{1,36}=0.224$, $p=0.639$). The initial mass of the pup was the only factor investigated that had a significant relationship with the DML rate of pups in March and July (Table 3.5), where the greater the initial mass of the pup the greater the rate of DML.

Mass-specific mass loss rate (MSMLR)

Table 3.6 ANCOVA table for MSMLR for March and July 2003 (DF = degrees of freedom, F = F-value, P = statistical significance - P<0.05)

	MARCH			JULY		
	DF	F	P	DF	F	P
Sex	1	4.08	0.06	1	0.06	0.81
Initial Mass	1	1.58	0.23	1	2.97	0.10
Sex x Initial Mass	1	3.80	0.07	1	0.02	0.88
Residual	16			16		

Sex and initial mass versus MSMLR was not significant in either March or July, indicating that the slopes for each sex were homogeneous. There was no significant relationship between initial mass and MSMLR in either month. This non-significant relationship was the same for males and females, and there was no significant difference in the MSMLR's between the sexes either (Table 3.6).

Table 3.7 Comparison of mean mass-specific mass loss rates (MSMLR) (kg/kg/day) of male and female New Zealand fur seal pups during 2003, Cape Gantheaume, Kangaroo Island. ANCOVA was used to test for differences between male and female MSMLR (sd=standard deviation, n = sample size, significance level: P<0.05).

Date	Sex	Mean MSMLR (kg/kg/day)	Sd	n	Statistical significance	
					F-Value	P
4-8 March	M	0.024	0.004	10	4.08	0.06
	F	0.026	0.004	10		
5- 8 March[a]	M	0.025	0.003	4	9.94	0.01
	F	0.028	0.003	6		
5-9 July	M	0.015	0.003	10	0.06	0.81
	F	0.016	0.002	10		

[a] only those pups where it was known exactly when they had begun fasting (known inflection point)

The only factor where MSMLR was found to significantly differ, was according to the period of time (March : n=20, July: $F_{1,36} = 82.16$, $p<0.0001$), where pups in July had lower mean MSMLR's than pups in March (March: n=20, mean=0.025 kg/kg/day, sd=0.004; July: n=20, mean=0.016, sd=0.003) (Figure 3.). As there was no significant relationship between sex and time versus MSMLR ($F_{1, 36}$, p=0.98), the slopes are therefore homogeneous for March and July. As such, the data was pooled (Table 3.8; Figure 3. 5).

Table 3.8 ANCOVA table for MSMLR for March and July combined, 2003 (DF = degrees of freedom, F = F-value, P = statistical significance - P<0.05)

	MARCH/JULY		
	DF	F	P
Sex	1	0.79	0.38
Initial Mass	1	65.57	<0.0001
Sex x Initial Mass	1	1.32	0.26
Residual	36		

Table 3.8 shows that for March and July combined, sex and initial mass versus MSMLR was not significant, hence the slopes are homogeneous. The relationship between initial mass and MSMLR is significant, and this relationship is the same for both sexes.

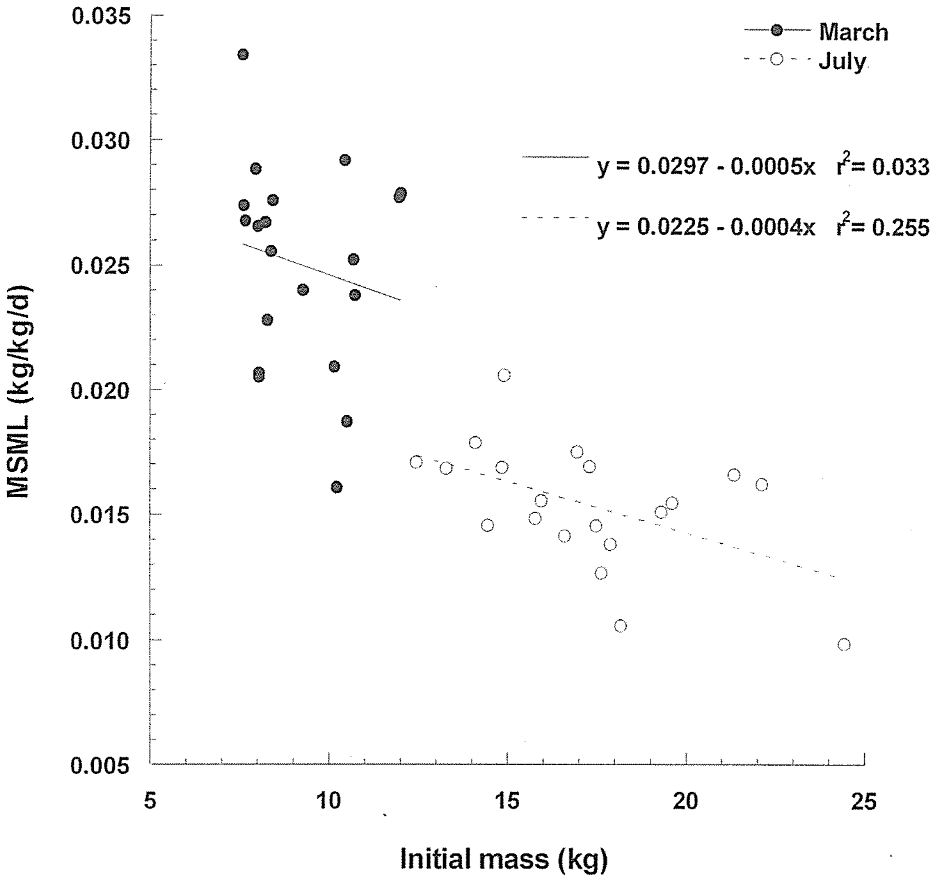

Figure 3.4 MSMLR during the study period showing March and July separately, as a function of initial mass for New Zealand fur seals at Cape Gantheume, 2003

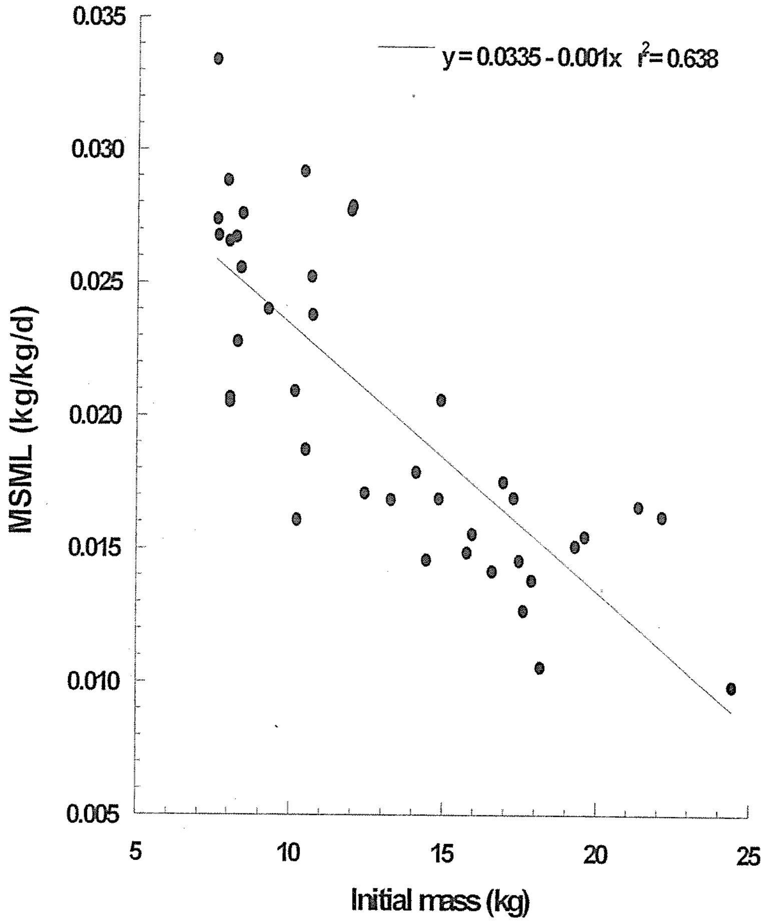

Figure 3.5 MSMLR during the study period showing March and July combined, as a function of initial mass for New Zealand fur seals at Cape Gantheume, 2003

3.3.2 MASS LOSS IN PUPS OF KNOWN FASTING DURATION

MSMLR before and after the gastric emptying of milk (Pre and post inflection points)

Ten pups from March had clearly detectable inflection points (males: n=4; females: n=6) (eg: figure 3.6), where in July there was an insufficient number (n=2) of pups with detectable inflection points to make any meaningful comparisons between months. Comparing the mean MSMLR of pups during the period when they were still assimilating milk (pre-inflection), to when they had undergone complete gastric emptying (post-inflection), revealed that pups had a significantly higher mean (average for all 3 days) MSMLR before the gastric emptying of milk (pre-inflection) ($F_{1,8}=26.72, p<0.001$) (Figure 3.7). There were no inter-sexual differences ($F_{1,8}<0.001, p=0.993$). Figure 3.7 shows the significantly higher mean MSMLR while residual milk was still being emptied from the stomach (pre-inflection) (Figures 3.6 and 3. 7).

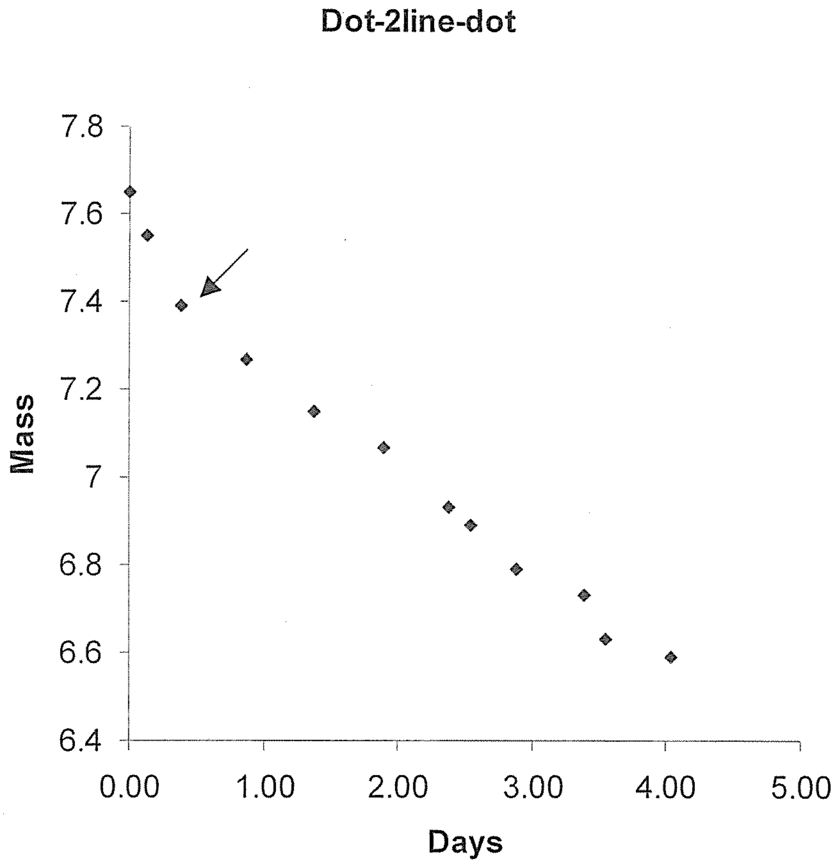

Figure 3.6 Example of a single pup's (Dot-2line-dot) daily mass loss over four days fasting (4-8 March 2003). Arrow shows the point of inflection where the complete gastric emptying of milk has taken place, illustrated by the change in the rate of mass loss after the inflection point. Mass recording on Day 0 is initial mass.

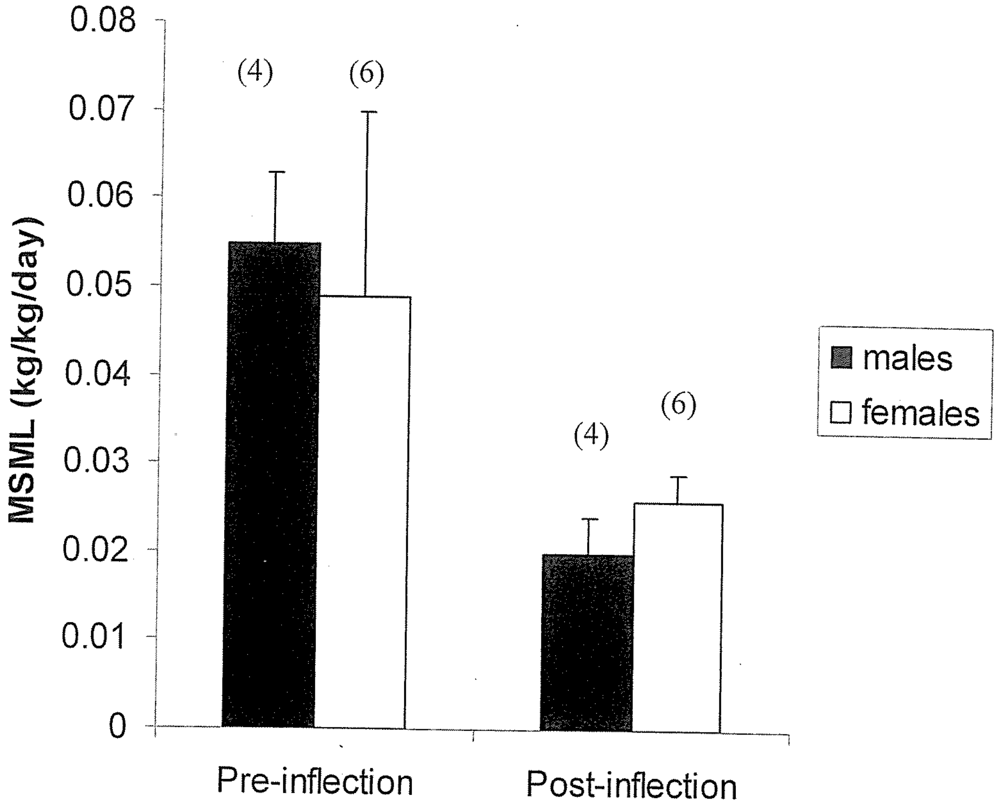

Figure 3.7 Comparison of the pre and post inflection mean mass-specific mass loss rate (MSMLR) of male and female pups with clearly detectable inflection points in March. Pre-inflection is prior to the gastric emptying of milk, while post-inflection is after gastric emptying. Error bars are standard deviation, numbers in brackets above are sample sizes.

Mass specific mass loss rate post- inflection

As we were able to determine when each pup began fasting, daily MSMLR's was compared. Females had a significantly higher mean daily MSMLR than males over the subsequent three days (repeated measures ANOVA: females: n=6, males: n=4; $F_{1,16}$=9.94., p=0.01) (Figure 3.8). Using ANCOVA, with the mean MSMLR as the dependent variable, initial mass as the independent variable and sex as a covariate, there was no significant relationship between MSMLR and initial mass ($F_{1,6}$=0.84, p=0.40).

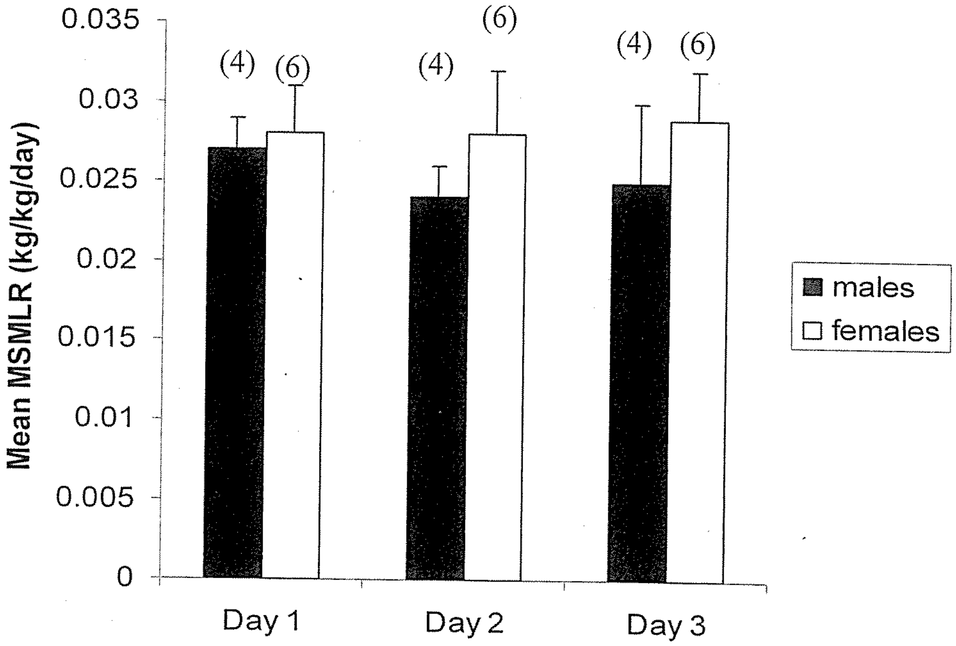

Figure 3.8 Comparison of the mean daily mass-specific mass loss rates of male and female New Zealand fur seal pups with identifiable inflection points, at Cape Gantheaume, Kangaroo Island, during 5-8 March 2003. Day 1 is MSMLR post-inflection. Error bars are standard deviation; numbers in brackets above are sample sizes.

3.4 BEHAVIOUR: PUP ACTIVITY DURING FASTING (ENCLOSURE)

Table 3.9 Comparison of daily activity rates (proportion) of male and female pups over time.

	MARCH				JULY			
	Day 2	Day 3	Day 4	**Mean**	Day 2	Day 3	Day 4	**Mean**
MALE	0.324	0.176	0.262	**0.254**	0.132	0.130	0.095	**0.119**
sd	0.1	0.06	0.07	**0.08**	0.07	0.09	0.1	**0.09**
FEMALE	0.316	0.163	0.228	**0.236**	0.069	0.111	0.071	**0.08**
sd	0.1	0.09	0.09	**0.09**	0.01	0.09	0.08	**0.06**

There were no intersexual differences in the mean daily activity rates of pups in March or July (arcsine transformed data, Repeated measures ANOVA: March: $F_{1, 26} = 0.488, p=0.497$; July: $F_{1, 30} = 1.299, p= 0.281$).

Pups were more active within the enclosure in March, than they were in July (arcsine transformed data, Repeated measures ANOVA: males, $F_{1, 22} = 16.95, p=0.002$; females, $F_{1, 24} = 28.01, p=0.0002$) (Figures 3.8 and 3. 9).

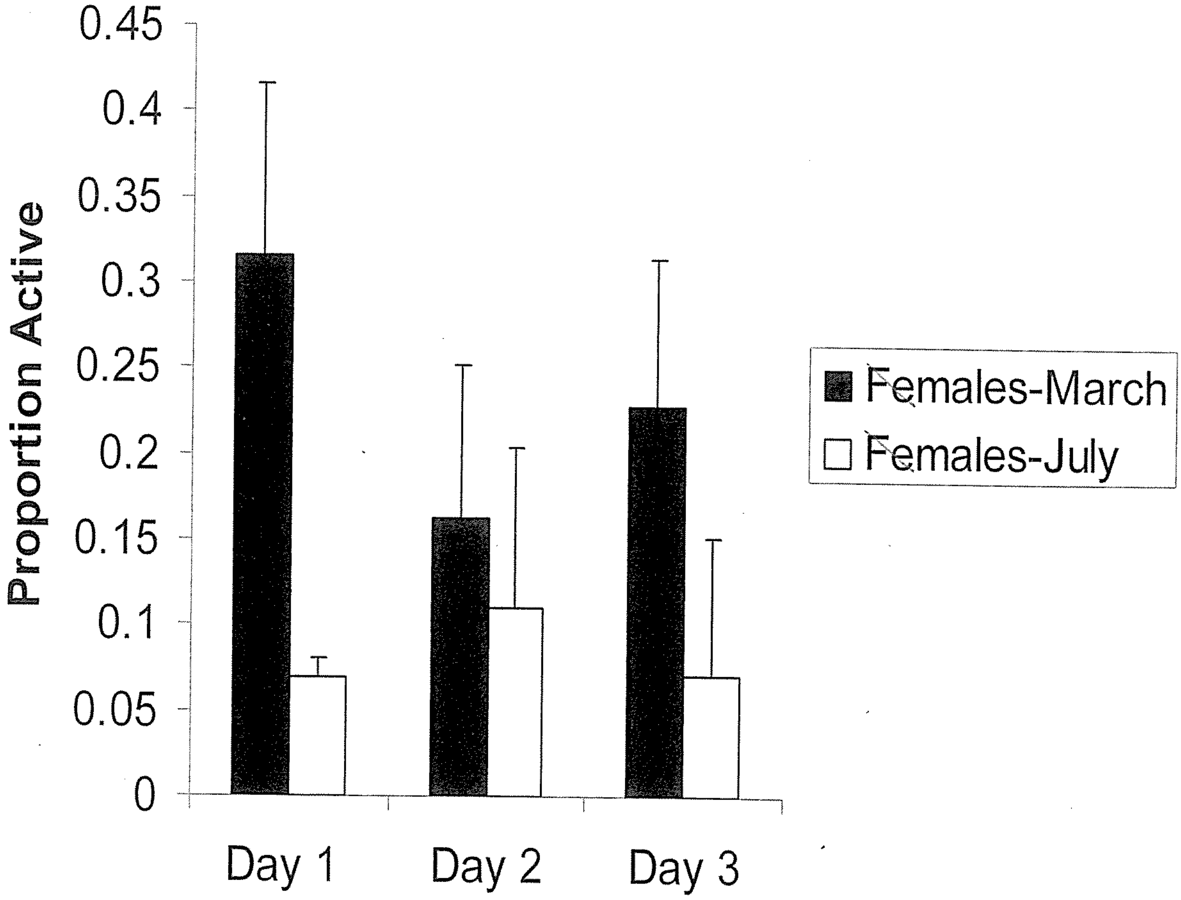

Figure 3.9 Day by day comparison (day 2-4) of the mean proportional activity of penned males from March with penned males from July 2003. Error bars are standard deviation, numbers in brackets above are sample sizes. Sample size: March, n=7; July, n=6

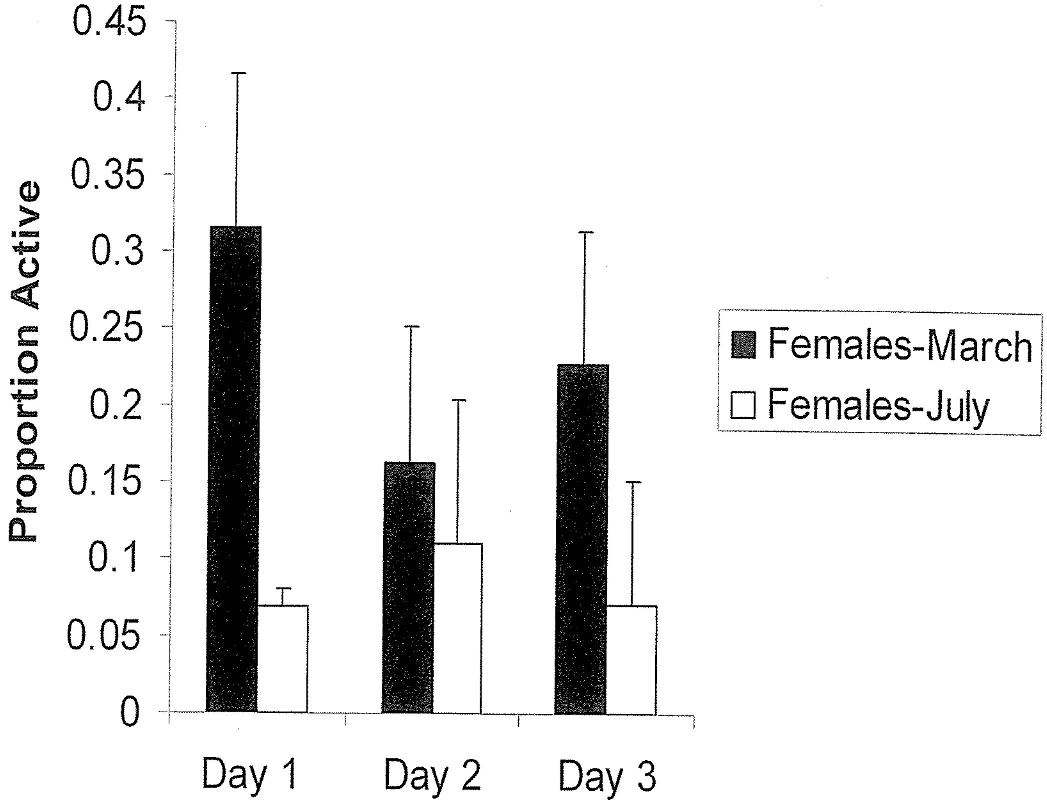

Figure 3.10 Day by day comparison (day 2-4) of the mean proportional activity of penned females from March with penned females from July 2003. Error bars are standard deviation, sample sizes: March, 8; July, 6

CHAPTER 4

DISCUSSION

There is an inherent difficulty in trying to decipher what may or may not seem like evidence for differential investment. For example, the findings from this study where males were larger and heavier than females, yet growing at the same rate, provide some support for differential investment based on the larger size of males, but as to why there is a similarity in growth rates is a little less apparent. Another possibility is that there is no differential investment occurring, but that males and females are possibly utilizing resources differentially. However, yet another explanation may be that there is equal maternal investment, but female pups have higher fasting mass loss rates, where they are losing more mass, and hence not achieving the same size as males. From this it can be seen that depending on what you think may be going on, there are a number of possible arguments to support it. This study, while if you view the findings from a superficial level, supports aspects of equality of investment, and that pups are possibly not only utilising resources differentially, but also have differential fasting strategies (fasting mass loss rates). However, the evidence for from fasting mass loss experiments (differential utilisation) is based on a subset of pups for which we were able to detect inflection points, hence, were able to compare pups which are experiencing a similar stage of fasting. There was no evidence of differential investment in cross-sectional data, and coupled with a low sample size, where the pups with known inflection points only numbered ten. The main finding from this study is that finding a particular result, and tying to interpret according to a restricted view point, undoubtedly creates as many questions as it does answers. The fact there is a number of possible interpretations of any one result, means that possibly the best way to investigate aspects of differential investment, equality of investment, and differential utilisation or fasting strategies, is to not limit the study to only one of a few aspects. The need for studies that encompass the broad range of possibilities and outcomes, may begin to unravel the conflicting evidence that exists today

4.1 POSSIBLE EXPLANATION FOR FINDINGS

For example, if males do exhibit larger mass and are growing at a faster rate than females in a given season, than typically in the past this would have been viewed as support for the TWM. However, even though this may well support the TWM, the paradigm shift in thinking, means that there is a number of ways in which such a finding may be viewed.

The initial aim of this study was to determine whether New Zealand fur seals, which have shown support for differential investment in the past (Goldsworthy, 1992), conform to the assumptions of the differential investment theory (TWM), or whether this evidence of differential investment is potentially due to differential utilisation and/or fasting strategies of pups. Male New Zealand fur seal pups in this study were recorded as being significantly heavier and longer throughout the year. This suggests that males had a faster growth rate than females. However, this study found that even though males were consistently longer and heavier throughout the study period, the growth rates of males and females were the same. This indicates that there are possibly other factors involved that require consideration. However, as no intersexual differences were found in any of the measures of maternal attendance behaviour indicates that New Zealand fur seals at Cape Gantheaume, from the results of this study, do not appear to readily conform to the assumptions of the differential investment theory (TWM). However, the question must be asked whether if there were differences in maternal attendance between offspring, are the techniques used alone enough to detect what might be a subtle interaction that is difficult to measure.

One of a number of presumptions in the past has been that if a mother was providing more care to her son, than she would bias her energy output, such as undertaking longer foraging trips in order to be able to deliver a greater milk volume and energy to her pup (Goldsworthy, unpublished data). The interaction of environmental conditions with the level of energy (milk) that is provided to pups is something to consider when investigating aspects of differential maternal care, such as maternal attendance. The relationship between food availability and the ability of lactating females to optimise the growth of their offspring is important, because if intersexual differences in maternal attendance are occurring then varying environmental conditions could make it difficult to detect (Boltnev, 1998). A number of studies have documented the effects of climatic change and its affects on pup growth. Goldsworthy (1992) documented that New Zealand fur seal females were lighter in 1989, than 1990, where 1989 was during an ENSO (El Nino Southern Oscillation) event associated with low resource availability (Bradshaw *et al.*, 20003a). Pup growth during the same time period revealed that male and female pups had the same growth rate in 1989, whereas in 1990 male pups had higher growth rates. Mattlin (1981) also documented that New Zealand fur seals on the Open Bay Islands were significantly lighter in the summer of 1974-5 compared to the following summer. He concluded that as environmental temperatures in 1974-5 were considerably higher, climatic conditions affected the availability of resources to offspring. Hence, it was thought that under the assumptions of the differential investment theory, that in 'good' resource years mothers were able to bias investment towards sons, while in 'bad' years she was unable to do so.

The results from this study may contradict this argument to some degree, in that pups born in 2002/ 2003, at least in the early stages after birth were below the long-term average weight of pups born over the last fifteen pupping seasons at Cape Gantheaume, and males still exhibited larger length and weight. This suggests that other factors may still be involved, however, it may mean that in order for larger males to actually have higher growth rates, and not just be larger and heavier, then it needs to be an above average season for resource availability. Kirkman *et al.*, (2002) found no evidence of ENSO events affecting subantarctic fur seal pup growth between 1993 and 1998. This illustrates that interpreting evidence of differential investment, may not be as clear cut as is expected, the interaction of environmental conditions (food availability), together with a mother's ability to deliver said resources and the strategies that the pups themselves adopt during extended fasts are all factors that may play a part in the growth rates of pups for any one season. Even though the effect of environmental conditions should be kept in mind when investigating aspects of differential investment, the conflicting evidence for or against differential maternal investment in pinnipeds remains however, even after research spanning a number of decades. This suggests that no one, as yet, has come up with the best way to investigate these aspects.

When attempting to determine the causes of intersexual differences in pup weights and length, there should also be consideration given to other factors, such as, mentioned previously, the effect of environmental conditions and/ or evidence of pups following their own growth strategies during their pre-weaning growth period. The extent of maternal care, how pups utilise this maternal care, in conjunction with environmental conditions are all likely to be extremely influential on the growth of pups (Arnould *et al.*, in press). The ability of mothers to provide nutritional resources to their pups has been the predominant approach when investigating differential investment theory in pinnipeds. Recently, where intersexual differences in the growth rates of pups were interpreted as evidence of differential investment (Boyd and McCann, 1989; Goldsworthy, 1995) increasingly such differences are being viewed at from the perspective of the pup, looking at its ability to efficiently utilise whatever level of resources their mothers' are able to provide to them.

The recent evidence of otariid pups receiving equal milk consumption (Arnould *et al.*, 1996; Arnould and Hindell, 2002; Donohue *et al.*, 2002), intersexual differences in how pups utilise resources, in terms of tissue deposition (i.e., females storing greater adipose tissue and males depositing relatively more lean tissue) (Arnould *et al.* 1996; Arnould and Hindell, 2001; Georges and Guinet, 2001, Bauplet *et al.*, 2003), and the rate of fasting mass loss in pups (Guinet *et al.*, 1999; Guinet *et al.*, 2000) has provided evidence that pups are much more involved in determining their future reproductive success than previously thought. As such, these studies may also provide some insight as to the possible reasons why male New Zealand fur seal pups in this study were consistently longer and heavier during 2003, whilst having the same rate of growth.

The fact that pups in this study appeared to be receiving equal maternal care, as well as that males may be directing a greater proportion of the milk they receive to a tissue that is relatively denser than adipose tissue, may explain why male and female pups are growing at the same rate, but males are consistently heavier and longer. Hence, this leads us to the second aim of the study, are New Zealand fur seal pups, in line with recent studies, adopting different growth strategies.

The fasting mass loss rates of New Zealand fur seal pups were investigated, but the results are presented with caution, as female New Zealand fur seal pups only had significantly higher mass-specific mass loss rates in March, and only when the time since gastric emptying of pup was known. The sample size of the pups with known inflection points was low for each sex as well. Guinet *et al.*, (1999) and Guinet *et al.*, (2000) suggested that the higher fasting mass loss rates of female Antarctic fur seal pups were possibly due to different activity and/ or metabolic rates. Hence, female and male pups were thought to have different strategies during periods of fasting. This study found no intersexual differences in the activity rates of the pups, suggesting that other factors may be involved. The literature has provided, as mentioned in chapter 1, no conclusive evidence that female pups exhibit higher activity or metabolic rates. In fact, an additional study that was being conducted concurrently, investigating the metabolic rates, using open-flow respirometry, of the same pups that were used for the mass loss investigations during March for this study, revealed that there was no significant intersexual differences in the resting metabolic rates of pups over the duration of the fast (Frappell, pers. com). In light of this, and the fact that this study found no differential rates of activity, poses the question of why female fur seal pups have a greater rate of mass-specific mass loss during fasting periods. This creates somewhat of a paradox, in that there is evidence of intersexual differences in pup growth, no apparent evidence of differential investment, male and female pups are possibly behaving differently causing greater mass specific mass loss during fasting, which is thought to be due to differences in metabolic and/ or activity rates, yet evidence thus far, as well from this study, do not appear to indicate activity differences. What is causing one sex to lose more weight during fasting than the other?

An interesting study by Bauplet *et al.*, (2003) on subantarctic fur seals on Amsterdam Island, investigated the body composition of pups as well as body composition changes during fasting. They discovered that there were intersexual differences in the body composition changes of males and females over the duration of the fast. Female pups were reported to rely more on protein catabolism than males (11% and 5% of total energy expenditure respectively) and as a result, male pups lost proportionately more lipid mass than did females during fasting. This finding is interesting in light of the fact that male pups utilise a greater proportion of the energy they receive to the laying down of lean tissue, yet appear to be adopting a form of protein sparing strategy. Similarly, female pups are, as mentioned previously, laying down a greater proportion of adipose stores, yet they appear to be adopting a lipid sparing strategy.

As females are utilising a greater proportion of a denser tissue (protein), and males more lipid reserves, may provide some insight as to why most studies on mass loss rates have reported female pups having a higher mass-specific mass loss rate. Even though the contribution of lipids to energy expenditure was predominant source of energy for males and females (> 50 %), females catabolized twice as much protein for energy during fasting. Hence, the findings of this study where females have the greater use of protein during fasting periods may have provided some of the best evidence thus far, as to why female fur seal pups, including New Zealand fur seals, have higher mass-specific mass loss rates whilst fasting. The findings of Bauplet *et al.*, (2003) where pups are utilising resources differentially, are perhaps as significant, as the study by Arnould *et al.*, (1996) where differences in body composition between male and female pups provided some of the first clear evidence that pups were adopting their own growth strategies. New Zealand fur seals, as most pinnipeds, are sexually dimorphic (Mattlin, 1981; Bradshaw *et al.*, 2003a), and as large size is presumed to aid in male-male interactions, size may provide an advantage and increase their reproductive success. Hence, selection should favour rapid lean body mass in male infants (Arnould *et al.*, 1996). In contrast the need for females to maintain bulk is not as prevalent. A greater accumulation of lipid reserves would tend to enhance survival prospects during the early post-weaning phase, when pups are likely to be inexperienced feeders and environmental conditions less favourable (Baker and Fowler, 1992; Lunn *et al.*, 1993; as cited Arnould *et al.*, 1996).

Female New Zealand fur seals for example, are likely to begin breeding within three to four years post-weaning (Dickie and Dawson, 2003). Hence, undertaking some form of 'lipid' sparing during pre-weaning fasting periods, may provide a dual aid of acting as a 'nutritional buffer' as well as enhancing a females thermoregulatory needs (Arnould *et al.*, in press), during the relatively short period between weaning and breeding when not only will a female need to learn to forage for herself, but also achieve the necessary capabilities of foraging for a pup as well. Male New Zealand fur seals have many more years (up to ten) to continue to forage independently and bulk up for later success at breeding. The concept that male and female pups are both sparing the resources that they deposition predominately, indicates that perhaps male and female pups are both under different selective pressures, and hence are adopting different strategies to enhance the future reproductive success of the species. It is not so difficult to consider, that a pup that spends the majority of its pre-weaning growth period fasting, has in one way or another, through various selective pressures adopted certain strategies to enhance its prospect of survival.

The recent paradigm shift in thinking that has emerged, where pups are thought to play a much more active role in how they utilise the resources they receive (Arnould *et al.*, 1996; Guinet *et al.*, 1999; Guinet *et al.*, 2000), highlights the need for studies that not only consider aspects of differential maternal care, but also the idea that pups have their own growth strategies. The pre-weaning growth period is a time during which fur seal pups must endure considerable periods of fasting, whilst at the same time optimise both their growth and the development of behavioural skills in order to successfully meet the demands of independent living (Arnould *et al.*, in press). The extent of maternal care, the pups own strategies during the early growth period and climatic conditions are all likely to be influential on the growth of pups.

In summary, it appears that from the findings of this study that while differential investment was not evident in the form of maternal investment in New Zealand fur seals, as well as the fact male pups were both consistently heavier and longer, suggests that pups may be following, at least to some degree their own strategies during growth. However, one must be cautious when simply trying to interpret a particular finding as support for TWM, or differential utilisation by pups. The finding that female pups have higher mass-specific mass loss rates and that activity, or metabolic rate over the fast was not accountable for this, creates somewhat of a paradox.

As stated previously, their needs to be a level of caution when interpreting the mass loss data from this study as evidence for differential fasting strategies of pups. The main finding from this study is that there was no definitive support for or against either differential investment, or that pups are following differential strategies. Hence, more studies are needed that cover both, aspects of maternal investment as well as looking at the various strategies of pups.

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