

The subantarctic fur seal pup switches its begging behaviour during maternal absence

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Abstract: Begging signals from the young are used to elicit parental care. Although honest and parent-directed signaling seems to be widely shared characteristic of begging behaviour, offspring might modify their strategy under some ecological or environmental constraints. In the subantarctic fur seal, *Arctocephalus tropicalis*, mothers forage at sea for 2–3 weeks at a time throughout the lactation period, resulting in regular separations of mothers and pups. Using playback experiments we investigated modifications of pups' begging behaviour during their mother's absence. From the 1st to the 5th day of maternal absence, pups rarely begged in response to other adult females' vocalizations (17.6–46.7% of tested pups), but always responded specifically to their mother's. After its mother had been absent for 5–10 days, the pup's response to playback of strange females' calls was stronger (46–69% of tested pups), but the specificity of the response to the mother remained. However, after the 11th day of maternal absence, pups become highly responsive to calls made by any adult female (up to 37% of tested pups). The variation in responsiveness of fur seal pups during their mother's absence may be explained by changes in their motivational state that were linked to their internal nutritional balance.

Résumé : Les signaux de quémante sont utilisés par les jeunes pour déclencher les soins parentaux. Bien que l'honnêteté des signaux et le fait qu'ils s'adressent aux parents soient des caractéristiques habituelles du comportement de quémante, les jeunes peuvent modifier leur stratégie dans certaines conditions écologiques. Chez l'otarie à fourrure subantarctique, *Arctocephalus tropicalis*, les mères cherchent leur nourriture en mer pendant 2–3 semaines, occasionnant ainsi de fréquentes séparations mère–petit durant toute la période d'allaitement. Nous avons noté les modifications du comportement des jeunes à l'émission d'enregistrement de cris de femelles adultes pendant l'absence de la mère. Durant les 5 premiers jours d'absence de la mère, les petits répondent peu aux cris des femelles adultes (17,6–46,7 % des jeunes testés), mais toujours spécifiquement à ceux de leur propre mère. Des jours 5–10, les jeunes répondent de plus en plus fortement aux cris de femelles (46–69 % des jeunes testés), mais toujours de façon spécifique aux cris de leur mère. Ce n'est qu'à partir du 11ème jour d'absence de la mère que les petits se mettent à répondre fortement aux cris d'autres femelles adultes (jusqu'à 37 % des jeunes). La variation des réactions des jeunes otaries en l'absence de leur mère peut s'expliquer par des modifications de leur motivation en rapport avec leur équilibre énergétique interne.

Introduction

Begging behaviour is performed by young to express hunger and energetic needs in order to elicit parental care (Kilner and Johnstone 1997). In his theory of parent–offspring conflict, Trivers (1974) considered begging behaviour to be selfish. Additional parental care elicited by begging represents a

benefit for the young but may result in additional energetic expenditure for parents (Krebs and Dawkins 1984; Stamps et al. 1989; Balcombe and McCracken 1992; Smolker et al. 1993). As begging behaviour may also be costly for offspring, since the production of vocalizations is energetically costly and calls may alert predators (Ryan 1988; Wells and Taigen 1989; Haskell 1994; McCarty 1996; Dearborn 1999),

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theoretical models suggest that begging signals should honestly express hunger in offspring (Godfray 1991, 1995). Indeed, most previous studies on the subject have shown that begging intensity reflects offspring need, and that parents allocate food to offspring as a function of their begging behaviour (Balcombe and McCracken 1992; Redondo and Castro 1992; Smolker et al. 1993; Mondloch 1995; Price and Ydenberg 1995; Weary and Fraser 1995; Iacovides and Evans 1998). However, some contradictory examples have also been documented. For example, competition among siblings sometimes induces exaggerated begging behaviours (Muller and Smith 1978; Smith and Montgomery 1991), and parents do not always direct their care to the offspring that beg most frequently (Cotton et al. 1999; Leonard and Horn 2001).

On the other hand, a widely shared characteristic of begging behaviour is that the young direct their begging only to their own parents. Indeed, offspring usually only encounter their own parents, and thus would have little opportunity to beg to others. However, in some colonial birds and mammals such as penguins, otariids, and bats, young are commonly observed begging to other adults (Riedman 1990; Balcombe and McCracken 1992; Reilly 1994; Aubin and Jouventin 2002). This suggests that although honesty and parent-directed signalling seem to be two widely shared characteristics of begging behaviour, young may use different begging strategies under some circumstances, such as, maybe, an increase in nutritional needs. Indeed, all previous studies of begging strategies have been performed on species in which parental care is available daily and continuously throughout the breeding period.

We investigated begging behaviour in the subantarctic fur seal, *Arctocephalus tropicalis*, a species in which the availability of maternal care varied greatly throughout the nursing period. In this species, lactation lasts for 10 months, on average, and consists of alternating foraging trips to sea (2–3 weeks) with suckling periods ashore (3–4 days). These long sea trips are a direct consequence of the long distance to appropriate resources for lactation (Georges and Guinet 2000). Pups are thus subjected to frequent and long fasting periods, which are especially challenging for developing animals. When the mother is ashore, the pup exhibits mother-directed begging behaviour, and this is supported by the fact that it is able to recognize its mother's voice among several hundred conspecific females (Charrier et al. 2001). Studies on other fur seal species have described mother–pup interactions such as reunion behaviour and vocal recognition (Trillmich 1981, 1990; Insley 1992, 2000; Charrier et al. 2001), and have focused on mother–pup pairs. In a recent study, Insley (2001) showed that northern fur seal (*Callorhinus ursinus*) pups sometimes seem to make recognition errors, responding to calling females other than their own mothers. However, one can hypothesize that these apparent misrecognitions are not due to imperfect discrimination abilities but represent attempts to get allomaternal care. From this perspective our work is the first study to treat the behaviour of searching pups as “begging behaviour”, i.e., vocal activity as a signal of need. Usually, fur seal pups beg in response to the calls of their own mother. Indeed, begging to a strange female can be costly for pups, since adult females may be very aggressive towards non-offspring that attempt to approach and steal milk (Riedman 1990; Harcourt 1991). However, given the

strong constraint imposed by the long fasting period, one can imagine that pups may beg to several females to try to obtain additional resources.

To investigate the pups' behaviour thoroughly, we propose here to describe the begging behaviour initiated by pups while mothers are foraging at sea. In our study we hypothesized that pups may change their begging strategy during the mothers' absence. First, begging behaviour should honestly reflect physiological energetic need and offspring should become progressively more responsive to calls while maternal absence lasts. Second, responses may become progressively less mother-specific as nutritional needs increase. To test these hypotheses, we played back to each pup the calls of its own mother and those of strange females, and recorded the pup's behavioural response to these playbacks.

Materials and methods

Study location and animals

This study was conducted on Amsterdam Island (37°55'S, 77°30'E) in the Indian Ocean during the pupping period (January–June) in 2000. The study colony was composed of 500–550 adult females. Some females had been tagged for several years, and their pups were marked a short time after birth using a numbered plastic label glued to their fur. When they were approximately 1 month old, pups were tagged in the web of both foreflippers using plastic tags (Rototag, Dalton, Nettlebed, U.K.). Pups ($n = 44$) were 1–7 months old.

Call recordings

For the playback experiments we used pup attraction calls emitted by mothers, which are known to be used in the process of mother–pup recognition (Paulian 1964; Trillmich 1981; Insley 1992; Phillips and Stirling 2000, 2001; Charrier et al. 2001). Calls were recorded with an omnidirectional Revox M 3500 microphone (frequency bandwidth 150–18 000 Hz, ± 1 dB) mounted on a 2 m long boom and connected to a Sony TC-D5M audiotape recorder. Calls were recorded when a female and her pup were searching for each other, e.g., when she returned from a feeding trip to sea or a short swim. During the recordings the distance between the vocalizing mother and the microphone was approximately 0.5 m. Though this distance was short, the behaviour of the female being recorded was never disturbed, since fur seals in the studied colony have become accustomed to humans. Calls were digitized with a 16-bit acquisition card at a sampling rate of 22 050 Hz with a 120 dB/octave anti-aliasing filter.

Playback procedure

Calls were broadcast using a Sony TC-D5M tape recorder connected to an Audax unidirectional loudspeaker via a customized 10-W amplifier (frequency response 1–9 kHz, ± 4 dB). The loudspeaker was placed 3–4 m from the pup. Tests were carried out during the mother's absence (average duration 15 days). The presence of the tagged mothers was checked daily to assess the exact day of departure for their trip to sea.

A playback session consisted of four series with three calls each: one series was made up of calls of the tested pup's mother and the three other series of calls produced by three different strange females (series duration was 10–15 s, allowing 5 min between series; total duration of a session

Table 1. Results of playback tests of subantarctic fur seal (*Arctocephalus tropicalis*) pups during maternal absences.

	Number of days after mother's departure							
	1	3	5	7	9	11	13	15
Percentage of tested pups exhibiting a positive response	17.6	29.6	46.7	69.2	68.2	82.4	75	73.3
Percentage of tested pups exhibiting a non-mother-specific response	0	0	6.7	7.7	13.6	16.7	37.5	26.7
Number of pups tested	17	27	15	13	22	12	8	15

was 20–25 min). To avoid pseudo-replication, the strange females' calls and the mother's calls were different and the order of presentation of the four series was randomized for each playback session. Calls were played at a natural sound pressure level (75 ± 10 dB, measured at a distance of 1 m with a Bruël and Kjaer sound-level meter type 2235). To avoid habituation, each pup was tested 2–3 times during its mother's absence (which lasts 15 days, on average), the tests being spaced at 4- to 5-day intervals. The pup's behavioural response was assessed during each series. We considered that the pup "responded" when it displayed typical begging behaviour during a series playback (emitting calls, making searching head movements, and approaching the loudspeaker) (Fig. 1). The responses of the pups were classified in two categories: "mother-specific response", when the tested pup responded to its own mother's calls but did not respond to the calls of strange females; and "non-mother-specific response", when the tested pup responded to calls from both its own mother and strange females.

Results from all tested pups were then pooled in different time sessions (days 1, 3, 5, 7, 9, 11, 13, and 15 after the mother's departure) to obtain two values: the percentage of pups exhibiting a "response" (either mother-specific or non-mother-specific) and the percentage of pups exhibiting only a non-mother-specific response.

Statistical analysis

We first analyzed the proportion of responding pups ("quantitative" behavioural parameter). To determine whether this proportion varied with the duration of the mother's absence, we performed a *G* test. To characterize the temporal variations in the proportion, we performed a regression on the time elapsed since the mother's departure (maximal duration 15 days, on average) and calculated the correlation between the proportion of responding pups and the number of days since the mother's departure. For this kind of analysis, the non-independence of samples does not constitute a constraint on the statistical analysis (for more details see Hassnaoui et al. 2000). Prior to the regression calculation, to obtain normal and homoscedatic values, all percentages were subjected to arcsine transformations (Sokal and Rohlf 1995).

Second, we analyzed (*G* test and regression) the proportion of pups exhibiting only a non-mother-specific response ("qualitative" behavioural parameter) in the same way.

Another point of the analysis was to determine the eventual effect of both pup age and pup sex on the change in begging behaviour (for example, whether female pups were more responsive than male pups or whether young pups tended to respond more frequently to strange females' calls than older pups did). Because samples were small, we chose to pool some data in age classes (three groups: 1–2, 3–4, and 5–6 months old) and time sessions (four groups: 1–3, 5–7, 9–11, and 13–15 days after the mother's departure). We used

Fisher's exact test to compare the results from male and female pups for each time session and a χ^2 test to compare results between the three age groups for each time session.

Results

The behavioural responses of pups to strange females' and mother's calls changed throughout the mother's absence (Fig. 1). There were both quantitative (proportion of responding pups) and qualitative (proportion of pups showing a non-mother-specific response) modifications of the pups' behavioural responses.

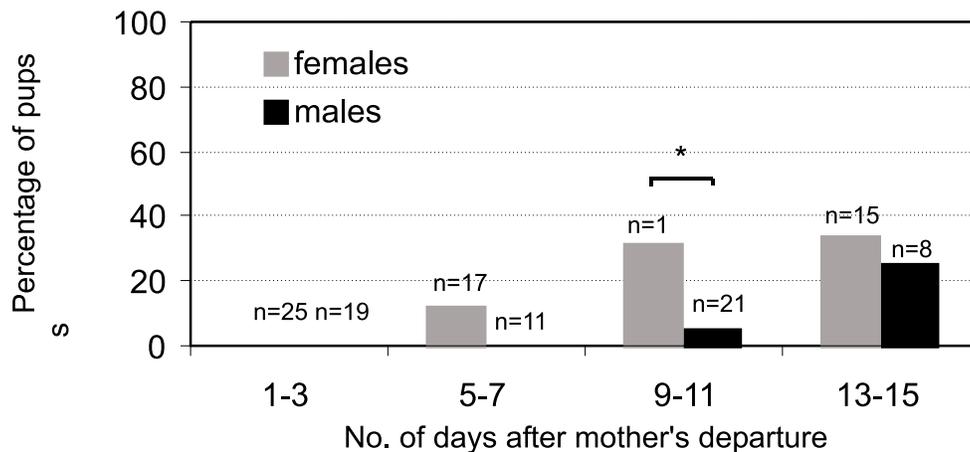
Quantitative modifications of the pup's responses

The proportion of responding pups varied significantly during the mother's absence (*G* test, $G = 28$, $df = 7$, $p < 0.05$). We found a strong positive correlation between the proportion of responding pups and the number of days since the mother's departure (double reciprocal model, $R^2 = 0.95$, $p < 0.05$; Fig. 1A). We showed that from the 1st to 7th days of maternal absence, the proportion of responding pups increased, i.e., pups became more and more responsive to females' calls (increasing from 17 to 69%; Table 1). In contrast, from the 7th to 15th days of maternal absence, the proportion of responding pups increased more slowly, though it remained high, and approached an asymptote (75%; Table 1). These variations in the pups' responsiveness were affected by neither pup age (χ^2 test, $df = 2$, $p > 0.05$) nor pup sex (Fisher's exact test, $p > 0.05$).

Qualitative modifications of the pup's responses

The proportion of pups showing a non-mother-specific response varied significantly during the mother's absence (*G* test, $G = 17.8$, $df = 7$, $p < 0.05$). We found a positive correlation between this proportion and the number of days since the mother's departure (square root *Y* model, $R^2 = 0.90$, $p < 0.05$; Fig. 1B). We showed that from the 1st to 9th days of maternal absence, the proportion of tested pups that responded to calls from strange females was low. In contrast, from the 9th to 15th days of maternal absence, the proportion of pups showing a non-mother-specific response strongly increased (from 13.6 to 37.5%; Table 1).

Variations in the proportion of pups exhibiting a non-mother-specific response for each age group and sex class increased throughout the mother's absence (as we found for the total sample, *G* test, $df = 3$, $p < 0.05$). We found a sex effect: female pups seemed to respond more rapidly to non-mother-specific calls than male pups did (Fig. 2), and this was particularly significant for the session 9–11 days after the mother's departure (Fisher's exact test, $p < 0.05$). In contrast, no difference was observed between age groups (χ^2 test, $df = 2$, $p > 0.05$).



Discussion

Adaptive perspective

The modifications of the pup's response during the mother's absence may be explained by changes in the motivational state of the pup that are linked to its internal energetic balance. The begging strategy of the subantarctic fur seal pup may constitute an adaptive response to the strong energetic constraints imposed by the environment of this species. Indeed, the foraging trips made by this species are among the longest (2–3 weeks; Georges and Guinet 2000) of any fur seal species (7–8 days in *Callorhinus ursinus*, Bartholomew 1959; Gentry and Holt 1986; 4.3 days in *Arctocephalus gazella*, Doidge et al. 1986; 4.7 days in *Arctocephalus australis*, Trillmich et al. 1986; 12.3 days in *Arctocephalus philippi*, Francis et al. 1998). The long duration of foraging trips is due to the unsuitability of resources for available for lactation around Amsterdam Island, which necessitates females having to cover a distance of several hundred kilometres (up to 500 km; Georges et al. 2000). When mothers come ashore, the pups, having withstood such a long fasting period (mortality is very high in this species, however; there is no difference between the sexes; Georges and Guinet 2000), use the

energy supply from the milk for growth and metabolism (Georges and Guinet 2000). We can hypothesize that during the first days after the mother's departure, the pups began to consume their body reserves and that only a small proportion of pups responded to playback of females' calls because their body condition was optimal. The hunger motivation seems to be too weak to elicit begging in response to any female's calls, even those of their own mother. As the fasting period continued, energetic needs increased and pups became more responsive to their mother's calls. The intensity of begging behaviour was then influenced by offspring need, and the pups' calling in response to their mother's vocalizations could be considered an honest signal.

After 11 days of maternal absence, on average, the pups began to respond to any female's calls, i.e., they directed their begging behaviour not only towards the calls of their own mother but also towards those of other females. These non-mother-specific responses may indicate a high state of hunger. In these circumstances it is unlikely that the pups failed to identify their mothers, since it has been shown that fur seal pups are still able to recognize their mother's calls at least 4 years after birth (Insley 2000). Female pups seem to show a non-mother-specific response before males do. This intersex difference might be explained by a difference in fat

storage or mass loss during the fasting period. Indeed, in a recent study on *A. gazella*, it was found that mass loss was greater in female pups than in male pups (Guinet et al. 1999).

The energy gains provided by extra-maternal feeding may assist pups while they are waiting for their mother's return. In contrast, during the first days of maternal absence, the energetic gains from extra-maternal care would not be essential for pups' survival, since pups can easily support a fasting period of a few days. Moreover, the cost incurred through its begging behaviour (including the energetic cost of producing vocalizations and the risk of being injured or even killed as a result of approaching a strange female) would reduce its survival potential for the remainder of its fasting period. Indeed, adult females are potentially dangerous to non-offspring. Individuality in the calls of both mothers and pups has certainly evolved to enable mother-pup recognition and thereby reduce the risk of making errors by pups in identifying their mothers, which might lead to injuries from strange females. In this species, as in most otariids and in contrast to phocids (Job et al. 1995; McCulloch et al. 1999), allo-suckling is exceptional (Bowen 1991; Lunn 1992; Georges et al. 1999), and while milk-stealing attempts often occur, they are rarely successful. Attempting to nurse from strange females probably has survival value when the mother's return is delayed, as the risk of being injured might then outweigh the risk of dying of starvation while waiting for the mother. This fact may explain why after 11 days of maternal absence, several pups approached and tried to steal milk from strange females (I. Charrier, unpublished data). At this stage, pups seem to switch from "pure" (mother-directed) honest signalling to more "opportunistic" signalling (Zahavi 1977).

Methodological perspective

This study shows that subantarctic fur seal pups are not always responsive to their mother's calls. We demonstrated the occurrence of a limited time window during maternal absence when pups are highly reactive to calls and show mother-directed responses. In this species, this time window ranges from the 5th to 9th days of maternal absence. This result will have to be considered in future investigations of the subantarctic fur seal, especially of the fine mechanisms governing mother-pup recognition. Moreover, we hypothesize that this kind of phenomenon has to be taken into account during investigations of other fur seal species, and even of other animal species if they show ecological similarities to the subantarctic fur seal, such as long maternal absences.

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