Colony-based foraging segregation by Antarctic fur seals at the Kerguelen Archipelago

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ABSTRACT: The foraging behaviour of conspecific female Antarctic fur seals (AFS) was compared simultaneously at 2 breeding colonies at Îles Kerguelen (S Indian Ocean). A remnant colony at Îles Nuageuses (IN) thought to have escaped sealing is hypothesized to be the source of increasing fur seal numbers at Cap Noir (CN) on the Kerguelen mainland. Inter-annual variability in foraging areas is known to occur in response to local oceanographic changes at CN. Given the distance between the 2 sites (~160 km), we hypothesize that seals from the 2 colonies may show spatial segregation in foraging due to variability in local prey resource availability, although the transfer of foraging knowledge between sites via emigration may override such behaviour. The foraging zones, diving activity, diet and foraging success of seals were compared between sites using satellite telemetry, dive recorders and faecal analysis. No evidence of spatial foraging overlap was observed, with seals from IN conducting longer foraging trips, typified by a longer initial transit phase, than CN seals, which spent less time diving at night and dived more deeply. Pups nevertheless received higher absolute and daily energy delivery rates at IN. Diet was superficially similar at ~98 % myctophid consumption; however, IN seals favoured the high-energy *Gymnoscopelus nicholsi*, indicating that local heterogeneity in marine resources likely influences the foraging zone choice of AFS. Finally, distribution patterns of 54 female AFS tracked during summer months from 1998 to 2006 reveal the importance of both on-shelf (<500 m) and shelf-break regions as foraging habitat. The core foraging area for CN in all years (10 400 km²) was small (~10 % of total foraging space); however, time spent in this region alone totaled 38 %. The likelihood of spatial overlap in foraging range is higher on the east coast of Kerguelen.

KEY WORDS: Fur seal · Segregation · Myctophid · Diving · Southern Ocean

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INTRODUCTION

Intra-specific spatial and dietary segregation is common between the sexes and the different age classes of top level marine predators like seals (Sterling & Ream 2004, Page et al. 2006), seabirds (Baird 1991) and penguins (Forero et al. 2002). Such differences may be explained by variation in body size and, consequently, diving ability, or in relation to temporal constraints on foraging behaviour related to breeding (Salamolard & Weimerskirch 1993, Charrassin et al. 1998), as in the case of central place foragers (Orians & Pearson 1979). High latitude species in particular,

such as seals and penguins, exhibit foraging plasticity both within and between sites in response to changes in physical oceanography and associated marine productivity (McCafferty et al. 1998, Tremblay & Cherel 2003, Lea et al. 2006, Trathan et al. 2006). Favourable foraging and reproductive success are likely positively influenced by the prevalence of proximal and/or predictable concentrations of prey (Mori & Boyd 2004, Trathan et al. 2006). Temporal and spatial variability in marine productivity and availability also influence individual and colony-wide foraging behaviour, while competition between similar niche species may be equally important in regulating foraging

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activity (Barlow et al. 2002). At sub-Antarctic South Georgia Island, where the majority of predators feed on Antarctic krill *Euphausia superba* during summer months, macaroni penguins *Eudyptes chrysocome* are a case in point. Penguins tracked from adjacent islands show considerable foraging overlap, while those from more distant breeding sites displayed no overlap whatsoever. A 7 yr study of foraging habitat at one breeding site helped interpret these data. In all years, penguins concentrated their foraging efforts on a bearing to the north of the colony, only varying the distance out to the shelf between years (Trathan et al. 2006), suggesting that inter-annual variability in shelf prey availability determined the extent of foraging movements.

Few sympatric, conspecific comparisons of pinniped, and particularly, otariid, foraging distribution patterns have been undertaken. Northern fur seals *Callorhinus ursinus* in northern sub-polar regions display a high degree of individual (Call et al. in press) and colony-related foraging site fidelity (Robson et al. 2004) during summer foraging trips, although the degree of overlap varies temporally within a season and between years (Call et al. in press). Again, at South Georgia, female Antarctic fur seals *Arctocephalus gazella* (AFS) from 2 colonies located only 90 km apart exhibited no spatial overlap, even though their potential foraging range was up to 300 km (Boyd et al. 2002).

At sub-Antarctic Îles Kerguelen, AFS numbers are recovering after considerable sealing pressure in the 1800s (Budd & Downes 1969). Breeding individuals on the Courbet Peninsula of Kerguelen were first discovered in the early 1980s (Bester 1981) and are thought to have immigrated from a remnant population in the northwestern sector of Îles Kerguelen (Bester 1981), subsequently shown to be at Îles Nuageuses (IN) (Jouventin et al. 1982). Studies of female AFS foraging behaviour conducted on the Courbet Peninsula between 1998 and 2000 have established high individual foraging-site fidelity (Bonadonna et al. 2001) and a strong correlation between many foraging parameters and change in environmental parameters such as sea surface temperature, the location of frontal structures, distance to the colony and the distribution of fish prey resources (Guinet et al. 2001, Lea & Dubroca 2003, Lea et al. 2006). To date, no studies of the foraging behaviour of seals from the remnant IN population have been undertaken. Given the inter-annual variability in foraging success exhibited by AFS at Cap Noir (CN) in response to changing oceanographic conditions and prey availability (Lea et al. 2006), and the foraging habitat preferences predicted for central place-foraging female AFS by Guinet et al. (2001), segregation in foraging distribution and diet may well be expected between the 2 colonies if prey availability is sufficient.

Previous foraging studies of AFS females from the CN breeding colony indicate that an area extending from the northeast to the east of the colony is an important foraging area (Lea et al. 2006). Given the potential importance of the IN population to the recolonisation of the Courbet Peninsula at Îles Kerguelen and the proximity of the 2 islands within the foraging range previously recorded for AFS at Îles Kerguelen (Bonadonna et al. 2001, Guinet et al. 2001, Lea et al. 2006), some overlap in foraging habitat between sites may also be expected to occur. Consequently, the primary aim of this study was to determine whether the AFS population at IN displays evidence of foraging segregation in terms of spatial foraging distribution, dive behaviour, foraging success (such as pup mass gain) and diet in comparison to seals from the derivative colony at CN.

MATERIALS AND METHODS

Study sites and population size. The Kerguelen Archipelago (49° 20' S, 70° 20' E) in the southern Indian Ocean (Fig. 1) is comprised of approximately 300 islands with a combined coastline greater than 3000 km. One of the most isolated land masses on Earth, it is located more than 3000 km from both Africa and Australia, and approximately 2200 km north of Antarctica.

The 2 study colonies were located 164 km apart at CN (49° 07' S, 70° 45' E) on the northeast coast of the Courbet Peninsula (CN, the site of a 3 yr study) and at Île de Croy (48° 38' S, 68° 38' E, IN, Fig. 1) in the IN. The colony at CN currently extends along the coast over a distance of approximately 1 km. Seals breed on pebbly beaches with mothers and pups moving onto the *Cotula plumosa* covered slopes and plateau as pups become more independent from their mothers. At the rarely visited IN colony, the majority of breeding activity is centred around a small, protected bay on the east coast of the island. In 1984 seals were reported as breeding on the headlands north and south of the bay and on an offshore islet to the southeast, with an estimated 1500 females on the headlands and over 5000 seals in total (Jouventin & Stonehouse 1985). The IN colony was visited from 5 to 20 January 2000, while an ongoing study was conducted at CN from December 1999 to March 2000. Analyses are restricted to the common period of 5 to 20 January 2000 in early summer.

Systematic whole colony counts of tagged and untagged pups at CN were made in late January in 1999 and 2000 as part of an ongoing 3 yr study (1998 to 2000) at this site (see Table 1 and Lea et al. 2006).

Fig. 1. *Arctocephalus gazella*. Time spent per 20×20 km grid cell for female Antarctic fur seals from Îles Nuageuses (west, $n = 5$) and Cap Noir (east, $n = 7$) in January 2000. Time spent (seal hours) is weighted by the number of seals and calculated for each colony separately. Inset map 13134 (Edition 1) courtesy of the Australian Antarctic Data Centre

A simplified mark-recapture technique using the number of flipper-tagged pups resighted as a proportion of those known to be tagged was used as a correction for counts of untagged pups. At IN, a single count of unmarked pups on the beaches and tussocks was made on 18 January 2000. A factor of 4.1 was used to convert pup counts to population size (Page et al. 2003).

Foraging activity. Time-depth recorders (TDRs, Wildlife Computers) or a TDR and platform terminal transmitter package (ST-10 PTT, Telonics Pty, packaged by Sirtrack) linked to the ARGOS satellite system were deployed on adult females to study the diving activity and foraging distribution of the seals (see Bonadonna et al. 2000, Guinet et al. 2001, Lea et al. 2002b, 2006). Seals were captured ashore using a hoop net and were subsequently weighed, a standard length measurement was recorded (nose to tail in ventral recumbancy) and an individual number was applied to

the fur on the rump with peroxide hair-dye (Bristol-Myers Squibb). During the attachment of the devices, adult seals were held on a wooden restraint board. Following the deployment, which lasted an average of 15 to 20 min, seals were released with their pups. The colonies were checked at least twice daily for the return of marked females overnight (0800) and during the day (1900).

Three types of dive recorders were deployed on seals from the 2 sites in January 2000. A single Mk7 TDR was attached dorsally to the fur 10 cm anterior to the rump of 9 seals at IN and 10 seals at CN using 2-part Araldite (AW 2101, Ciba Specialty Chemicals) for the study of diving behaviour. TDR/PTT packages were also deployed on seals at both sites for the study of at-sea distribution patterns. At CN, Mk7 TDR/PTT packages (Lea & Dubroca 2003) were deployed on 8 seals, while at IN, Mk5 TDR/PTT packages (Bonadonna et al. 2000, Guinet et al. 2001) were

deployed on 7 seals (Table 1). Relatively large seals with healthy pups were selected for these deployments. These packages were attached dorsally between the scapulae.

In total, devices were attached to 33 seals (15 at IN and 18 at CN). During the course of the study 1 seal returned without the TDR/PTT device (CN), 1 seal was not

Table 1. *Arctocephalus gazella*. Pup production counts at Cap Noir (CN) and Île de Croix (Îles Nuageuses) breeding colonies in 1999 and 2000

Date	Size	Pups counted Tagged Untagged	Actual no. tagged pups	Estimated pup production	Est. colony Size
22 Jan 1999	Cap Noir	130 545	140	724	2968
29 Jan 2000	Cap Noir	137 512	158	748	3067
18 Jan 2000	Île de Croix	– 3279	–	~3600 ^a	14 700

^aAdditional pups seen on inaccessible islet in east harbour

recaptured and thus PTT data were available without dive data (IN), and in 4 cases (2 per colony), the Mk7 TDR failed to record dive data. PTTs (2 MK10-A satellite GPS tags, Wildlife Computers, and 3 ST-10 PTT) were also deployed on 16 females at Pointe Suzanne on the southeastern Courbet Peninsula from 22 January to 21 February 2006. The movements of these adult females, together with those at IN (from 2000) and CN (from 1998 to 2000), constitute the total tracking research undertaken at Îles Kerguelen and consequently provide the most complete island-wide estimate of foraging habitat use.

Transit and foraging phases were determined from the onset and ending of bout diving during the foraging trip (see Lea et al. 2002b for bout analysis details). Inter-site comparisons of diving behaviour have been restricted to those seals at each site carrying the small, rump-mounted Mk7 TDRs to minimize the device effects associated with carrying larger PTTs. An analysis of similarity (ANOSIM) and a similarity of percentages (SIMPER) analysis with site as a factor were conducted using PRIMER 5.0 (Primer-E Limited). Seven dive parameters were included in the analyses: mean dive depth (m), dive duration (min), foraging trip length (d), proportion of time spent diving, proportion of dives in bouts, mean dives per bout and dive frequency (h^{-1} , see Lea et al. 2002b for greater detail). Proportional data were arcsine-transformed and other data were log-transformed.

Spatial analyses. Argos movement data of location quality 0 to 3 (see Bonadonna et al. 2001) were filtered for an upper speed of 3.0 m s^{-1} using the filtering algorithm in the R-Software Trip package (Sumner 2006). The resulting track was split into 60 min segments, which were then summed within $20 \times 20 \text{ km}$ grid cells to create time spent in area plots for habitat use. Time spent in cells was converted to a proportion by colony or year to standardize effects of sample size for the various deployments. The centroid of the $20 \times 20 \text{ km}$ grid cells was spatially joined in ArcMap (ESRI) to the nearest bathymetry value (GEBCO One Minute Grid) to provide a water depth measurement per cell. Bathymetric domains were defined as inner shelf ($<500 \text{ m}$), outer shelf (500 to 1000 m), shelf break (1000 to 1500 m), and deep waters ($>1500 \text{ m}$).

Diet. Faecal samples were collected from female haul-out sites in the colonies at CN and IN during the course of the study (6 January to 23 January 2000). Individual samples were frozen at -20°C on site and returned to the laboratory for sorting and prey identification. Samples were elutriated overnight and subsequently sieved with a 1 mm and 500 μm mesh. The frequency of occurrence (FO) of fish (otoliths, scales and bones), squid (beaks, radulas, pens and eye lenses), invertebrates (amphipods, isopods, nematodes and

annelids) and other miscellaneous items in faeces was noted. Percentage FO is expressed as a percentage of the number of faeces containing prey items. Numerical abundance of fish and squid was estimated by the sorting and identification to species level of otoliths (sagitta, asteriscus and lapillus) when possible. See Lea et al. 2002a for further details.

Dietary comparisons between sites were conducted using a stepwise Discriminant Function Analysis (Systat 9.0, SPSS) with tolerance level set at 0.15 and p values of 0.05. Measures of mass gain were compared between sites using a 2-sample t -test. All variables were tested for normality and homogeneity of variance with Levene's statistic.

Foraging success. Inter-site comparisons of pup mass: A random cross-sectional sample of pups ($n = 100$) was weighed at each breeding site on 14 January 2000 to test for differences in mean size of pups between populations. Pups were weighed using a Salter Weightronix spring balance ($25 \pm 0.02 \text{ kg}$) by field teams moving systematically through the colony to prevent the repeat weighing of individuals. Comparisons were made per sampling period by 2-way ANOVA on log-transformed mass data with 'sex' and 'site' as factors (SPSS).

Pup mass gain per foraging cycle: Mass gained by a pup during a foraging cycle (1 foraging trip and subsequent shore bout) has been shown to represent a relatively easily obtainable measure of maternal energy transfer to the pup in several studies (Georges & Guinet 2000, Guinet et al. 2000). The pups of females equipped with PTT and/or TDRs were weighed each day during the fasting period while females were at sea, prior to the arrival of the female and again immediately after her departure, to estimate the mass gained by the pup during the foraging cycle (FC). In instances where the body mass was not recorded on the arrival day of the female, it was estimated by linear regression of pup mass lost during the previous fasting bout. A control group consisting of pups from unequipped females was also monitored simultaneously at each colony (IN: $n = 12$; CN: $n = 21$).

RESULTS

CN-IN comparison

Foraging habitat use

There was no overlap in the foraging zones used by seals tracked simultaneously at IN ($n = 5$) and CN ($n = 7$) in January 2000 (Fig. 1). Seals from the CN colony foraged within a $\sim 240 \text{ km}$ arc from the NE to the SE of the island (Table 2, Fig. 1), whilst the majority of

Table 2. *Arctocephalus gazella*. Summary statistics for female Antarctic fur seals studied at Iles Nuageuses (IN) and Cap Noir (CN), Iles Kerguelen. L: length; PTT: platform transmitter terminal; TDR: time-depth recorder; Mk7: Mk7 TDR; y: yes; BDG: Behaviour Dive Group (Lea et al. 2002b)

Site	Unit	Seal	BDG	Deploy date	Length (cm)	Mass (kg)	Pup sex	Pup L (cm)	Pup Mass (kg)	Dives	PTT	TDR	Trip duration (d)	Maximum distance (km)
CN	Mk7	J1	2	7 Jan	107.5	24.5	F	61.5	6.0	1213	–	Y	6.0	–
CN	Mk7	J2	2	7 Jan	109.5	24.8	F	69.5	3.2	706	–	Y	3.2	–
CN	Mk7	J3	2	6 Jan	109.5	26.8	M	71	5.1	1118	–	Y	5.1	–
CN	Mk7	J6	2	7 Jan	113	26.9	M	65	8.1	2230	–	Y	8.1	–
CN	Mk7	J7	2	8 Jan	120.5	32.4	M	73	7.9	2186	–	Y	7.9	–
CN	Mk7	J9	2	8 Jan	119.5	33.0	F	71	5.8	1100	–	Y	5.8	–
CN	Mk7	J10	2	8 Jan	111	24.9	F	66.5	4.3	1299	–	Y	4.3	–
CN	PTT	H2	1	15 Jan	117.5	34.3	M	74	6.8	1163	Y	Y	6.8	230
CN	PTT	H3	3	29 Jan	114.5	34.8	F	77.5	12.3	2453	Y	Y	12.3	448
CN	PTT	H4	1	30 Jan	113	29.4	M	76	8.9	2055	Y	Y	8.9	193
CN	PTT	H5	1	30 Jan	110	29.7	F	73.5	6.2	1141	Y	Y	6.2	186
CN	PTT	H6	2	31 Jan	117	33.9	M	80.5	9.3	2863	Y	Y	9.3	259
CN	PTT	H7	2	29 Jan	115	28.3	F	79	8.8	2855	Y	Y	8.8	251
CN	PTT	H8	1	31 Jan	119.3	31.5	M	83	5.16	915	Y	Y	5.2	114
IN	Mk7	IN8	1	Mean	114.6 ± 1.2	30.1 ± 1.0		72.9 ± 1.5	6.7 ± 0.7	1599.4 ± 195.9	–	Y	7.0 ± 0.6	240.1 ± 39.3
IN	Mk7	IN10	2	5 Jan	112.5	29.4	F	73.5	7.3	1213	–	Y	7.3	–
IN	Mk7	IN11	4	6 Jan	128	41.0	M	75.5	8.3	2226	–	Y	8.3	–
IN	Mk7	IN12	2	8 Jan	112	30.7	F	68	6.5	1178	–	Y	6.5	–
IN	Mk7	IN13	2	6 Jan	114	30.0	F	65.5	9.1	2847	–	Y	9.1	–
IN	Mk7	IN14	1	8 Jan	120.3	36.8	F	71.5	9.0	1674	–	Y	9.0	–
IN	Mk7	IN15	2	7 Jan	126	35.5	M	83	8.2	2335	–	Y	8.2	–
IN	Mk7	IN15	1	8 Jan	122	40.0	M	74	6.9	1367	–	Y	6.9	–
IN	PTT	IN1	1	7 Jan	121.3	36.8	M	76	8.7	2155	–	Y	8.7	–
IN	PTT	IN2	1	6 Jan	112.3	33.7	M	70	8.8	2015	Y	Y	8.8	281
IN	PTT	IN3	1	5 Jan	113	31.4	M	74.5	7.5	1410	Y	Y	7.5	202
IN	PTT	IN4	3	5 Jan	112.3	28.0	F	73	8.9	1718	Y	Y	8.9	201
IN	PTT	IN5	1	8 Jan	114	32.7	F	73	11.4	1809	–	Y	11.4	–
IN	PTT	IN6	1	10 Jan	123	37.0	M	71	10.0	–	Y	Y	8.8	253
IN	PTT	IN7	1	7 Jan	112.8	32.2	F	66.5	8.3	1845	Y	Y	8.3	301
IN	PTT	Mean		Mean	117.4 ± 1.5	33.9 ± 1.1		72.5 ± 1.2	8.5 ± 0.3	1830.2 ± 134.5			8.4 ± 0.3	247.6 ± 20

seals at IN foraged within a ~250 km arc to the W and SW of the colony (224° to 278°). The foraging range of females was similar between the 2 colonies ($t_{10} = 0.149$, $p > 0.05$), although the range in maximum distance traveled from CN was highly variable (114 to 448 km, Table 2). Time spent in different bathymetric regions varied considerably between sites. Females at IN spent more time on the inner shelf (39%) and in deep waters (33%) than on the outer shelf (14%) and shelf break (12%). At CN females spent more time in deeper waters (36%) and on the outer shelf (26%) than on the inner shelf (17%) and shelf break (16%).

There is some evidence for device effects, with PTT females recording longer foraging trips than TDR females ($F_{1,25} = 5.185$, $p = 0.038$, Table 3). Consequently, we have only included TDR dive statistics in analyses for 7 females at each site (3 TDRs at CN and 1 TDR at IN failed, and 1 TDR at IN was not retrieved). Absolute and proportional transit and foraging phases of PTT females were similar between sites. Trip durations of TDR females at IN were significantly longer than those at CN (Table 3), as were transit times to the start of the first foraging bout (0.70 d cf. 0.41 d; $t_{11.87} = -2.370$, $p = 0.036$). No significant differences in return transit phase, foraging phase length (time between transit phases), or the proportion of any phase in relation to trip duration were detected between sites, although the foraging phase tended to be longer at IN (Table 3). Foraging phase length was positively related to trip duration (Fig. 2).

The diving behaviour of females at each site (IN: 12840 dives, CN: 9852 dives) differed markedly when compared by ANOSIM, at $p = 0.023$. Foraging trip duration, mean dive depth and the number of dives per hour accounted for 65.2% of the inter-site dissimilarity (Table 4). Trips were longer, dives deeper and the frequency of diving less at IN (Table 4). If trip duration was removed from the analysis, mean dive depth and dive frequency alone accounted for 52.4% of the dissimilarity between sites ($p = 0.044$). Mean dive depth was also significantly negatively correlated to foraging phase duration at IN ($r_{1,7} = -0.904$, $p = 0.005$) but not at

Fig. 2. *Arctocephalus gazella*. Relationship between trip duration and foraging phase length for females at Îles Nuageuses (IN) ($n = 7$) and Cap Noir (CN) ($n = 7$). FT: foraging trip duration; FP: foraging phase

CN ($r_{1,7} = 0.425$, $p > 0.05$). The timing of diving activity varied significantly between sites ($t = -3.780$, $p = 0.008$) with females at CN conducting 94.5 ± 1.0 (SE) % of their diving nocturnally (Fig. 3, Table 4), compared with females from IN at 68.6 ± 6.8 % (33 to 87 %).

Dietary preferences

The frequency of occurrence of fish in the diet of female seals was high, with fish remains predominating at both study sites (83% at IN and 89% at CN, Table 5). Evidence of cephalopod ingestion was considerably higher at CN than at IN, with beaks occurring in 67% of scats samples at CN (cf. 33% at IN). Crustaceans and other invertebrates were relatively uncommon by comparison, occurring in only one-third of samples from both sites.

In total 18 species of fish were recorded in the diet of female fur seals at IN and 15 species at CN (Table 6). The diet at both sites was dominated by myctophids, which accounted for 97.8% at IN and 98.8% at CN. In total, 1727 sagittal otoliths were recovered from the scats. Although the mean number of otoliths per scat was highest

Table 3. *Arctocephalus gazella*. Mean durations and proportions of foraging and transit phases for females Antarctic fur seals from Îles Nuageuses (IN) and Cap Noir (CN). Sample sizes in parentheses

Duration of trip	IN (7)		CN (7)		<i>t</i>	<i>df</i>	<i>p</i>
Phases (days)	Mean	SE	Mean	SE			
Transit phase 1 (T1)	0.70	0.09	0.41	0.08	-2.370	12	0.035
% time in T1	0.93	0.52	1.05	0.42	-0.501	12	0.625
Foraging phase (FP)	6.78	0.37	5.14	0.74	-1.991	12	0.070
% time in FP	85.79	1.33	87.33	3.33	-0.431	12	0.674
Transit phase 2 (T2)	0.41	0.17	0.20	0.09	-1.102	12	0.292
% time in T2	6.16	2.48	6.23	3.08	0.018	12	0.986
Total trip length	7.89	0.38	5.76	0.67	2.768	12	0.017

Table 4. *Arctocephalus gazella*. Mean comparisons and analysis of dissimilarity for dive parameters between female at Îles Nuageuses (IN) and Cap Noir (CN). PMG: pup mass gain during foraging trip (kg); PM: night

Parameter	IN (n = 7)	CN (n = 7)	T	p	Cumulative % dissimilarity
1. Trip length (d)	7.89 ± 0.38	5.76 ± 0.67	2.768	0.017	26.9
2. Mean depth (m)	59.7 ± 6.92	43.1 ± 1.44	2.343	0.054	48.3
3. Dives per hour	9.5 ± 0.9	10.1 ± 0.7	-0.470	0.646	65.2
4. Mean dive duration (min)	1.59 ± 0.13	1.29 ± 0.06	8.482	0.069	81.8
5. Dives per bout	10.1 ± 0.3	11.6 ± 0.7	-1.971	0.083	93.9
6. Time spent diving (%)	21.4 ± 0.01	24.2 ± 0.01	1.927	0.078	
7. Proportion dives in bouts	97.6 ± 0.003	97.1 ± 0.004	0.794	0.443	
8. Proportion dives PM	68.6 ± 0.07	94.5 ± 0.01	-3.780	0.008	
9. Time spent diving PM	41.7 ± 0.04	58.0 ± 0.02	-3.390	0.005	
10. Prop Vertical depth PM	50.0 ± 6.5	87.1 ± 3.3	-5.103	0.000	
11. Dives per hour PM	20.7 ± 3.6	29.3 ± 2.0	-2.127	0.055	
PMG (TDR)	3.1 ± 0.3	1.7 ± 0.3	-3.049	0.011	
PMG_FT (TDR)	0.394 ± 0.04	0.278 ± 0.02	-2.144	0.055	
PMG_FC (TDR)	0.312 ± 0.04	0.223 ± 0.02	-2.548	0.027	

Discriminant Function Analysis (DFA) of log-transformed abundance data (Wilks' Lambda = 0.2474, approx. $F_{11,16} = 4.4249$, $p < 0.01$). A backwards-stepwise DFA conducted on the same data indicated that 3 species, *Gymnoscopelus nicholsi*, *Electrona carlsbergi* and *Gobionotothen acuta* accounted for the distinction in diet between sites (Wilks' Lambda = 0.2526, approx. $F_{3,24} = 23.6758$, $p < 0.001$). Using these 3 species as discriminators, only 2 of 28 samples were incorrectly assigned (Jackknife matrix 93% success, IN: 100%; CN: 86%).

at IN (71.6 ± 22.4 [SE], range 1 to 238), it did not differ significantly to that at CN (51.8 ± 11.6). Diet samples from IN were dominated by *Gymnoscopelus nicholsi* (31.2%) and *G. fraseri* (29.1%), with *Kreftlichthys anderssoni* (12.0%) also important to several individuals. At CN the prevalence of *G. fraseri* in the diet (40.8%) outweighed that of all other species, while *Electrona subaspera* was also more common than in samples from IN (Table 6, Fig. 4).

A significant difference in the dietary composition between sites was detected by a complete linear

Foraging success

Body mass of pups was highly variable between individuals, ranging from 3.9 to 13.6 kg and 3.8 to 13.4 kg at CN and IN, respectively. Male pups were heavier than females pups ($F_{1,99} = 26.50$, $p < 0.001$) and IN pups were heavier than CN pups ($F_{1,99} = 7.22$, $p < 0.01$, Table 7).

Mass gained by pups (PMG) after a maternal foraging trip was measured for pups of control animals (IN: 2.7 ± 0.2 [SE] kg, $n = 8$; CN: 2.2 ± 0.2 kg, $n = 20$), PTT females

Fig. 3. *Arctocephalus gazella*. Diurnal variability in maximum dive depth at (a) Cap Noir ($n = 7$) and (b) Îles Nuageuses ($n = 7$). Shaded regions denote night

Table 5. *Arctocephalus gazella*. Frequency of occurrence by number and percentage of prey items recorded in Antarctic fur seal scats in January 2000 at Île de Croy (Iles Nuageuses) and Cap Noir, Kerguelen Archipelago. Number of scats sampled and the number containing prey items are in parentheses

	Île de Croy (37/18)		Cap Noir (26/18)	
	n	%	n	%
Fish	15	83.3	16	88.9
Otoliths	13	72.2	14	77.8
Eye lenses	9	50.0	13	72.2
Bones	14	77.8	12	66.7
Vertebrae	10	55.6	11	61.1
Myctophids	9	50.0	15	83.3
(scales or jaw bones)				
Channichthyids	1	5.6	0	0.0
(jaw bones or opercles)				
Nototheniids (jaw bones)	1	5.6	1	5.6
<i>Paradiplospinus gracilis</i>	1	5.6	0	0.0
(teeth or vertebrae)				
<i>Harpagifer spinosus</i>	0	0.0	1	5.6
(opercles)				
Cephalopods	6	33.3	13	72.2
Beaks	4	22.2	12	66.7
Eye lenses	3	16.7	10	55.6
Gladii	2	11.1	6	33.3
Crustaceans	6	33.3	6	33.3
<i>Themisto gaudichaudii</i>	5	27.8	4	22.2
Other amphipods	3	16.7	0	0.0
Isopods	1	5.6	1	5.6
Copepods	0	0.0	1	5.6
Others				
Nematodes	12	66.7	10	55.6
Pebbles	5	27.8	15	83.3
Mollusk shells	2	11.1	1	5.6
Feathers (penguin)	1	5.6	0	0.0

(IN: 2.9 ± 0.2 kg, $n = 4$; CN: 2.8 ± 0.2 kg, $n = 6$) and TDR females (Table 4). PMG varied significantly in relation to unit type only at CN, where pups of TDR females gained less mass than PTT pups ($F_{32,2} = 4.672$, $p = 0.016$) while control pups were intermediate (Fig. 5a). Overall, pups of TDR females at IN gained more absolute mass and daily mass per trip and foraging cycle than pups at CN (Table 3). A multi-linear regression indicated trip duration (FT) and maternal length (ML) contributed equally to absolute PMG ($PMG = 0.318FT + 0.098ML - 10.534$, $p < 0.001$, $r = 0.939$, Fig. 5b).

Regional habitat use

Females from the previously unstudied colony at Pointe Suzanne on the Courbet Peninsula dispersed to the SE over the Kerguelen Plateau towards Heard Island (Fig. 6a). Effort in terms of seal hours is relatively evenly distributed, although more time was spent by seals at the outer reaches of the foraging zone on the inner/outer shelf boundary (SE) and the shelf break (E and S). Fig. 6b summarizes previous summer

Fig. 4. *Arctocephalus gazella*. Percentage abundance of 11 myctophid species observed in the diet of Antarctic fur seals at Cap Noir (CN) and Îles Nuageuses (IN). Species abbreviations listed in Table 6

(January to March) tracking studies for 33 females from CN. Black cells demarcate the concentrated core foraging region common to seals in all 3 yr (1998 to 2000, Table 8), representing 9.7% of the total foraging region.

Finally, the foraging habitat use of seals from all 3 sites is presented in Fig. 6c. Foraging effort represents a combined 403 seal days for 54 individuals encompassing 281 20×20 km grid cells (112400 km²). Although not sampled simultaneously, the potential spatial overlap between the combined foraging range of CN seals and Pointe Suzanne females was high at 31.4%; however, the overlap with the core CN region was low at 3%. Bathymetric domains favoured by seals in order of importance were: outer shelf (34.3%), deep water (30%), inner shelf (19.9%) and shelf break waters (15.9%).

DISCUSSION

Between site comparisons in the same year

Spatial distribution and diving activity

Given the likely emigration of seals from IN to CN, some degree of similarity in foraging locations might be anticipated for seals from both sites. However, spatial overlap analyses of the foraging patterns of adult females from IN and CN in 2000 indicate complete foraging segregation at the 20×20 km scale. Sample sizes

Table 6. *Arctocephalus gazella*. Frequency of occurrence (FO), numbers, otolith (OL) or lower rostral beak length (LRL) of fish and squid prey of Antarctic fur seals at Île de Croÿ (Îles Nuageuses) and Cap Noir in January 2000. Values are mean $\pm$ SE. Numbers in parentheses: (no. of samples/no. of samples with prey items)

Fish	Île de Croÿ (37/23)				Cap Noir (26/12)			
	n	%	n	No.	OL (mm) (n)	FO n	%	OL (mm) (n)
Myctophidae								
<i>Gymnoscopelus nicholsi</i> ^a (Gn)	12	85.71	313	31.24	4.45 $\pm$ 0.04 (97)	9	64.29	58 8.00 4.74 $\pm$ 0.13 (8)
<i>Gymnoscopelus fraseri</i> (Gf)	10	71.43	292	29.14	3.58 $\pm$ 0.03 (86)	10	71.43	296 40.83 3.49 $\pm$ 0.06 (33)
<i>Gymnoscopelus</i> sp. (eroded) ^b	9	64.29	145	14.47	—	10	71.43	110 15.17 —
<i>Kreftichthys anderssoni</i> (Ka)	5	35.71	120	11.98	1.20 $\pm$ 0.03 (36)	4	28.57	15 2.07 1.26 $\pm$ 0.04
<i>Electrona carlsbergi</i> ^a (Ec)	5	35.71	48	4.79	3.75 $\pm$ 0.07 (11)	2	14.29	22 3.03 3.62 $\pm$ 0.06
<i>Gymnoscopelus piabilis</i> (Gp)	5	35.71	33	3.29	6.07 $\pm$ 0.07 (3)	6	42.86	23 3.17 5.24 (1)
Myctophidae (eroded) ^b	7	50.00	12	1.20	—	10	71.43	69 9.52 —
<i>Protomyctophum bolini</i> (Pb)	1	7.14	5	0.50	1.73 $\pm$ 0.03 (5)	3	21.43	4 0.55 1.77 $\pm$ 0.01 (2)
<i>Electrona Antarctica</i> (Ea)	4	28.57	4	0.40	—	7	50.00	12 1.66 1.51 $\pm$ 0.11 (2)
<i>Electrona subaspera</i> (Es)	2	14.29	3	0.30	3.72 $\pm$ 0.25 (3)	12	85.71	69 9.52 3.33 $\pm$ 0.15 (8)
<i>Protomyctophum choriodon</i> (Pc)	1	7.14	2	0.20	2.09 (1)	7	50.00	25 3.45 1.90 $\pm$ 0.03 (4)
<i>Protomyctophum tension</i> (Pt)	2	14.29	2	0.20	—	5	35.71	13 1.79 —
<i>Gymnoscopelus bolini</i> (Gb)	1	7.14	1	0.10	—	0	0.00	0 0.00 —
				97.81				98.76
Other fish								
<i>Icichthys australis</i>	4	28.57	12	1.20	—	1	7.14	2 0.28 —
<i>Gobionotothen acuta</i> ^a	2	14.29	3	0.30	—	0	0.00	0 0.00 —
<i>Scopelosaurus hamiltoni</i>	1	7.14	2	0.20	—	1	7.14	2 0.28 —
Channichthyidae sp. (eroded)	1	7.14	2	0.20	—	0	0.00	0 0.00 —
<i>Paradiplosinus gracilis</i>	1	7.14	1	0.10	3.21 (1)	0	0.00	0 0.00 —
<i>Benthalbella elongata</i>	1	7.14	1	0.10	—	0	0.00	0 0.00 —
? <i>Nansenia Antarctica</i>	1	7.14	1	0.10	—	1	7.14	2 0.28 —
<i>Magnisudis prionosa</i>	0	0.00	0	0.00	—	1	7.14	1 0.14 —
<i>Osteichthyes</i> sp. (eroded)	0	0.00	0	0.00	—	2	14.29	2 0.28 —
Total			1002	100				725 100
Mean per scat (range)			71.6 (1–238)				51.8 (1–138)	
Squid								
<i>Moroteuthis knipovitchi</i>	—	—	—	—	LRL (mm)	1	7.14	2 LRL (mm)
<i>Slosarczykovia circumantarctica</i> ^c	3	21.4	4	—	—	9	64.3	38 2.85 (1)
<i>Kondakovia longimana</i>	1	7.14	1	—	1.38, 1.88 (2)	—	—	2.19 $\pm$ 0.08 (20)
Undetermined squids	0	0.00	—	—	—	3	21.43	—

^aSignificant contribution in DFA; ^bNot included in discriminant function analyses; ^cPreviously described as *Brachioteuthis friisei* (Cherel et al. 1997, Lea et al. 2002a)

Table 7. *Arctocephalus gazella*. Mean pup body mass at Cap Noir (CN) and Iles Nuageuses (IN) in January 2000

Colony	Pup sex	Body mass ($\pm$ SE, kg)	n
CN	M	7.64 $\pm$ 0.25	43
CN	F	6.48 $\pm$ 0.19	57
IN	M	8.21 $\pm$ 0.25	52
IN	F	7.08 $\pm$ 0.21	48

for IN were small and consequently should be interpreted with some degree of caution. However, concurrent differences in diet, diving behaviour and indirect foraging success in terms of mass gain also support the idea of segregated foraging. Seals from IN concentrated their foraging effort westwards and to the SW along the shelf edge towards the Skiff Bank region in association with inner shelf and deep waters (Fig. 6). CN females, by comparison, dispersed widely from the colony to the east and south, focusing effort in deep water to the NE and along the outer shelf and southwards along the Kerguelen Plateau. The area to the NE of CN is highly productive, supporting one of the largest seasonal phytoplankton blooms in the Southern Ocean and high fish abundances associated with the flow of the Antarctic Polar Front (Duhamel et al. 2000, Blain et al. 2007). Consequently, it is regionally important for Antarctic fur seals and other marine predators (Guinet

et al. 2001, Bost et al. 2002, Charrassin et al. 2004, Lea et al. 2006) and fisheries (Cherel et al. 1996). The only previous records of fur seals to the west of Kerguelen include large groups sighted at sea (Ensor & Shaughnessy 1990), and more recently sightings and interactions of fur seals with fishing vessels (Capdeville 1997). The western slope of the Kerguelen shelf and the Skiff Bank region have been the focus of longline fisheries since the early 1990s (Duhamel 1992, Duhamel et al. 2005).

Clearly, local marine productivity is sufficiently high on both the east and west coasts of the island to enable distinct foraging segregation between the 2 colonies irrespective of their close proximity (~160 km). Such a distance would take ~18 hr to cover at average surface swim speeds of 2.5 m s⁻¹ (Watson 2007). Transit times to and from feeding areas and maximum distance traveled did not vary significantly for tracked seals (Fig. 1); however, there does appear to be some effect of carrying the PTT/TDR devices as foraging trips were longer for these females than those carrying only a tail-mounted TDR. Transit time to feeding areas and foraging trip durations were, however, significantly longer for TDR females from IN than CN, implying that the onset of foraging occurs earlier at CN. In addition to increased foraging times, IN females spent more time diving during the day, to deeper depths (~60 m) than their CN counterparts (see Lea et al. 2002b). It is likely that females are foraging over the extended shelf

Fig. 5. *Arctocephalus gazella*. (a) Regression of absolute mass gained by pups (PMG) against maternal trip duration for control (n = 28), TDR-equipped (Mk7; n = 14) and PTT-equipped females (n = 10); and (b) regression of PMG against maternal length for TDR equipped females; CN: Cap Noir; IN: Iles Nuageuses; black: CN; grey: IN

Fig. 6. *Arctocephalus gazella*. Time spent in seal hours per 20° × 20 km grid by adult female Antarctic fur seals at: (a) Pointe Suzanne (2006, n = 16); (b) Cap Noir (1998–2000, n = 33); and (c) all 3 colonies at Îles Kerguelen in 1998, 1999, 2000 and 2006 (n = 54). Black circles denote core summer foraging region for female seals from Cap Noir. Grey circles denote overlap between females from Cap Noir and Pointe Suzanne

Table 8. *Arctocephalus gazella*. Habitat use and spatial foraging overlap for adult female Antarctic fur seals from Cap Noir (CN), Îles Nuageuses (IN) and Pointe Suzanne (PS)

Colony comparisons	n	Seal foraging hours	Number 20 × 20 km cells	Foraging area (km ²)	Mean area per seal (km ²)	Mean water depth
CN: Jan 00	7	1414	95	38 000	5429	1611 ± 102
IN: Jan 00	5	1090	55	22 000	4400	1041 ± 87
CN: summer 98–00	33	5694	184	73 600	2230	1696 ± 79
PS: summer 06	16	2892	113	45 200	2825	839 ± 51
All colonies	54	9676	281	112 400	2082	1443 ± 58
Overlap		% overlap			Sum time spent (%)	
Core CN: Summer 98–00	–	9.7	26	10 400	38.0	854 ± 114
Core CN & PS	–	3.6	14	5600	11.8	886 ± 120
CN Summer & PS	–	31.4	71	28 400	37.7	876 ± 69

region to the west of IN during daytime transits to productive shelf-break regions and access to preferred pelagic prey resources. Local oceanographic features, such as current movements, may contribute to the outward direction (Park et al. in press) taken by adult females in addition to an individual's prior knowledge of seasonal food resources (Bonadonna et al. 2001); the persistence of oceanic prey 'hot spots' may also enable predators to reduce foraging effort (Gende & Sigler 2006).

Dietary segregation

Identifiable squid remains occurred in more than 70% of scats at CN and were relatively rare by comparison at IN (33%). The primary species taken by CN females, *Slosarczykovia circumantarctica*, is a relatively small, abundant, pelagic migratory species from Antarctica (Cherel & Hobson 2005). Commonly consumed by predators—including fish, seabirds, seals and penguins—at both Crozet and Kerguelen (Cherel et al. 2004), it was also the primary squid species taken by fur seals at CN during previous diet studies (Lea et al. 2002a). Although squid consumption is likely underestimated by the faecal analysis technique employed (as many squid beaks are regurgitated, Kirkman et al. 2000), fur seal diet at Îles Kerguelen is dominated by myctophid fish.

The fish assemblage in the Polar Frontal zone waters near Kerguelen is comprised primarily of Myctophidae (Duhamel et al. 2000) which constitute the largest biomass in the Southern Ocean after krill (Loots et al. 2007). The most numerous of the circum-Antarctic species are *Gymnoscopelus nicholsi* and *Electrona antarctica* (Sabourenkov 1990). Myctophids are an important dietary component for many sub-Antarctic marine predators, notably the king penguin (Bost et al. 2002) and fur seals—in particular at Kerguelen (Cherel et al.

1996, Lea et al. 2002a, Lea et al. 2006) and Heard island (Green et al. 1989). At IN in 1994, *G. nicholsi* was the most numerous prey item taken by male, female and juvenile fur seals (Cherel et al. 1996). In 2000, the diet of AFS at both sites was dominated by myctophids. We confirm the importance of *G. nicholsi* in the diet of adult females at IN and highlight the common occurrence of *G. fraseri* at CN and IN. *G. nicholsi* is mesopelagic/epibenthic, generally distributed along the shelf breaks and over the shelf at depth (Duhamel et al. 2005), migrating vertically to the top 100 m at night to feed (Pusch et al. 2004). Given the high occurrence of *G. nicholsi* in the diet of fur seals at IN, and its general absence at CN, it is reasonable to assume that shelf waters W and SW of IN are prime habitat for *G. nicholsi*. Rare research surveys to this productive region corroborate the existence of *G. nicholsi* (Koubbi et al. 2000) here and to the NE of Kerguelen along the shelf break (Duhamel et al. 2005). *G. nicholsi* is comparable in calorific content to *G. fraseri* per gram at ~10 kJ (Lea et al. 2002c); however, the average size of fish consumed varies considerably. A 7.5 cm *G. fraseri* yields approximately 45 kJ while an 11 cm *G. nicholsi* yields 3 times more energy, around 145 kJ (see Lea et al. 2002c). This discrepancy may offset the longer transit times, foraging trips and deeper dives recorded for IN seals. Milk fat content also increases concomitantly with increasing myctophid content in the diet, potentially further offsetting increased foraging effort by IN females by increasing the calorific content of their milk available to their pups (Lea & Dubroca 2003).

Recently Reid et al. (2006) have shown that local marine topography and oceanographic variability likely explain the temporal and spatial variability recorded in AFS diet in the Atlantic sector of the Southern Ocean. Zeppelin & Ream (2006) have confirmed such influences, showing that colony-specific dietary preferences of northern fur seals persist over many years and are indicative of foraging in distinct hydro-

graphic domains. The differences in habitat use and prey selection observed between CN and IN would be further clarified by simultaneous prey surveys in east and west coast bathymetric domains utilized by fur seals.

Provisioning success

Pup body mass and mass gained per foraging trip were both significantly higher at IN than at CN, perhaps indicating higher prey availability at IN. Although median birth dates have not been measured at either site, they are similar at both South Georgia and Marion Island (see Hofmeyr et al. 2007), which are much farther apart, indicating that pup body mass data may constitute a valid index of relative prey availability. Daily PMG per foraging trip was also significantly higher at IN, with longer, potentially older, females transferring more mass to pups than smaller females. This finding implies that experienced females may be more efficient foragers, and that body size also confers advantages in terms of energy transfer rates (Beauplet & Guinet 2007). Females at CN dive more frequently during restricted bouts of night diving (29 dives h^{-1}), while IN females tend to spend less time diving over the course of foraging trips, due to longer transit times. Foraging trips at CN averaged 5.7 d, while IN females averaged 7.9 d. So although mass gain rates were higher at IN, overall, pup growth rates at both sites may be similar due to the discrepancies in mean foraging trip length. Pups at CN would have 20.7 feeding events over the 4 mo lactation period compared with 15.2 feeding events at IN. At this stage, without the benefit of multi-year studies, it is difficult to state whether one breeding site promotes more favourable pup rearing conditions than the other. However, the rapid population growth of colonies on both coasts suggests that fur seals have not yet attained carrying capacity at Îles Kerguelen.

Multi-year and site comparisons of Antarctic fur seal habitat use

Niche overlap theory predicts that overlap should decrease with increasing environmental variability and with increasing numbers of species (Pianka 1974). The waters surrounding Kerguelen are highly dynamic and variable in terms of local productivity. This is reflected in the inter-annual variability of foraging zones utilized by female AFS at CN (Lea et al. 2006). Although seals concentrated foraging in a core area along the shelf break to the NE of the colony in all years, in 2000, a year of high pup growth at CN, much

foraging effort was focused to the SE along the Kerguelen Plateau (Lea & Dubroca 2003, Lea et al. 2006). This region is also an important foraging habitat for king penguins *Aptenodytes patagonicus* breeding on the east coast of Kerguelen (Bost et al. 2002). Potential competition between these 2 myctophid specialists is minimized by the diel feeding habits of both predators, with king penguins feeding primarily during the day at greater depths than the nocturnal fur seals. King penguins have been shown to access the cold thermocline waters below 100 m along the eastern edge of the Kerguelen Plateau (Charrassin et al. 2004), while fur seals tend to dive in the upper 50 m of the water column, only descending to greater mean depths in years of anomalously warm sea surface temperatures and reduced prey availability (Lea et al. 2006).

The potential overlap between Pointe Suzanne seals and all CN individuals occurs primarily in this region over outer shelf waters. Animals from Pointe Suzanne (2006) and CN (1998 to 2000) were not tracked simultaneously and, consequently, interpretation of overlap between sites is somewhat limited. Although it is unclear whether overlap is persistent or more likely in years of high and dispersed prey availability, seals from the Courbet Peninsula clearly utilize common inner and outer shelf domains. Our findings concur with those on other central place foraging marine predators. Trathan et al. (2006) showed that overlap in foraging zones was high for closely adjacent macaroni penguin colonies and minimal for more distant colonies. Boyd et al. (2002) reported no overlap for AFS females from colonies 300 km apart, which is well within the foraging range of the species, while Robson et al. (2004) noted greater overlap between northern fur seals from colonies on the same island than between islands which were only 72 km apart.

Population-level foraging distribution patterns and habitat use by AFS at Îles Kerguelen in 1998, 1999, 2000 and 2006 confirm the importance of inner and shelf regions, and deep water habitats within a 250 km range of breeding colonies. Guinet et al. (2001) predicted the likely habitat use of central place foraging AFS at Îles Kerguelen based on bathymetry, oceanographic features and fish distribution for 1998. The actual foraging distribution of Kerguelen seals (this study) confirms these predictions when distance to the colony is excluded, indicating a preference for shelf and shelf break areas to the SW (IN) and E and NE (CN).

CONCLUSIONS

Habitat use by the increasing fur seal population at Îles Kerguelen is variable between colonies and between years. Competition between conspecifics from

west and east coast colonies appears low, with no spatial overlap and distinct differences in the species composition observed within the diet. Despite the close proximity of these colonies, indications are that high relative prey densities adjacent to the breeding colonies and observed differences within the diving behaviour are sufficient to prevent inter-colony resource competition. Thus, it also appears that high local prey densities also over-ride the potential transfer of knowledge of favourable foraging sites transmitted through emigration between islands. The potential for inter-species competition with king penguins is minimized on the east coast through temporal and behavioural differences in diving. Although both species utilize the same regions, foraging times and prey species preferences differ markedly between the myctophid specialists. Overlap between years and between east coast colonies suggests a continuum of foraging zones between CN and Pointe Suzanne colonies, which may be variable in response to annual changes in oceanographic parameters. Core habitat regions were common to seals from CN in all summers, and although relatively small in size, they are important in terms of time spent foraging. Future management of commercial fisheries in the waters surrounding Kerguelen might consider the possibility of differential impacts on the foraging behaviour of females from various colonies, given the importance of locally productive regions to fur seal breeding success.

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