

Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal

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Summary

1. We studied feeding frequency in free-ranging grey seals using stomach temperature telemetry to test if previously reported sex differences in the diving, movement and diet were reflected in the temporal pattern of foraging success.
2. Data were retrieved from 21 of 32 grey seals from 1999 to 2001, totalling 343 days and 555 feeding events, with individual record length varying from 2 to 40 days (mean: 16.33 ± 2.67 days/seal).
3. Seals fed on $57.8 \pm 6.46\%$ of days sampled and had an average of 1.7 ± 0.26 meals per day, but individual variability was apparent in the temporal distribution of feeding as evidenced by high coefficients of variation (coefficient of variation = 69.0%).
4. Bout analysis of non-feeding intervals of six grey seals suggests that feeding intervals of individuals were varied and probably reflect differences in prey availability. Grey seals tended to have many single feeding events with long periods separating each event, as would be expected for a large carnivore with a batch-reactor digestive system.
5. We found significant sex differences in the temporal distribution of feeding. The number of feeding events per day was greater in males (2.2 ± 0.4 vs. 1.0 ± 0.2), as was time associated with feeding per day (56.6 ± 5.8 min vs. 43.9 ± 9.4 min).
6. The number of feeding events varied with time of day with the least number occurring during dawn. Feeding event size differed significantly by time of day, with greater meal sizes during the dawn and the smallest meals during the night.
7. The length of time between meals increased with the size of the previous meal, and was significantly less in males (541.4 ± 63.5 min) than in females (1092.6 ± 169.9 min).
8. These results provide new insight into the basis of sex differences in diving and diet in this large size-dimorphic marine predator.

Key-words: distribution of feeding, grey seals, meal frequency, predators, sex differences.

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Introduction

The spatial and temporal distribution of predator foraging behaviour introduces heterogeneity in prey mortality, which can have significant effects on prey and community dynamics (Estes & Duggins 1995; Krebs *et al.* 1995; Boyd 1996; Estes *et al.* 1998). Temporal variation in predator foraging behaviour may also provide insight into the spatial distribution of highly dynamic prey that may be difficult to track in other

ways (Mangel & Adler 1994; Weimerskirch *et al.* 1997a; Litzow *et al.* 2000), given that temporal variation in prey patch structure often constitutes a major source of spatial patchiness (Wiens 1976). The temporal distribution of feeding can provide valuable information about the way in which predators perceive the patchiness of prey, which currently represents a gap in our ability to model predator–prey relationships (e.g. Abrams 1991).

However, feeding frequency in large marine predators is poorly understood. This information is needed to help to address pressing issues concerning the effects of upper trophic level predators on commercially important (Mohn & Bowen 1996; Yodzis 1998) and endangered prey species (Springer *et al.* 2003). Direct

observation of feeding can be difficult because many species feed in dense cover, feed at night or forage over large and remote areas. In particular, the temporal distribution of successful foraging is largely unknown in marine predators, as direct observation is precluded because feeding occurs generally during diving. Consequently, the timing of foraging has been inferred from the functional analysis of the two-dimensional time–depth profile of dives (Schreer & Testa 1996; Le Boeuf *et al.* 2000), the temporal structure of bouts of diving (Boyd 1996; Beck *et al.* 2003a) and, for some species (e.g. Murie & Lavigne 1986), the state of digestion of stomach contents. These proxies have provided useful insights, but fall short of providing quantitative data on the frequency of feeding in marine mammals.

Furthermore, despite the application of new methods that have resulted in a better understanding of the diets of marine animals (e.g. Schell, Saupe & Haubenstein 1989; Iverson *et al.* 2004), we still have little indication of when feeding occurs or how animals might structure their food intake over time. Thus, rapid growth in our knowledge of marine mammal and seabird diving behaviour and diet and, by inference, their foraging behaviour (Grémillet *et al.* 1999; Lesage, Hammill & Kovacs 1999; Le Boeuf *et al.* 2000; Wilson *et al.* 2002), has not been mirrored by an increase in our understanding of the timing or frequency of foraging success.

The development of stomach temperature telemetry (Carey, Kanwisher & Stevens 1984; Wilson, Cooper & Plotz 1992) has enabled feeding frequency to be studied in free-ranging marine animals. This method is based on the principle that the body temperature of prey in the marine environment is colder than that of the core body temperature of its endothermic predators, resulting in a predictable drop in stomach temperature following prey ingestion (Wilson *et al.* 1992; Pütz & Bost 1994; Hedd, Gales & Renouf 1995). Stomach temperature telemetry has been used with considerable success on free-ranging seabirds, e.g. albatross (*Diomedea exulans*; Wilson *et al.* 1992), king penguins (*Aptenodytes patagonicus*; Pütz & Bost 1994) and northern gannets (*Sula bassana*; Garthe, Grémillet & Furness 1999).

The use of stomach temperature telemetry in marine mammals has been limited by the difficulty of keeping the temperature transmitter in the stomach (Bjørge *et al.* 1995; Wilson *et al.* 1995, 1998; Lesage *et al.* 1999). However, captive studies with harbour seals (*Phoca vitulina*; Bekkby & Bjørge 1995; Hedd, Gales & Renouf 1995), harp seals (*P. groenlandica*; Gales & Renouf 1993) and Steller sea lions (*Eumetopias jubatus*; Andrews 1998) have shown that stomach temperature telemetry can reliably identify when feeding has occurred and therefore holds great promise in examining the temporal pattern of feeding in free-ranging pinnipeds.

Sex differences in foraging behaviour are evident in several taxa (Pérez-Barbería & Gordon 1999; Le Boeuf *et al.* 2000; Jormalainen *et al.* 2001; Ishikawa & Watanuki 2002) and may affect the temporal distribution of feeding. In grey seals (*Halichoerus grypus*), males

and females exhibit different seasonal patterns of diving at several temporal scales (Beck *et al.* 2003a,b). Adult grey seals also tend to differ in the way in which they search for food, with females typically using smaller foraging ranges than males (Austin, Bowen & McMillan 2004). The energetic consequences of body-size dimorphism (males are approximately 1.5 times heavier than females, Beck, Bowen & Iverson 2003c), differences in diet (Beck *et al.* 2005) and seasonal differences in energy storage (Beck *et al.* 2003c) suggest that sexes might also differ in the temporal pattern of feeding.

Variation in foraging behaviour independent of sex has also been reported in a number of taxa (Bolnick *et al.* 2003). Based on reconstructed tracks from satellite telemetry, adult grey seals exhibit three broad types of movement, but show considerable individual variation within each type (Austin *et al.* 2004). Individual variation is also evident in the diets of grey seals (Beck 2002) which might, in turn, affect the temporal pattern of feeding, particularly given that prey distributions differ in both time and space. For example, the distribution of some commonly eaten grey seal prey, such as capelin (*Mallotus villosus*) and sandlance (*Ammodytes dubius*), are highly clustered in time and space and can be found in large schools (Scott & Scott 1988). However, other important non-schooling prey items such as flatfish (Beck 2002) are less heterogeneous in their spatial and temporal distribution (Valiela 1995; Litzow *et al.* 2004). Thus, prey characteristics may affect encounter rate and the probability of single prey vs. multiple prey meals (see Bowen *et al.* 2002). Therefore, the temporal distribution of feeding may reflect differences in diet between individual seals.

We studied feeding in free-ranging grey seals using stomach temperature telemetry with two objectives. The first was to characterize the frequency and temporal distribution of feeding in a marine predator, and the second was to test hypotheses about the effects of sex, time of day and between-meal duration on the temporal pattern of feeding. Given the pronounced sex differences in foraging behaviour noted above, we hypothesized that males would feed more often given their larger body size and metabolic demands. Because prey behaviour and predator perception of prey might differ with time of day, we predicted that we would observe daily variation in the frequency of feeding success; in particular, we hypothesized that females would show diurnal feeding patterns reflecting their diving behaviour. Finally, we expected that the time between feeding events would be affected by feeding motivation, and thus dependent on the size of the last meal, such that larger meals would lead to an increase in the post-feeding interval.

Methods

Seals were studied on Sable Island (44°53' N, 60°00' W), a vegetated sand bar in the Northwest Atlantic, approximately 300 km from Halifax, Nova Scotia, Canada in

September/October from 1999 to 2001. Known-aged, adult grey seals were caught using hand-held nets (Bowen, Oftedal & Boness 1992) and weighed to the nearest 0.5 kg prior to being anaesthetized with Telazol® (Tiletamine/Zolazepam, A. H. Robbins Co., Richmond, VA, USA). Males and females received an average dose of 0.45 mg/kg body mass and 0.90 mg/kg body mass, respectively (Bowen, Beck & Iverson 1999).

DATA SAMPLING

The stomach temperature telemetry system consisted of two separate instruments: a stomach temperature radio transmitter (STT; 56 × 20 mm, 32 g) placed in the stomach of the seal, and a radio receiver with an integrated microprocessor data logger (10 × 50 × 70 mm, 60 g), attached to the seal's pelage along the dorsal midline over the stomach using 5-min epoxy (both from Wildlife Computers, Redmond WA, USA). The receiver was programmed to record stomach temperature every 3 s in 1999 and 2000 and every 10 s in 2001. To ensure that the STT remained in the stomach of the animal, we devised an assembly that increased the size of the device without endangering the health of the animal. To minimize the potential for rejection of the device, the STT was glued into the centre of an oval-shaped piece (15 × 12 × 2 cm) of biodegradable ethafoam with 10-min epoxy. The sides of the STT remained exposed to gastric fluids and ingested prey in the stomach. We assumed that the estimated response time of our STT assembly to changes in stomach temperature was similar to the 6-s response time measured in harbour seals (Lesage 1999).

The STT was delivered to the stomach of an anaesthetized seal by fastening the assembly to the end of an equine intubation tube. Prior to intubation, the STT assembly was compressed with biodegradable paper tape to reduce its cross-sectional area and lubricated. Once in the stomach, the STT assembly was dislodged using a rod inserted through the equine tube. The assembly expanded back to its full size as the paper tape was broken down by stomach acids and peristalsis. Through consultation with veterinarians, the assembly was made large enough to delay passage but small enough so that, as the foam broke down in the stomach over time, it would eventually be passed. We calculated that the pill assembly represented about 4.8% and 3.2% of the estimated full stomach volume (W. D. Bowen, unpublished data) of adult females and males, respectively.

To provide information about movement, animals were instrumented with satellite relay data loggers (SRDLs; Wildlife Computers, Redmond, WA, USA or ST-18-Telonics; Mesa, AZ, USA). Instruments were secured to netting and then the netting was attached to the pelage on top of the head or neck of the anaesthetized animals using 5-min epoxy. Each instrument weighed ≤ 650 g (< 0.6% of body mass). To examine diving behaviour, each animal was also instrumented with a time–depth recorder (TDR) secured to the pelage

between the shoulders along the dorsal midline of the anaesthetized individual using 5-min epoxy. TDRs recorded depth every 20 s. These instruments and their epoxy mounts weighed between 65 and 300 g (< 0.3% of animal's body mass at deployment) depending on the model used (Mk3e, Mk5, Mk 6 and Mk7; Wildlife Computers). Seals returned to Sable Island during the breeding season in December/January at which point they were re-weighed and the stomach temperature data logger removed. Instrumented females were not recaptured until several days post-partum to permit females to form a strong bond with their pup. To account for total mass gained during foraging and prior to giving birth, we corrected the mass at recapture to initial post-partum mass using a linear rate of mass lost as 4.3 kg/day (Mellish, Iverson & Bowen 1999). Male grey seals were usually captured within several days of appearing on the island in December/January. We used the average daily mass lost during the breeding season (2.5 kg/day, Godsell 1991) to back-calculate male body mass on arrival.

DATA ANALYSIS

Stomach temperature data were downloaded using software provided by the manufacturer. The resulting file was then run through a custom software program (VISUAL BASIC within Microsoft Access) designed to identify individual feeding events. A feeding event was considered to have begun when temperatures were > 2 standard deviations of the calculated running mean (prefeeding temperature) for ≥ 2 min. A feeding event ended when the difference between the mean stomach temperature for each 1-min period and the prefeeding temperature was less than 2%. A random sample of 50 putative feeding events was scored manually to ensure that identified feeding events showed the characteristic precipitous drop followed by a slow asymptotic rise (e.g. Fig. 1a). For each feeding event, we measured: prefeeding stomach temperature, minimum temperature, time to reach the minimum temperature, time to return to prefeeding temperature, rate of temperature decrease (amplitude of temperature drop/time to minimum temperature) and time between the end of one feeding event to the onset of the next. Grey seals feed on non-schooling demersal fish and schooling pelagic fish, hence a feeding event might involve the ingestion of single or multiple prey. Each feeding event was scored as either single, corresponding to a single drop in temperature (Fig. 1a), or multiple, corresponding to a large drop followed by multiple smaller drops in temperature representing the ingestion of additional prey (Fig. 1b).

To test if the STT instrument package had negative effects on grey seal behaviour, our TDR data were analysed using the methods reported in Beck *et al.* (2003a) and mean dive depth, mean dive duration, mean bottom time, accumulated bottom time/day and dives/day were then compared to a sample of grey seal adults that did

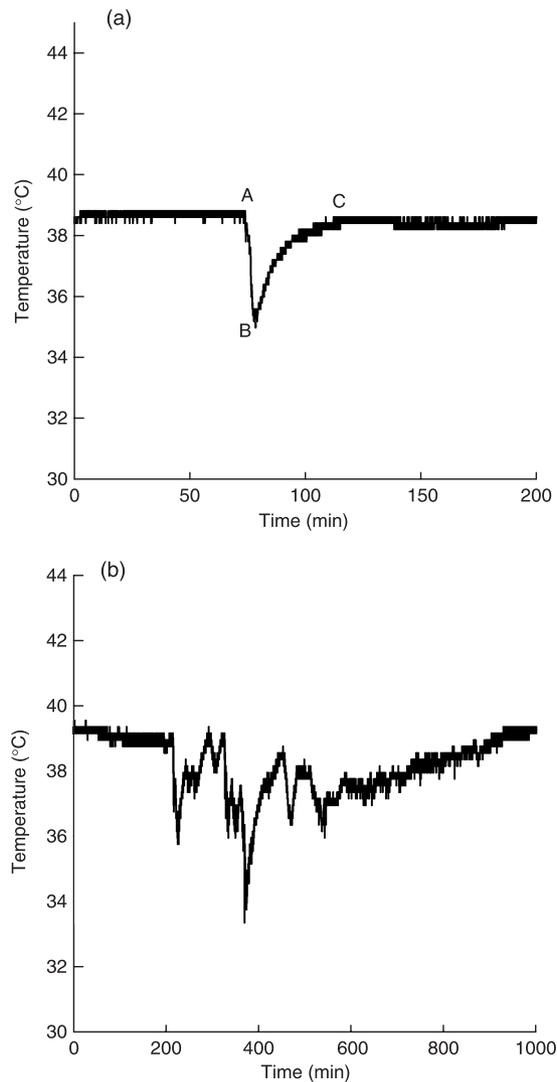


Fig. 1. Example of a stomach temperature profile over time, demonstrating (a) a typical single feeding event (where A = prefeeding stomach temperature, B = minimum temperature attained during feeding and C = recovery temperature) and (b) a typical multiple feeding event.

not carry the STT using a generalized linear model (GLM) with a Gamma distribution and a log link. To compare body mass on arrival at the breeding colony and rate of mass gain per day (mass change/deployment duration) of STT instrumented seals vs. non-STT instrumented seals, we used data from Beck *et al.* (2003c), and a GLM with a Gamma distribution and a log link. Geographic locations from satellite transmitters were processed using the methods in Austin *et al.* (2004), and mean daily locations were used to illustrate distribution patterns of STT animals in this study.

Hedd *et al.* (1996) found it was not possible to quantitatively estimate meal size in harp seals (*P. groenlandica*) using stomach temperature telemetry, as has been carried out in seabirds (Wilson *et al.* 1992), due to the confounding effects of diving activity, variation in heat transfer, stomach fullness and the degree of stomach churning. As a result, we used the area above the curve only as a relative quantitative index of meal size

(Wilson *et al.* 1995). For convenience, the area above the temperature curve, bounded by points A–C (Fig. 1a) was calculated using a geographical information system (ARCVIEW 3.1, Environmental Systems Research Institute, Inc., Redlands, CA, USA, 1996). We used the extension Xtools (Mike Delaune 1999; Oregon Department of Forestry, Salem, Oregon, USA <http://www.odf.state.or.us.sfgis>) point to polygon function and determined the spatial area bounded by the curve in an unprojected planar view.

To investigate the temporal pattern of feeding, we conducted runs tests at three temporal scales (1 day, 12 h and 6 h) on those seals having records ≥ 14 days ($n = 12$). The runs test procedure is used to test whether the order of occurrence of two values of a variable (presence or absence of feeding) is random. A run is a sequence of like observations in which a sample with too many or too few runs suggests that the sample is not random. To increase further our understanding of the pattern of feeding over time, we examined the non-feeding interval, i.e. the time between feeding events. The satiety concept (LeMagnen 1985; Tolkamp *et al.* 1998; Tolkamp & Kyriazakis 1999) predicts a low probability that animals will initiate a feeding event shortly after terminating one, but as the duration of non-feeding increases, hunger or motivation will also increase, thereby increasing the probability of feeding. Under this model, feeding will not be distributed randomly in time and the distribution of intervals between feeding will correspond to the physiological state of the animal. We used bout analysis, as outlined in Tolkamp *et al.* (1998), to estimate the distribution and duration of feeding events (Sibly, Nott & Fletcher 1990) of six grey seals having the longest stomach temperature records. To do this, we estimated the critical time interval that determined whether successive events were part of the same meal or part of a different meal. We binned non-feeding intervals into 24 equal time bins of 1 h and used a maximum likelihood to fit log-transformed intervals (Tolkamp *et al.* 1998). We estimated the percentage of intervals that occurred within and between meals, and estimated the mean inter-meal interval for each seal.

Grey seals exhibit day–night variation in diving behaviour (Beck *et al.* 2003a). To examine if feeding was related to time of day, we binned time of day into 6-h blocks corresponding to light levels throughout a 24-h period (dusk, night, dawn and day) and calculated the number of feeding events per bin. We chose these time bins given that prey vulnerability to predation may differ with light level. To test for the effects of sex and time of day on meal size and meal frequency, we used Generalized Linear Mixed Models (GLMM) with Penalized Quasi-Likelihood (PQL) estimation where the random effect was the individual seal and the error distribution was Gamma (meal size) and Poisson (meal frequency) using a log link. To determine if the percentage of single vs. multiple prey ingestion events varied between males and females, we used a GLM with a quasi error distribution and the logit link. To test

Table 1. Number of days in which stomach temperature was sampled in 21 grey seals and number and proportion of days with feeding

Seal id	Sex	Year	Record length (days)	Days with feeding (days)
6122	Female	2001	32.0	10 (31.3%)
24	Female	2000	28.0	17 (60.7%)
5683	Female	2000	28.0	12 (42.3%)
5108	Female	1999	24.0	16 (66.7%)
5110	Female	1999	14.0	9 (64.3%)
6116	Female	2001	6.0	4 (66.7%)
6120	Female	2001	5.0	0 (0%)
3271	Female	2000	4.0	2 (50.0%)
2690	Female	2001	3.0	1 (33.3%)
6117	Male	2001	40.0	13 (32.5%)
5114	Male	1999	36.0	24 (66.7%)
6124	Male	2001	32.0	19 (59.4%)
5111	Male	1999	17.0	7 (41.2%)
5684	Male	2000	17.0	7 (41.2%)
5687	Male	2000	17.0	14 (82.3%)
5112	Male	1999	14.0	13 (92.9%)
6125	Male	2001	8.5	7 (82.4%)
6126	Male	2001	6.0	6 (100%)
3661	Male	2000	5.0	5 (100%)
5116	Male	1999	4.5	0 (0%)
5685	Male	2000	2.0	2 (100%)

if sex or meal size might affect the time elapsed between feeding events, we used a GLMM with log-transformed inter-meal duration as the response variable and meal size and sex as predictor variables, using a Gaussian error distribution. All possible models with two-way interactions were examined and residuals were examined for lack of fit. To determine the best predictive GLM or GLMM, models having the lowest Akaike's information criterion (AIC) were selected. GLM and GLMM models were fitted in *s* PLUS version 6.2 (©1988, 2003 Insightful Corp., Seattle, WA, USA). Other statistical analyses were conducted using *SPSS* version 11.5 (©2002 SPSS Inc., Chicago, IL, USA). Means are reported with standard errors.

Results

Thirty-two (16 males and 16 females) grey seals were equipped with STTs: eight in 1999 and 12 each in 2000

and 2001. Four of those animals did not return to the breeding colony the following January, although one detached data logger was recovered on Sable Island during the breeding period. Of the 29 recovered recorders, eight recorders collected no data, leaving 21 with stomach temperature data. We recovered 23 TDRs with dive data (three seals did not return and six instruments did not function). However, of these 23 animals, only 16 seals had collected valid stomach temperature records. Three of the 16 animals had concurrent satellite transmitters that failed, leaving a final sample size of 13 individual grey seals for which data on distribution were available.

The number of days of stomach temperature sampled was highly variable among seals (Table 1). Records from 12 seals were ≥ 14 days, to a maximum of 40 days. One recorder sampled 8 days and the remaining eight instruments recorded for < 1 week. Two instruments recorded no feeding events, although it appears that the instrument was retained in the stomach for almost a week. A total of 343 days of stomach temperature data was collected from the 21 seals, for an average of 16.3 ± 2.67 days/seal. Mean sampling duration did not differ between males (15.9 ± 3.46 days) and females (16.1 ± 3.95 days; $t_{19} = 0.106$, $P = 0.92$).

A comparison of dive variables for animals carrying STTs and TDRs (this study) against animals that carried TDRs alone (Beck *et al.* 2003a) indicated no significant differences (Table 2). Similarly, there are no differences in mass gain or body mass at arrival to the breeding colony between the two groups (Table 2). Together, these results indicate that the STT did not have an overall negative effect on the foraging behaviour of our study animals.

During the period that we collected stomach temperatures, the 13 animals with satellite locations used relatively uniform habitat mainly in the vicinity of Sable Island (Fig. 2). This habitat is characterized largely by clean well-sorted sandy substrate (G. Fader, Bedford Institute of Oceanography, Department of Fisheries and Oceans Dartmouth, NS, Canada) and depths of 50 m or less (Fig. 2). Given that animals tagged on Sable Island in autumn are more likely to remain in the area around the island than travel to more distant foraging areas (Austin *et al.* 2004), we assumed that the eight seals without satellite data had similar foraging distributions.

Table 2. Comparison of mean dive parameters and mass gain for grey seals deployed with STTs and TDRs vs. grey seals deployed with TDRs only

	STT deployed seals (this study)		TDR only seals (Beck <i>et al.</i> 2003a)		GLM results t (P) (d.f. = 1, 32)	
	Males ($n = 11$)	Females ($n = 5$)	Males ($n = 7$)	Females ($n = 12$)	STT vs. non-STT	Sex
Mean dive parameters						
Depth (m)	45.65 \pm 2.69	47.42 \pm 6.73	48.66 \pm 0.44	53.41 \pm 3.94	1.03 (0.30)	-0.81 (0.42)
Duration (min)	5.44 \pm 0.22	6.65 \pm 0.49	4.66 \pm 0.31	6.52 \pm 0.21	-5.33 (0.10)	-1.66 (> 0.001)
Bottom time (min)	3.21 \pm 0.19	4.28 \pm 0.40	2.76 \pm 0.14	4.37 \pm 0.25	-0.79 (0.43)	-5.33 (> 0.001)
Accumulated bottom time (h/day)	11.5 \pm 1.22	13.89 \pm 1.19	8.16 \pm 2.00	11.67 \pm 2.21	-1.34 (0.18)	-1.43 (0.15)
Number of dives/day	90.15 \pm 11.02	76.08 \pm 9.93	70.16 \pm 15.62	63.82 \pm 12.01	-1.16 (0.247)	0.69 (0.489)
Mean mass at breeding (kg)	305.12 \pm 13.86 ($n = 11$)	210.71 \pm 9.75 ($n = 8$)	306.61 \pm 7.90 ($n = 24$)	210.13 \pm 5.01 ($n = 23$)	0.54 (0.59) (d.f. = 1, 63)	-12.60 (> 0.001) (d.f. = 1, 63)
Rate of mass gain/day (kg/day)	0.79 \pm 0.097 ($n = 11$)	0.32 \pm 0.075 ($n = 8$)	0.52 \pm 0.04 ($n = 24$)	0.35 \pm 0.02 ($n = 23$)	-0.84 (0.398) (d.f. = 1, 63)	-4.72 (> 0.001) (d.f. = 1, 63)

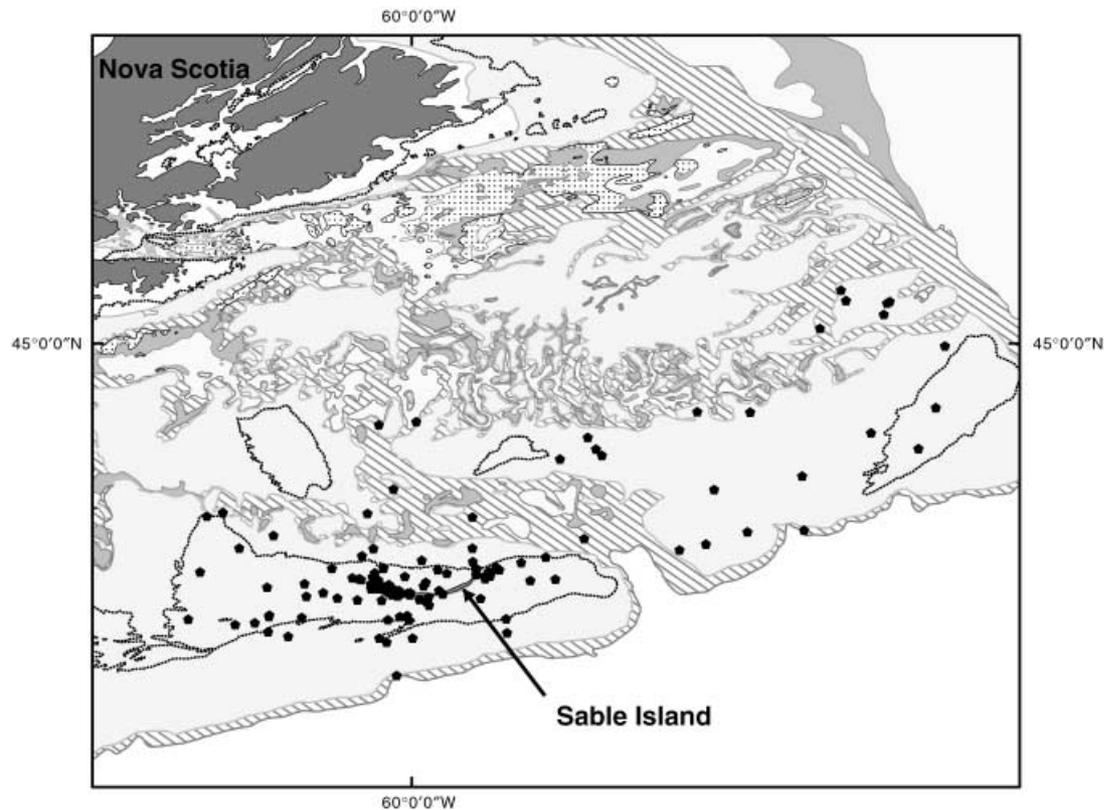


Fig. 2. Daily locations for 13 seals with concurrent satellite and stomach temperature telemetry records. The 50 m isobath is shown by the hashed line, while the dominant substrate types are as follows: light grey = clean well-sorted sand, dark grey = clay and sand with gravel, white = silty clay, stipples = muddy sand with gravel, diagonal bars = muddy sand.

Table 3. Results of maximum likelihood fitting of log normal distributions to the non-feeding intervals of six seals. Given P -values are based on the goodness of fit, $P < 0.05$ indicate significantly poor model fit. *Indicates the best fitting distribution. Mean non-feeding interval is transformed back from the log value and is given in minutes with upper and lower confidence intervals in brackets. The T_c describes the point in time where the two log normal distributions intersect and therefore all between-feeding intervals $< T_c$ occurred within a meal and all between-feeding intervals $> T_c$ represent separate meals

Seal id	Single log-normal P -value	Double log-normal P -value	Mean non-feeding interval length (min)	T_c (min)
24	0.400*	0.997	253.5 (140.6, 457.1)	
5108	0.381*	0.896	346.7 (192.3, 625.2)	
5112	0.157*	0.992	190.5 (118.6, 306.2)	
5114	0.058	0.180*	0.82 (0.66, 1.0)/108.7 (76.8, 153.8)	1.6
6117	0.506*	0.705	154.9 (82.4, 291.1)	
6124	0.005	0.746*	1.6 (1.4, 1.9)/189.2 (117.8, 304.1)	20.0

We recorded a total of 555 feeding events in the 21 seals with an average of 26.4 ± 5.56 events per seal (median = 22 events). Mean feeding event duration was 56.9 ± 6.88 min. There was considerable individual variation in the frequency of feeding (Fig. 3) and feeding did not occur daily in most seals. For example, seal 6122 went 13 days without feeding, while seal 5112 fed on each of 13 consecutive days of its 14-day record (Fig. 3). Seal 5114 appeared to alternate between 3 or 4 days of feeding and several days of not feeding (Fig. 3).

Seals fed on $57.8 \pm 6.46\%$ of days sampled and had an average of 1.7 ± 0.26 meals per day (including non-feeding days), but the number of meals per day was highly variable among seals [coefficient of variation (CV) = 69.0%; Fig. 3]. Results from the runs test indi-

cates that at the scale of 1 day, the temporal distribution of feeding was significantly different from random in only five of the 12 seals (Fig. 3). As we reduced the temporal scale to 12 h and 6 h, the number of seals showing a significant pattern of feeding increased to seven of 12. Seals with a significant temporal pattern of feeding events were those having the longest records (i.e. greater than 2 weeks), suggesting that the probability of detecting temporal patterns of feeding is greater in longer records.

For the six seals with the longest records, bout analysis revealed that each animal had a different distribution of non-feeding intervals, and that the best fit to the data varied from a log-normal to a double log-normal model (Table 3, Fig. 4). Four of the animals

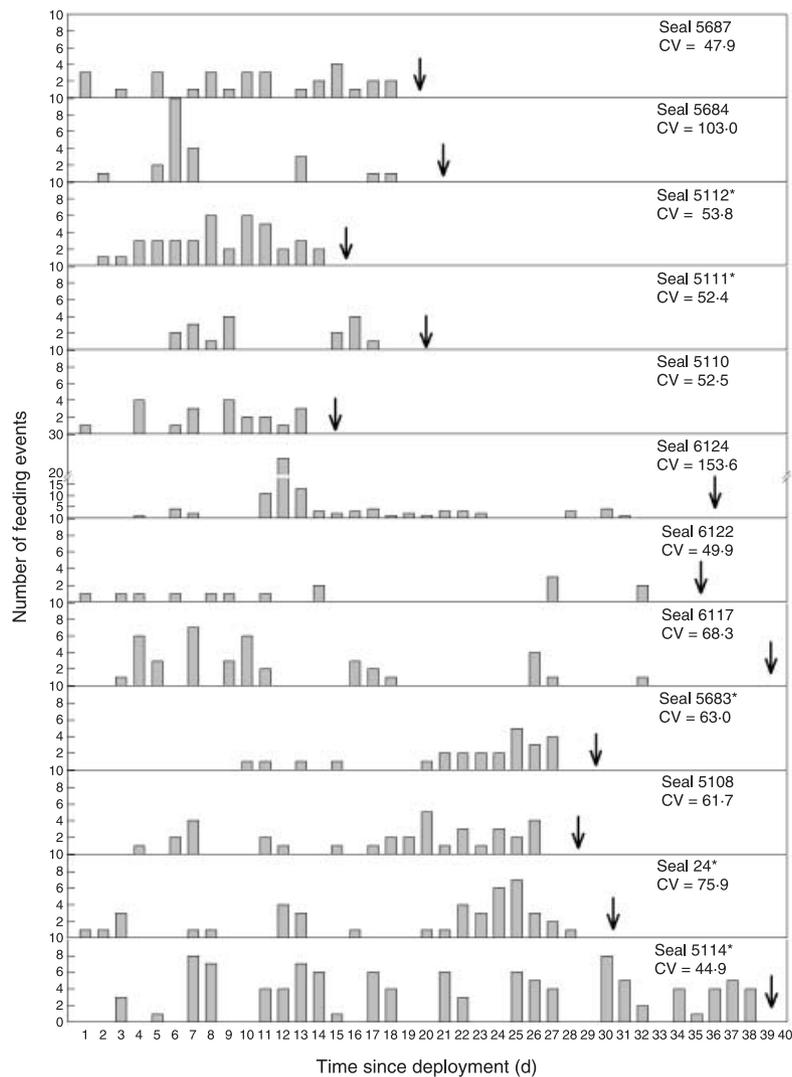


Fig. 3. Frequency of feeding events by day in individual seals having stomach temperature records ≥ 2 weeks ($n = 12$). Time is measured as days since deployment. Arrows indicate the end of the stomach temperature record. Seals marked with an asterisk are those with a significant runs test. Coefficients of variation (CV) are given for each seal.

fitted a log-normal distribution, indicating that there was no evidence for discontinuity in the length of time between feeding intervals. When transformed back from the log scale, the geometric mean non-feeding interval for these animals ranged from 0.8 to 346.7 min (the geometric mean is closer to the median value of the interfeeding event time across all seals = 145.2 min). Intervals from two seals fitted a double log-normal model (Table 3), resulting in two populations of intervals: short intervals within meals and longer intervals effectively separating individual meals (> 75% of all intervals). For these two animals, we calculated the mean non-feeding interval of the first and second populations of intervals. Using model parameters, we calculated a meal criterion (T_c) where the two log-normal distributions intersect, such that between-feeding intervals $< T_c$ occurred within a meal and between-feeding intervals $> T_c$ represented separate meals (Table 3).

SEX DIFFERENCES

The average age of seals was 22.4 ± 1.2 years for males and 20.1 ± 2.5 years for females. At the time of deployment, males were significantly heavier than females ($t_{19} = 4.28$, $P < 0.001$), with mean body mass 1.3 times larger in males (223.5 ± 8.5 kg) than in females (173.8 ± 2.8 kg). At the time of recapture males were again significantly larger, approximately 1.4 times larger than females ($t_{19} = 5.57$, $P < 0.001$; Table 2). The daily rate of mass gain was also significantly greater in males than in females ($t_{17} = 3.51$, $P = 0.003$; Table 2). There was no difference in the length of time the STT remained in the stomach between males (15.3 ± 3.12 days) and females (15.0 ± 3.56 days; $t_{19} = 0.052$, $P < 0.001$).

There were significant sex differences in the temporal distribution of feeding. The mean number of feeding events per day was significantly greater in males (2.2 ± 0.38) than in females (1.0 ± 0.20 ; $t_{19} = 2.45$, $P = 0.024$).

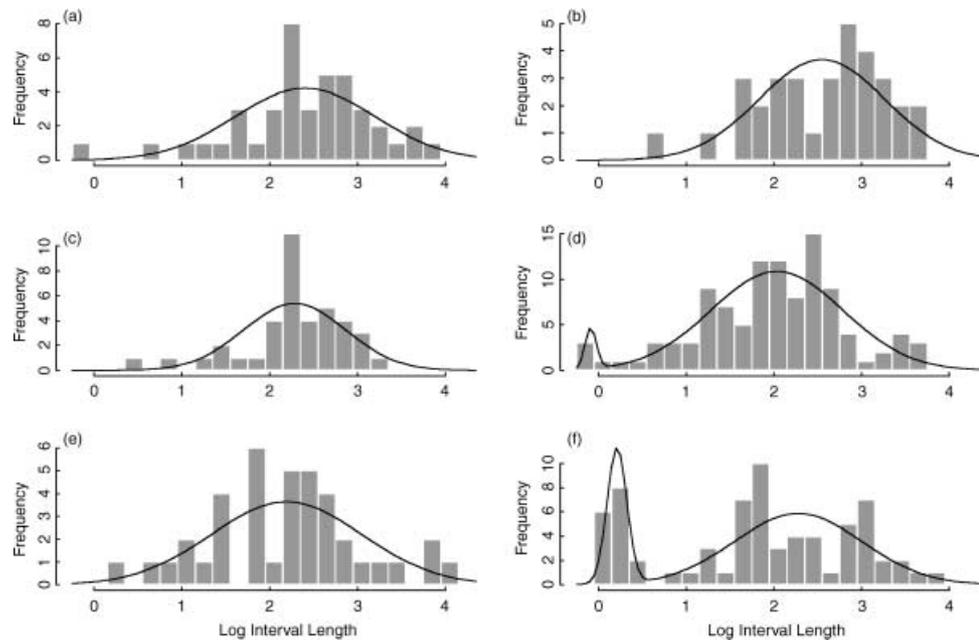


Fig. 4. Frequency distribution of log-transformed intervals between feeding events. Solid line demonstrates fit to a single or double log-normal distribution. (a) seal 24; (b) seal 5108; (c) seal 5112; (d) seal 5114; (e) seal 6117; and (f) seal 6124.

Table 4. Model fitting procedure for GLMM models with factors affecting meal size and feeding frequency. The best-fitting model was chosen according to the lowest Akaike's information criterion (AIC). The difference in AIC from the best-fitting model (Δ AIC) and the Akaike weights (w_i) are also provided. K is the number of model parameters

GLMM model	K	AIC	Δ AIC	w_i
(1) Meal size ($n = 555$)				
(a) Time of day (TOD)	4	2065.3	0.0	0.61
(b) Sex	2	2067.9	2.6	0.17
(c) Sex + TOD	6	2067.4	2.1	0.21
(d) Sex + TOD + (sex \times TOD)	7	2072.5	7.2	0.02
(2) Feeding frequency ($n = 67$)				
(a) Time of day (TOD)	4	179.41	0.68	0.28
(b) Sex	2	187.23	8.50	0.01
(c) Sex + TOD	6	179.19	0.46	0.32
(d) Sex + TOD + (sex \times TOD)	7	178.73	0.00	0.40

Similarly, the average time spent feeding per day was greater for males (56.6 ± 5.84 min) than females (43.8 ± 9.42 min; $t_{17} = 1.70$, $P = 0.05$). Males had a greater percentage of days with feeding ($66.5 \pm 9.32\%$) than females ($46.2 \pm 7.38\%$), but this difference was not significant ($t_{19} = 1.71$, $P = 0.10$). Apparent meal size was greater in males ($58\,667 \pm 14\,743$ units) than in females ($53\,338 \pm 27\,619$ units), although this difference was also not significant (Table 4). Apparent meal size differed significantly among time bins (GLMM, $B_{(3,535)} = -0.004 \pm 0.0019$, $P = 0.02$; Table 4), with greater meal sizes during the dawn and the smallest meals during the night (Fig. 5). Although males tended to have larger meals during dusk, night and dawn, and females tended to have larger meals during the day (Fig. 5), there was no sex effect (Table 4). The number of feeding events

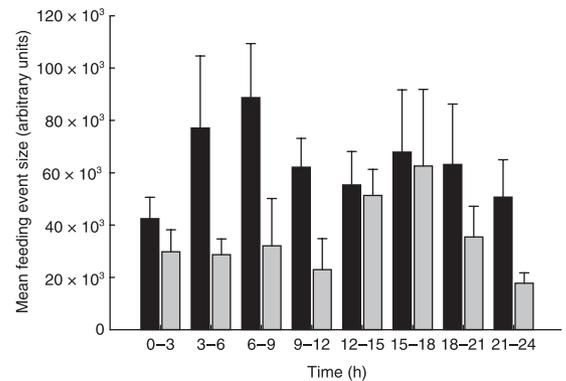


Fig. 5. Mean feeding event size by time of day and sex. Male grey seals are shown by dark bars and female grey seals by lighter bars. Standard error bars given.

varied with time of day (GLMM, $B_{(3,47)} = 0.22 \pm 0.08$, $P = 0.007$; Table 4), with the least number of feeding events occurring during dawn. Sex was not a significant factor in the number of feeding events by time of day, nor was the sex–time of day interaction (Table 4).

The length of time between meals was affected significantly by the size of the previous meal (GLMM, $B_{1,517} = 1.0 \times 10^{-6} \pm 3.0 \times 10^{-7}$, $P = 0.0004$; Table 5). Sex was also a significant predictor of the between-meal duration (GLMM, $B_{1,16} = 0.50 \pm 0.10$, $P = 0.0002$; Table 5), with males having shorter between-meal durations (541.4 ± 63.5 min) than females (1092.6 ± 169.9 min). Single feeding events accounted for an average of 45% of meals. The ratio of single to multiple feeding events did not vary significantly by sex (GLM; $B_{1,17} = 0.045 \pm 0.48$, $P = 0.92$), although females tended to have a higher percentage of multiple meals ($63 \pm 3.1\%$) than males ($51 \pm 4.4\%$).

Table 5. Model fitting procedure for GLMM models with factors affecting the time between feeding events

GLMM model	K	AIC	Δ AIC	w_i
Time between feeding events ($n = 536$)				
(a) Sex	4	1374.8	10.40	0.003
(b) Meal size	1	1375.8	11.40	0.002
(c) Sex + meal size	5	1364.4	0.00	0.584
(d) Sex + meal size + (sex \times meal size)	6	1365.1	0.70	0.411

Discussion

Although used previously with success in free-ranging seabirds (Grémillet & Plos 1994; Wilson *et al.* 1995; Weimerskirch, Wilson & Lys 1997b), this study is the first quantitative analysis of feeding frequency in a free-ranging marine mammal based on data collected by stomach temperature telemetry. We obtained data records of > 2 weeks from a number of animals, which demonstrated that in this large marine predator there is a considerable degree of individual variation in the temporal distribution of feeding. Feeding distribution varied by time of day and meal size was a predictor of the time between meals. As predicted, we found significant differences in the number of feeding events and the time spent feeding between males and females. These results provide new insight into the basis of sex differences in diving and diet in this size-dimorphic species.

We found little evidence of adverse effects of the stomach temperature assembly on the diving behaviour, mass gain or body mass on arrival to the breeding colony of adult grey seals, suggesting that our results are unlikely to be artefacts arising from the experimental procedure. This may have been due partly to the small size of the SST assembly relative to the volume of a relatively full stomach. Nevertheless, we acknowledge that we could not test for effects of the SST assembly on the size or level of satiation of individual meals. Also, we cannot rule out the possibility that some of the longer intervals between meals may have been influenced by the presence of the SST assembly.

Variation in behaviour among individuals has often been overlooked by ecologists, such that interesting phenomena have been obscured in pursuit of simplification and the creation of general ecological theories (Judson 1994; Bolnick *et al.* 2003). However, advances in wildlife telemetry and data loggers have resulted in a shift to individual-based research, resulting from the ability to collect large amounts of information pertaining to a single organism. Although optimal foraging theory has been used traditionally to predict population-level foraging behaviour (Charnov 1976; Stephens & Krebs 1986), recent studies have indicated that individuals within a single population often exhibit marked individual variation, or specialization, in foraging behaviour (Bolnick *et al.* 2003; Estes *et al.* 2003). Given that natural selection operates at the level of the individual, ecological concepts that paint all individuals with the same sweeping brush effectively disregard this sort of variation (Judson 1994).

A high degree of variability in feeding frequency between individuals was one of the most interesting findings of this study and was comparable to the level of individual variability found in the movement paths of adult grey seals (Austin *et al.* 2004). Individual variability in feeding frequency has also been found in other marine predators, such as wandering albatross, *Diomedea exulans* (Weimerskirch *et al.* 1997a) and king penguins, *Aptenodytes patagonicus* (Pütz & Bost 1994). In both these species, individual variation in feeding frequency may be related to the characteristics of predominant prey species: wandering albatross consume a variety of squid species which are distributed unpredictably at the water's surface (Weimerskirch *et al.* 1997b), whereas king penguins feed predominantly on schooling myctophid fishes, which are correspondingly distributed patchily (Pütz & Bost 1994).

The source of the observed variability in feeding frequency in grey seals is unclear. However, it may also reflect the patchiness of prey consumed and differences in the search tactics of individuals. The temporal pattern of feeding departed from a random sequence in four of the seven animals with records longer than a month, suggesting that some seals may be exploiting prey that are predictably located and captured in time while others rely on less predictably located prey. Evidence from quantitative fatty acid signature analysis (Iverson *et al.* 2004) suggests that grey seals exhibit two foraging tactics: semipelagic, feeding primarily on redfish, *Sebastes* sp. and sand lance, *Ammodytes dubius* and a benthic tactic, feeding predominantly on flatfishes (Pleuronectidae, Austin, Bowen & Iverson, unpublished data). Presumably the temporal distribution of feeding will reflect to some extent the characteristics of an individual's diet. Furthermore, prey distribution will vary with prey type, such that the distribution of pelagic prey tends to be more clumped in time and space, whereas benthic prey are typically more uniformly distributed. For example, the distribution of sand lance, an important grey seal prey (Bowen & Harrison 1994), is linked tightly to a specific bottom substrate (Scott & Scott 1988), such that seals may be able to cue into particular areas where there is a high probability of encountering prey. In contrast, other grey seals may have long periods without success, which may reflect foraging on highly mobile pelagic fishes such as herring (*Clupea harengus*, Scott & Scott 1988), which are also known to be consumed frequently by grey seals (Bowen, Lawson & Beck 1993).

Indeed, most grey seals did not feed every day, and it was not uncommon for many days to separate individual feeding events. During the breeding and moulting periods, adult grey seals fast for 3–4 weeks (Lidgard *et al.* 2005; Beck *et al.* 2003c; Iverson *et al.* 1993). The ability to withstand extended periods of non-feeding is undoubtedly related to large body size and capacity of marine mammals to store energy in blubber, which gives them a degree of insurance against periods of non-feeding (Iverson 2002). However, given the small prey size to predator size ratio in grey seals and other pinnipeds, extended periods of fasting outside the moult and breeding season were unexpected. We expected that grey seals would feed more frequently than predators that gorge on large prey since they tend to feed on small prey (0.01–3.0 kg) relative to their body size (150–350 kg, < 1% body size). In contrast, African lions (*Panthera leo*) consume typically 7–11 kg (approximately 5% body size) in a single feeding event, followed subsequently by several days of non-feeding (Schaller 1972). In wolves (*Canis lupus*), which also consume large prey, time between predation events on ungulates can vary from 3 to 19 days (Hayes *et al.* 2000). We hypothesize that the inconsistent pattern of feeding seen in grey seals reflects the difficulty in locating prey patches of suitable quality rather than constraints imposed by handling and the digestion of prey.

Grey seals tend to have many meals composed of a single feeding event with a relatively long period separating each event, as might be expected given the small prey size to predator size ratio. Recently, using underwater video on four individuals over a period of 4–8 days, Williams & Yeates (2004) observed that Weddell seals (*Leptonychotes weddelli*) feed intermittently in a series of approximately 16-min dives, consuming up to 20 fish (900–1000 g) per dive, interspersed with brief resting periods throughout the day.

Our findings and those from studies on terrestrial carnivores differ considerably from the distribution of feeding in herbivores or domestic animals, where the typical feeding structure involves many short within-meal intervals and fewer long intermeal intervals, with a clear distinction between the two populations of intervals (Simpson & Ludlow 1986; Langton, Collett & Sibly 1995; Tolkamp *et al.* 1998). Herbivores often have a continuous supply of food and therefore feed to satiation with occasional brief interruptions in feeding for predator vigilance, social interactions or searching for a new food patch. In contrast, grey seals search actively for prey and therefore feeding is more likely to be limited by opportunity rather than stomach fullness. Therefore, timing of meals will reflect hunting success which will depend on factors such as prey distribution and abundance, both of which may vary with the habitat. However, in this study grey seals occupied a relatively uniform habitat (Fig. 2) so we assume that, on average, individuals had similar opportunities to feed. Furthermore, most carnivores employ a ‘batch-reactor’ type of digestion, which involves the consumption of discrete

meals consisting of large amounts of food at intermittent time intervals. Typically, digestion is characterized by well-mixed stomach contents and separated by idle periods in which the stomach is emptied of products from the preceding digestion, reloaded with enzymes and prepared for the next cycle. The ideal batch reactor operates intermittently and remains idle between additions of food, as opposed to herbivores, which use a ‘continuous-flow-reactor’ system, characterized by a continuous flow of material (Penry & Jumars 1987).

The time between feeding increased with the size of the preceding meal suggesting that stomach fullness in grey seals may result in reduced feeding motivation. Similarly, the duration of non-feeding intervals is correlated directly with stomach fullness in shrews (*Sorex* sp., Saarikko & Hanski 1990). Alternatively, increasing meal size may be a response to temporal uncertainty of feeding (Rosen & Trites 2004). Other experimental laboratory studies have shown that, as the energetic cost of feeding is made to increase, animals may initiate meals less often, but consume more each time, thereby conserving overall intake (Collier, Johnson & Morgan 1997). Although we do not have a measure for feeding costs in this study, we suggest that if prey were scarce, such that the time between feeding increases with increased search costs, one might predict that seals would compensate by eating more at each prey encounter (e.g. schools of fish).

SEX DIFFERENCES

As predicted, males spent more time feeding and had longer feeding events than females. Grey seal males are on average 50% heavier than females (Beck *et al.* 2003c), although in this study they ranged from being 30% heavier in the autumn and 45% at start of the breeding period. As absolute metabolic requirements increase with body size (Klieber 1961), a larger animal requires greater energy intake and may forage differently as a result (Clutton-Brock, Guinness & Albon 1982). Male hamadryas baboons (*Papio hamadryas*), the larger sex, fed more often and had larger meals than females (Zinner 1999). Male grey seals require about 1.3 times the energy intake of females (Mohn & Bowen 1996), suggesting that size dimorphism may be largely responsible for our findings. Seasonal patterns of energy storage may also influence sex differences in feeding. Males begin to accumulate energy stores only during the prebreeding foraging period following a 6-month period of loss in body energy (Beck *et al.* 2003c). Energy gain increases in September and continues throughout the autumn, corresponding to our study period. In contrast, females have a more consistent strategy of energy accumulation throughout the year, and do not demonstrate as marked an increase in the autumn months (Beck *et al.* 2003c). In early autumn, time spent diving continuously in bouts is greater in males than in females (Beck *et al.* 2003a). This indicates that males are perhaps

foraging with greater intensity during this time period. In addition, males also appear to have a broader dietary niche breadth than females by including more benthic prey species of lower energy density (Beck 2002). By consuming prey of lower energetic value, males may have to feed more often to meet energetic requirements.

Feeding event size also tended to be greater in males, although not significantly so. However, the interpretation of this difference is problematic because of the theoretical effects of body size on warming ingested prey. Given their small body size, females should have about a 10% greater mass-specific heat production than males (Cossins & Bowler 1987), which might suggest that females would warm ingested prey faster than males. Nevertheless, males are heavier than females, and hence would warm the ingested prey faster than females because heat storage capacity is proportional to body mass (Cossins & Bowler 1987; Berteaux 2000). Therefore, if males warm ingested prey faster for the same quantity of prey eaten, feeding event size in males ought to be smaller than in females. However, we observed the opposite phenomenon, which suggests that the difference in feeding event size was even greater than that observed and that males probably do have larger meals than females. By contrast, females consume a higher percentage of pelagic and semipelagic prey species of higher energy density. Thus, larger meal sizes in males may result from the more frequent ingestion of large single prey, whereas females may forage to a greater degree on smaller schooling prey.

We have demonstrated that the temporal distribution of foraging success is highly variable among individuals and between the sexes, providing new insights into the basis of sex specific differences in foraging behaviour and diet in this size dimorphic species. Future studies linking the temporal record of feeding with a concurrent measure of diving effort and foraging distribution will offer insights into how foraging success affects diet and behaviour in large marine predators.

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