Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal

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Both body size dimorphism and sex differences in the relative costs and benefits associated with acquiring energy for reproduction have been advanced to explain the evolution of sex differences in foraging behaviour. We examined the extent to which these factors influenced sex differences in the diving behaviour of a size-dimorphic, capital breeder, the grey seal, *Halichoerus grypus*. Using time-depth data loggers, we examined the diving behaviour of 46 male and 49 female grey seals for 7 months before parturition and mating. Males and females showed significantly different seasonal patterns in the characteristics of individual dives and dive effort. Compared with males, females showed significantly higher levels of dive effort immediately following moult and in the 3 months before parturition. Females also had longer dives (5.5 versus 4.9 min) and spent more time at depth (3.4 versus 2.7 min), whereas males dived deeper (57 versus 49 m). Males dived consistently throughout the day, whereas females showed strong diurnal patterns in dive depth, duration and frequency. The diving behaviour and rates of mass gain by females suggested a pattern of foraging consistent with early accumulation of body energy to support pregnancy and the subsequent lactation period during which females fast. Males, on the other hand, showed diving behaviour and rates of mass gain consistent with a more gradual accumulation of energy stores. Our results suggest that sex differences in the seasonal patterns of diving behaviour reflect sex differences in the costs and benefits of stored energy for reproduction rather than the influence of body size dimorphism alone.

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Survival, growth and reproductive success are ultimately linked to an individual's ability to acquire food energy. Foraging behaviour should therefore maximize an individual's fitness, subject to trade-offs between foraging and other activities such as predator avoidance and mate acquisition. Extrinsic factors, such as the spatial and temporal distribution of prey, prey quality, risk of predation and environmental stochasticity influence the strategy used to obtain food (e.g. Oaten 1977; Orians & Pearson 1979; Stephens & Charnov 1982). However, intrinsic factors, such as sex, can also influence the foraging behaviour of an individual (e.g. Jenkins 1979; Clutton-Brock et al. 1982; LeBoeuf et al. 1993; Ginnett & Demment 1997).

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Intraspecific differences in the foraging behaviour of males and females have been found in a variety of taxa (e.g. Williams 1980; Clutton-Brock et al. 1982; Petit et al. 1990; LeBoeuf et al. 2000). Among the explanations for these differences, the three most prominent hypotheses to account for the occurrence of sex differences in foraging behaviour are sexual size dimorphism, reduced intersexual competition for food, and the differential roles of each sex during reproduction and parental care.

Sexual size dimorphism is common with male-based size dimorphism being more prevalent in birds and mammals (Fairbairn 1997). As absolute metabolic requirements increase with body mass, larger individuals require more energy per unit time than smaller ones (Klieber 1961). Therefore, to attain and maintain their larger size, the larger sex requires a higher energy intake and thus may forage differently than the smaller sex (e.g. red deer, *Cervus elaphas*: Clutton-Brock et al. 1982; giraffes, *Giraffa camelopardalis*: Ginnett & Demment 1997). Competition for resources between male and female conspecifics may account for differences in foraging behaviour (Schoener

1969; Hughes 1980; Clarke et al. 1998). In the downy woodpecker, *Dendrocopos pubescens*, sexes differ not only in their pattern of foraging activity, but also in foraging technique and diet composition, thereby reducing competition for food resources (Williams 1980). Sex differences in foraging behaviour have also been attributed to the different parental duties of males and females (Morse 1968; Williamson 1971; Petit et al. 1990). For example, in prothonotary warblers, *Protonotaria citrea*, males and females partition their foraging range vertically, with males maintaining territorial vigilance and feeding in the higher branches and females feeding lower, closer to the nest (Petit et al. 1990).

Males and females may also forage differently because of differences in the sex-specific energetic costs of reproduction (Clutton-Brock et al. 1983; Petit et al. 1990; Parmelee & Guyer 1995; Ginnett & Demment 1997). These costs may differ not only in origin, but also in magnitude. In mammals, the immediate energetic expenditure to females for gestation and lactation often outweigh the immediate expenditure of males in acquiring mates and defending resources (Gittleman & Thompson 1988; Perrigo 1990; Wilkinson & Barclay 1997). The fitness consequences associated with not acquiring sufficient resources to support these expenditures may also differ, such that the trade-off between the costs and benefits of storing energy for reproduction differs between males and females. For example, in polygynous mammalian species where females are capital breeders (i.e. relying only on stored body energy for reproduction), females that fail to store sufficient energy before the breeding season may not successfully wean the current offspring, or wean an offspring that have a low probability of survival (e.g. Hall et al. 2001). In species where males compete for mates, males that return to the breeding grounds in poor condition may have reduced mating opportunities, but may still obtain some matings by using alternate mating tactics (e.g., sneak matings), and thus the loss of fitness may be less dramatic for males than for females.

Sex differences in foraging behaviour among birds have been studied mainly during the breeding season (but see Williams 1980; Morrison & With 1987). Among mammals, sex differences in the foraging behaviour of ungulates have been studied throughout the year (eg. Main et al. 1996; Ruckstuhl 1998; Barboza & Bowyer 2000) and have been interpreted in relation to size dimorphism and reproduction. With the exception of the extremely sexually size-dimorphic northern, *Mirounga augustrioustris* (LeBoeuf et al. 2000) and southern elephant seals, *M. leonina* (Slip et al. 1994), little is known about the sex differences in foraging behaviour of marine mammal species. Although there is a considerable understanding of the allocation of time between foraging and reproduction during the breeding season in female pinnipeds (e.g. Goebel et al. 1991; Bowen et al. 1999b; Arnould & Hindell 2001), few studies have examined the diving behaviour of both males and females before the breeding season (LeBoeuf et al. 2000).

Grey seals, *Halichoreus grypus*, are a polygynous, size-dimorphic species in the family Phocidae, with males and

females in the northwest Atlantic population reaching lengths of up to 2.65 m and 2.20 m, respectively (McLaren 1993). Grey seals alternate periods of terrestrial fasting during moulting and breeding periods with foraging at sea. As a result of this life-history strategy, individuals go through dramatic seasonal changes in body mass and composition; however, adults males are approximately 1.5 times heavier than adult females throughout the year (Beck 2002).

Female grey seals use stored body energy accumulated over the previous 7-month period to support the high energetic cost of lactation and their own metabolic expenditures during the breeding season. Females with low body mass (and hence energy stores) at parturition tend to wean smaller pups or wean their pups prematurely (Iverson et al. 1993; Mellish et al. 1999; Pomeroy et al. 1999), increasing the probability of juvenile mortality (Coulson 1960; Coulson & Hickling 1964; Hall et al. 2001). Male grey seals use a variety of mating strategies, ranging from tenure of several weeks on land to roving, in which males alternate short foraging trips to sea with attempts at mate acquisition on land (Boness & James 1979; Amos et al. 1993; Twiss et al. 1994; Lidgard et al. 2001). Despite these trips to sea, males still rely on energy stores accumulated prior to breeding to compete for and acquire mates. Although the quantity of stored energy is important for this purpose, Godsell (1991) and Lidgard et al. (2001) found that for adult male grey seals on Sable Island, Nova Scotia, Canada, the correlation between body mass at the start of the breeding season and mating success is weak. Hence, reproductive success of males appears to be less dependent on the amount of stored body energy at the beginning of the breeding season than is the reproductive success of females.

The benefits associated with storing energy for reproduction are reasonably well understood (Jönsson 1997; Chapin et al 1990; Bonnet et al. 1998). However there may be fitness costs associated with storing energy for long periods (Witter & Cuthill 1993; Gosler et al. 1995; Bonnet et al. 1998; Gentle & Gosler 2001). Such costs could include an increased risk of predation or increased cost of transport during diving. For example, studies on the effect of buoyancy on air-breathing aquatic foragers (Webb et al. 1998; Beck et al. 2000) indicate that, at the level of individual dives, descent rate decreases as animals fatten. As a result, it takes animals longer to reach depth and they spend longer periods underwater (Beck et al. 2000), perhaps at increased energetic cost.

In this study, we investigated sex differences in the diving behaviour of adult grey seals, a species in which size dimorphism and a capital breeding strategy are expected to influence foraging behaviour before breeding. As has been shown with ungulates, studying foraging behaviour during the nonbreeding season may provide valuable insight into how each sex prepares for reproduction, and because foraging is necessarily associated with diving in marine mammals, factors that influence foraging will also affect their diving behaviour. Thus, we hypothesized that both size dimorphism and sex differences in the relative costs and benefits associated with acquiring energy for reproduction would be reflected in

diving behaviour prior to reproduction. As the larger sex, males were expected to show higher levels of dive effort than females in order to acquire the higher level of energy intake imposed by a larger body size (Klieber 1961). We also predicted that males and females would differ in their seasonal patterns of diving behaviour. Male and female grey seals are in the poorest condition following the spring moult (Table 5.1, Figure 5.3 in Beck 2002). Evidence from a variety of mammalian species indicates that females in poor condition are less likely to be pregnant or carry the pregnancy to term (Boyd 1984; Albon et al. 1986; Stewart et al. 1989; Cameron et al. 1993; Lunn & Boyd 1993; White et al. 1997; Pitcher et al. 1998). Therefore, female grey seals ought to recover body condition quickly to support early pregnancy and to begin storing the body energy required to support the high energetic cost of lactation. On the other hand, we expected males to recover body condition more gradually, increasing energy storage only as the breeding season approaches, because the accumulation of body energy should be mediated by fitness costs associated with supporting increased body mass for long periods (Jönsson 1997). Although females will also have to deal with such costs, they may do so differently, because the predicted reproductive benefit from early storage of body energy is higher for females than for males.

METHODS

The study was carried out between May 1992 and January 2000 on Sable Island (43°55′N, 60°00′W), a crescent-shaped, partially vegetated sandbar approximately 300 km southeast of Halifax, Nova Scotia, Canada. Sable Island is the largest haul-out and breeding location for grey seals in the northwest Atlantic population. Animals congregate in large numbers on the island in May and June to moult, in late December and January to rear offspring and mate, and in smaller numbers throughout the year between foraging trips.

Grey seals, of known age (8–27 years), were captured onshore following the spring moult (May and June) or in the autumn (late September and early October) using hand-held nets (Bowen et al. 1992). Seals were weighed to the nearest 0.5 kg and anaesthetized using Telazol (equal parts of teletamine and zolazepam), with males and females receiving an average dose of 0.45 mg/kg of body mass and 0.90 mg/kg of body mass, respectively (Bowen et al. 1999a). Beginning in 1995, dorsal standard length (DSL; McLaren 1993) was measured on all animals while anaesthetized.

To study diving behaviour, time-depth recorders (TDRs) were glued to the pelage along the dorsal midline of the seal's lower back using a 5-min epoxy. Instruments weighed between 65 and 300 g (<0.3% of animal's initial body mass) depending on the model used. In January, when animals returned to Sable Island for the breeding season, instrumented animals were recaptured to remove the data loggers and then released. Beginning in January 1998, instrumented animals were also weighed at recapture.
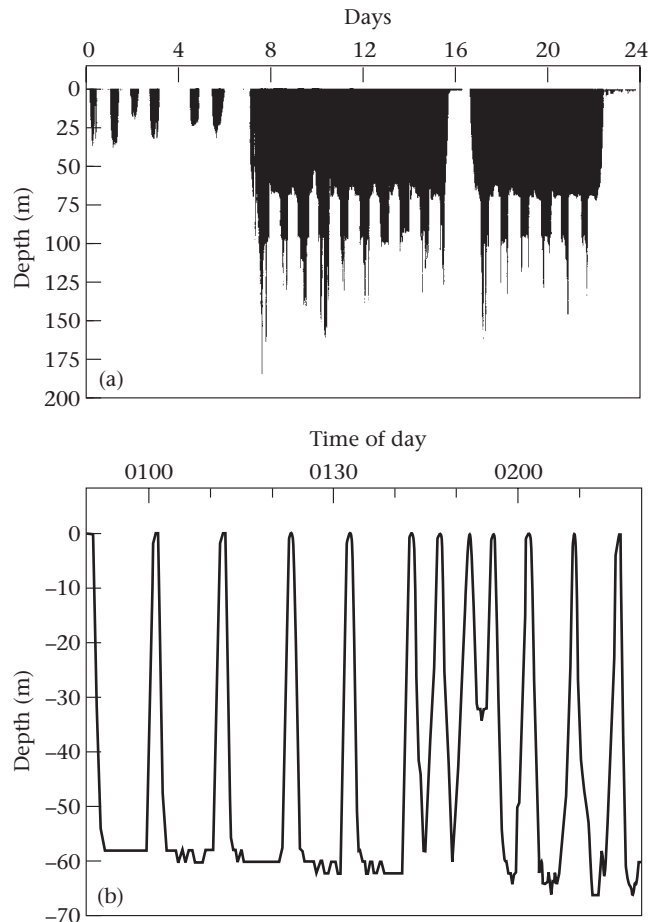

Figure 1. (a) Diving behaviour in an adult female grey seal over a 27-day period. Data are compressed such that every third sample is plotted. Peaks between groups of dives represent time spent 0–4 m from the sea surface or on land. (b) Diving behaviour in the same animal over a 90-min period. All data sampled during this period were plotted to illustrate the characteristics of individual dives.

Instrument Sampling

Various models of TDRs (Mk3e, Mk5, Mk 6 and Mk7, Wildlife Computers, Redmond, Washington, U.S.A.) were used to collect information on diving behaviour. These instruments recorded depth every 20 s to a resolution of 2 m and had a wet/dry sensor that was used to determine when the animal was hauled out on land. Most TDRs were duty-cycled to prolong the memory and battery life over the deployment period. Depending on the duty cycle, between 33 and 100% of diving behaviour was sampled over the length of deployment (3–8 months).

Dive Analysis

TDR data were processed using software supplied by the manufacturer (Wildlife Computers). Initially, data were examined graphically (Strip Chart) to provide a visual representation of the diving pattern of each individual (Fig. 1). Zero-offset correction (ZOC) software was used to account for shifts in the calibration of the pressure transducer of the instrument over the data collection

period. Within the software, this correction was done semiautomatically. ZOC breaks the depth data into sections, which usually represent three to five dives. Corrections are made for each section automatically until a change in zero-offset of greater than ± 2 m is observed. The user then manually adjusts the section to a new zero. Dive analysis (DA) software was then used to automatically analyse the corrected records and provide numerical descriptions of each dive (see Boness et al. 1994 for definitions of dive variables). We determined that the default settings of DA provide reliable estimates of each dive variable by visually examining all dives in DA from a random sample of 20 animals.

Transducer drift and sea surface conditions introduce noise in depth measurements that cannot be completely removed by the zero-offset correction. Therefore, we excluded dives of 4 m or less (two times the resolution of the TDR) from the analysis. Dives longer than 30 min were also excluded from analysis because visual inspection of these long dives showed that they generally represented situations where two dives were not properly separated by the zero-offset correction software. These erroneous dive durations accounted for less than 0.05% of the total number of dives sampled. Based on the visual examination of all dives from the 20 randomly selected individuals, dives less than 30 min were properly identified as individual dives.

To examine the effects of age on diving behaviour, we assigned animals to one of three age classes (young: <17 years; middle: 17–22 years; old: >22 years). Age classes represent the 33rd and 66th percentiles of age for all study animals. We chose this approach to avoid creating groups based on inspection of the data that could bias the analysis. Similarly, we classified seals as one of three length classes (small: <183.5 cm; medium: 183.5–208 cm; large: >208 cm) based on the 33rd and 66th percentile values of DSL to examine the effect of overall body size on diving behaviour.

Individual dive characteristics

To examine seasonal changes in diving behaviour, we averaged data by month for each individual. Only individuals with at least 3 months of dive data were used in the seasonal analysis. May was excluded from all seasonal analysis because so few males were sampled. We used linear mixed effects models (LME; S-Plus 4.5) to examine the effect of month, sex and age on individual dive characteristics of adult grey seals. Given the nature of the data, we assumed an autoregressive (i.e. AR1) variance–covariance matrix for the within-subject error terms. All possible models with two-way interactions were examined and all models were compared to the mean model: $y=\mu+\varepsilon$. To select the best predictive model, the five models with the lowest Akaike's information criterion (AIC) were compared using a log-likelihood ratio test. We used this approach, rather than relying only on the lowest AIC, because of the nonorthogonal nature of our data (i.e. not all animals were measured in each month). The explained variance was calculated using Cox & Snell's (1989, pp. 208–209) generalized coefficient of determination (R^2) modified to incorporate the effective

degrees of freedom (edf; W. Blanchard, personal communication) using the following formula:

$$R^2 = 1 - (\text{log-likelihood mean model/log-likelihood of best model})^{2/edf}$$

where edf is the number of observations × (1 − serial correlation parameter of the model). Other statistical analyses were performed using SPSS 10.0.

Diurnal pattern of depth and duration distribution

To determine whether male and female grey seals dived differently throughout the day, we conducted two analyses. First, we compared the distributions of dive depths and durations during the day and night based on the times of sunrise and sunset at Sable Island using two-way, repeated measures analysis of variance (ANOVAs). Then, to investigate diurnal behaviour in greater detail, we examined the effect of month, time period (eight 3-h periods), sex and age class on the distributions of mean dive depths, durations and dive activity (percentage of dives) using repeated measures LME analysis. For both analyses, dive depth and dive duration were binned at 30-m and 2-min intervals, respectively.

Dive Shape Classification

The shape of individual dives can be represented in two dimensions as a function of time and depth (Fig. 1b). Different shapes are thought to represent different behaviours in a variety of diving species (LeBoeuf et al. 1988; Bengtson & Stewart 1992; Asaga et al. 1994; Crocker et al. 1994; Slip et al. 1994; Wilson et al. 1996; Martin et al. 1998; Hochscheid et al. 1999; Lesage et al. 1999). We classified dive shapes using a combination of manual identification and discriminat function analysis (DFA) as described by Scheer & Testa (1996). Briefly, we individually inspected a random subset of 2000 dive profiles, stratified by sex and classified each profile as one of five shapes: (1) square, (2) wiggle, (3) V, (4) left-skewed square and (5) right-skewed square. Discriminat functions were derived from this subset using the following dive variables: depth, duration, bottom time, bottom time/depth, rate of descent, rate of ascent and skew (ascent/descent). We also used the presence or absence of wiggles (vertical movement at depth) to classify individual dives. DFA correctly classified 96.1% of the dives in the training sample with a jackknife cross-validation error rate of 4.0%. We used the discriminant functions resulting from this analysis to classify the larger data set. Repeated measures MANOVA was used to examine the effect of month, year, sex and age on the distribution of dive shapes by individuals. Given our sampling rate of 20 s, dives of 1 min or less were V-shaped by definition. To avoid introducing a bias, we excluded all dives less than or equal to 1 min from this analysis.

Dive Effort

We measured dive effort using three indexes: accumulated dive time/day, accumulated bottom time/day, and

Table 1. Age, body length and rate of mass gain in adult grey seals

	Males				Females				
	N	$\bar{X}$	SE	CV	N	$\bar{X}$	SE	CV	P
Age (years)	46	19	0.7	0.236	49	17	0.9	0.341	0.166*
Length (m)	38	2.12	0.02	0.044	38	1.78	0.01	0.048	<0.001*
Mass (kg)									
June	24	200.8	7.0	0.17	37	141.0	3.2	0.14	<0.001*
October	14	227.4	6.6	0.11	16	167.0	5.0	0.12	<0.001*
January	28	303.7	6.9	0.12	26	208.1	4.6	0.11	<0.001*
Mass gain (kg/day)									
June–January	19	0.47	0.03	0.25	16	0.34	0.03	0.34	0.003†
October–January	9	0.76	0.08	0.33	10	0.39	0.08	0.61	0.001†

*Independent samples t test.
†ANCOVA.

vertical distance travelled/day. These three measures of effort were highly correlated such that all measures of effort produced the same statistical results. Thus, we present only the results of accumulated bottom time. We believe that this was the best measure of effort because grey seals appear to be benthic foragers (Thompson et al. 1991) and the absolute difference in dive depths by males and females, although statistically significant, was relatively small. We calculated accumulated bottom time (ABT) from individual dive records as follows:

$$ABT = \left[\left(\sum_{d=1}^{k} BT \right) / 60 \right] / N$$

where BT is bottom time for individual dives (min), d and k are dive number and the number of dives recorded for each individual, respectively, and N is the number of days sampled. Repeated measures LME models (as described above) were used to examine the influence of month, sex and age class on accumulated bottom time/day.

RESULTS

As expected, adult male grey seals were significantly heavier and longer than adult females throughout the year (Table 1). Rates of mass gain differed significantly between males and females, with males having a higher gain/day than females (ANCOVA with initial mass as a covariate: $F_{1,32}=10.59$, $P=0.003$ (June–January); $F_{1,16}=18.24$, $P=0.001$ (October–January)). Rate of gain by females was similar between the two deployment periods (i.e. June–January versus October–January, Table 1), however, males had significantly higher rates of mass gain during the October–January period compared with the longer deployment period (ANCOVA with initial mass as a covariate: $F_{1,28}=16.66$, $P<0.001$; Table 1). Ranges for dorsal standard length were 2.0–2.4 m in males and 1.5–2.0 m in females. The mean age of study animals did not differ between sexes and all animals were sexually mature (Table 1).

Between spring 1992 and autumn 1999, 130 instruments were deployed on adult grey seals (54 males, 71 females). Of these animals, 111 (85.4%) returned to Sable Island the following January, but detailed dive data were obtained from only 95 individuals (46 males, 49 females) due to instrument loss or failure. On average, we recorded $10\,238 \pm 768.5$ dives from males and 9774 ± 622.9 dives from females, with a median sampling period of 189 and 142 days for males and females, respectively. There was no significant difference in the number of dives sampled in males and females (independent samples t test: $t_{93}=0.471$, $P=0.639$).

Characteristics of Individual Dives

Overall, mean dive variables of males and females differed significantly (MANOVA: $F_{6,54}=7.32$, $N=95$, $P<0.001$) with females diving longer and spending longer at the bottom of dives (Table 2) but diving shallower than males. Dive variables did not differ by age class or year (MANOVA: age class: $F_{12,110}=1.36$, $P=0.197$; year: $F_{42,354}=1.18$, $P=0.219$) nor were there any significant interaction terms. Once the effect of sex had been removed, length class had no significant effect on dive variables. Given that sex accounted for the variability seen between length classes, length class became a redundant factor and was removed from further analysis.

Overall, $95.9 \pm 0.60\%$ of dives by 95 adult grey seals were less than 120 m and $90.8 \pm 0.79\%$ of dives were less than 8 min. The maximum dive depths recorded for a male and female grey seal were 412 m and 354 m, respectively. Although, mean maximum dive depths differed by more than 30 m between males and females, this difference was not statistically significant ($t_{93}=1.90$, $N=95$, $P=0.061$; Table 2). Mean maximum dive duration and mean maximum bottom time also did not differ significantly between males and females (Table 2).

Seasonal changes were evident in three of the six dive variables: duration, bottom time and rate of descent. For these variables, the sex and age class of individuals influenced the observed seasonal pattern of behaviour. In both males and females, dive duration (Fig. 2a) and bottom time (Fig. 2b) steadily increased from June through to September, and then decreased from October through to

Table 2. Dive characteristics of adult grey seals

| Dive variables	Males, N=46			Females, N=49			
	$\bar{X}$	SE	CV	$\bar{X}$	SE	CV	P*
Depth (m)	57	1.7	0.201	49	2.1	0.299	0.009
Duration (min)	4.9	0.09	0.129	5.5	0.15	0.188	0.002
Bottom time (min)	2.7	0.08	0.196	3.4	0.12	0.246	<0.001
Surface time (min)	2.2	0.12	0.367	2.4	0.17	0.505	0.350
Descent rate (m/s)	1.0	0.03	0.232	1.0	0.04	0.313	0.242
Ascent rate (m/s)	−0.8	0.03	−0.218	−0.9	0.05	−0.413	0.265
Maximum depth (m)	252	12.9	0.349	219	11.6	0.370	0.061
Maximum duration (min)	20.3	1.05	0.352	22.0	0.75	0.240	0.179
Maximum bottom time (min)	16.2	0.94	0.395	17.8	0.74	0.290	0.175

*Independent samples t test.
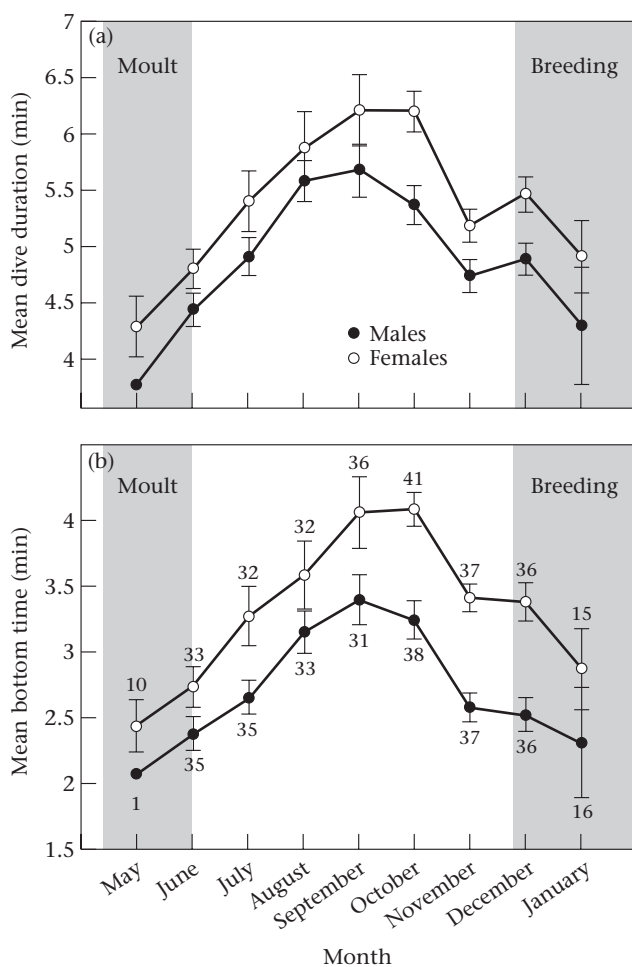
Figure 2. Seasonal changes in (a) duration (min) and (b) bottom time (min) of dives by male and female grey seals. Values are means±1 SE. Numbers above or below each mean represent sample size (i.e. number of individuals) in each month and are the same for both panels. May was not included in statistical analysis because only one male was sampled.

January. From June through to September, males and females did not differ significantly in their dive durations or in the amount of time spent at the bottom of the dive.

However, from October through to December, females spent significantly more time at the bottom of dives than did males (Fig. 2b). Younger seals had longer dives (5.5 min versus 5.2 min) and spent more time at the bottom of dives (3.5 min versus 3.0 min) than the two older age classes throughout the foraging period (P<0.02; Table 3). The best predictive models for duration (R^2=0.184) and bottom time (R^2=0.255) included a quadratic month term, sex and age class. However, there was a significant interaction in dive duration, indicating that the seasonal pattern differed between males and females (Table 3).

Seasonal changes also were observed in the rate at which individuals descended to depth. Overall descent rate decreased from a peak of 0.98 ± 0.04 m/s in July to 0.66 ± 0.05 m/s in January. However, this seasonal pattern was generated by changes in male behaviour alone. From June to September males had faster rates of descent than did females, however, from October to January descent rates were similar for both sexes, resulting in a significant month/sex interaction term (Table 3). Age class also had a significant effect on descent rate, with older animals descending to depth more slowly (0.88 m/s) than the middle and younger age classes (1.01 m/s). However, the best predictive model explained only 8.7% of the variability in descent rate (Table 3).

Although statistically significant, differences in dive variables (dive duration, bottom time and descent rate) between the three age classes were small and presumably of minor biological significance. Given that all animals in our study were adults, these minor differences were not considered further.

Diurnal Patterns of Dive Depth and Duration

The distribution of dive depths differed between day and night (repeated measures ANOVA: $F_{7,87}$=16.566, $P<0.001$). At night, 73.9% of dives were less than 60 m, whereas only 59.4% of daytime dives were less than 60 m. This difference was generated by the behaviour of females alone. During the day females dived significantly more often to depths between 90 and 150 m, whereas at night, dives were concentrated in shallower depths. The depth

Table 3. Best predictive linear mixed effects model of individual dive variables*

Dive variable (N)	Source	Coefficient	SE	Z score	P value	df	Pseudo R^2
Depth (87)	Constant	63.54	4.73	13.446	<0.001		
	Sex	−8.25	2.95	−2.792	0.003	85	0.023
Duration (87)	Constant	−1.70	1.26	−1.349	0.089		
	Month	1.71	0.23	7.374	<0.001	409	
	Month^2	−0.09	0.01	−7.247	<0.001	409	
	Sex	−0.27	0.46	−0.625	0.268	85	
	Age class	−0.74	0.36	−2.079	0.019	84	
	Month^2*sex	0.40	0.21	1.862	0.031	71	0.184
Bottom time (87)	Constant	−4.20	0.92	−4.563	<0.001		
	Month	1.52	0.20	7.777	<0.001	409	
	Month^2	−0.08	0.01	−7.676	<0.001	409	
	Sex	0.63	0.14	4.519	<0.001	85	
	Age class	−0.23	0.08	−2.806	0.003	84	0.255
Surface interval (87)	Constant	0.74	0.06	12.063	<0.001		
Descent rate (85†)	Constant	1.59	0.17	9.300	<0.001		
	Month	−0.05	0.02	−2.997	0.001	397	
	Sex	−0.27	0.11	−2.597	0.005	83	
	Age class	−0.04	0.02	−2.022	0.022	82	
	Month*sex	0.02	0.01	1.918	0.028	389	0.087
Ascent rate (83†)	Constant	−0.78	0.02	−50.46	<0.001		

*Based on lowest AIC and log-likelihood ratio tests.
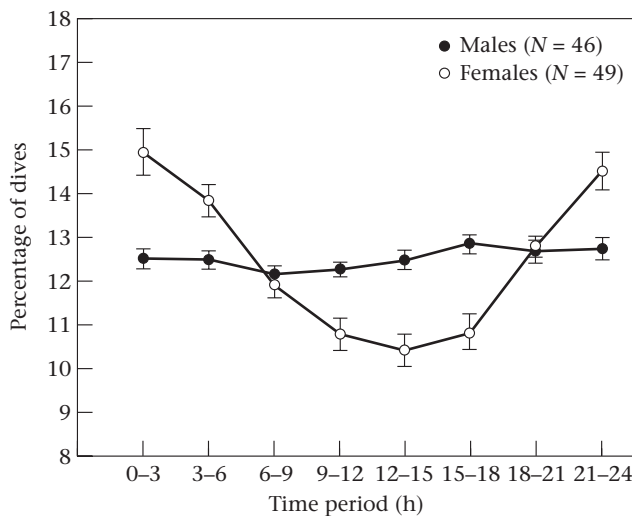†Outliers removed prior to analysis.

Figure 3. Diurnal pattern of dive activity by male and female grey seals. Values are means±1 SE of the percentage of total dives that occurred during each time period.

distribution of male dives was similar during both periods. As with depth, the distribution of dive duration differed between day and night and between sexes (repeated measures ANOVA: $F_{7,87}=3.409$, $P=0.003$). Again, female behaviour generated most of the diurnal difference, with more short dives at night (71.1% <6 min) compared with daytime (63.8% <6 min). The distribution of dive durations of males was similar throughout the day.

Diurnal patterns of diving activity differed between males and females and by month. Males distributed their dive activity evenly throughout the day (Fig. 3), whereas females showed increased dive activity between 1800 and 0600 hours local time and a corresponding decrease in activity during midday. These patterns of dive activity were relatively consistent during the 7-month period, although there were significant month*time period and month*sex interactions, again indicating that the seasonal pattern of diving activity by males and females differed (Table 4). Mean dive depth varied with time of day and sex, but not with month (Table 4). There was a significant interaction between sex and time period, with female dive depths differing throughout the day and male dive depths remaining more consistent (Table 4). Both sexes showed the deepest diving during midday. As with diving activity, there was a significant month*time-period interaction in dive duration. Although the seasonal pattern was similar in males and females, the significant sex*time period interaction indicated differing diurnal patterns, with females diving longer than males during the day, but not at night (Table 4).

Dive Shape

One of five shapes was assigned to the 923 477 dives from 95 individuals (Table 5). Square dives were most common, relatively deep and of medium duration. Right-skewed square dives were the second most common shape. These dives were also deep and of medium duration, but had faster rates of descent than of ascent. Left-skewed dives were shallow, of medium duration and had slower rates of descent than of ascent. V-shaped dives were also shallow and of short duration, with no significant amount of time spent at depth. Finally, wiggle dives tended to be deep and long relative to other dive types (Table 5).

The distribution of dive shapes differed significantly between males and females (repeated measures MANOVA: $F_{3,92}=6.566$, $N=95$, $P<0.001$). Having found significant overall differences, we used univariate tests to

Table 4. Best predictive linear mixed effects model of diurnal patterns in dive variables*

Diurnal patterns (N)	Source	Coefficient	SE	Z score	P value	df	Pseudo R^2
Dive activity (87)	Constant	14.249	0.819	17.394	<0.001		
	Month	0.300	0.078	3.845	0.001	3815	
	Sex	1.162	0.532	2.128	0.017	85	
	Time period	−2.393	0.202	−11.845	<0.001	3814	
	Time period^2	0.312	0.030	10.432	<0.001	3814	
	Month*time period^2	−0.118	0.056	−2.110	0.017	3766	
	Month*sex	−0.005	0.002	−2.576	0.005	3808	0.054
Dive depth (87)	Constant	6.206	0.124	50.145	<0.001		
	Sex	−0.359	0.109	−3.301	<0.001	85	
	Time period	0.526	0.036	14.561	<0.001	3814	
	Time period^2	−0.059	0.004	−15.031	<0.001	3814	
	Sex*time period^2	0.002	0.001	2.562	0.005	3806	0.268
Dive duration (87)	Constant	0.538	0.190	2.835	0.002		
	Month	0.373	0.041	9.121	<0.001	3815	
	Month^2	−0.020	0.002	−9.159	<0.001	3815	
	Sex	0.051	0.021	2.390	0.008	85	
	Time period	0.044	0.009	5.088	<0.001	3814	
	Time period^2	−0.004	0.001	−3.968	<0.001	3814	
	Month*time period^2	−0.00001	5×10^{-6}	−2.127	0.015	3766	
	Sex*time period^2	0.0003	2×10^{-4}	2.031	0.021	3806	0.105

*Based on lowest AIC and log-likelihood ratio tests.

Table 5. Characteristics of shapes assigned to dives by 95 grey seals

Dive shape	Profile	%Dives	Depth (m)	Duration (min)	Bottom time (min)	Descent rate (m/s)	Ascent rate (m/s)	Skew ratio (ascent/descent)
Square	\/	68.2±1.70	62±3.5	5.5±0.86	3.3±0.07	1.0±0.03	0.9±0.04	0.96±0.132
Right skewed Square	_/	14.2±1.08	53±3.9	5.4±0.12	3.0±0.09	1.5±0.05	0.6±0.02	0.41±0.004
Left skewed Square	_/	7.0±0.59	32±1.7	5.2±0.07	3.0±0.06	0.4±0.05	1.2±0.12	3.65±.117
V-shaped	V	5.7±0.70	26±1.1	3.3±0.13	0.1±0.03	0.5±005	0.7±0.11	3.19±0.46
Wiggle	\w/	5.0±0.70	57±1.6	6.8±0.23	4.4±0.20	1.0±0.04	0.9±0.08	1.43±0.108

determine where those differences occurred. Females had a significantly higher proportion of left-skewed dives than did males (independent samples t test: $t_{94}=−3.426$, $P=0.001$), whereas males had a significantly higher proportion of right-skewed square dives ($t_{94}=2.441$, $P=0.016$). The proportion of square, wiggle and V-shaped dives did not differ between males and females ($t_{94}=−0.610$, $−0.980$ and 1.895, $P=0.543$, 0.329 and 0.061, respectively). Dive shape distribution also did not differ between age classes (ANOVA: $F_{6,178}=1.402$, $N=95$, $P=0.209$) or by year ($F_{12,213}=1.516$, $P=0.120$).

Dive shapes used by grey seals changed seasonally in a nonlinear pattern ($F_{18,30}=7.274$, $N=49$, $P<0.001$; Fig. 4). There was a significant decrease in the proportion of square dives from June to August, then a significant increase from October through December followed by a significant decrease in January. January was not included in the above repeated measures analysis due to reduced sample size ($N=30$). However, there was a sharp increase in the proportion of V-shaped (6.0 ± 0.58–$16.3 \pm 3.75\%$) and left-skewed (6.1 ± 0.64–$12.1 \pm 2.29\%$) dives from December to January with a corresponding decrease in square dives (74.3 ± 1.59–$57.9 \pm 4.71\%$; Fig. 4).

From June to December, the seasonal change in dive shape distribution did not differ between age classes ($F_{36,60}=1.299$, $N=49$, $P=0.182$) or between males and females ($F_{18,30}=1.581$, $N=49$, $P=0.130$). We reexamined sex as a factor using a larger sample where months were grouped into two periods (June–September and October–December). Using this larger sample, dive shape distribution of males and females did not differ during the June–September period ($F_{9,51}=1.706$, $N=61$, $P=0.112$), but differed significantly in the October–December period ($F_{6,64}=4.848$, $N=71$, $P<0.001$). During the 3 months prior to breeding, males showing a greater proportion of V-shaped dives and a reduced proportion of square dives compared with females. In contrast, females showed a greater proportion of left-skewed dives and increased the proportion of square dives as breeding approached.

Dive Effort

Dive effort differed significantly between males and females and by month. Overall, females spent 7.69 h/day at depth compared with the 6.47 h/day spent at depth
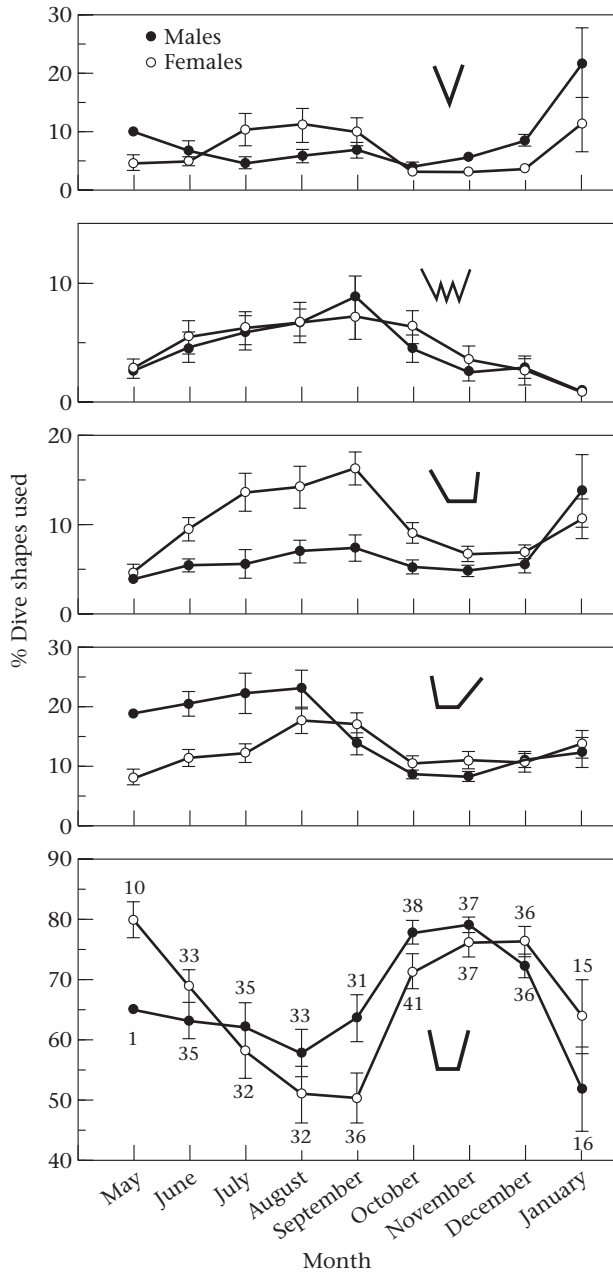
Figure 4. Seasonal changes in the percentage of dive shapes used by male and female grey seals. Shape profiles are indicated in each panel. Values are means±1 SE. Numbers above or below each mean in the bottom panel indicate the number of animals sampled in each month and are the same for all panels. May and January were not included in statistical analysis because only one male was sampled in May and inclusion of January would have reduced the sample size in the other months.

by males (independent samples t test: $t_{93} = -3.421$, $P=0.001$). The best predictive model for this index of dive effort explained about 52% of the variation. Again, there was a significant month × sex interaction showing that the seasonal pattern of accumulated bottom time/day differed between males and females (Fig. 5, Table 6). Age-class had no significant effect on seasonal patterns of dive effort.
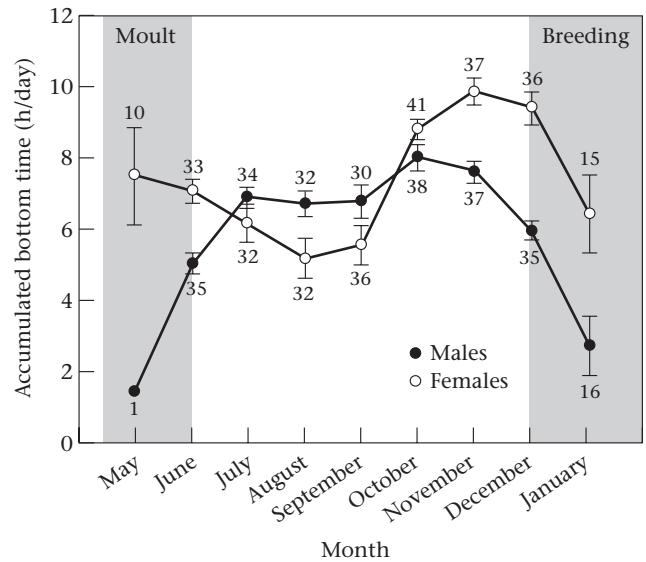

Figure 5. Seasonal changes in accumulated bottom time (h/day). Values are means±1 SE. Numbers above or below each mean indicate the number of individuals sampled in each month. May was not included in statistical analysis because only one male was sampled.

DISCUSSION

Our findings demonstrate pronounced sex differences in diving behaviour of adult grey seals. These differences occurred at the level of individual dives (e.g. duration, shape), diurnal patterns of diving and dive effort. However, the most prominent feature of these differences was the sex-specific seasonal pattern in diving behaviour, suggesting that males and females have different long-term foraging strategies because much of their diving activity is likely to be associated with foraging. We interpret these sex differences in the seasonal pattern of diving as evidence that males and females make different foraging decisions as a result of sex-specific costs and benefits associated with storing energy for reproduction (see below).

Given that adult grey seal males require about 1.3 times more energy than do females (Mohn & Bowen 1996), sex differences in the foraging behaviour of adult grey seals were not unexpected. However, the direction of the observed differences was contrary to that predicted based on the energy requirements of the larger sex, with males showing less overall effort, having shorter dives and spending less time at the bottom of individual dives compared with females. Using accumulated bottom time/day as a measure of dive effort does not account for the energy and time expended by animals travelling to and from depth. However, two other indices of effort (accumulated dive time/day and vertical distance travelled/day) that do take dive depth into account, showed similar overall and seasonal results. Thus, the finding that males have a lower level of dive effort is not an artefact of males diving deeper and thereby spending more time and energy travelling to and from depth. Rather, males perform shorter dives despite the fact that

Table 6. Best predictive linear mixed effects model of dive effort*

Foraging measure	Source	Coefficient	SE	Z score	P value	df	Pseudo R^2
Accumulated bottom time (h/day)	Constant	35.38	5.829	6.069	<0.001		
N=87	Month	−10.53	1.996	−5.274	<0.001	409	
	Month^2	1.23	0.221	5.592	<0.001	409	
	Month^3	−0.05	0.007	−5.845	<0.001	409	
	Sex	0.06	0.294	0.208	0.417	85	
	Month^3*Sex	0.0005	0.0001	4.307	<0.001	401	0.517

*Based on lowest AIC and log-likelihood ratio tests.

they dive deeper than females, contrary to the expected result based on a higher energy requirement and predicted higher level of effort in males. Two possible explanations for this inconsistency are that males are more efficient predators than females or they are less selective when searching for prey. Because mass-specific energy requirements decrease with body mass and gut capacity scales isometrically, larger males should be able to digest lower-quality foods more easily than females, and thus be less selective foragers (Mysterud 2000). As a result, in size-dimorphic herbivore species, males are more efficient, spending less time foraging than females despite their larger size and absolute energy requirement (e.g. Ginnett & Demment 1997; Ruckstuhl 1998; Pérez-Barberia & Gordon 1999). These scaling relationships imply that grey seal males should have a higher ratio of gut capacity to metabolic requirement than females and as such could be more efficient foragers than are females. Females, with a lower gut capacity/metabolic requirement ratio, may be more selective than males and thus make longer dives in search of more profitable prey types. Males may also be more efficient forgers than females if their larger size allows them to capture and handle larger prey more easily; however, there are currently no data to examine this possibility.

Sexual size dimorphism in grey seals also does not explain the sex-specific seasonal patterns of diving behaviour seen in this study. Perhaps females alter their seasonal patterns of diving to reduce intraspecific competition with males. Males and females may forage in different locations (Schoener 1969; Clarke et al. 1998), on different prey (Hughes 1980; Williams 1980) or at different times within the same habitat to reduce competition. Sex differences in both foraging areas and diurnal patterns of dive depth have been observed in northern elephant seals (DeLong & Stewart 1991; LeBeouf et al. 2000). In that species it is thought that males feed on demersal prey whereas females feed on vertically migrating pelagic prey, however, direct evidence of sex differences in diet is still needed (Le Beouf et al. 2000). Nevertheless, the observed sex differences in both location and diving behaviour are consistent with the intraspecific competition hypothesis in northern elephant seals.

In contrast, at-sea locations from satellite telemetry and geolocation time-depth recorders show that there is a broad overlap in the distribution of adult male and female grey seals in this study population (Beck 2002). Thus, it seems likely that foraging areas also overlap. As a result, males and females should be affected by the same seasonal changes in environmental conditions and prey availability. It is also possible that males and females use these areas differently and that the sex differences in diurnal patterns of diving we observe (Fig. 3) reflect this. Differences in behaviour could indicate that males and females reduce intraspecific competition by consuming different prey. However, current evidence based on fatty acids signatures indicates that the diets of adult males and females in this population overlap considerably (Beck 2002). Thus, the differences in the diving behaviour of male and female grey seals are unlikely to be the result of differences in diet. We conclude that it is unlikely that males and females show seasonal differences in foraging behaviour to reduce intraspecific competition.

Given this, the seasonal differences in the foraging behaviour of males and females seems better explained as evidence of a sex-specific trade-off between the costs associated with storing body energy and the benefit of having stored that energy for reproduction. This argument is similar to the 'reproductive strategy hypothesis' used to explain the ecological segregation of male and females in size-dimorphic ungulate species (Main et al. 1996; Mysterud 2000).

We suggest that female grey seals have a lower cost/benefit ratio for stored body energy than do males because the reproductive benefit to females is greater than the reproductive benefit to males and may have greater consequences for female fitness. Coulson (1960) and Hall et al. (2001) showed that undersized grey seal pups have lower survival probability than average- or above-average-sized pups at weaning. Female size and milk energy output are the best predictors of weaning mass in grey seals (Iverson et al. 1993; Mellish et al. 1999), emphasizing the importance of maternal energy storage to offspring survival and female fitness. In contrast, mating success in male grey seals is more flexible with respect to body energy reserves and as a result is more variable (Anderson & Fedak 1987; Godsell 1991; Lidgard et al. 2001). Age, body mass, operational sex ratio and length of stay within a breeding colony all influence the reproductive success of grey seal males (Boness & James 1979; Godsell 1991; Twiss et al. 1994; Lidgard et al. 2001). In addition, recent studies have shown that some males take short foraging trips during the breeding season

presumably to supplement energy stores (Lidgard et al. 2001). Therefore, in this species, female reproductive success is much more dependent on energy stores available at the start of the breeding season than is male mating success.

Immediately following the spring moult females showed high levels of dive effort in which approximately 80% of all dives were square-shaped (Figs 4, 5). Maternal condition has an important influence on early fetal development in grey seals, and other mammals, with females in poorer condition implanting later than females in better condition (Boyd 1984; Albon et al. 1986; White et al. 1997; Pitcher et al. 1998). Thus, females need to recover body condition quickly to ensure maintenance of pregnancy. Given that this early recovery of body condition is not required in males, it is not unexpected that the diving behaviour of females and males differed in the first 2 months following the moult (Fig. 5). Seasonal changes in sternal blubber thickness, a measure of energy storage, show an earlier increase in grey seal females than in males following the moult (B. Beck, personal communication).

During the late summer and early autumn female grey seals reduced their dive effort and their proportion of square-shaped dives. This reduction may indicate that females are simply maintaining body condition during this period. Given that there are likely to be costs associated with the accumulation and maintenance of stored body energy over long periods of time (Jönsson 1997), females may not benefit from further accumulation of energy stores during this period. These costs could include increased metabolic costs associated with maintaining and transporting additional body mass (Jönsson 1997), including an increased cost of transport during the descent phase of dives due to increases in buoyancy (Webb et al. 1998; Beck et al. 2000). Although we cannot quantify these costs at present, even small increases in the cost of transport could be important given that a grey seal will perform approximately 48 000 dives between the moult and the beginning of the breeding season based on an average of 200 dives/days (Beck 2002). Increased foraging effort in the months immediately prior to parturition suggests that the benefits of additional accumulation of body energy during this period outweigh these costs.

The seasonal pattern of diving behaviour and effort observed among male grey seals was less variable than that observed among females. This was also reflected in a more constant use of square-shaped dives throughout the spring and summer relative to females. Following the moult, male dive effort increased gradually, reaching a peak in late autumn and declining just before the breeding season. Rate of mass gain in males was significantly lower during June–January (0.47 ± 0.03 kg/day) than during the second half of the foraging period (October–January; 0.76 ± 0.08 kg/day). This result suggests that, in males, much of the body energy stored for reproduction is accumulated during the last 4 months of the foraging period. Given the less certain reproductive payoff in males associated with energy stores (see above), the costs associated with storage and transportation of extra body mass throughout the entire 7-month foraging period may outweigh the benefit of early accumulation of stored

energy to fitness. Although male dive effort declined just before the breeding season, this decline may reflect a shift to increased travel as males return to the breeding colony. An increase in the proportion of V-shaped dives used by males during December and January supports this hypothesis (Fig. 5). V-shaped dives are known to represent horizontal travel in elephant seals and may serve a similar function in other diving species, although direct evidence is needed to confirm this (Fedak & Thompson 1993; Asaga et al. 1994; Slip et al. 1994; Martin et al. 1998; LeBoeuf et al. 2000).

Of the 32 species of pinnipeds, only sufficient numbers of grey seals (this study) and elephant seals have been studied to make reasonable inferences about the foraging ecology of both sexes (Slip et al. 1994; LeBoeuf et al. 2000). However, unlike grey seals, elephant seals are highly migratory and foraging is organized into two major trips each year, during which diving is virtually continuous (LeBoeuf et al. 1988, 1989, 1993, 2000). In the size-dimorphic southern elephant seal, females make longer dives than males Slip et al. (1994); however, in northern elephant seals, males and females have similar mean dive durations despite the larger body size of males (LeBoeuf et al. 1993, 2000). In a less size-dimorphic species, the harbour seal, *Phoca vitulina*, males make longer dives during the breeding season than do females (Coltman et al. 1997; Bowen et al. 1999b), but female diving may be constrained by the diving ability of her pup during this period.

Although size dimorphism may account for some of the observed differences in the diving behaviour of male and female grey seals (e.g. dive depth), we suggest that seasonal differences in diving, and thus foraging, behaviour result from sex differences in the trade-offs associated with long-term energy storage for reproduction. If this hypothesis is correct, we would not expect a sex–season interaction in diving behaviour of juvenile grey seals, given that juveniles are not storing energy for reproduction. Thus, an understanding of the diving behaviour of juveniles and a better understanding of the costs associated with foraging and energy storage are needed.

Acknowledgments

this study were in accordance with the principles and guidelines of the Canadian Council on Animal Care.

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