

Foraging behaviour of sympatric Antarctic and subantarctic fur seals: does their contrasting duration of lactation make a difference?

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Received: 8 November 2006 / Accepted: 12 March 2007 / Published online: 5 April 2007
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Abstract The duration of periods spent ashore versus foraging at sea, diving behaviour, and diet of lactating female Antarctic (*Arctocephalus gazella*, AFS) and subantarctic (*A. tropicalis*, SFS) fur seals were compared at Iles Crozet, where both species coexist. The large disparity in lactation duration (SFS: 10 months, AFS: 4 months), even under local sympatry, has led to the expectation that AFS should exhibit higher foraging effort or efficiency per unit time than SFS to allow them to wean their pups in a shorter period of time. Previous evidence, however, has not supported these expectations. In this study, the distribution of foraging trip durations revealed two types of trips: overnight (OFT, <1 day) and long (LFT, >1 day), in common with other results from Macquarie Island. However, diving behaviour differed significantly between foraging trip types, with greater diving effort in OFTs than in LFTs, and diving behaviour differed between fur seal species. OFTs were more frequent in SFS (48%) than in AFS (28%). SFS performed longer LFTs and maternal attendances than AFS, but spent a smaller proportion of their foraging cycle at sea (66.2 vs. 77.5%, respectively). SFS dove deeper and for

longer periods than AFS, in both OFTs and LFTs, although indices of diving effort were similar between species. Diel variation in diving behaviour was lower among SFS, which foraged at greater depths during most of the night time available than AFS. The diving behaviour of AFS suggests they followed the nychthemeral migration of their prey more closely. Concomitant with the differences in diving behaviour, AFS and SFS fed on the same prey species, but in different proportions of three myctophid fish (*Gymnoscopelus fraseri*, *G. piabilis*, and *G. nicholsi*) that represented most of their diet. The estimated size of the most important fish consumed did not vary significantly between fur seal species, suggesting that the difference in dive depth was mostly a result of changes in the relative abundance of these myctophids. The energy content of these fish at Iles Crozet may thus influence the amount and quality of milk delivered to pups of each fur seal species. These results contrast with those found at other sites where both species coexist, and revealed a scale of variation in foraging behaviour which did not affect their effort while at sea, but that may be a major determinant of foraging efficiency and, consequently, maternal investment.

Communicated by O. Kinne.

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Introduction

Temporospatial separation of foraging and breeding is a defining characteristic of pinnipeds, and may constrain their evolution (Costa 1991). Unlike most phocid seals, otariid (fur seals and sea lions) lactating females cannot fast for the entire period of lactation, as they are too small to store all the required energy (Boness and Bowen 1996). Therefore, they alternate their time at sea foraging with visits ashore to nurse their pup. Otariid lactation varies in duration from 4 months (Antarctic *Arctocephalus gazella* and northern *Callorhinus*

ursinus fur seals) to 3 years (Galápagos fur seals *A. galapagoensis*), and single foraging trips range from several hours to about 50 days in duration, depending on the species, stage of lactation, population, and location (Beauplet et al. 2004; Schulz 2004). Such large variation has prompted efforts to identify the proximate and ultimate factors that determine what particular strategy an otariid adopts.

Studies on temperate species have emphasized the importance of prey ecology and variability of the physical environment in relation to otariid maternal strategies. For example, Juan Fernández (*A. philippii*) and subantarctic (*A. tropicalis*) fur seals both have a 10-month lactation, during which lactating females feed on epipelagic fish (mean depths <30 m), mostly at night (Ochoa-Acuña and Francis 1995; Beauplet et al. 2004). Mean duration of foraging trips increases in both species from 1–2 days early in lactation, to 25–50 days just prior to weaning. In contrast, foraging trips of Australian fur seals (*A. pusillus doriferus*) rarely exceed 10 days during lactation, and females feed at much greater depths on benthic prey at all times of day (Gales and Pemberton 1994; Arnould and Hindell 2001). These three species inhabit temperate latitudes with similar seasonal regimes, so differences among them have challenged an early hypothesis set forth to explain the variation in fur seal foraging behaviour, that presents environmental seasonality as the main determinant of interspecific differences in foraging–nursing cycles (Gentry et al. 1986).

A drawback of interspecific comparisons using samples from different locations is that environmental variation is usually unaccounted for. However, several examples of different species breeding on the same islands exist, offering the opportunity to control for this factor. Here we compare the foraging behaviour of sympatric Antarctic (*A. gazella*) and subantarctic (*A. tropicalis*) fur seals (AFS and SFS, respectively, hereafter), two phenotypically similar sister species with large differences in duration of lactation. AFS breed mainly on islands south of the Antarctic Polar Front, while SFS do so mainly on islands just north of it, but they breed sympatrically in three groups of islands: Macquarie Island, Iles Crozet, and the Prince Edward Islands (Bonner 1999). Lactation is 116 days long in AFS (Costa et al. 1988; Lunn et al. 1993) and 300 days long in SFS (Kerley 1987; Guinet and Georges 2000), and this trait appears to be constant throughout their distribution. SFS pups were shown to have lower energy requirements and higher body fat stores, compared to AFS pups (Arnould et al. 2003), even though rate of milk consumption was only slightly higher in AFS. Therefore, AFS females have <50% of the time that SFS females have for investing in their offspring, but their offspring's energy demands may be higher (Arnould et al. 2003). Understanding how individuals of these species forage when in sympatry, yet under such different pressures, can thus help reveal which elements of

foraging behaviour are species-specific and relatively invariant, and which ones are plastic and adaptively responsive to environmental influences.

The foraging ecology of AFS and SFS has been studied at various locations throughout their range, over several time scales. The diet of AFS varies geographically, with Antarctic krill (*Euphausia superba*) being the main food resource in the southern Atlantic Ocean (South Georgia, Doidge and Croxall 1985; Reid and Arnould 1996; Bouvetøya, Kirkman et al. 2000), although fish complements their diet along the Antarctic peninsula (Casaux et al. 2003) and South Shetland Islands (Daneri 1996). In the southern Indian Ocean, fish is the main prey (Marion Island, Klages and Bester 1998; Iles Kerguelen, Lea et al. 2002a; Heard Island, Green et al. 1997). Based on scat analyses, SFS at Marion Island feed predominantly on myctophid fish (Klages and Bester 1998), although stomach content analyses suggest that at Marion (Ferreira and Bester 1999) and Gough (Bester and Laycock 1985) islands they feed mostly on cephalopods and on myctophid fish at Amsterdam Island (Beauplet et al. 2004). Some studies suggest that such intraspecific dietary differences are related to the analytical techniques used, but are also associated with differences in dive behaviour, both in terms of depth and diel activity patterns (AFS at South Georgia, Croxall et al. 1985; Boyd and Croxall 1992; AFS at Iles Kerguelen, Lea et al. 2002b; SFS at Amsterdam Island, Georges et al. 2000b).

If foraging behaviour is mainly determined by prey ecology, then dietarily similar sympatric fur seal species would be expected to differ little in foraging behaviour. At the level of entire foraging trips, this expectation has been supported in studies of AFS and SFS at Macquarie Island (Goldsworthy et al. 1997; Goldsworthy 1999; Robinson et al. 2002) and Iles Crozet (Bailleul et al. 2005). The species were similar in diet at Macquarie Island and exhibited similar foraging behaviour at both sites, with females diving close to the surface, mostly at night. Summer foraging areas of the species also overlapped considerably. Other data from Marion (Bester and Bartlett 1990; Kirkman et al. 2002, 2003) and Macquarie islands (Goldsworthy 1999; Robinson et al. 2002) suggest there are no interspecific differences in the duration of foraging trips, except at Iles Crozet, where AFS made longer trips (Bailleul et al. 2005).

To date, comparisons of foraging behaviour of AFS and SFS have used the scale of the foraging trip (Bester and Bartlett 1990; Robinson et al. 2002; Kirkman et al. 2003; Bailleul et al. 2005). However, such a scale may not reveal ecologically important interspecific differences on finer scales. Night diving by fur seals is linked to the diel vertical migration of their prey (Croxall et al. 1985; Gentry 1998; Wells et al. 1999), so foraging behaviour optima are expected to show a diel pattern, particularly during the night (Mori 1998). Therefore, important interspecific differences in the

temporal distribution of dive effort and depth utilization may exist. Determining when and where the species concentrate their foraging effort in the water column, in relation to the prey they exploit, may reveal patterns that are related to their different lactation strategies. Moreover, the presence of overnight and longer foraging trips in both species at some locations raises the question of whether their functions differ. These questions have not been addressed, so the objectives of this study were to compare: (1) maternal attendance and foraging trip durations; (2) diel patterns in diving, and how they vary between overnight and longer foraging trips; and (3) diet of sympatric AFS and SFS at Iles Crozet. Because of their briefer lactation and the physiological differences between AFS and SFS pups outlined above, AFS females were expected to show briefer maternal attendance periods and foraging-trip durations. For the same reasons, they also were expected to spend greater effort while diving.

Materials and methods

Fur seal study colonies

Research was carried out at La Mare Aux Elephants (MAE; 46° 22' 29'' S, 51° 40' 13'' E), at the western end of Ile de la Possession, Crozet archipelago, Southern Indian Ocean, during the 2001–2002 (December 4th–March 25th) and 2002–2003 (December 1st–March 16th) breeding seasons (2001 and 2002 hereafter). MAE consists of two adjacent AFS and SFS colonies, which are on different types of substrate. AFS used the northern part of the beach, composed of small- to medium-sized pebbles, with gentle slopes behind; while SFS used the southern part of the beach, composed of large boulders eroded from the steep hinterlands. Both species gave birth close to shore, but the AFS colony grew in size as the season progressed, while the other species tended to remain close to shore during the same period.

A total of 277 (AFS: 153, SFS: 124) pups were individually marked as previously described (Georges and Guinet 2000a; Arnould et al. 2003; Bailleul et al. 2005). Pup production and mean date of pupping were estimated using total pup counts (both years; including dead and living pups) on a weekly basis until no more births were observed. Peak pupping dates were 5 and 15 December (164 and 167 pups in 2001 and 2002, respectively) for AFS, and 25 and 30 December (80 and 91 pups in 2001 and 2002, respectively) for SFS. Therefore, there were inter-annual differences of up to 10 days, which suggests large environmental differences between study years (Lunn and Boyd 1993). However, Lunn and Boyd (1993) suggested that variation in pupping date at Bird Island, South Georgia, may reflect differences in environmental conditions during late gesta-

tion, rather than postpartum, which is our study period, so inter-annual differences in foraging behaviour were not fully analysed. Populations of both species have been increasing at an annual rate of about 18%, at least until 1994 (Guinet et al. 1994).

Instrumentation, maternal attendance and diving behaviour

Animal capture and handling procedures were described in Bailleul et al. (2005) Briefly, lactating females of each species were captured on land during their nursing visits. Each individual was weighed to the nearest kg, and placed on a restraint board for attachment of instruments. One of 3 different time-depth recorder (TDR) models was glued to the dorsal fur between the scapulae, using a two-component glue (AW 2101 Ciba Specialty Chemicals): MK5, MK7, and MK8 (Wildlife Computers, Redmond, Washington, USA). There were no significant differences in foraging trip duration, dive depth, nor dive duration between animals instrumented with different TDR models ($P > 0.5$ in all cases), so data from the three models were pooled for inter-specific comparison purposes. TDRs were programmed to record time and depth every 5 s when the seals were at sea, with a 1 m depth resolution. The characteristics and composition of sampled females are summarized in Table 1. Instruments were left on the seals for 1–11 foraging trips, and were recovered by cutting the fur beneath them, upon the seals' return to the colony.

TDR data were downloaded to a portable computer on the same day the instrument was recovered, to allow redeployment of TDRs on different individuals. Visualization and analyses of the resulting regular time series of dive data were performed using custom written software, available as GNU R (R development Core Team 2006) package diveMove (Luque 2007). Before analyses, depth readings were corrected for shifts in the pressure transducer of the TDR. Sections of each record were identified as foraging trips if continuous wet activity (i.e. continuous depth readings) was recorded for at least 6 h. This limit was imposed to

Table 1 Summary of data on lactating female Antarctic (AFS) and subantarctic (SFS) fur seals fitted with time-depth recorders (TDRs) on Iles Crozet, in the breeding seasons of 2001–2002 and 2002–2003

Species	Breeding season	Body mass (kg)	TDR model				Foraging trips
			MK5	MK7	MK8	All	
AFS	2001	33.2 ± 0.44	5	16	16	37	102
	2002	31.6 ± 0.58	3	4	5	12	30
	Both	32.7 ± 0.36	8	20	21	49	132
SFS	2001	30.6 ± 0.55	3	17	17	37	113
	2002	30.4 ± 0.78	2	4	4	10	32
	Both	30.5 ± 0.45	5	21	21	47	145

exclude short excursions to sea, for activities other than foraging because they contained isolated shallow dives and mainly surface behaviour, in contrast to the bout-organized dives typical of longer excursions (Mori et al. 2001). Therefore, maternal attendance and foraging trip durations were obtained from TDR records.

Dives were defined as departures from the surface to depths ≥ 4 m plus the ensuing return to the surface. Dives to lower depths were not considered because they were indistinguishable from noise remaining after adjustment of pressure transducer drifts, which was greater than the resolution of the instrument (Beck et al. 2000). Each dive was divided into descent, bottom, and ascent phases, where: (1) descent started at the surface and ended when no further increases in depth were detected; (2) ascent was defined from the end of the dive and, with the reversed time series, ending when no further increases in depth were detected; and (3) the bottom was the period between descent and ascent phases. Dives were subsequently described by duration, maximal depth, and post-dive duration. The duration of each phase of the dive, the vertical distance covered during descent and ascent, and the cumulative vertical displacements (“wiggles”) during the bottom phase also were computed by the program. These basic dive descriptors were used to estimate descent and ascent rates as $r = \delta x / \delta t$, where r is the rate (m/s), δx is vertical distance, and δt is the duration of the corresponding phase.

Dive rate was used as an index of diving effort, calculated as the sum of ascent and descent distances, plus the vertical distance covered during the bottom phase, divided by total night time spent at sea. The index has been used previously to estimate vertical distance travelled per unit time (Costa and Gales 2000). For comparison with previous studies, a second index of diving effort was calculated as the total time spent diving, divided by the total night time spent at sea. Total night time at sea was calculated following algorithms available from the National Oceanic and Atmospheric Administration (NOAA) at <http://www.srrb.noaa.gov/highlights/sunrise/sunrise.html>.

Diet

Scat samples, weighing an average of 50 g, were collected at each species' colony during January and February 2002 (2001 breeding season). Although species were spatially segregated on land, seals of both species occasionally used the periphery of the colony to commute between land and sea. Therefore, samples were collected only within core areas used by lactating females and pups of each species. Samples were frozen at -20°C , until laboratory analysis.

In the laboratory, scat samples were thawed overnight in warm water, and washed through 1 and 0.5 mm diameter mesh sieves. Remains of fish (otoliths, scales and bones),

cephalopod (beaks), mollusc (shells), bird (feathers), and invertebrates were sorted under a dissecting microscope and stored in 70% alcohol until identification. Remains were identified to the species level where possible, using available guides (Clarke 1986; Williams and McEldowney 1990; Smale et al. 1995) and our own reference collection at CEBC, Chizé, France. Standard length of the most frequent prey for each fur seal species was estimated using available regression equations (Williams and McEldowney 1990) of fish length against measured otolith standard length (to the nearest mm). Diet was quantified by calculating the relative numerical abundance of each prey taxon (number of individuals found relative to the total number of individuals), and frequency of occurrence of each taxon (number of samples containing the item divided by the total number of samples).

Statistical analyses

Dives from the same seal were not independent of one another. Furthermore, the number of foraging trips, and hence the number of dives per individual were not the same. To give each seal the same statistical weights in analyses, and to avoid pseudoreplication, the mean of each dive variable was calculated per individual during initial foraging-trip scale analyses, thus allowing comparison with other studies (Hurlbert 1984). The mean also was used to represent data from each individual and each hour of the day, for studying diel variation in foraging behaviour.

Variability in dive depth was used as a measure of how closely AFS and SFS followed the vertical movements of prey, if they consumed the same prey species, or else as a measure of variability in prey vertical movements. To test for differences in this variability, the coefficient of variation (CV) was calculated for each individual, and a one-way Analysis of Variance was used to test whether it differed between species.

Results are presented as means \pm SE, unless noted otherwise. The Shapiro–Wilks statistic and Fligner–Killeen test were used to evaluate assumptions of normality of data distributions and homogeneity of variances, respectively, prior to analyses of variance. Effects of foraging-trip duration, species, and their interaction, on each dive variable were tested using linear mixed-effects models (Pinheiro and Bates 2000). Dietary differences were tested using two-sample Wilcoxon tests. All analyses were carried out in the GNU R system (R development Core Team 2006).

Results

We obtained data for >250 foraging trips from >90 females, split roughly equally between the species (AFS, $n = 49$;

SFS, $n = 47$; 1–11 per female Table 1). Data from two SFS females deployed in winter 2003 (June 11th–July 15th) to determine their foraging behaviour during late lactation, were analysed but excluded from interspecific comparisons, because no additional SFS females could be instrumented then.

Maternal attendance and foraging-trip duration

Most seals departed the colony to forage at sea between 17:00 and 20:00 local time, although departures during all afternoon were observed for AFS (Fig. 1). Arrival times were more variable, but occurred mostly during the morning for both species. AFS females departed from the colony significantly earlier in the afternoon (Kruskal–Wallis $\chi^2 = 27.56$, $P < 0.001$), and returned to it later in the morning ($\chi^2 = 26.48$, $P < 0.001$). Median departure and arrival times were 17:30 and 09:31 for AFS, and 18:39 and 06:44 for SFS, respectively.

A subsample of 70 seals for which complete foraging cycles (i.e. foraging trip and the subsequent maternal attendance) were documented, showed that AFS spent significantly more time at sea ($F_{1, 68} = 7.69$, $P = 0.007$, arcsine transformed data) and a larger proportion of their foraging cycle at sea than SFS (AFS: $77.5\% \pm 0.30$, $n = 36$; SFS: $66.2\% \pm 0.54$, $n = 34$). The proportion of time at sea did not vary significantly throughout the breeding season ($P > 0.1$ for both AFS and SFS).

Foraging trips lasted from 0.3 to 32 days, but with a highly skewed right distribution, and an absence of trips of durations 1.00–1.25 days (Fig. 2). Furthermore, 43% of all trips lasted <1 day, so a distinction between foraging trips lasting <1 day and >1 day was necessary. Brief, overnight foraging trips (OFT) were significantly more frequent for SFS (48 vs. 28% for AFS, Pearson's $\chi^2 = 5.15$, $P = 0.02$, Table 2).

Although an analysis of inter-annual variation was not the focus of this study, a comparison of durations of long forag-

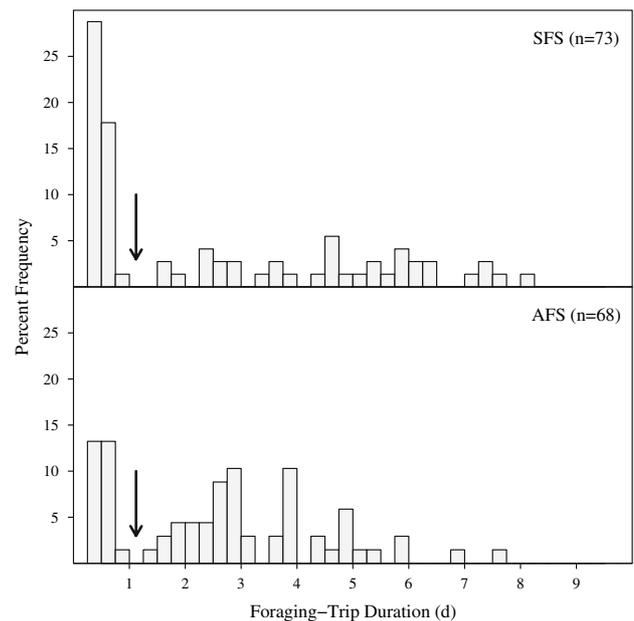


Fig. 2 Frequency distributions of foraging-trip durations for sympatric lactating female Antarctic (AFS) and subantarctic (SFS) fur seals at Iles Crozet are variable and highly skewed. A discontinuity in duration is apparent (arrows), which was used to distinguish between brief and long trips (see text). Data were binned at 0.25 days

ing trips (LFT) between years did not differ significantly for either species (Kruskal–Wallis test, $P > 0.1$). Therefore, inter-annual variation in foraging and maternal attendance behaviour was not considered in subsequent analyses.

OFTs were not limited to any particular period of the breeding season because seals alternated irregularly between OFTs and LFTs throughout that period (Fig. 3, upper). OFTs averaged approximately half a day in duration and did not differ significantly between species (Table 2). However, LFTs were about 50% significantly longer in SFS females (Table 2). LFTs increased significantly in duration over the breeding season (slope = $0.92 h \times d^{-1}$, $P < 0.05$),

Fig. 1 Sympatric lactating female Antarctic (AFS) and subantarctic (SFS) fur seals at Iles Crozet differ significantly in times of morning returns from foraging trips (left) and of afternoon departures for foraging trips (right). Shaded area time between dusk and dawn; dashed vertical lines median times

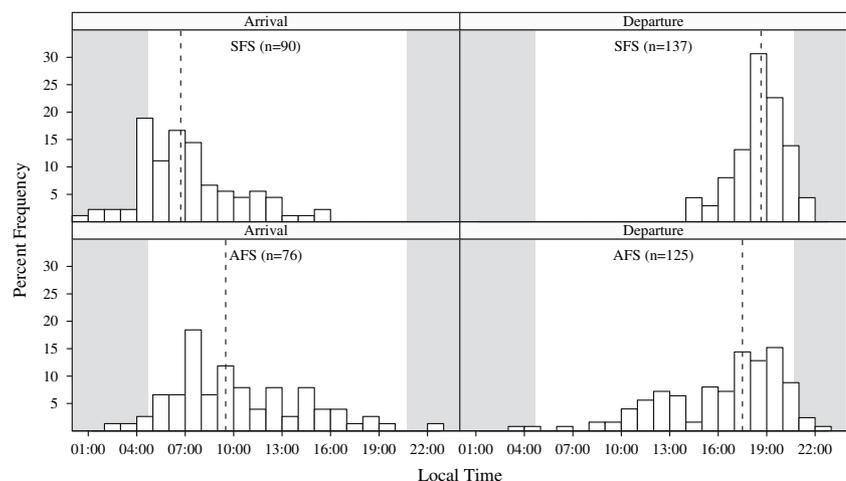


Table 2 Summary of durations of overnight (OFT) and long (LFT) foraging trips, and of the ensuing period ashore, for Antarctic (AFS) and subantarctic (SFS) fur seals on Iles Crozet. Mean \pm SE (N) are shown

Activity	Species	Duration (d)	
		OFT	LFT
At-sea	AFS	0.52 \pm 0.03 (19)	3.47 \pm 0.20 (49)
	SFS	0.48 \pm 0.02 (35)	5.23 \pm 0.51 (38)
	<i>F</i> -ratio	$F_{1,52} = 1.72$	$F_{1,85} = 12.4^b$
Ashore ^a	AFS	0.74 \pm 0.17 (17)	1.18 \pm 0.09 (31)
	SFS	1.17 \pm 0.12 (28)	1.94 \pm 0.19 (19)
	<i>F</i> -ratio	$F_{1,43} = 4.63^b$	$F_{1,48} = 16.0^b$

^a Periods ashore were grouped according to duration of the preceding foraging trip

^b $P < 0.01$ between species

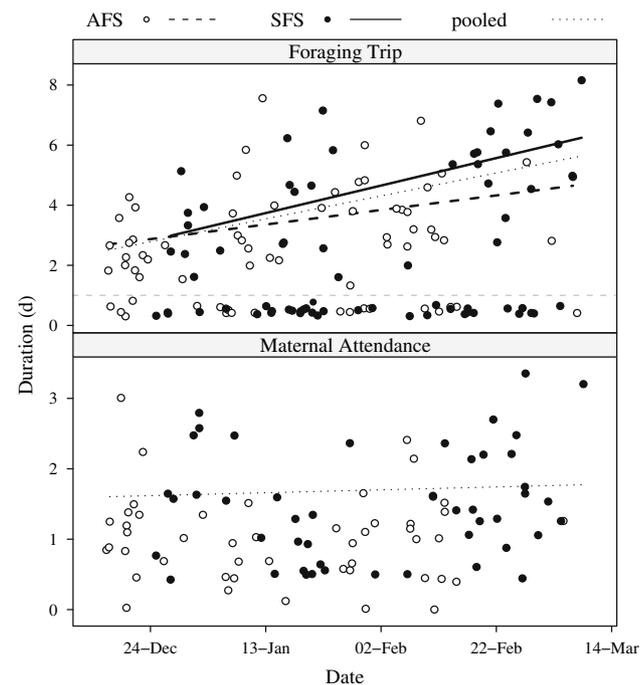


Fig. 3 Long foraging trips increased in duration over the breeding season (*upper*) but periods of maternal attendance on land did not (*lower*), for sympatric lactating female Antarctic (AFS) and subantarctic (SFS) fur seals at Iles Crozet. Lines represent fitted linear regressions. The thin gray dashed line (*upper*) at 1 day separates overnight and long foraging trips

although variation was large ($r^2 = 0.29$); rate of increase was similar between species (ANCOVA $F_{1,81} = 2.67$, $P = 0.11$, Fig. 3). Data from two SFS individual females in winter included one foraging trip each, with a duration of 30.2 and 31.9 days, respectively, much greater than values recorded during the summer.

Maternal attendances were significantly longer in SFS, following either OFTs or LFTs (Table 2). Concomitant

Table 3 Overall summary of diving behaviour of Antarctic (AFS) and subantarctic (SFS) fur seals on Iles Crozet. Mean \pm SE (N) are shown

Dive variable ^a	AFS	SFS	F-ratio
Total number of dives	59,636	56,795	
Night dives (% of total)	97.8 \pm 0.04	98.5 \pm 0.04	4.71 ^b
Mean dive depth (m)	29.2 \pm 0.24	39.7 \pm 0.31	14.3 ^c
Median dive depth (m)	23.7 \pm 0.33	39.9 \pm 0.39	19.8 ^c
Maximum dive depth (m)	122.9 \pm 0.66	99.8 \pm 0.34	17.4 ^c
Deepest dive (m)	193	141	
Mean dive duration (s)	78.5 \pm 0.42	93.2 \pm 0.46	10.6 ^b
Median dive duration (s)	74.5 \pm 0.57	94.5 \pm 0.57	11.5 ^c
Maximum dive duration (s)	219.0 \pm 0.63	206.9 \pm 0.58	3.77
Longest dive (s)	295	310	
Mean descent rate (m s ⁻¹)	0.92 \pm 0.003	1.07 \pm 0.004	19.9 ^c
Mean ascent rate (m s ⁻¹)	1.07 \pm 0.004	1.23 \pm 0.005	12.6 ^c
Mean bottom time (s)	31.8 \pm 0.14	36.4 \pm 0.19	7.1 ^b
Time spent diving at night (% of night time)	34.5 \pm 0.19	33.4 \pm 0.17	0.29
Night dive rate (m h ⁻¹)	988.5 \pm 7.84	1,116.6 \pm 8.97	2.23

^a For each individual, the mean was used to avoid pseudoreplication

^b $P < 0.05$ between species

^c $P < 0.001$ between species

with these differences, female seals stayed ashore longer after LFTs than after OFTs ($F_{1,93} = 10.2$, $P = 0.002$; non-significant species \times trip-type interaction, $P > 0.1$).

Diving behaviour

Information from 133,010 dives was obtained from all seals overall, but 16,579 of those were from two individuals deployed in winter, so 116,431 were from the summer (Table 3). Diving was restricted almost entirely to the night in both species. While at sea at night, both species dove 34% of the available time, on average.

Overall, diving behaviour differed significantly between species, with SFS diving deeper and for longer periods (Table 3). However, maximal dive depths were higher for AFS. Mean rates of descent and ascent, as well as time spent at the bottom, were higher in SFS. Despite those differences, both species spent nearly the same effort when diving, as no significant differences were found in time spent diving (mean, 34%) or the rate of diving (mean, 1,053 m \times h⁻¹) during the night.

Seasonal changes in diving behaviour were apparent for SFS, as the two lactating females instrumented during winter showed reduced mean diving depths and durations (24.6 \pm 0.38 m and 80.2 \pm 5.6 s, respectively), compared to summer values. Maximal dive durations increased to 337.5 \pm 8.8 s. Diving was mainly nocturnal (mean, 99.1%), as during the summer.

Diving behaviour varied significantly with type of foraging trip (OFT vs. LFT, linear mixed effects models, $P < 0.05$ all cases), and this factor did not show any significant interactions with species for any of the dive attributes studied ($P > 0.05$ all cases). However, the inclusion of this factor did not affect interspecific comparisons. During OFTs, seals dove to significantly greater depths, for longer periods ($F_{1, 46} = 28.7$ and $F_{1, 46} = 40.0$, $P < 0.001$ both cases). The deepest and longest dives for each seal were recorded during OFTs (Table 4). Similarly, mean descent and ascent ($F_{1, 46} = 8.4$, $F_{1, 46} = 9.9$) plus nocturnal dive rates ($F_{1, 46} = 5.4$), were significantly greater during OFTs ($P < 0.05$ all cases).

Table 4 Quantitative summary of diving behaviour of Antarctic (AFS) and subantarctic (SFS) fur seals on Iles Crozet, during overnight (OFT) and long (LFT) foraging trips. Mean \pm SE (N) are shown

Dive variable ^b	AFS	SFS
<i>OFT</i>		
Total number of dives	4,088	8,573
Mean dive depth (m)	29.7 \pm 0.25	37.8 \pm 0.35
Median dive depth (m)	24.2 \pm 0.33	37.4 \pm 0.46
Maximum dive depth (m)	122.0 \pm 0.67	99.9 \pm 0.36
Deepest dive (m)	193	141
Mean dive duration (s)	78.7 \pm 0.44	88.1 \pm 0.51
Median dive duration (s)	74.5 \pm 0.58	88.3 \pm 0.66
Maximum dive duration (s)	218.2 \pm 0.65	207.2 \pm 0.69
Longest dive (s)	295	310
Mean descent rate (m s ⁻¹)	0.92 \pm 0.003	1.07 \pm 0.004
Mean ascent rate (m s ⁻¹)	1.08 \pm 0.004	1.23 \pm 0.006
Mean bottom time (s)	31.5 \pm 0.15	34.9 \pm 0.22
Time spent diving at night (% of night time)	35.4 \pm 0.20	33.1 \pm 0.21
Night dive rate (m h ⁻¹)	1,008.9 \pm 8.17	1,105.8 \pm 10.92
<i>LFT</i>		
Total number of dives	54,850	48,064
Mean dive depth (m)	29.6 \pm 0.89	43.7 \pm 0.48
Median dive depth (m)	29.7 \pm 1.10	45.7 \pm 0.57
Maximum dive depth (m)	92.1 \pm 1.78	89.3 \pm 0.70
Deepest dive (m)	151	134
Mean dive duration (s)	90.6 \pm 1.37	103.7 \pm 0.72
Median dive duration (s)	94.6 \pm 1.79	108.0 \pm 0.86
Maximum dive duration (s)	185.0 \pm 1.40	180.2 \pm 1.03
Longest dive (s)	220	255
Mean descent rate (m s ⁻¹)	0.80 \pm 0.01	1.04 \pm 0.006
Mean ascent rate (m s ⁻¹)	0.93 \pm 0.02	1.22 \pm 0.008
Mean bottom time (s)	39.6 \pm 0.56	39.5 \pm 0.38
Time spent diving at night (% of night time)	34.5 \pm 0.68	33.1 \pm 0.34
Night dive rate (m h ⁻¹)	833.2 \pm 24.16	1,082.4 \pm 14.68

^a See text for results of statistical comparisons

^b For each individual, the mean was used to avoid pseudoreplication

Despite the trends just reported on, median dive depth was shallower ($F_{1, 46} = 5.5$, $P = 0.02$), and mean and median dive duration ($F_{1, 46} = 17.0$ and $F_{1, 46} = 20.7$), as well as mean bottom time ($F_{1, 46} = 20.5$) were briefer during OFTs ($P < 0.001$ in all cases). Mean dive depth and time spent diving at night did not vary with type of foraging trip ($P > 0.1$ all cases).

Differences in diving behaviour between foraging trip types and between species became more evident when diel patterns in dive depth and duration were considered (Fig. 4). During OFTs, AFS females dove to mean depths of 28 m for most of the night, but increased dive depths to 61 m at dawn. In contrast, SFS females began diving at dusk to relatively shallow depths (24 m), but dive depths increased steadily to mean depths of 48 m at midnight, and decreased thereafter to mean depths of 39 m (Fig. 4a). Nonetheless, the coefficient of variation (CV) in dive depth between dusk and dawn was similar between species during OFTs ($F_{1, 52} = 0.004$, $P = 0.95$). Dive duration followed a similar pattern during these short trips, when AFS females made the longest dives at dusk and dawn. Dive durations were much less variable throughout the night among SFS females, despite relatively large changes in dive depths (Fig. 4b).

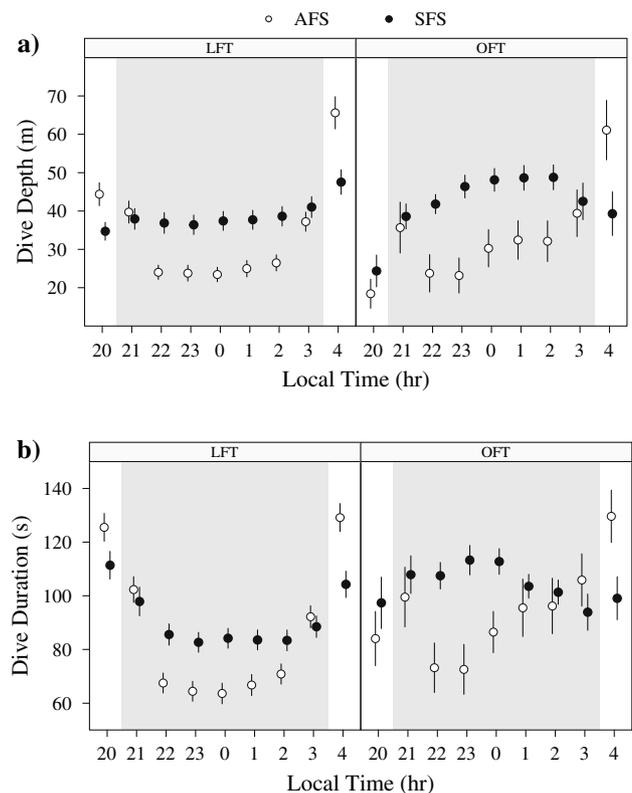


Fig. 4 Diel patterns in depth (a) and duration (b) of foraging dives differed between sympatric lactating female Antarctic (AFS) and subantarctic (SFS) fur seals at Iles Crozet, for overnight (OFT, right) and long (LFT, left) foraging trips. Values are mean \pm SE

Diel changes in dive depth differed between LFTs and OFTs (Fig. 4). AFS females made their deepest dives at dusk and dawn (mean 44 and 65 m, respectively), but dove to relatively shallow depths (mean 28 m) for most of the night. Dive depths varied little from dusk until the end of the night in SFS (mean 37 m), and they increased to approximately 48 m at dawn (Fig. 4a). Concomitant with these differences, the CV of nocturnal dive depths during LFTs was higher in AFS ($F_{1,96} = 17.1$, $P < 0.001$). Again, dive durations followed approximately the same pattern in AFS, with the longest dives at dusk and dawn, and the briefest dives in the middle of the night. Dive durations of SFS females were similar to, though less pronounced than, those of AFS (Fig. 4b).

Dive rates were lowest at dusk and dawn, regardless of foraging-trip type or species. However, they showed different diel patterns between species and between foraging-trip types (Fig. 5a). While on OFTs, dive rates varied greatly for SFS, being highest in the middle of the night and higher than those of AFS during that period. Dive rates were more homogeneous in LFTs for both species, but were again higher for SFS in the middle of the night. They showed peaks at dusk and dawn for AFS, associated with the deeper dives they performed during those hours. Changes in time

spent diving per hour of night showed the same differences between foraging-trip types, although differences between species were evident only for the hours following dusk and prior to dawn in LFTs (Fig. 5b).

SFS females instrumented in winter dove close to the surface between dusk and dawn, and at considerably lower mean depths (15–30 m) than those in summer. Winter dive durations were 50–110 s, with the longest dives after midnight and before dawn. Mean dive rates and time spent diving varied greatly, but were relatively constant throughout the night at $80 \text{ m} \times \text{h}^{-1}$, and $90 \text{ s} \times \text{h}^{-1}$, respectively; considerably lower than in summer.

Diet

A total of 82 scat samples were analysed (41 from each fur seal species), yielding 2,354 sagittal otoliths, 143 cephalopod beaks, and 22 crustacean remains useful for identification. Species from the family Myctophidae dominated the fish component of the diet of both species (90.8 and 92.2% of total number of prey, respectively). The genus *Gymnoscopelus* was the most common representative of that family (AFS: 71.1%; SFS: 70.0%, Fig. 6), and seven other fish species (from 7 families) were also identified, albeit in very low numbers (<1%). Seven species of cephalopod were also identified, but only one of them represented >1% of all prey numbers (Fig. 6).

AFS and SFS consumed the same prey species, but in different proportions ($\chi^2 = 213.2$, $P < 0.001$; test based on ten species for which relative numbers were larger than 5 for both fur seal species). The difference was due to differences in the proportions of *Gymnoscopelus* species (*G. fraseri*, *G. piabilis*, *G. nicholsi*, and other unidentified species) and, to a lesser extent, *Electrona subaspera* and the brachioteuthid cephalopod *Slosarczykovia circumantarctica* (Fig. 6). SFS consumed *G. fraseri* and *E. subaspera* in higher numerical proportions than did AFS, and *G. nicholsi* and the cephalopod *S. circumantarctica* were more common in the diet of AFS.

Based on regression analysis of otolith size (see [Materials and methods](#)), standard length of *G. fraseri* consumed by the two fur seal species was similar (AFS, $82.8 \pm 6.3 \text{ mm}$, $n = 12$; SFS, $81.5 \pm 6.4 \text{ mm}$, $n = 102$; Mann-Whitney, $U = 645.0$, $P = 0.76$). *G. piabilis* consumed by AFS was slightly larger ($132.5 \pm 9.8 \text{ mm}$, $n = 14$), but not significantly so ($U = 776.5$, $P = 0.07$), than that consumed by SFS ($129.7 \pm 7.7 \text{ mm}$, $n = 85$).

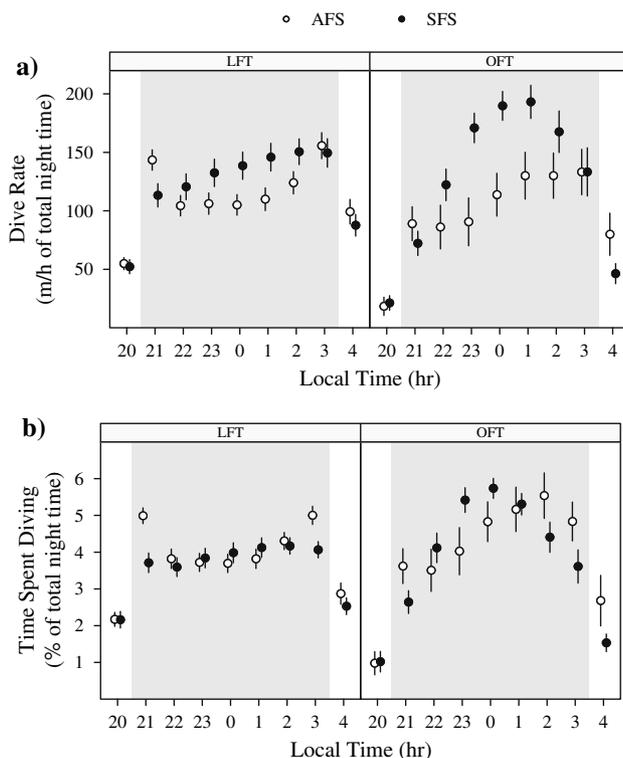
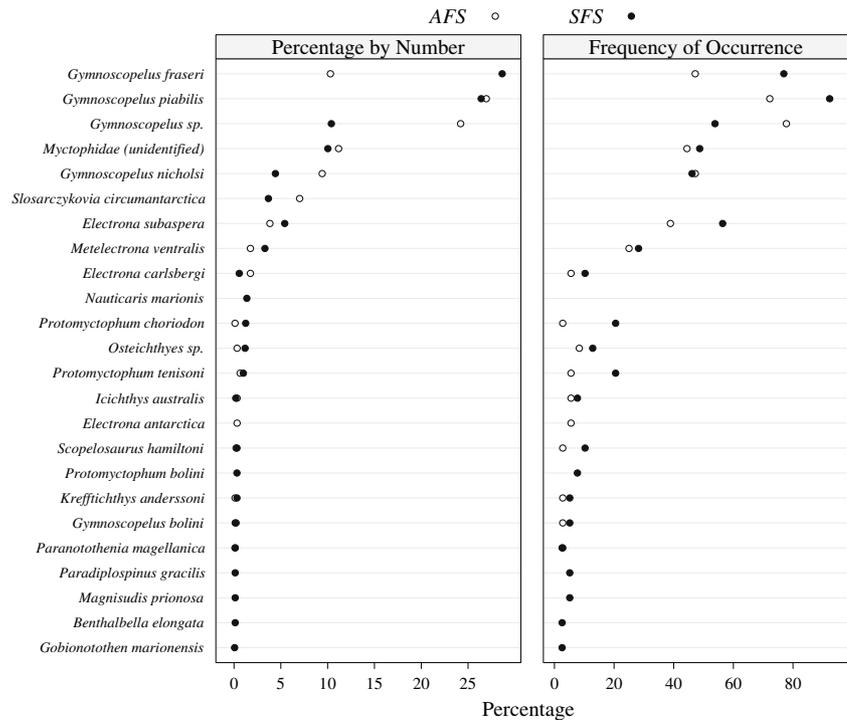


Fig. 5 Diel patterns in nocturnal dive rate (vertical meters travelled per night hour (a)), and time spent diving (b) differed between sympatric lactating Antarctic (AFS) and subantarctic (SFS) fur seals at Iles Crozet, for overnight (OFT, right) and long (LFT, left) foraging trips. Values are mean \pm SE

Discussion

Antarctic and subantarctic fur seals are locally sympatric (syntopic) at Macquarie Island, Marion Island, and Iles

Fig. 6 Percentage by number (of total prey items) and relative frequency of occurrence of identified prey in scat samples of Antarctic (AFS) and subantarctic (SFS) fur seals from MAE, Iles Crozet. Only those species with relative frequency or frequency of occurrence higher than 1% are shown



Crozet, where they feed on the same species. At Macquarie Island and Iles Crozet they were shown to use similar foraging areas, dive to similar depths, and stay submerged for about the same amount of time. These similarities in foraging behaviour have been used to support the notion that prey ecology is the major determinant of the predators' foraging characteristics. However, the large difference in duration of lactation and in pup physiology (e.g. energy budgets and fat stores, as noted above) suggested to us that some interspecific differences in foraging ecology must occur. The results of the present study revealed interspecific differences in foraging behaviour which were not previously evident from foraging-trip scale analyses.

Differences in maternal attendance and foraging-trip duration

Several studies have used the interval between departure from the colony and the first dive as an indication of travel time to the first foraging patch (Boyd et al. 1991; Page et al. 2005). In our study, the late afternoon departure and early morning arrival from the colony for most individuals indicated that both species travelled to foraging areas close to the colony, because seals dove almost exclusively at night, in common with other fur seals that dive predominantly at night (Gentry and Kooyman 1986). Indeed, this was documented in a previous satellite-tracking study, in which both species were shown to forage 50–100 km from the colony (Baillieul et al. 2005).

We observed two distinctly different kinds of foraging trip in both species: brief (OFT) or long (LFT). This also has been observed in these species at Macquarie Island (Goldsworthy 1999). However, mean foraging-trip duration varies both geographically and temporally in AFS (2.5–13.1 days: Boyd and Croxall 1992; Green 1997; Lea et al. 2002b; Kirkman et al. 2003), and the LFT durations we observed in this study (mean, 3.47 days) fall near the lower end of values in that range. At Marion Island, which has a similar marine environment around it as that found around Iles Crozet, LFT durations averaged considerably longer for AFS females: 6.0–9.4 days (Kirkman et al. 2003), suggesting they fed closer to the colony at Iles Crozet.

The LFT durations we observed for SFS (mean 5.23 days) were similar to those observed at Marion Island (Kirkman et al. 2002), but much briefer than those observed in an allopatric population at Amsterdam Island, where summer foraging trip durations averaged 11 days (Georges and Guinet 2000b). SFS females at Amsterdam Island forage in the Subtropical Front (Georges et al. 2000a), which is found much farther from the colony, and increasingly so throughout lactation, than the Polar and Subpolar Fronts around Iles Crozet (Sparrow and Heywood 1996), where this species finds food. Therefore, the proximity of these two oceanic fronts around Iles Crozet may account for the briefer durations of foraging-trips in this SFS population. This may also be the case for SFS at Marion Island (Kirkman et al. 2002).

A finding common to all three sites where AFS and SFS breed sympatrically is the longer duration of SFS maternal

attendance, compared to AFS females (Goldsworthy 1999; Bester and Bartlett 1990). Increased frequency of brief foraging trips, and reduced duration of maternal attendance, both suggest higher energy transfer rates to offspring (Boyd et al. 1994; Arnould et al. 1996; Boyd 1999). In the Amsterdam Island SFS population, however, pups from mothers making very brief or very long foraging trips suffered reduced growth rates, compared to those from mothers making trips 9–13 days in duration (Georges and Guinet 2000b), so OFTs may not always be the most profitable for mother and pup. Otherwise, females of both species would be expected to use OFTs as much as possible. Therefore, SFS females may have increased the proportion of OFTs at a cost of reducing energy transfer rates to their pups. This foraging strategy may be optimal for species with relatively long lactation, with offspring that must fast for long periods during which they have reduced energy requirements (Arnould et al. 2003). In contrast, lactating female AFS may be under stronger pressure to perform foraging trips >1 days in duration, to transfer sufficient energy to sustain pup activity and growth during maternal absence. Indeed, lactating female AFS spent a greater proportion of their foraging cycle at sea.

Interspecific differences in diving behaviour and diet

The major aspects of diving behaviour of lactating female AFS and SFS in our study differed little from allopatric populations of those species (Boyd and Croxall 1992; Georges et al. 2000b; Lea et al. 2002b). However, AFS may have greater versatility in diving behaviour, as they also dive frequently during the light hours in some populations (McCafferty et al. 1998; Lea et al. 2002b); presumably this is related to variation in diet. In contrast, our study and another one carried out at Amsterdam Island, <1% of all SFS dives occurred during light hours, and SFS diet consisted primarily of myctophid fish (Beauplet et al. 2004).

We documented diel changes in dive characteristics, which revealed some fine-scale ecological differences between AFS and SFS: (i) relatively deep and long dusk and dawn diving, with shallow, brief diving for most of the night in AFS, particularly during LFTs, (ii) dives to relatively constant depths and durations for most of the night, with a depth increase at dawn, and dive duration maxima at dusk and dawn during LFTs for SFS, and (iii) deep diving around midnight, decreasing to minima at dusk and dawn, with relatively constant dive duration for most of the night during OFTs for SFS.

These patterns resulted in SFS diving deeper and for longer periods overall. The associated changes in night dive rate and time spent diving also indicated that they concentrated diving efforts at different times of the night. Thus,

AFS females focused their diving effort in the hour immediately after dusk and before dawn during LFTs, and in the hours between midnight and dawn during OFTs. In comparison, SFS females progressively increased diving effort between dusk and dawn during LFTs, and concentrated most of it around midnight during OFTs.

The first feature (i) of AFS female dives, noted above, has been considered typical of fur seals closely tracking the vertical migration of their prey (Goebel et al. 1991; Croxall et al. 1985); such as myctophid fish in our study. Most myctophids are known to undergo migrations from deep (200–800 m) layers in the water column during the daytime, to a few tens of metres from the surface at night (Robison 2003). Therefore, the deep crepuscular dives performed by AFS in both types of foraging trip suggest they were following their prey, as they return to their deeper daytime locations.

The diel diving pattern of SFS in LFTs suggests that this species did not follow the vertical migrations of their prey closely (feature ii, as noted above). Consistent with this observation, variability in dive depth throughout the night was lower in SFS, and their dives were concentrated deeper in the water column, so foraging exhibited some vertical segregation between species during LFTs. This was not mirrored in nocturnal dive rates or time spent diving, as diel patterns in those variables were similar between species. The diving behaviour of SFS during LFTs is similar to that of benthic feeding otariids (Costa and Gales 2003; Arnould and Hindell 2001); however, both SFS and AFS are pelagic foragers (Bailleul et al. 2005) and the bottom phase of dives was characterized by numerous “wiggles”, which is not typical of benthic feeders. The overall similarity in the diets of both species suggests that they exploit the same prey resource, but in slightly different ways, as they distribute their diving effort differently over time and through the water column.

AFS and SFS females differed most strikingly in OFT diving characteristics. During OFTs, some of these differences resulted in vertical segregation of approximately 20 m around midnight. The nocturnal dive rate at dusk and dawn was very low for these trips among SFS, even lower than among AFS, hence they made very few dives at these times. Consistent with the reduction in diving effort at dawn, SFS females arrived at the colony earlier, and the later arrival of AFS females reflects their greater effort diving deeply at dawn.

The diet and diving behaviour of SFS have only been studied previously at Amsterdam Island. The myctophids consumed there differ greatly from those we identified (Beauplet et al. 2004), with none of the same species being noted. However, diving behaviour is strikingly similar between the two sites. Although OFTs do not occur at Amsterdam Island, LFT dives of SFS from both sites

showed relatively constant depths throughout the night, and our limited data from winter also show similarities between the two sites. This contrasts with AFS studies showing broad differences in diving behaviour, in association with differences in diet. SFS may thus be less flexible in their diving behaviour than their southern cousins.

The vertical distribution and migration of myctophids consumed by fur seals in waters around Iles Crozet are unknown, but data from Iles Kerguelen (1,400 km to the southeast) provide some indications. The three most important myctophids identified in Iles Crozet fur seal scats have been found in the upper 50 m layer of waters around Iles Kerguelen (Duhamel et al. 2000). *G. fraseri* shows strong vertical migrations there, but is less abundant than *G. nicholsi* near the surface at that location. If the same pattern exists around Iles Crozet, it may explain the higher frequency of *G. fraseri* in SFS and of *G. nicholsi* in AFS scats. Interestingly, *G. nicholsi* from that location is richer in lipid content than *G. fraseri* (18.0 vs. 11.6% wet mass; Lea et al. 2002c). Therefore, AFS may forage more efficiently by trading off the larger abundance of an energetically poorer prey deeper in the water column, for a richer prey closer to the surface. The consequences of such foraging behaviour differences between sympatric fur seals with contrasting lactation durations need to be investigated in terms of mother–offspring energetics.

Acknowledgments This work was possible thanks to the financial and logistic support from the Institut Polaire Français Paul Emile Victor (IPEV), the Draney-Anderson Foundation, and a graduate student fellowship from the Department of Biology of Memorial University (SPL). We are very grateful to the members of the 39th and 40th missions to Iles Crozet, who participated in many aspects of field work. Research was conducted in accordance with the guidelines provided by IPEV.

References

- Arnould JPY, Hindell MA (2001) Dive behaviour, foraging locations, and maternal attendance patterns of Australian fur seals (*Arctocephalus pusillus doriferus*). *Can J Zool* 79:35–48
- Arnould JPY, Boyd IL, Socha DG (1996) Milk consumption and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups. *Can J Zool* 74:254–266
- Arnould JPY, Luque SP, Guinet C, Costa DP, Kingston J, Shaffer SA (2003) The comparative energetics and growth strategies of sympatric Antarctic and Subantarctic fur seal pups at Îles Crozet. *J Exp Biol* 206:4497–4506
- Bailleul F, Luque SP, Dubroca L, Arnould JPY, Guinet C (2005) Differences in foraging strategy and maternal behaviour between two sympatric fur seal species at the Crozet Islands. *Mar Ecol Progress Ser* 293:273–282
- Beauplet G, Dubroca L, Guinet C, Cherel Y, Dabin W, Gagne C, Hindell M (2004) Foraging ecology of subantarctic fur seals *Arctocephalus tropicalis* breeding on Amsterdam Island: seasonal changes in relation to maternal characteristics and pup growth. *Mar Ecol Progress Ser* 273:211–225
- Beck CA, Bowen WD, Iverson SJ (2000) Seasonal changes in buoyancy and diving behaviour of adult grey seals. *J Exp Biol* 203:2323–2330
- Bester MN, Bartlett PA (1990) Attendance behaviour of Antarctic and subantarctic fur seal females at Marion Island. *Antarct Sci* 2:309–312
- Bester MN, Laycock PA (1985) Cephalopod prey of the Subantarctic fur seal, *Arctocephalus tropicalis*, at Gough Island. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer, Berlin, pp 551–554
- Boness DJ, Bowen WD (1996) The evolution of maternal care in pinnipeds. *Bioscience* 46:645–654
- Bonner N (1999) Seals and sea lions of the world. Blandford, London
- Boyd IL (1999) Foraging and provisioning in Antarctic fur seals: inter-annual variability in time–energy budgets. *Behav Ecol* 10:198–208
- Boyd IL, Croxall JP (1992) Diving behaviour of lactating Antarctic fur seals. *Can J Zool* 70:919–928
- Boyd IL, Lunn NJ, Barton T (1991) Time budgets and foraging characteristics of lactating Antarctic fur seals. *J Anim Ecol* 60:577–592
- Boyd IL, Arnould JPY, Barton T, Croxall JP (1994) Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. *J Anim Ecol* 63:703–713
- Casaux R, Baroni A, Arrighetti F, Ramón A, Carlini A (2003) Geographical variation in the diet of the Antarctic fur seal *Arctocephalus gazella*. *Polar Biol* 26:753–758
- Clarke MR (1986) A handbook for the identification of squid beaks. Clarendon Press, Oxford
- Costa DP (1991) Reproductive and foraging energetics of pinnipeds: implications for life history patterns. In: Renouf D (ed) The Behavior of Pinnipeds. Chapman and Hall, London, pp 300–344
- Costa DP, Gales NJ (2000) Foraging energetics and diving behavior of lactating New Zealand sea lions, *Phocartos hookeri*. *J Exp Biol* 203:3655–3665
- Costa DP, Gales NJ (2003) Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecol Monogr* 73:27–43
- Costa DP, Trillmich F, Croxall JP (1988) Intraspecific allometry of neonatal size in the Antarctic fur seal (*Arctocephalus gazella*). *Behav Ecol Sociobiol* 22:361–364
- Croxall JP, Everson I, Kooyman GL, Ricketts C, Davis RW (1985) Fur seal diving behaviour in relation to vertical distribution of krill. *J Anim Ecol* 54:1–8
- Daneri GA (1996) Fish diet of the Antarctic fur seal, *Arctocephalus gazella*, in summer, at Stranger Point, King George Island, South Shetland Islands. *Polar Biol* 16:353–355
- Doige DW, Croxall JP (1985) Diet and energy budget of the Antarctic fur seal, *Arctocephalus gazella*, at South Georgia. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer, Berlin, pp 543–550
- Duhamel G, Koubbi P, Ravier C (2000) Day and night mesopelagic fish assemblages off the Kerguelen Islands. *Polar Biol* 23:106–112
- Ferreira SM, Bester MN (1999) Chemical immobilization, physical restraint, and stomach lavaging of fur seals (*Arctocephalus* spp.) at Marion Island. *S Afr J Wildl Res* 29:55–61
- Gales R, Pemberton D (1994) Diet of the Australian fur seal in Tasmania. *Aust J Mar Freshw Res* 45:653–664
- Gentry RL (1998) Behavior and ecology of the northern fur seal. Princeton University Press, Princeton
- Gentry RL, Kooyman GL (1986) Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton
- Gentry RL, Costa DP, Croxall JP, David JHM, Davis RW, Kooyman GL, Majluf P, McCann TS, Trillmich F (1986) Synthesis and conclusions. In: Gentry RL, Kooyman GL (eds) Fur seals: maternal

- strategies on land and at sea. Princeton University Press, Princeton, pp 220–264
- Georges JY, Guinet C (2000a) Early mortality and perinatal growth in the subantarctic fur seal (*Arctocephalus tropicalis*) on Amsterdam Island. *J Zool (Lond)* 251:277–287
- Georges JY, Guinet C (2000b) Maternal care in the Subantarctic fur seals on Amsterdam Island. *Ecology* 81:295–308
- Georges JY, Bonadonna F, Guinet C (2000a) Foraging habitat and diving activity of lactating Subantarctic fur seals in relation to sea-surface temperatures at Amsterdam Island. *Mar Ecol Progress Ser* 196:291–304
- Georges JY, Tremblay Y, Guinet C (2000b) Seasonal diving behaviour in lactating Subantarctic fur seals on Amsterdam Island. *Polar Biol* 23:59–69
- Goebel ME, Bengtson JL, DeLong RL, Gentry RL, Loughlin TR (1991) Diving patterns and foraging locations of female northern fur seals. *Fishery Bull* 89:171–179
- Goldsworthy SD (1999) Maternal attendance behaviour of sympatrically breeding Antarctic and subantarctic fur seals, *Arctocephalus* spp., at Macquarie Island. *Polar Biol* 21:316–325
- Goldsworthy SD, Hindell MA, Crowley HM (1997) Diet and diving behaviour of sympatric fur seals *Arctocephalus gazella* and *A. tropicalis* at Macquarie Island. In: Hindell MA, Kemper C (eds) Marine mammal research in the Southern hemisphere: status, ecology and medicine, vol 1. Surrey Beatty & Sons, Chipping Norton, pp 151–163
- Green K (1997) Diving behaviour of Antarctic fur seals *Arctocephalus gazella* Peters around Heard Island. In: Hindell MA, Kemper C (eds) Marine mammal research in the Southern hemisphere: status, ecology and medicine, vol 1. Surrey Beatty & Sons, Chipping Norton, pp 97–104
- Green K, Williams R, Burton HR (1997) Foraging ecology of Antarctic fur seals *Arctocephalus gazella* Peters around Heard Island. In: Hindell MA, Kemper C (eds) Marine mammal research in the Southern hemisphere: status, ecology and medicine, vol 1. Surrey Beatty & Sons, Chipping Norton, pp 105–113
- Guinet C, Georges JY (2000) Growth in pups of the subantarctic fur seal (*Arctocephalus tropicalis*) on Amsterdam Island. *J Zool (Lond)* 251:289–296
- Guinet C, Jouventin P, Georges JY (1994) Long term population changes of fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet) and subtropical (St. Paul and Amsterdam) islands and their possible relationship to El Niño Southern Oscillation. *Antarct Sci* 6:473–478
- Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54:187–211
- Kerley GIH. (1987) *Arctocephalus tropicalis* on the Prince Edward islands. In Croxall JP, Gentry RL (eds) NOAA Technical Report NMFS 51, US Department of Commerce, pp 61–64
- Kirkman SP, Bester MN, Hofmeyr GJG, Pistorius PA, Makhado AB (2002) Pup growth and maternal attendance patterns in Subantarctic fur seals. *Afr Zool* 37:13–19
- Kirkman SP, Bester MN, Makhado AB, Pistorius PA (2003) Female attendance patterns of Antarctic fur seals at Marion Island. *Afr Zool* 38:402–405
- Kirkman SP, Wilson W, Klages NTW, Bester MN, Isaksen K (2000) Diet and estimated food consumption of Antarctic fur seals at Bouvetoya during summer. *Polar Biol* 23:745–752
- Klages NTW, Bester MN (1998) Fish prey of fur seals *Arctocephalus* spp. at subantarctic Marion Island. *Mar Biol* 131:559–566
- Lea MA, Cherel Y, Guinet C, Nichols PD (2002a) Antarctic fur seals foraging in the Polar Frontal zone: inter-annual shifts in diet as shown from fecal and fatty acid analyses. *Mar Ecol Progress Ser* 245:281–297
- Lea MA, Hindell M, Guinet C, Goldsworthy S (2002b) Variability in the diving activity of Antarctic fur seals, *Arctocephalus gazella*, at Iles Kerguelen. *Polar Biol* 25:269–279
- Lea MA, Nichols PD, Wilson G (2002c) Fatty acid composition of lipid-rich myctophids and mackerel fish (*Champscephalus gunnari*)—Southern Ocean food-web implications. *Polar Biol* 25:843–854
- Lunn NJ, Boyd IL (1993) Influence of maternal characteristics and environmental variation on reproduction in Antarctic fur seals. In: Boyd IL (ed) Symposia of the Zoological Society of London, vol 66. Clarendon Press, Oxford, pp 115–129
- Lunn NJ, Boyd IL, Barton T, Croxall JP (1993) Factors affecting the growth rate and mass at weaning of Antarctic fur seals at Bird island, South Georgia. *J Mammal* 74:908–919
- Luque SP (2007). Diving behaviour analysis in R. *R News* 7 (in press)
- McCafferty DJ, Boyd IL, Walker TR, Taylor RI (1998) Foraging responses of Antarctic fur seals to changes in the marine environment. *Mar Ecol Progress Ser* 166:285–299
- Mori Y (1998) Optimal choice of foraging depth in divers. *J Zool (Lond)* 245:279–283
- Mori Y, Yoda K, Sato K (2001) Defining dive bouts using a sequential differences analysis. *Behaviour* 138:1451–1466
- Ochoa-Acuña H, Francis JM (1995) Spring and summer prey of the Juan Fernández fur seal, *Arctocephalus philippii*. *Can J Zool* 73:1444–1452
- Page B, McKenzie J, Goldsworthy SD (2005) Inter-sexual differences in New Zealand fur seal behaviour. *Mar Ecol Progress Ser* 304:249–264
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer, Heidelberg
- R development Core Team (2006) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-00-3. <http://www.R-project.org>
- Reid K, Arnould JPY (1996) The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biol* 16:105–114
- Robinson SA, Goldsworthy SD, van den Hoff J, Hindell MA (2002) The foraging ecology of two sympatric fur seal species, *Arctocephalus gazella* and *Arctocephalus tropicalis*, at Macquarie Island during the austral summer. *Mar Freshw Res* 53:1071–1082
- Robison BH (2003) What drives the diel vertical migrations of Antarctic midwater fish? *J Mar Biol Assoc U K* 83:639–642
- Schulz TM (2004) Pinniped lactation strategies: evaluation of data on maternal and offspring life history traits. *Mar Mammal Sci* 20:86–114
- Smale MJ, Watson G, Hecht T (1995) Otolith atlas of southern African marine fishes. JBL Smith Institute of Ichthyology, Grahamstown
- Sparrow MD, Heywood KJ (1996) Current structure of the south Indian Ocean. *J Geophys Res* 101:6377–6391
- Wells RS, Boness DJ, Rathbun GB, Rommel SA (1999) Behavior. In: Reynolds JE III (ed) Biology of marine mammals, Smithsonian Institution Press, Washington, pp 324–422
- Williams D, McEldowney A (1990) A guide to the fish otoliths from the waters off the Australian Antarctic Territory, Heard and Macquarie Islands. ANARE Res Notes 75:1–173