

Ontogeny of aquatic behaviours in Antarctic fur seal (*Arctocephalus gazella*) pups in relation to growth performances at Kerguelen Islands

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Abstract In diving marine predators, such as pinnipeds, the development of diving and foraging skills prior to weaning might be critical to post-weaning survival. Here, we examined the effect of pup mass growth on the amount of time devoted to aquatic activities and the dive performance of Antarctic fur seal, *Arctocephalus gazella*, pups on Kerguelen Island. Maternal attendance and mass-specific growth rate were assessed for 85 pups. Two types of monitoring were applied: visual observations of behaviours for 60 pups and the deployment of time-depth recorders (TDRs) on 19 female pups. At approximately 2 months of age, pups demonstrated minimal diving behaviour, but displayed considerable aquatic activity. While mothers were foraging at sea, pups fasted on land (6.0 ± 1.3 d). As the mass-specific growth rate was different between sexes, only data on female pups were analysed ($n = 31$). Mass-specific growth rate was related to maternal attendance patterns and impacted the amount of time allocated by pups to aquatic activities. The time spent in the water by pups was quadratically related to fasting progress. This study shows the importance of growth and fasting progress on the quantity of time pups devoted to aquatic activities. Our results suggest that greater post-weaning survival of heavier pups may be due not only to their greater body reserves, as reported in several studies, but also possibly to from their greater aquatic skills and physiological adaptations developed during the suckling period.

Keywords Fur seal · Pups · Aquatic activity · Growth rate · Fasting · Kerguelen

Introduction

In marine mammals, pinnipeds differ from cetaceans in their dual dependence on the marine environment for feeding and the shore habitat for reproduction. This spatiotemporal segregation between marine and terrestrial habitats induces specific life history traits and physiological, behavioural and ecological adaptations (Cappozzo 2001). Young pinnipeds must therefore develop capabilities essential to marine life, over a relatively short lactation period.

Lactation in otariids generally lasts 10 months; however, short lactation periods (4 months) are observed for the two high latitude fur seal species: the Antarctic fur seal (*Arctocephalus gazella*) and Northern fur seals (*Callorhinus ursinus*). Pups from these species exhibit the highest mass-specific growth rates reported for otariids (Stirling 1983; Lunn et al. 1993). During this short lactation duration, pups have to develop sufficient aquatic skills to survive the weaning process. Diving skills and frequency of diving behaviours were found to increase over the time (Baylis et al. 2005) in New Zealand fur seal pups that have a 10-month lactation period. Factors influencing the ontogeny of these abilities are the age, physiological development (thermoregulation, metabolism) and the experience of the pup (McCafferty et al. 1998a; Baker and Donohue 2000; Baylis et al. 2005).

Mortality in mammals is generally the highest just after weaning during the early part of life (Beauplet et al. 2005). In two previous studies of otariids with short and long lactation periods, pup post-weaning survival positively

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correlated with pup pre-weaning growth rate and weaning mass (Baker and Fowler 1992; Beuplet et al. 2005). Heavy weaners may be able to rely on greater body stores which may be critical while foraging just after weaning. Beuplet et al. (2005) also found that subantarctic fur seal (*A. tropicalis*) pups weaning with greater mass had a higher post-weaning survival probability than lighter ones. In the Southern elephant seal (*Mirounga leonina*), an extra 5 kg in weaning mass increased pup fasting abilities at sea by 10 days, and heavier pups were also found to have a higher survival rate (McMahon et al. 2000) and improved diving abilities (Hindell et al. 1999).

Consequently, we could expect that Antarctic fur seal pups receiving more milk may allocate more energy to growth but also for sustaining physical activity. Ontogeny of swimming and diving, manoeuvrability as well as thermoregulation adaptation is likely to represent increased energy expenditures. Moreover, resting metabolic rate of Antarctic fur seal pups is higher in water than in air likely due to increased thermoregulation costs (Baker and Donohue 2000; Arnould et al. 2003). Devoting time to the behavioural development of aquatic skills could thus induce high levels of energy expenditure which may potentially reduce a pup's post-weaning fasting abilities. Indeed, these abilities may be crucial during the early period of nutritional independence, while foraging efficiency may still be low (Birgersson and Ekvall 1997).

On the other hand, if pups stay ashore, energy expenditures are likely to decrease, but pups have to compromise with the development of their aquatic skills which might be also critical for post-weaning survival (Chambellant et al. 2003). As a consequence, we can hypothesize that pups receiving more energy from their mothers are able to grow faster but also to allocate more time to the ontogeny of aquatic behaviours (Baker and Donohue 2000).

Otariids are an ideal group for investigating this topic as females give birth to a single offspring, which they then rear and suckle alone until weaning (Stirling 1983; Guinet et al. 2000). Nutritional needs are entirely covered by milk throughout most of the lactation period, and there is no post-weaning maternal care (Arnould et al. 2001). Furthermore, during lactation, mothers alternate short suckling periods ashore and foraging trips to sea during which their pups fast (Bester and Bartlett 1990). While the female forages at sea, pups fast ashore and rely on their body reserves to fuel their activities. We therefore hypothesize that with the extension of fast duration and the depletion of their body reserves pups should allocate less time to aquatic activities which require more energy.

The aims of this study were therefore to determine (1) whether Antarctic fur seal pups exhibiting high growth rates devoted more time to aquatic activity and (2) how

pups allocate their time to aquatic activity in relation to fasting progress.

Materials and methods

Study area

Fieldwork was conducted at Pointe Suzanne, Kerguelen Island (49°00'S, 70°00'E) in a colony of around 900 pups. It took place between December 20th 2008 and February 18th 2009, i.e. during the first 2 months of the breeding cycle.

Pup growth performances

At the beginning of the study, 85 pups were caught and tagged using numbered, plastic tags (Rototag, Dalton supply UK) on the trailing edge of each foreflipper. Pups were weighed using a spring balance (± 100 g), and their standard length (from the snout tip to the tail tip) was measured to the nearest centimetre every week, over a period ranging from 4 to 8 weeks.

Mass-specific growth rates were determined as the slope rate of the linear regression of body mass (kg) against time (days) for each pup. The use of the mass-specific growth rate, as a proxy of pup growth performances, was preferred to the size-specific growth rate and to the body condition index which are dependent on body length. Moreover, the mass-specific growth rate was found to explain a greater percentage of the observed variability in our data compared to the size-specific growth rate and body condition index (results of a PCA).

Maternal attendance

The provisioning attendance patterns of the tagged pups ($n = 85$) were monitored twice a day by direct observation of the presence or absence of their mothers. From these data, the mean trip duration and the regularity of foraging trip for each mother were estimated. This regularity was determined as the standard deviation of mean female trip duration (Lea et al. 2006). The mother provisioned regularly (i.e. made trip of consistent duration) when the value was lower. From these data, the fasting progress (the time elapsed since the mother's departure) in days (d) was also determined for each pup.

Pup behaviour

Two types of monitoring were used to investigate the aquatic activity of pups. First, the behaviour of tagged pups ($n = 60$) was directly observed twice per day during

16 days between 3 and 18 February 2009. The following data were recorded for each sighting of a tagged pup: date, observation period (morning/afternoon), observation area (in water/ashore) and general behaviour (active/rest). Simultaneously, nineteen tagged pups were also equipped with time-depth recorders (TDR, GLS-Lotek LAT 1100 Series, Canada, 35 mm, 8 mm, 5 g) to monitor the time spent in the water (dry-wet) and their diving behaviour. Due to sex differences in growth rates (Stirling 1983; Arnould et al. 2001) and limited equipment, only female pups were monitored with loggers to avoid any differences in behaviour which might be sex-related. Equipped female pups were chosen along a gradient of mass-specific growth rate and according to their fasting stage (beginning of the fast). The logger was attached to the flipper-tag using two nylon cable ties (Advanced Cable Ties, USA) and black adhesive paste (3 M, France).

TDRs were programmed to sample water depth (± 1 m) every 1 s, while pups were in the water and luminosity every 20 s. Thus, recordings allow the detection of dry and wet periods, i.e. the time spent by an individual in water or on land, during day and night.

Analyses of TDR data

TDR data were downloaded, and depth sensor drift over time was individually corrected in each time series using custom-made software developed under R (The R Foundation for Statistical Computing 2009). A linear interpolation was applied to luminosity data to estimate light level for each second. Due to TDR resolution (1 m) and the quality of depth data collected, we were unable to identify true dives characterized by descent, bottom and ascent phases. However, we could quantify for each pup the amount of time spent in the water and some diving performances. The following aquatic behaviour parameters were thus calculated for each individual: proportion of time wet (total wet time/total deployment period), daily proportion of time wet, proportion of time wet during four periods (sunrise, daytime, sunset, night) and duration of each wet period. The four periods of the day were determined using the luminosity profiles, e.g. a luminosity ascent phase corresponds to the sunrise. We also calculated for each pup: mean and maximum dive depth (m) reached over the entire recording.

Data analyses

Factors influencing pup behaviour were examined by using mixed-effect models implemented under the R software (nlme package). As only females were monitored with TDRs, only visual observation data on females were used in the models. The response variable was the daily

proportion of time spent wet ($n = 19$) or the observation area (in water/ashore, $n = 31$). A binomial distribution was used for the observation area response variable. Explanatory variables included mean foraging trip duration, regularity of foraging trip, mass-specific growth rate, fasting day and observation period. The random effect used was the date that was selected using AIC (Akaike Information Criterion) and LRT (Likelihood Ratio Test). Model selection was also performed using these two criteria removing step-by-step non-significant variables to get a final model with only significant variables. An autocorrelation test was also performed to account for repeated-measures in time in a same day.

Additional statistical analyses were performed by fitting linear regression to test the effect of maternal attendance on pup mass-specific growth rate and the effect of the latter one on diving performances. Student's *t* tests were also performed to test the time spent in water according to the four periods of the day.

Results

Effect of maternal attendance on pup mass-specific growth rate

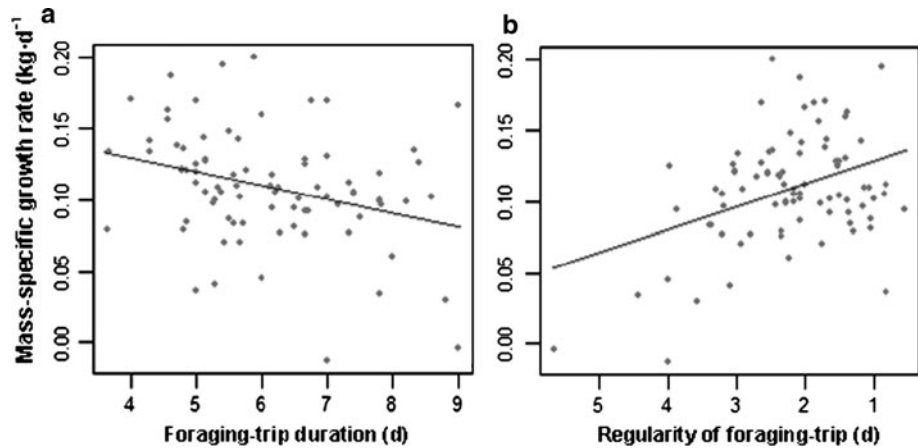
The mass-specific growth rate of the tagged pups was 0.109 ± 0.039 kg d⁻¹. The mass-specific rate was significantly higher for males (0.122 ± 0.041 kg d⁻¹) than for females (0.094 ± 0.031 kg d⁻¹). Mean foraging trip duration determined during this study was 6.0 ± 1.3 d ($n = 85$, ranging from 1 to 15 d), and the mean regularity of the foraging trip was 2.2 ± 0.9 d (ranging from 0.54 to 5.66 d).

Mass-specific growth rate was found to be negatively related to mean foraging trip duration (LM: -0.010 ± 0.003 ; $t = -2.983$; $P = 0.004$; Fig. 1a) and positively related to regularity of foraging trip (LM: 0.016 ± 0.004 ; $t = 3.713$; $P < 0.001$; Fig. 1b). Thus, if two mothers are, on average, making trips of the same duration, the mother provisioning more regularly should have a larger pup. However, if two mothers are making regular trips (with the same CV), the mother making shorter trips should have a larger pup.

General behaviour patterns

Visual observation records were obtained for 31 two-month-old female pups, and TDR-recorded aquatic behaviour was monitored for 19 pups equipped for 2–7 days each, over a 14-day monitoring period. TDR records reveal that at this age, pups demonstrated minimal diving activity, displaying mostly a swimming behaviour at

Fig. 1 Relationships between mass-specific growth rate of pups and **a** foraging trip duration of fur seal females, *Arctocephalus gazella*; and **b** the regularity of their foraging trip



shallow depths (3.4 ± 0.3 m, $n = 19$) with a mean maximum diving depth of 14.1 ± 3.0 m. No clear diving pattern and dives exhibiting the same structure as adult females (a descent-bottom and ascent phases) could be detected. Equipped pups spent most of their time ashore ($74 \pm 5\%$) compared to water ($26 \pm 5\%$), and water visits tended to be brief (0.31 ± 0.25 h). Similarly, 75% of visual observations concerned pups ashore (e.g. 73% for non-equipped pups).

TDR data revealed that the aquatic activity displayed a daily pattern with the majority of aquatic activity taking place during daylight hours (t test: $P < 0.001$) and in particular during the morning (Table 1). Additionally, the factor ‘date’ that was selected as the random effect in the models explained between 8 and 25% of the total variance depending on models.

Time spent in water

The effects of four factors (mean foraging trip duration, regularity of foraging trip, mass-specific growth rate and fasting day) on the two response variables, i.e. the daily proportion of time wet assessed from TDRs and the observation area (in water/ashore) assessed from visual observations, were tested. No auto-correlations were found in data.

The response variables were found to be independent from the mean foraging trip duration and the regularity of foraging trips (Table 1).

However, the probability of being in water estimated from visual data was positively related to the mass-specific growth rate (Table 1, Fig. 2a). Nevertheless, no correlation was found between the mass-specific growth rate and the daily proportion of time wet (TDR data).

Additional models performed from visual observation data, restricted to the 14-day TDR deployment period, also failed to identify significant correlation between the probability of being in water and the overall mass-specific growth rate.

The daily proportion of time wet (TDR) and the probability of being in water (Visual) were significantly related to the fasting progress. However, these relationships were not linear but quadratic (Table 1, Fig. 2b). The time spent in water (daily proportion of time wet and probability of being in water) was initially low, while the mother was ashore (0 day of fasting), then increased with fasting to reach a maximum at day 3–4 of the fast before decreasing progressively with increasing fast duration.

Additional models performed from visual observation data showed, during the early part of the fasting period, a positive correlation between the probability of being in water and the overall mass-specific growth rate (GLMM: 1.656 ± 0.654 ; $P = 0.011$). However, for the latter part of the fast during which the aquatic activity decreased, no significant correlation was found between the probability of being in water and the overall mass-specific growth rate.

Discussion

Potential effect of the logger

An increasing number of ecological and physiological studies on marine animals rely on the use of external recorders raising the question of the effect of these instruments on animal performances, behaviours or energetic expenditure (Hazekamp et al. 2010). However, in our study, equipped pups displayed similar behaviours ($\sim 75\%$ of the time spent ashore) to non-equipped ones indicating that loggers had no detectable detrimental effect on pup behaviour, and this could be explained by their very small size/weight that represents less than 0.5% of pup body mass.

Pup growth

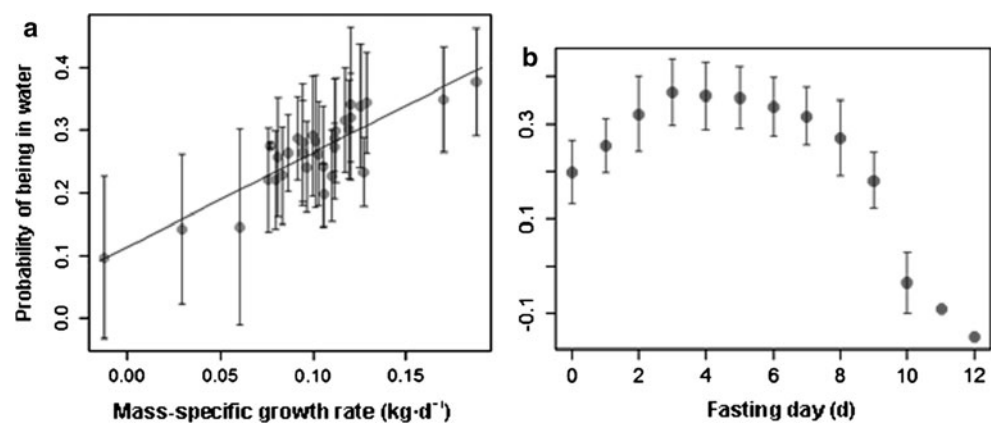
During this study, the mass-specific growth rate estimated was similar to that reported for pups from the South

Table 1 Summary of the mixed-effect models that were fitted on the data coming from the two monitoring types (loggers and visual observations) in Antarctic fur seal pups, *Arctocephalus gazella*

Model selection				Final model	
	AIC	LRT	<i>P</i> value	Coefficients + se	<i>P</i> value
Loggers: daily proportion of time wet					
Full model	-39.3				
Tested variables					
Fasting	-30.5	10.80	0.002	0.131 ± 0.042	0.003
Fasting ²	-34.3	6.99	0.014	-0.022 ± 0.009	0.017
Mass-specific growth rate	-40.1	1.24	0.294		
Mass-specific growth rate ²	-39.4	1.90	0.192		
Mean foraging trip duration	-39.7	1.60	0.023		
Regularity of foraging trip	-41.3	0.01	0.917		
Direct observations: 'observation area' (in water/ashore)					
Full model	303.0				
Tested variables					
Fasting	306.0	5.05	<0.001	0.077 ± 0.022	<0.001
Fasting ²	314.0	13.08	0.002	-0.008 ± 0.003	<0.001
Observation time (morning)	310.9	9.87	0.027	0.096 ± 0.044	0.031
Mass-specific growth rate	301.4	0.44	0.511	1.244 ± 0.595	0.037
Mass-specific growth rate ²	301.0	0.003	0.956		
Mean foraging trip duration	301.0	0.03	0.871		
Regularity of foraging trip	304.2	3.23	0.076		

The 'Model selection' part (on the left) shows all the tested variables, and the 'Final model' part (on the right) shows coefficient values and *P* values of selected variables

Fig. 2 Probability of being in water estimated from mixed-effect models fitted on visual observations data in relation to **a** the mass-specific growth rate and **b** the fasting progress of Antarctic fur seal pups, *Arctocephalus gazella*



Shetland Islands (Vargas et al. 2009) and Kerguelen Island during good years (Lea et al. 2006) and higher than those measured for others breeding site such as South Georgia (McCafferty et al. 1998b), the South Shetland Islands or Kerguelen Island in poor years (Guinet et al. 1999).

Pups displayed high variability in the mass-specific growth rate, with pups provisioned more regularly and/or more frequently growing faster than pups fed less regularly and/or frequently. A positive relationship was also detected between the mass-specific pup growth rate and

the probability of being in water. This indicates that faster growing pups were able to allocate more time to aquatic activity which means that high growth rates were not achieved at the expense of aquatic activity. Thus, contrary to *A.tropicalis* pups (Beauplet et al. 2003) which can get bigger thanks to both maternal investments and an economy strategy (i.e. resting on land rather than swimming actively at sea), Antarctic fur seal pups may get bigger thanks to maternal investments only.

Effect of maternal attendance on pup behaviour

No direct relationship between maternal attendance pattern and time spent in water assessed by either TDR or visual data was found.

Nevertheless, the presence/absence pattern of mothers was found to influence pup behaviours. Indeed, when the mothers is present ashore (Fig. 2b), pups minimize the time they spend in water probably to maximize their milk intake. After the mother departs, the time devoted to aquatic activities gradually increased but did not reach maximum values immediately. This suggests that milk digestion may constrain the activity of the pup. In fact, previous studies have shown that the mass loss rate is higher during the first 48 h following the departure of the mother and that was associated with milk digestion and tissue synthesis (Guinet et al. 2000; Goldsworthy et al. 2004).

Subsequently, the amount of time spent in the water reached maximum values from 3 to the 6th day of the fast before decreasing as fast duration increased. Such a decrease in aquatic activity suggests that at this stage of the fast, pups start to adjust their aquatic activity, probably in relation to increasing energetic constraints. Furthermore, previous studies have shown that *A. gazella* pups exhibited lower mass loss rates in relation to increasing fast duration. In fact, it was suggested that they achieve this by reducing their activity and in particular aquatic activity (Guinet et al. 2000).

Interestingly, it is worth noticing that the mean foraging trip duration for females lasted about 6 days which corresponded to fasting duration inducing no restriction in the amount of time allocated to aquatic activity by the pups.

During the early fasting stage, the amount of time devoted to aquatic activity by pups was positively related to their mass-specific growth rate indicating that faster growing pups were able to allocate more time to the ontogeny of aquatic behaviours. As fasting progresses, no relationship between growth rate and the amount of time devoted to aquatic activity was found, suggesting that regardless of their growth rate, pups tend to adopt an energy saving strategy by reducing their aquatic activity. Thus, pups provisioned regularly and with foraging lasting less than 6 days should be able to allocate the greatest amount of time to aquatic life. It is worth considering as well that while pups may want to save energy as the fasting progresses, they may also choose to remain near the place they last suckled in order to maximize the chances of finding their mothers.

Effect of environmental conditions on pup strategies

In this study, we selected date as the random factor. This factor had a strong effect on the time spent by pups in water. In fact, the amount of time allocated to aquatic

activities and the probability of being ashore varied greatly between days regardless of the growth rate and the fasting stage of the pups. Furthermore, when analysing TDR data, no relationship was found between the mass-specific growth rate and the daily proportion of time wet. This was likely to be related to the short deployment period of the loggers. Indeed, when selecting the observation data (in water/ashore) collected on the same short deployment period as the TDRs, no correlation was found between the two variables. This result could be explained by the effect of environmental conditions, such as extreme temperature, which may exercise strong constraints on pups. Several studies have shown for instance that pups spend less time in water as rainy and windy conditions increase (Baker and Donohue 2000), and pups are less likely to be found in water during rough sea conditions (C. Guinet and M. Viviant personal observation).

By about 2 months of age, pups in our study exhibited minimal diving activity and, no clear dive structure could be identified. However, clear dive patterns and structures were identified in older *A. gazella* pups (McCafferty et al. 1998a). This thus indicates a progressive development of the diving aptitude of *A. gazella* pups between 2 and 4 months of age. In our study, we did not exactly know the age of equipped pups but they were maximum 2 weeks apart. In future studies, it will be important of taking pups of known age. Nevertheless and according to our prediction, our study clearly establishes that faster growing pups were able to devote more time acquiring aquatic behaviours (and skills) by increasing the time they spent in water. Furthermore, this time is also mediated by their fasting stage and environmental conditions, which need to be further investigated. Previous studies have shown that the proportion of time spent in the water increased for *A. gazella* pups (McCafferty et al. 1998a) throughout their rearing period. However, the inverse was found to be true for *A. tropicalis* pups possibly due to a decreasing delivery rate by their mothers (Guinet et al. 2005; Verrier et al. in revision).

Thereby, our results suggest that the greater post-weaning survival of heavier pups may not only be due to their greater body reserves, as reported in several studies, but also possibly to their greater aquatic skills and physiological adaptations developed during the lactation period. In order to test this hypothesis, one needs to investigate the influence of growth performance and fasting stage, through longitudinal monitoring, on the diving performance of pups between 2 and 4 months of age and just after weaning.

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