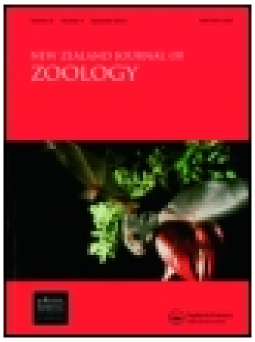

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Suckling behaviours and growth rates of New Zealand fur seals, *Arctocephalus forsteri*, at Cape Foulwind, New Zealand

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Abstract This study investigated suckling behaviours and mother/pup attendance patterns of New Zealand fur seals, *Arctocephalus forsteri*, to determine the effects these behaviours have on pup growth rates. The study was carried out at Cape Foulwind, New Zealand, over the 6 month period from February to July 1993.

The growth rates of pups at Cape Foulwind during this study were the highest recorded for this species in New Zealand, with females averaging 37.1 g/day ± 3.7 SE (n = 108) and males 44.3 g/day ± 3.6 SE (n = 154) over the 140 day period. Male pups were heavier and grew faster than female pups from 60 to 200 days old, but relative sexual dimorphism did not increase significantly. The time mothers spent ashore suckling their pups decreased from 1.7 days ± 0.13 (69) in February to 1.2 ± 0.06 (94) in July. Suckling bout duration was significantly longer for males (27 min ± 2.4 (176)) than females (22 min ± 2.1 (108)). There was a trend for males to suckle more per hour (35 min/h ± 1.5 (197)) than females (33 min/h ± 1.7 (196)), especially during May. Pups terminated 82% of suckling bouts, which, assuming milk was still available, suggests that they are primarily responsible for their own resource allocation while their mothers are ashore. These results are discussed in relation to the factors influencing sexual dimorphism in fur seals.

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Keywords *Arctocephalus forsteri*; New Zealand fur seal; suckling behaviour; sexual dimorphism; pup growth; Cape Foulwind

INTRODUCTION

The New Zealand fur seal, *Arctocephalus forsteri*, is a sexually dimorphic, polygynous species. The breeding season is from early November until January, with females, pregnant from the previous breeding season, arriving at the colony about 2 days before parturition (McNab & Crawley 1975; Miller 1975). They remain with their pup continuously for 8–10 days after birth, and during this time mate with the resident male (Miller 1975). During the next 8–11 months the mothers lactate, dividing their time between caring for their pup ashore and foraging at sea (Crawley & Wilson 1976).

As adults, males are considerably larger than females (Crawley & Wilson 1976), apparently as a consequence of their polygynous breeding system. Males need to be large to be able to gain and defend breeding territory. Previous studies have shown that male fur seal pups have greater birth weight, faster growth, and later average weaning date than females (Crawley 1975; Mattlin 1981; Goldsworthy 1992). These are all indications of a higher allocation of maternal resources to sons rather than daughters (Crawley 1975; Mattlin 1981; Goldsworthy 1992).

The aim of this study was to measure suckling behaviours and mother/pup attendance patterns of New Zealand fur seals, at Cape Foulwind, New Zealand, to determine how these behaviours change throughout lactation and if they are influenced by pup sex. Pup weights and growth rates were used to determine the extent of sexual dimorphism in pup weights over the 6 month period, February–May 1993. The effects of differing suckling behaviours observed, as a result of age and/or sex of pup, were compared with weight data to determine if suckling behaviours are a mechanism that initiates sexual dimorphism of New Zealand fur seals.

MATERIAL AND METHODS

Study area

Fur seals were studied at Cape Foulwind (41°45′S, 171°28′E), Westland, New Zealand. This was a large accessible mainland colony where pups were already tagged and therefore easily identified. In January 1993, the Department of Conservation (DoC) tagged 200 seal pups at Cape Foulwind (100 of each sex), to help monitor the fur seal population along the West Coast. These tagged pups were used in this study.

Pup growth

Pups were weighed by H. Best (unpubl. data) and DoC staff on 8 February 1993, 1 week before this study began. We weighed pups again on 10–11 May and 5–6 July. Pups were caught by hand, sexed, identified (if tagged), placed in light nylon sacks, and weighed to the nearest 100 g on a 0–20 kg spring balance. All captured pups were temporarily marked on the tail with water-resistant paint to ensure that none were weighed more than once that month.

Observations

Fur seal pups and their mothers were observed at Cape Foulwind in February, May, and July of 1993, when pups were about 60, 140, and 200 days old. Each study period consisted of 8–9 days observations, 8–10 h/day during daylight hours, from cliff vantage points overlooking the colony. Observing from the cliffs allowed a good view of seals on the rocky terrain, and meant the colony was not disturbed by the observers. There was usually only one observer; however, during May and July, a second observer was present for 4 days. Each observer could confidently observe two to three closely situated mother/pup pairs at one time. We checked for possible bias between observers, but this was not significant. Seals were observed using a Kowa 20× telescope and Pentax 35 × 7 binoculars. Seals were selected for observation using the following criteria: (1) only females with tagged pups in attendance (not necessarily suckling) were selected (because we did not know the sex of the untagged pups); and (2) identifiable mother/pup pairs were not sampled more than twice in any one day (to avoid repeated sampling of the most visible pairs).

Field records were kept of: (1) date; (2) pup sex and identification number; (3) time that each observation period began and ended; (4) duration of suckling bouts; (5) who terminated suckling bouts; and (6) number of consecutive days mother/pup pairs had been observed, or if the mother had been sighted returning to the colony and had joined with her pup for the first time that day. If possible, each mother/pup pair was kept under observation for a minimum of an hour, which allowed pups to suckle several times in one sample. An observation was terminated if both mother and pup were obscured from view for more than 2 min. Mothers terminated suckling bouts by rolling away from pups, or by using their tails or flippers to prevent pups from suckling; pups terminated by detaching themselves from their mother's teat and beginning some other activity such as play, sleep, or swimming.

The amount of time mothers spent ashore was assessed from the number of consecutive days each mother/pup pair was observed. (Females were not tagged, and may have been ashore for some time before being seen with their pups. However, we were usually able to observe mothers returning, calling, and reuniting with their pups.) The three observation periods (February, May, and July) differed in length, so data on mothers' attendance were truncated to a standard 8 day period for each visit.

A "suckling bout" was defined as the period the pup suckled, including any short (<2 min) breaks during this bout. Bouts of <2 min were excluded from analysis. An "intersuckling bout" was defined as the interval between suckling bouts, provided these were longer than 2 min. These definitions of suckling and intersuckling bout, while arbitrary, follow Goldsworthy (1992) and Oftedal et al. (1987), who considered a suckling bout to consist of both suckling on the teat and the short breaks as pups changed teats.

Pup age and growth rates

To calculate the ages and growth rates of pups, we needed an estimate of their average birth date. The birth dates of pups at the Cape Foulwind colony are unknown so we used the mean birth date of 16 December calculated for seals at Taumaka, Open Bay Islands (the closest seal colony to Cape Foulwind for which information is available; Mattlin 1981). Assuming a 16 December birth date, pups were approximately 60, 140, and 200 days of age when we weighed them.

Three pup growth rates were calculated: 60–140, 140–200, and 60–200 days. Differences in growth rates between sexes were examined using two-sample *t*-tests. Unless otherwise stated, all means in the text are presented ±1 SE.

Suckling behaviour

Data were standardised using the following criteria: (1) observation periods of <30 min were omitted, as they usually did not allow the recording of a complete suckling bout; and (2) observations for which a complete suckling bout was not observed were excluded from the analysis of mean bout length.

Four measures of suckling behaviour were estimated: (1) suckling bout length, in minutes; (2) intersuckling bout length, in minutes; (3) bouts per hour; and (4) minutes per hour suckling. Minutes per hour suckling does not include the periods of restlessness within a suckling bout. Hence, minutes per hour is not equal to suckling bout length times bouts per hour.

General linear models (GLM procedure in Systat; Wilkinson 1992) were used to test the effects of month, pup age, pup sex, and maternal attendance patterns on the measures of suckling behaviour given above. These data were not strictly independent because repeated measures were taken from some mother/pup pairs. However, the level of repeated measures was low (a maximum of 2 per day and a mean of 1.4 per day). Data were tested for normality by plotting residuals. Some analyses were repeated with data log-transformed to improve variance structure, but as these produced virtually identical results to analyses of raw data, they are not presented. Chi-square tests of association were used to investigate the effects of pup sex and age on termination of suckling bouts and the pattern of maternal attendance and its effect on suckling behaviour.

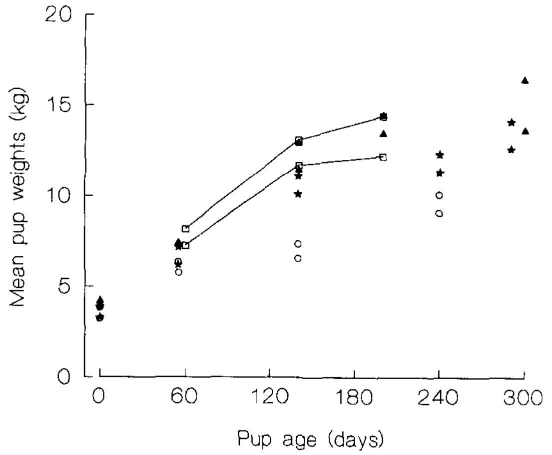

Fig. 1 Comparison of New Zealand fur seal (*Arctocephalus forsteri*) pup weights from Cape Foulwind (□, this study), Open Bay Island (○, 1975; ★ 1976; Mattlin 1981), and Cape Gantheaume, Kangaroo Island, Australia (▲, Goldsworthy 1992). Male pups are represented by the upper weights for each dataset.

RESULTS

Pup weights and growth

The mean weights of male and female pups at 60, 140, and 200 days old are given in Table 1. Male pups were significantly heavier than female pups at all ages (Fig. 1). Percentage sexual dimorphism tended to increased with age (Table 1), the difference was not significant (2-way ANOVA: pup sex × age interaction $P = 0.09$).

Mean pup growth rate from 60 to 200 days was 44.3 g/day ± 3.6 (154) for males and 37.1.0 g/day ± 3.7 (108) for females. Pup growth rates were highest from 60 to 140 days, averaging 61.3 g/day ± 4.4 (112) weight increase for males and 55.0 g/day ± 5.1 (80) for females. Growth rates then slowed significantly, and the average weight gains from 140 to 200

Table 1 Average mean weights ± SE (*n*) of New Zealand fur seal (*Arctocephalus forsteri*) pups at Cape Foulwind, New Zealand, in 1993. Dimorphism is estimated as the difference between male and female weights expressed as a percentage of male weight.

Month	Age (days)	Male pups (kg)	Female pups (kg)	Average body size dimorphism (%)	Intersexual difference in growth rates (%)
Feb[1]	60	8.2 ± 0.20 (50)	7.3 ± 0.15 (50) ($P < 0.001$)	12	17.7
May	140	13.1 ± 0.27 (62)	11.7 ± 0.39 (30) ($P < 0.004$)	12	11.5
Jul	200	14.4 ± 0.46 (42)	12.2 ± 0.49 (28) ($P < 0.002$)	18	63.2

[1] H. Best (unpubl. data).

days were 21.7 g/day ± 8.8 (104) for males and 8.3 g/day ± 10.5 (58) for females.

Suckling behaviour

All four measures of suckling behaviour varied significantly with pup age. Mean suckling bout length increased, so the corresponding number of suckling bouts per hour declined (Table 2). Mean suckling interval was similar in February and May, but increased significantly in July. Minutes per hour suckled increased between February and May, but decreased slightly between May and July (Table 2).

Suckling bouts were longest on the days mothers were observed to haul-out and reunite with their pups, but decreased significantly thereafter (Table 3, $P = 0.02$). The minutes per hour pups suckled showed the same trend ($P = 0.08$). The length of time mothers spent ashore decreased significantly with pup age (Table 4, $P < 0.001$).

Suckling bout termination

Pups ended more suckling bouts than mothers (78% in February, 72% in May, 95% in July; $P < 0.02$ for pooled data). Male and female pups were equally likely to terminate (male 84%, female 81% NS).

Effect of pup sex on suckling behaviour

Mothers spent significantly more days ashore with female pups (1.79 days ± 0.12 (34)) than with male pups in February (1.51 ± 0.13 (35) $P = 0.04$), but not in May or July (Table 4). Mean suckling bout length was significantly greater for males than for females (Table 5; $P = 0.006$); females had more suckling bouts per hour than males (Table 5; $P = 0.16$); males

Table 2 Changes in the suckling behaviours of New Zealand fur seal (*Arctocephalus forsteri*) pups at Cape Foulwind, New Zealand, in 1993. Means ± SE (*n*).

	Pup age			
Parameter	60 days (Feb)	140 days (May)	200 days (Jul)	Significance of month
Bouts per hour	1.9 ± 0.1 (102)	1.6 ± 0.1 (147)	1.2 ± 0.03 (144)	$P < 0.001$
Mean bout length (min)	19.5 ± 1.2 (93)	29.5 ± 1.7 (147)	33.7 ± 1.7 (112)	$P < 0.001$
Minutes per hour	31.1 ± 1.2 (102)	38.4 ± 1.2 (147)	37.5 ± 1.1 (144)	$P < 0.001$
Mean interval length (min)	14.1 ± 1.6 (62)	14.6 ± 1.4 (75)	24.5 ± 1.9 (82)	$P < 0.001$

Table 3 Changes in the suckling behaviour of New Zealand fur seal (*Arctocephalus forsteri*) pups, in relation to the time their mother has been ashore, at Cape Foulwind, New Zealand, in 1993. Means ± SE (*n*). NS = not significant.

	Mother ashore		
Parameter	First day (min)	All other days (min)	Significance
Mean bout length	32.1 ± 3.3 (53)	27.5 ± 1.0 (299)	$P = 0.02$
Bouts per hour	1.6 ± 0.1 (56)	1.6 ± 0.1 (337)	$P = 0.48$ NS
Minutes per hour	37.4 ± 1.9 (56)	36.0 ± 0.7 (337)	$P = 0.08$ NS
Mean bout interval	17.9 ± 2.2 (35)	18.6 ± 1.1 (184)	$P = 0.56$ NS

Table 4 Changes in maternal attendance periods of New Zealand fur seals (*Arctocephalus forsteri*) during lactation at Cape Foulwind, New Zealand, in 1993. Means ± SE (*n*). NS = not significant.

Month	Female (days)[1]	Male (days)[1]	Significance
Feb	1.79 ± 0.12 (34)	1.51 ± 0.13 (35)	$P = 0.04$
May	1.27 ± 0.09 (44)	1.50 ± 0.10 (38)	$P = 0.08$ NS
Jul	1.14 ± 0.05 (50)	1.16 ± 0.06 (44)	$P = 0.79$ NS

[1] Mean number of consecutive days ashore.

and females had similar mean bout intervals (Table 5); and males suckled more minutes per hour than females (Table 5; $P = 0.3$).

In May, male pups had significantly longer and fewer suckling bouts than females (Table 5; $P < 0.01$). These significant results combined to show a trend ($P = 0.09$) for males to suckle more minutes per hour than females in May (Table 5).

DISCUSSION

Pup weight and growth

Pups in this study grew faster between the ages of 60–200 days (44.3 g/day males and 37.1 g/day females) and were notably heavier at 200 days (males 14.4 kg ± 0.5 (42) and females 12.2 kg ± 0.5 (28)) than has been reported elsewhere for New Zealand fur seals. At Taumaka, Open Bay Islands, Mattlin (1981) recorded growth rate, between 55 and 235 days of 19.9 g/day and 17.5 g/day for male and female pups, in 1974–75, and 29.4 g/day and 28.5 g/day in 1975–76. Mean weights for these pups at 235 days were 10.1 kg ± 0.3 (94) for males and 9.1 kg ± 0.3 (81) for females. Crawley (1975) recorded growth rates between the ages of 60 and 240 days of only 7 g/day and 11 g/day for male and female pups, at Taumaka during the 1970–73 breeding seasons. These weighed 9.25 kg ± 0.7 (31) for males and 9.2 kg ± 0.8 (33) for females at 240 days of age.

These differences between studies presumably reflect environmental and human factors, including differences in site latitude, climate, fisheries, food availability, and the changes in the seal colonies over the past 20 years.

Pup body size dimorphism

Before investigating whether suckling behaviours and maternal attendance varied between sexes and influenced dimorphism in New Zealand fur seal pups, the extent of sexual dimorphism needed to be established. As adult New Zealand fur seals show extreme dimorphism, it was anticipated that dimorphism would be apparent from an early age, with males being significantly larger and having proportionally greater growth rates than females. However, the growth rates shown by male and female pups were similar (Table 1). Males were significantly heavier than females at all ages, and the extent of sexual dimorphism did not increase significantly with pup age (Table 1).

As dimorphism in pup size was not pronounced, and did not increase markedly over the 6 month study period, it is likely that any effect of pup sex on suckling behaviour and maternal attendance effects will also be subtle, and thus difficult to detect.

Suckling bout termination

Pups terminated most suckling bouts, indicating that they are primarily responsible for their own resource

Table 5 Changes in the suckling behaviour of New Zealand fur seal (*Arctocephalus forsteri*) pups, in relation to pup sex and age, at Cape Foulwind, New Zealand, in 1993. Means ± SE (*n*). NS = not significant.

	Female pups	Male pups	Monthly significance	Overall significance
Suckling bout length (min)				
Feb (60 days)	17.2 ± 2.2 (42)	16.3 ± 1.5 (51)	NS	
May (140 days)	21.5 ± 1.9 (76)	31.6 ± 2.7 (71)	$P = 0.01$	$P = 0.006$
Jul (200 day)	29.0 ± 2.1 (58)	32.6 ± 2.9 (54)	NS	
Suckling bouts per hour				
Feb	2.1 ± 0.2 (46)	1.9 ± 0.1 (56)	NS	
May	1.8 ± 0.1 (76)	1.5 ± 0.1 (71)	$P = 0.01$	$P = 0.16$ NS
Jul	1.2 ± 0.04 (74)	1.3 ± 0.05 (70)	NS	
Minutes per hour suckled				
Feb	29.9 ± 1.9 (46)	29.5 ± 1.6 (56)	NS	
May	34.8 ± 1.7 (76)	38.9 ± 1.5 (71)	$P = 0.09$ NS	$P = 0.3$ NS
Jul	36.5 ± 1.5 (74)	35.5 ± 1.5 (70)	NS	
Suckling bout interval (min)				
Feb	15.0 ± 2.3 (28)	14.7 ± 2.2 (34)	NS	
May	16.8 ± 1.9 (42)	16.0 ± 1.7 (33)	NS	$P = 0.9$ NS
Jul	24.8 ± 2.4 (44)	26.1 ± 2.9 (38)	NS	

allocation from their mother. We assumed that when pups ended their suckling bouts it was because they were full, although it is possible that the mother had sometimes run out of milk. Males and females terminated bouts in similar proportions.

Seasonal changes in suckling behaviours

The total time pups spent suckling increased with age, primarily through increased suckling bout length. This increased suckling is presumably linked to the greater energy demands of older, larger pups (Oftedal 1984). Suckling bout length increased to meet this demand, so the number of bouts per hour showed a corresponding decrease.

The total time pups spent suckling in May and July were similar, despite pups growing rapidly in the intervening period. It is possible that changes in milk fat and protein composition later in lactation enabled pups to spend the same time suckling, yet obtain greater energy input (Ponce de Leon 1984 cited in Harcourt 1990). Furthermore, older pups may begin catching other foods to supplement their milk intake. Information on changes in milk content throughout lactation, mothers' diet, and pup foraging at different ages would provide a more complete understanding of maternal investment in this species.

Influence of time mother spends ashore on suckling behaviours

More time was spent suckling on the first day mothers hauled out than on subsequent days (Table 3). The decline in time spent suckling during the maternal shore bouts may indicate satiation of pups and/or depletion of maternal milk resources or body reserves (Goldsworthy 1992). Studies by Gentry & Holt (1986) on northern fur seals, *Callorhinus ursinus*, found that if pups were artificially fed or mother/pup reunions were delayed, the length of time mothers spent ashore was extended. This suggests that females may have the capacity to produce only a certain volume of milk to pass on to their pup. Therefore, the pups may obtain more milk on the first day, and as the availability of milk decreases on subsequent days, pups suckle less. The same pattern has been reported for South American fur seals, *Arctocephalus australis* (Harcourt 1990), New Zealand fur seals in Australia (Goldsworthy 1992), and Galapagos fur seals, *Arctocephalus galapagoensis* (Trillmich 1986).

Effect of pup sex on maternal attendance

If females have only a certain volume of milk to pass on to their pups (Goldsworthy 1992), the duration and intensity of pup suckling could affect their mother's time ashore. If pups of one sex demand more milk than pups of the other sex, then the length of time their mothers are ashore may be reduced by faster depletion of milk and/or body reserves. This study did not specifically record the time mothers spent ashore or foraging. Instead, the presence of identifiable pup/mother pairs on consecutive days, over the standardised 8-day observation periods, was used as an index of the period mothers spent with their pups. There was a significant negative correlation between the number of days mothers spent ashore and pup age (Table 4; $P < 0.001$), which apparently resulted from greater demand for food by older pups (cf. Oftedal 1984). Similar decreases in shore times have been reported for the New Zealand fur seal (Goldsworthy 1992); South American fur seal (Harcourt 1990); northern fur seal (Gentry & Holt 1986); Antarctic fur seal, *A. gazelle* (Doidge et al. 1986); South African fur seal, *A. pusillus* (David & Rand 1986); and the Galapagos fur seal (Trillmich 1990).

In February, mothers of females spent significantly longer time ashore than mothers of males (Table 4; $P < 0.04$). However, there was no significant difference in time spent ashore by mothers of pups of different sexes in either May or July. Similar results were found for New Zealand fur seals in Australia in January and February (Goldsworthy 1992). Early in lactation, males may deplete their mothers' milk supply faster than do females. However, this effect was not found later in lactation.

Effect of pup sex on suckling behaviour

Goldsworthy (1992) noted that mothers of male fur seal pups spend proportionally longer time foraging at sea (72% ± 0.1 ($n = 11$)) than mothers of female pups (64.5% ± 0.1 ($n = 17$)), but spend similar periods onshore. This suggests that feeding opportunities for males are likely to be fewer than for females, so that males should adopt a different suckling pattern to females (Goldsworthy 1992).

In this study, the suckling pattern differed between the sexes only in May, when minutes per hour suckled showed a non-significant tendency to be longer for males. Goldsworthy (1992) reported similar trends. From the results of this study, it seems that behavioral and physiological differences among pups start to have an effect on growth mid-way through lactation (May). Subsequent observations (July) reflected the effect of these difference on weight and growth rates.

Other factors that could have affected July's results include a change in the composition of milk, and effects of pup size or sex on suckling efficiency. The influence of such factors on the suckling behaviour of New Zealand fur seal pups is unknown.

General discussion and study limitations

There were several limitations evident in this short study. There was no information on pup birth weights or the mean birth date from the Cape Foulwind colony, so we used data collected at a colony 430 km to the south. Second, the study was discontinued before weaning. Third, direct measurement of maternal foraging trip lengths could have provided a better correlation between maternal attendance and pup growth (cf. Goldsworthy 1992; Harcourt 1990).

To date, no study has investigated the correlation between suckling behaviour and milk intake for New Zealand fur seal pups. Goldsworthy (1992) concluded that differing maternal attendance patterns reflected the greater energy demand of male pups (also shown in their faster growth rates) and therefore a greater milk intake, despite similar suckling behaviours between the sexes. Higgins et al. (1988) studied the suckling behaviour of Steller sea lion, *Eumetopias jubatus*, pups to estimate milk intake and concluded that suckling behaviour was a poor indicator of milk ingestion. The relationship between the suckling behaviour parameters measured and milk intake may therefore be questionable.

Milk fat and protein content have been shown to change during lactation in several species of fur seals (Riedman 1990). For example, the composition of South American fur seal milk changes from 30% fat in the first month of lactation to 54% when pups are 11 months of age (Ponce de Leon 1984 cited in Harcourt 1990). If New Zealand fur seals also make this change in milk composition, an understanding of the factors controlling milk changes (e.g., seasonality, pup age, size, and sex) would be important in determining the significance of changes in maternal effort through lactation.

More accurate determination of the effects of suckling behaviours on weights and growth rates of pup sexes will require consideration of various other factors, including: behavioral and morphological differences between pup sexes, the changes in these parameters as they grow older and increase in size, and the mothers' behaviours and physiology, in relation to pup age and sex.

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