

Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal

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Summary

1. Sex differences in the timing and magnitude of energy expenditure for reproduction may result in sex-specific seasonal patterns of energy storage and utilization, particularly among capital-breeding species. We studied the seasonal patterns of energy storage in adult grey seals, *Halichoerus grypus*, a capital-breeding, marine carnivore, to test the prediction that males and females differ in their seasonal pattern of energy storage and expenditure.

2. We measured body mass and composition in 135 (67 males, 68 females) adult grey seals at five key points throughout the annual cycle. Longitudinal changes in body composition were also measured in 73 individuals (35 males, 38 females) to examine individual variability.

3. There were significant sex differences in seasonal patterns of total body energy, with females exhibiting greater energy content (after accounting for body mass) throughout the year. Females gained body energy following both the spring moult and the breeding season, whereas males only gained body energy following an extended period of loss that included both breeding and moulting, a period of some 6 months.

4. Mass loss of females during the breeding season was similar in magnitude and composition to that gained during the 7-month pre-breeding foraging period. In contrast, mass loss of males during the breeding season was more similar to that gained during the last three months of the pre-breeding foraging period.

5. Our results suggest that the balance of costs and benefits of storing body energy for reproduction differs between males and females. Females appear to be risk-averse, committing themselves to, and preparing for, reproduction at a much earlier stage in the annual cycle compared to males. As a result, females accumulate body energy stores earlier and carry a higher level of insurance against environmental uncertainty leading up to the breeding season relative to males.

Key-words: body composition, body mass, fitness-maximizing strategy, grey seals, reproduction, seasonal, sex.

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Introduction

Recent interest in state-dependent life histories recognizes the importance of the physical state of an animal to its reproductive decisions and fitness (McNamara & Houston 1996; Boyd 2000; Glazier 2000). An individual's state is expected to affect its ability to survive to a given age, where state may incorporate (but is not limited to) aspects of body size, energy content, territory quality and foraging skills (McNamara & Houston

1996). Thus, state-dependent analysis of life-history strategies may provide more insight into how individuals balance reproduction with other vital activities and the consequences of this balancing on fitness (McNamara & Houston 1996; Boyd 2000).

Body mass and energy content are important components of an individual's state and are expected to vary throughout an individual's lifetime. For instance, many northern and temperate herbivores go through seasonal changes in body mass and composition that coincide with the seasonal changes in food availability (Mautz 1978; Adamczewski *et al.* 1987; Chan-McLeod, White & Russell 1999). However, seasonal changes in mass and body condition are also linked to reproduction

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(e.g. Kenagy, Sharbaugh & Nagy 1989; White, Rowell & Hauer 1997). Reproduction represents a period of increased energy demand associated with rearing offspring, mate acquisition and resource defence. These reproductive costs can alter the magnitude and timing of seasonal fluctuations in body mass brought about by changes in food availability (Leader-Williams & Ricketts 1981; Hewison *et al.* 1996). More directly, reproductive behaviour may severely limit foraging (e.g. in many pinnipeds, baleen whales, Holarctic bears and male ungulates) such that individuals must use previously stored body energy to meet maintenance metabolic requirements and the additional costs of reproduction. Individuals that rely solely on previously stored energy during offspring rearing are referred to as 'capital breeders' (Sibly & Calow 1986; Jönsson 1997) and are subject to especially pronounced seasonal patterns of energy accumulation and depletion.

In mammals, the magnitude of reproductive costs differ between males and females (Gittleman & Thompson 1988) with the energetic costs to females (gestation and lactation) often being higher than the energetic costs to males (mate acquisition and resource defence). The timing and duration of reproductive costs also differ between the sexes. In most mammalian species, males do not contribute to parental care, such that male reproductive costs are generally limited to the breeding period. In contrast, females incur energetic costs from the early stages of gestation until the offspring is weaned. The fitness consequences of not obtaining sufficient energy to meet these energetic costs can also differ between males and females. A male's fitness is most closely associated with the number of mating opportunities whereas a female's fitness is more closely associated with her energetic ability to successfully wean offspring (Trivers 1972). Consequently, fitness-maximizing strategies of males and females typically differ (Clutton-Brock & Parker 1992; Jormalainen *et al.* 2001) and may be expected to influence the foraging behaviour and pattern of energy storage of each sex differently.

Despite the number of studies that have examined sex differences in seasonal changes of body energy, only a few carnivore species have been studied (Buskirk & Harlow 1989; Prestrud & Nilssen 1992; Poulle, Crete & Huot 1995). In capital breeding carnivores, depletion of body energy stores can be extreme. For example, in polar bears, *Ursus maritimus*, females lose approximately 44% of their stored body energy during the denning period (calculated from Atkinson & Ramsay 1995). Among pinnipeds, territorial male Antarctic fur seals, *Arctocephalus gazella*, lose on average 24% of their body mass during the breeding season with fat accounting for 53.4% of mass loss (Boyd & Duck 1991). Thus, capital breeding carnivores provide a good opportunity to examine seasonal patterns of energy storage and allocation in males and females.

We examined the seasonal patterns of body mass and energy storage and allocation in male and female grey seals, *Halichoerus grypus*. The grey seal is a

polygynous, size-dimorphic species (Family Phocidae), with adult males being approximately 1.5 times heavier than adult females in the North-west Atlantic population (Mohn & Bowen 1996). Female grey seals are capital breeders, relying solely on stored body energy accumulated prior to parturition to support the high energetic costs of lactation and their own metabolic expenditures during the breeding season. Females with low body mass (and hence low energy stores) at parturition tend to wean smaller pups or wean pups prematurely (Iverson *et al.* 1993; Mellish, Iverson & Bowen 1999; Pomeroy *et al.* 1999), increasing the probability of juvenile mortality (Coulson 1960; Hall, McConnell & Barker 2001). Female grey seals enter oestrous and are mated during the late stages of lactation, however, implantation does not occur for 3–4 months (Boyd 1984). Male grey seals use a variety of mating tactics during the breeding season. These strategies range 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; Twiss, Pomeroy & Andersen 1994; Lidgard, Boness & Bowen 2001). Despite these trips to sea, males rely on energy stores accumulated prior to breeding to extend the period of time they can remain ashore competing for and acquire mates. Although the quantity of stored energy is important for this purpose, Godsell (1991) and Lidgard *et al.* (2001) found that the correlation between body mass and male mating success is weak. Hence, reproductive success of males seems less dependent on the amount of stored body energy at the beginning of the breeding season than is the reproductive success of females. Both males and females return to sea immediately following the breeding season, but experience another period of mass loss during the annual moult on land some 4–5 months later.

As a result of these alternate periods of terrestrial fasting and foraging at sea, grey seals go through dramatic seasonal changes in body mass and composition. Both sexes deplete body mass and energy stores during periods of terrestrial fasting, however, we predicted sex differences in the seasonal pattern of energy accumulation due to sex-specific reproductive costs (magnitude and timing) and differential fitness consequences associated with having insufficient stored body energy to meet reproductive needs. Female mammals in poor condition are less likely to become pregnant or carry the pregnancy to term (Thomas 1982; Boyd 1984; Albon *et al.* 1986; White *et al.* 1997). Thus, we predicted that female grey seals would recover body condition early following the breeding and moulting periods, both to support pregnancy and the future energetic costs of lactation. We predicted a more gradual accumulation of energy stores in males as there is no immediate reproductive requirement following the breeding period and thus, there appears to be a lower risk to future reproduction associated with reduced body condition early in the year.

While the benefits of stored body energy are well understood, there are also potential costs associated

with the storage of body energy and increased body mass (Witter & Cuthill 1993; Gosler, Greenwood & Perrins 1995; Gentle & Gosler 2001). In phocids, such costs could include an increased risk of predation, decreased mobility on land, and increased cost of transport during diving due to increases in buoyancy (Webb *et al.* 1998; Beck, Bowen & Iverson 2000). The way in which male and female grey seals deal with these costs are likely to differ since the relative reproductive benefit from early storage of body energy is predicted to be higher for females. Thus, we predicted that the seasonal pattern of energy storage and allocation would differ between male and female grey seals as a result of the sex-specific trade-off between storing energy for reproduction and the costs of storing that energy over long periods of time.

Materials and Methods

The study was carried out between January 1997 and May 2000 on Sable Island (43°55' N, 60°00' W), a crescent-shaped, partially vegetated sandbar approximately 300 km south-east of Halifax, Nova Scotia, Canada. Sable Island is the largest haul-out location for grey seals in the North-west 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.

Known-aged, adult grey seals (branded or tagged as pups) were captured on shore using hand-held nets (see Bowen, Oftedal & Boness 1992) at five points throughout their annual cycle (Fig. 1): start of the moult, end of the moult, mid-foraging period (early October), start of breeding (late December/early January), and end of

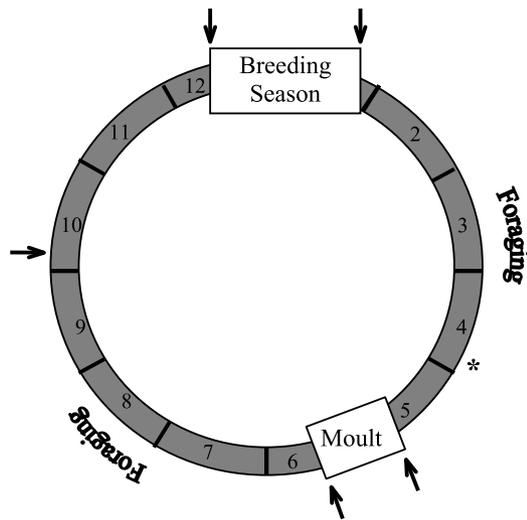


Fig. 1. Annual cycle of terrestrial fasting and at-sea foraging for grey seals in the North-west Atlantic. Numbers indicate month of the year. Periods of terrestrial fasting and their associated activities are shown in boxes, arrows depict times of sampling and the star denotes approximate time of implantation.

breeding (February). This allowed us to compare how males and females stored and allocated energy throughout the year. In grey seals the timing of the moult differs between the sexes with females moulting in May, about one month earlier than males. As a result, the moulting condition of the animal was used to assess ‘start’ and ‘end’ of moult rather than a particular date. Individuals were considered to be at the start of the moult if 95% or more (visual estimate) of the previous year’s pelage was still present. Individuals were considered to be at the end of moult only when they were fully moulted. In addition to the cross-sectional sampling described above, a subset of males and females sampled at the end of moult or in October were sampled again the following January and February to examine individual variability in energy storage and energy allocation to reproduction.

Individuals were weighed to the nearest 0.5 kg using Salter spring balances and then administered a known quantity of tritiated water (HTO; 0.5 mCi mL⁻¹ (1 Ci = 37 GBq); at 0.02 g kg⁻¹ body mass). HTO was injected intramuscularly (IM) and the needle and syringe were rinsed with unlabeled water (also injected) to insure complete delivery of the weighed isotope. A blood sample was taken from the extradural vein at 90 min post-administration and again 15–20 min later to confirm that isotope equilibration had occurred. Previous studies on grey seals have shown that HTO injected IM equilibrates with body water in ≤ 90 min and that 15–20 minute intervals are sufficient to detect any continued changes (Mellish 1999; Beck 2002).

Blood samples were collected into Vacutainers without additives and then centrifuged for 20–30 min. Serum aliquots (5 mL) were stored frozen (–20 °C) in cryovials until analysis. Water was recovered from each sample in triplicate by distilling 50 µL aliquots of serum directly into pre-weighed scintillation vials, using the evaporated-freeze-capture method described by Ortiz, Costa & Le Boeuf (1978). The vials were then re-weighed to obtain the mass of distillate to the nearest 0.1 mg and 10 mL of Scintiverse II was added to each vial. Each sample was analyzed in triplicate and counted for 5 min in a Beckman scintillation counter. The average specific activity was expressed as count per minute per gram distillate (CPM g⁻¹). In cases where the triplicate samples had a coefficient of variation greater than 2%, the two closest samples were used. The specific activity of the injectant was determined at the same time as that of the serum samples.

HTO dilution space was calculated as in Bowen, Beck & Iverson (1999) and total body water (TBW) was estimated from a regression of isotope dilution space on TBW (Bowen & Iverson 1998). Total body fat (TBF), protein (TBP) and energy (TBE) were calculated from the following equations developed for grey seals by Reilly & Fedak (1990):

$$\%TBF = 105.1 - 1.47(\%TBW)$$

$$\%TBP = 0.42(\%TBW) - 4.75$$

$$\text{TBE (MJ)} = 40.8(\text{Body Mass}) - 48.5(\text{TBW}) - 0.4.$$

In January, females were not recaptured until 1–3 days postpartum to allow mothers time to bond with their pups. For females sampled 1–3 d postpartum and at the end of the breeding season, we corrected mass and composition to postpartum levels using each individual's rates of mass and composition loss, which is known to be linear (Mellish *et al.* 1999). In cases where mass and composition of an individual were not obtained at the end of breeding, we used the average rate of mass and fat loss in female grey seals during early lactation (Mellish *et al.* 1999 and this study) to back-calculate postpartum body mass and composition. Thus, mass and energy gained by females or lost during lactation did not include birth mass of her pup. Male grey seals were captured within 2 days of appearing on the breeding grounds based on daily surveys of the island. During the breeding season, male grey seals on Sable Island lose mass at an approximate rate of 2.5 kg day⁻¹ with fat comprising 62% of mass loss (Godsell 1991). These rates of loss were used to correct body mass and composition of males to arrival conditions. As with females, when males were sampled at both the beginning and end of the breeding season, we used each individual's rate of mass and composition loss to correct mass and composition to arrival levels.

Statistical analyses were conducted with SPSS 10.1. Standard error (SE) is given as a measure of variability about the mean. Total body energy was significantly correlated with body mass (Pearson's correlation = 0.900, $P < 0.001$). As a result, analysis of covariance with body mass as a covariate was used to examine sex differences in the seasonal pattern of TBE. Homogeneity of regression slopes between groups was tested prior to conducting the covariance analysis. This method was considered the most appropriate way of correcting for the effects of body mass given that the two variables are not isometrically related (Raubenheimer & Simpson 1992; Raubenheimer 1995). To avoid pseudoreplication in

the cross-sectional analysis, only a single randomly selected observation was used in cases where a seal was sampled more than once. For the longitudinal data, independent samples of individuals were used to compare rates and composition of gain from the end of moult to start of breeding and from mid-foraging to start of breeding periods. We had insufficient data to conduct a repeated-measures analysis using all three periods (i.e. including start to end of breeding).

Results

CROSS-SECTIONAL CHANGES IN BODY MASS AND COMPOSITION

Body mass and composition was measured in 135 adult grey seals (67 males and 68 females, Table 1). It was not possible to sample at all time periods in every year of the study due to logistic constraints. However, start and end of breeding samples were collected for both sexes in 1998, 1999 and 2000. Animals were sampled at the start of the moult in May of 1999 and 2000, the end of the moult in June of 1997, 1998 and 1999, and mid-foraging samples were collected in October of 1997 and 1999. Given the relatively small sample size when stratified by period and year, we could not investigate inter-annual changes in body composition. However, equal numbers of males and females were sampled in each year/season group. The age of study animals ranged from 8 to 28, but did not differ by season (ANOVA: $F_{3,71} = 0.863$, $P = 0.464$) or sex ($F_{1,71} = 1.905$, $P = 0.172$) and there was no significant season by sex interaction ($F_{3,71} = 1.731$, $P = 0.168$).

In addition to the potential influence of age and year on our results, we were also concerned with the potential of a sampling bias at the mid-foraging sampling period. This is a concern because the probability of capturing an individual during this period may be related to condition, with animals in better condition more likely to be resting ashore and therefore sampled.

Table 1. Mean \pm SE (CV) seasonal mass and body composition of 135 adult male and female grey seals

	Sex	Sampling period				
		End of breeding	Start of moult	End of moult	Mid-foraging	Start of breeding
Body mass (kg)	M	241 \pm 10.5 (0.14)	240 \pm 6.4 (0.10)	199 \pm 9.7 (0.19)	239 \pm 11.9 (0.17)	291 \pm 7.7 (0.10)
	F	144 \pm 4.7 (0.11)	160 \pm 4.6 (0.11)	133 \pm 5.9 (0.17)	153 \pm 4.0 (0.09)	207 \pm 8.5 (0.16)
Water (%)	M	57.1 \pm 1.03 (0.06)	58.8 \pm 0.69 (0.05)	63.7 \pm 0.97 (0.06)	56.2 \pm 1.15 (0.07)	52.9 \pm 1.01 (0.07)
	F	59.5 \pm 1.54 (0.9)	55.9 \pm 0.72 (0.05)	60.9 \pm 1.01 (0.06)	56.9 \pm 0.99 (0.06)	49.4 \pm 0.85 (0.07)
Protein (%)	M	19.2 \pm 0.42 (0.07)	19.9 \pm 0.29 (0.06)	22.0 \pm 0.40 (0.07)	18.8 \pm 0.49 (0.09)	17.4 \pm 0.42 (0.09)
	F	20.2 \pm 0.65 (0.11)	18.7 \pm 0.30 (0.06)	20.8 \pm 0.43 (0.08)	19.2 \pm 0.42 (0.08)	16.0 \pm 0.36 (0.09)
Fat (%)	M	21.2 \pm 1.51 (0.24)	18.7 \pm 1.00 (0.21)	11.5 \pm 1.41 (0.47)	22.5 \pm 1.68 (0.26)	27.5 \pm 1.51 (0.20)
	F	17.7 \pm 2.26 (0.42)	23.0 \pm 1.07 (0.18)	15.6 \pm 1.49 (0.37)	21.4 \pm 1.45 (0.23)	32.5 \pm 1.25 (0.15)
Total body energy (MJ)	M	3180 \pm 223.8 (0.23)	2956 \pm 125.7 (0.16)	2014 \pm 196.3 (0.38)	3292 \pm 272.7 (0.29)	4460 \pm 246.9 (0.23)
	F	1729 \pm 134.5 (0.26)	2205 \pm 110.6 (0.19)	1534 \pm 142.9 (0.36)	2030 \pm 110.9 (0.19)	3504 \pm 187.0 (0.21)
N	M	11	15	15	12	14
	F	11	15	15	12	15

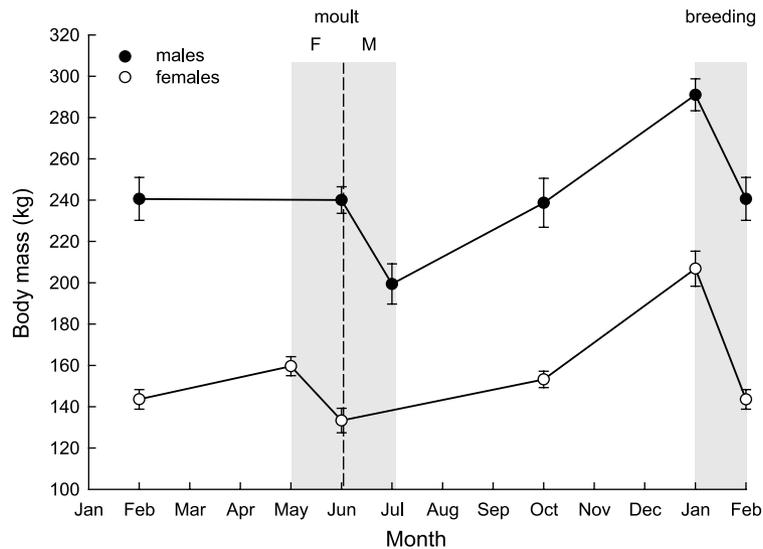


Fig. 2. Seasonal changes in body mass in adult male and female grey seals (mean ± SE). Sample sizes are given in Table 1. Shaded areas represent the two periods of terrestrial fasting. Note that females begin and end moult about a month earlier than males. The post-breeding sample is plotted twice to better illustrate the overall annual patterns.

If this were true we might expect to see a smaller coefficient of variation (CV) in body mass in the October samples. However, the CV of body mass was similar at all sampling times (Table 1) suggesting that we were sampling from the population in a similar way throughout the year. Additionally, a test of homogeneity of variance showed no significant difference in the variance of body mass between sampling periods (Levene's test: test statistic = 1.147, d.f. = 4, 130, $P = 0.338$). The CV of total body energy was also similar among sampling periods, with the exception of the end of moult sample, which was more variable than the other sampling times (Table 1). The higher variance in body energy at this time was the result of two study animals (1 male and 1 female) being in exceptionally good condition (24% and 30% fat, respectively) for this time of year.

As expected, males were heavier than females at all sampling times (Fig. 2). Males were lightest following the spring moult compared to other times of the year (ANOVA: $F_{4,62} = 13.52$, $P < 0.01$; *post hoc* comparisons between seasons: all $P < 0.030$) and heaviest at the start of the breeding season 7 months later (*post hoc* Bonferroni comparisons: all $P < 0.004$). Similarly, females were heaviest at the start of the breeding season compared to other times of the year (ANOVA: $F_{4,63} = 23.53$, $P < 0.001$; *post hoc* Bonferroni comparisons: all $P < 0.001$). Females were lightest following the spring moult (Table 1). However, average female mass at the end of the moult was not significantly different than female mass at the end of the breeding season (Table 1; *post hoc* Bonferroni comparison: $P = 0.998$).

Males had greater TBE at all sampling times (Table 1), but as males are larger than females this was expected. Once the effect of body mass was accounted for, males and females showed significantly different seasonal patterns of energy storage and depletion, as

Table 2. Results of ANCOVA on total body energy of 135 adult males and females

Source of variation	d.f.	F	P
Body mass (covariate)	1	501.97	< 0.001
Sex	1	65.48	< 0.001
Season	4	6.00	< 0.001
Sex × season	4	2.48	0.047
Error	124		

indicated by a significant sex–season interaction (ANCOVA with body mass as the covariate, Table 2). Additionally, when corrected for differences in body mass, females had a higher energy content than males throughout the year (Fig. 3). By the beginning of the spring moult, females had increased their TBE by 27.5% relative to their end of breeding condition whereas males had lost a further 7.1% of TBE (Table 1, Fig. 3). Both sexes lost mass and body energy during the spring moult (Fig. 3), but females remained in significantly better condition than males, as measured by percentage body fat (Fig. 4; $P = 0.048$). By the mid-foraging period, there was no significant difference in the fat content of males and females (Fig. 4; $P = 0.629$). From the end of the moult to the beginning of the breeding season both males and females more than doubled their body energy stores (Table 1). However, males gained more TBE between the end of moulting and mid-foraging season, whereas females gained more TBE during the three months prior to parturition (Fig. 3). Both sexes lost body energy during the breeding period, with females losing more energy than males both in absolute (1775 MJ vs. 1280 MJ) and relative terms (50.7% vs. 28.7%).

Within the annual cycle, both the mass and energy gained during foraging roughly balanced that which was spent during periods of terrestrial fasting and

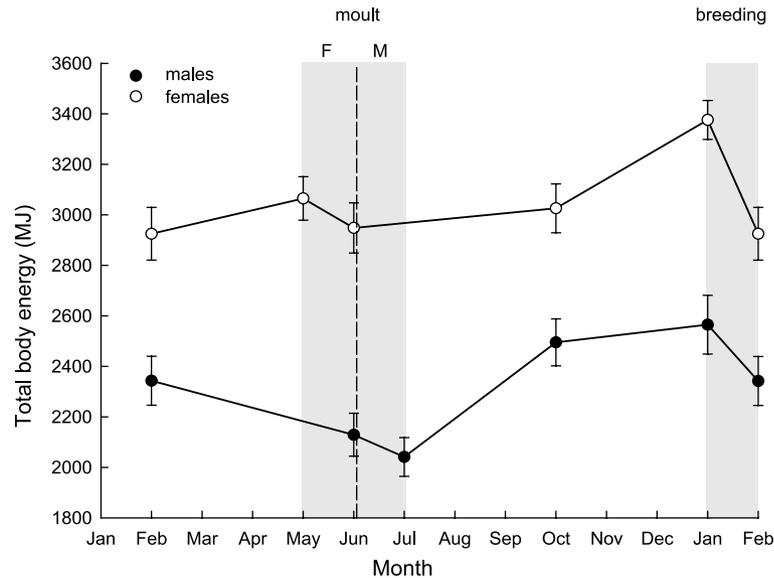


Fig. 3. Seasonal changes in total body energy in adult male and female grey seals. Values are means \pm SE corrected for the effect of body mass from an ANCOVA with body mass as the covariate. Sample sizes are given in Table 1. Shaded areas represent the two periods of terrestrial fasting. Note that females begin and end moult about a month earlier than males. The post-breeding sample is plotted twice to better illustrate the overall annual patterns.

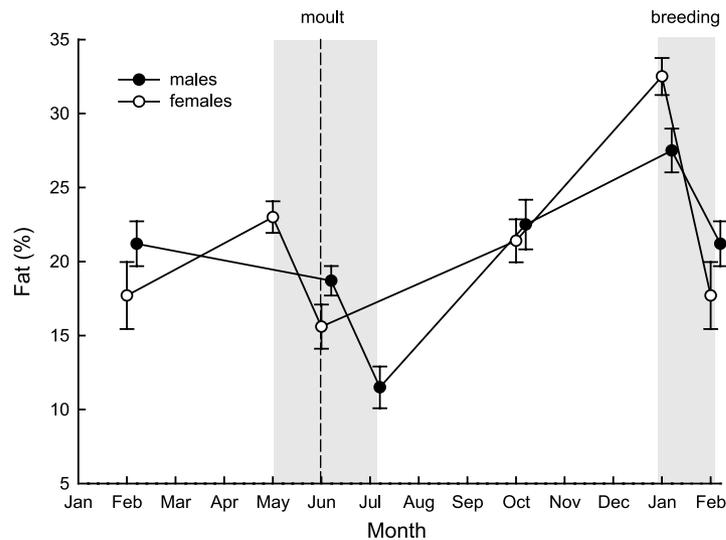


Fig. 4. Seasonal changes in percentage body fat in adult male and female grey seals (mean \pm SE). Male and female sampling times are offset to show error bars. Sample sizes are given in Table 1. Shaded areas represent the two periods of terrestrial fasting. Note that females begin and end moult about a month earlier than males. The post-breeding sample is plotted twice to better illustrate the overall annual patterns.

reproduction. However this balance occurred differently for males and females. Males accumulated energy only during the pre-breeding foraging period and continuously lost body energy from the start of the breeding season through the end of the moult, some 6 months later (Fig. 3). In contrast, females accumulated body energy during both the pre-moult and pre-breeding foraging periods and expended this energy during the moult and breeding seasons, respectively (Fig. 3). Thus females paid for each period of mass loss with a preceding period of energy storage, whereas males did not.

LONGITUDINAL CHANGES IN BODY MASS AND COMPOSITION

Longitudinal data were obtained from 73 individuals (35 males and 38 females). A total of 52 individuals were sampled prior to the start of the breeding (end of moult or mid-foraging) season and again at the start of breeding. Twenty-three of these individuals were sampled a third time at the end of the breeding season and an additional 21 individuals were sampled at the start and end of breeding, accounting for the sample size of 96 listed in Table 3. These longitudinal data

Table 3. Mean ± SE (CV) of rate of mass and energy change in adult grey seals studied longitudinally. See Table 4 for statistical results and Results for description of sample sizes

	Sex	Period of mass/energy change		
		End of moult to start of breeding	Mid-foraging to start of breeding	Start to end of breeding
Mass change (kg)	M	97 ± 5.3 (0.24)	65 ± 7.0 (0.33)	-52 ± 2.9 (0.24)
	F	75 ± 6.7 (0.35)	34 ± 7.0 (0.62)	-65 ± 1.5 (0.12)
Rate of mass change (kg day ⁻¹)	M	0.47 ± 0.03 (0.25)	0.76 ± 0.08 (0.33)	-2.45 ± 0.09 (0.16)
	F	0.34 ± 0.03 (0.34)	0.39 ± 0.08 (0.62)	-4.22 ± 0.10 (0.12)
Total body energy change (MJ)	M	2727 ± 172.9 (0.28)	1512 ± 212.9 (0.42)	-1285 ± 161.8 (0.55)
	F	2002 ± 191.2 (0.37)	1081 ± 181.7 (0.50)	-1724 ± 60.3 (0.18)
Rate of energy change (MJ/d)	M	13.1 ± 0.83 (0.27)	17.7 ± 2.50 (0.43)	-59.0 ± 6.54 (0.48)
	F	9.0 ± 0.82 (0.36)	12.5 ± 2.12 (0.51)	-114.9 ± 4.02 (0.17)
N	M	19	9	19
	F	15	9	25

complimented the cross-sectional analyses by allowing us to examine individual variability in mass and energy gain from the end of moult until the beginning of the breeding season.

The amount of mass gained from the end of moult to the beginning of the breeding season was quite variable among individuals with females exhibiting more variability than males (Table 3). However, this difference in variability of mass gain between males and females was not significant (Levene statistic = 0.016, d.f. = 1, 32; $P = 0.901$). The maximum and minimum gains for individuals over the 7-month pre-breeding period were 139 kg (70%) and 57 kg (28%) for males and 113 kg (86%) and 26 kg (13%) for females. Mass gain between mid-foraging period and the start of breeding tended to be more variable within sex compared to the variation in mass gain over the entire period (Table 3); however, this difference in variability by season was not significant for males (Levene statistic = 0.009, d.f. = 1, 26; $P = 0.925$) or females (Levene statistic = 0.273, d.f. = 1, 22; $P = 0.607$).

To examine the temporal pattern of mass and energy gain, we compared the rate of gain in animals sampled in the last 3-months of the pre-breeding foraging period to that of individuals studied over the entire 7-month period (Table 4). There was no significant correlation between body mass and the rate of mass gain for either time period ($P = 0.26$ and 0.19), therefore there was no need to use body mass as a covariate in this analysis. Rates of mass gain differed significantly between males and females and time periods, but there was also a significant sex–time period interaction (Table 4). Females gained mass at a relatively constant, but significantly lower rate than males throughout the pre-breeding foraging period (Table 3). Between post-moult and pre-breeding, males gained mass at a rate of 0.47 kg day⁻¹, however, rate of mass gain in the 3 months prior to breeding (0.76 kg day⁻¹) was significantly higher than the 7-month average. Mean energy gain during the 7-month foraging period was 2727 MJ

Table 4. Results of two-way ANOVA on longitudinal rates of mass and energy gain

Source of variation	d.f.	<i>F</i>	<i>P</i>
Rate of mass gain			
Sex	1	26.60	< 0.001
Time period (EM – SB or MF – SB)	1	12.06	< 0.001
Sex × time period	1	5.97	0.018
Error	48		
Rate of energy gain			
Sex	1	10.52	0.002
Time period	1	8.05	0.007
Sex × time period	1	0.13	0.724
Error	48		

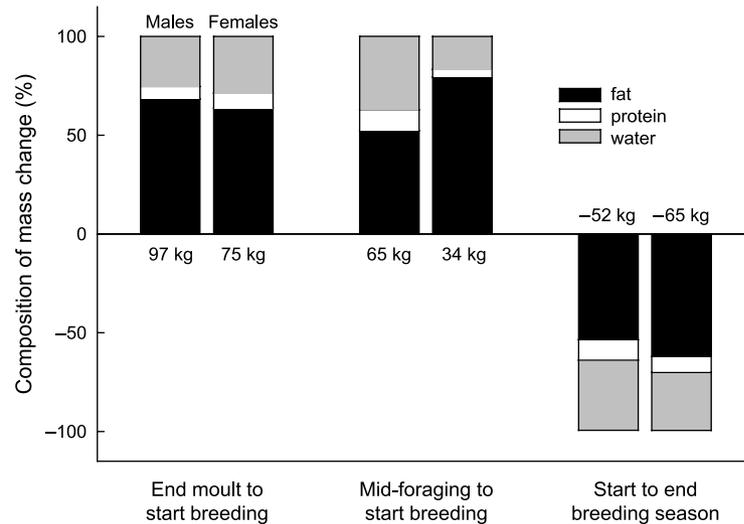
for males and 2002 MJ for females. Females had a significantly lower rate of energy gain than males during this period (Table 3), however, in both sexes, rate of energy gain during the three months prior to breeding was significantly higher than the 7-month average (Tables 3 and 4).

During the breeding season both absolute mass and energy loss were significantly higher in females than in males ($t_{42} = 3.79$, $P = 0.001$ and $t_{42} = 2.80$, $P = 0.008$, respectively; Table 3). Daily rate of mass loss was also significantly higher in females than in males ($t_{42} = 13.46$, $P < 0.001$) as was rate of energy expenditure ($t_{42} = 7.630$, $P < 0.001$) during the breeding season.

Composition of mass gained during the pre-breeding season also differed significant by sex (2-way ANOVA: $F_{1,48} = 5.66$, $P = 0.021$) and there was a significant sex–time period interaction ($F_{1,48} = 8.96$, $P = 0.004$). Over the entire 7-month foraging period the composition of mass gain did not differ significantly by sex (Table 5, Fig. 5), however, the composition of mass gained during the last 3-months prior to the breeding season did (Fig. 5). During this period, fat accounted for most of the mass gain by females, whereas body water and protein mass accounted for more of the gain by males

Table 5. Longitudinal estimates of the composition of seasonal mass change in male and female grey seals. Total mass change for each period is shown in Table 3. Sample size represents the number of animals sampled at the beginning and end of each period, also see Results

Composition of mass change	End of moult to start of breeding (7 months)		Mid-foraging to start of breeding (3 months)		Start to end of breeding (1 month)	
	Male	Female	Male	Female	Male	Female
TBW (%)	25.5 ± 3.79	28.4 ± 2.93	37.1 ± 3.60	16.6 ± 4.67	35.4 ± 4.63	29.2 ± 1.64
Protein (%)	6.3 ± 1.42	7.5 ± 1.05	10.7 ± 1.52	3.9 ± 1.34	10.4 ± 1.72	8.1 ± 0.79
Fat (%)	68.3 ± 5.17	63.0 ± 4.08	52.2 ± 5.51	79.0 ± 6.11	53.5 ± 6.77	62.1 ± 2.38
N	19	15	9	9	19	25

**Fig. 5.** Composition of mass change in adult male and female grey seals between key points in the annual cycle. Numbers represent the average change in mass within each sex and time period. Bars on the left and right represent male and female mass change, respectively.

(Table 5, Fig. 5). During the breeding season, fat accounted for 62% of mass loss in females compared to 54% in males. However this difference was not significant ($F_{1,42} = 1.9$, $P = 0.18$).

We were also interested in the balance between energy gain during foraging and loss during reproduction within individuals. Paired data from the end of moult through to the end of breeding was obtained for 9 males and 7 females. Among these individuals, the energy lost by females during reproduction was not significantly different than that gained over the 7-month foraging period (paired t -test: $t_6 = 0.88$, $P = 0.411$). In contrast, the energy lost by males during reproduction was significantly less than that gained over the entire pre-breeding foraging season (paired t -test: $t_8 = -7.06$, $P < 0.001$). Paired data from animals sampled at mid-foraging, start and end of breeding was available for only 3 males and 4 females, limiting statistical analysis. Nevertheless, the composition and magnitude of mass loss in males during the breeding season (i.e. 52 kg, 54% fat) was more similar to that gained during the 3-months prior to breeding (65 kg, 52% fat) than to that gained over the entire 7-month foraging period (Fig. 5, Table 5). In contrast, female mass loss during the

breeding season (i.e. 65 kg, 62% fat) was approximately double that gained in the 3 months prior to breeding (34 kg) and more similar in both magnitude (75 kg) and composition (63% fat) to that gained over the entire 7-month foraging period (Fig. 5).

Discussion

The manner in which an individual allocates energy between survival and reproduction depends on the animal's current condition, the energetic demand of reproduction and the time until reproduction (McNamara, Merad & Houston 1991). Individuals are expected to employ the strategy that maximizes their lifetime reproductive success and hence fitness. In this paper, we demonstrate that males and females in a capital-breeding carnivore differ in their patterns of seasonal body mass, energy storage and expenditure during both reproduction and moulting. Females store body energy before both periods of terrestrial mass loss, thus paying the energetic costs of these expenditures before they occur. By contrast, males only accumulate body energy during the pre-breeding foraging period, which is then spent during breeding and the post-breeding period

through to the end of the moult, a period of approximately 6 months. The male pattern is inherently more risky than that used by females as energy storage occurs at only one time of year. We suggest that this difference reflects the earlier reproductive costs in females and differences in the sex-specific trade-off between the benefit of stored body energy for reproduction and the cost of mass and energy storage over long periods.

Given the critical role of stored energy in female reproductive success, females should reduce uncertainty in future reproductive success by accumulating body energy as soon as possible. Maternal condition has an important influence on early foetal development in grey seals, with females in poorer condition implanting later than females in better condition (Boyd 1984). Thus, females ought to recover body condition quickly following the breeding season to ensure successful implantation. Consistent with this prediction, females increased their total body energy by 27.5% from the end of the breeding season to the beginning of the moult. In contrast, although males maintained body mass during the post-breeding to pre-moulting foraging period (Fig. 2), they continued to lose body energy (Fig. 3) while increasing the proportion of lean body tissue. This may reflect the need for males to replace lean body mass lost during the breeding season and the lack of early reproductive costs. This also implies that subsequent reproductive success in males is relatively insensitive to energy stores during the pre-moult foraging period. Sex-differences in the seasonal pattern of diving (and hence foraging) behaviour of adult grey seals in this population are consistent with this interpretation, with females exhibiting a high level of dive effort immediately following the moult compared to a more gradual increase in dive effort by males (Beck 2002).

Our observation that the amounts of mass gain and energy stored during the pre-breeding foraging period appears to balance that which is spent during reproduction further suggests that there must be both costs and benefits to storing body mass and energy as found in other taxa (Witter & Cuthill 1993; Jönsson 1997; Bonnet, Bradshaw & Shine 1998). The differing seasonal patterns of energy storage and expenditure in male and female grey seals suggest that each sex has a different solution to this trade-off, reflecting different fitness-maximizing strategies (Trivers 1972; Jormalainen *et al.* 2001). Based on our longitudinal study, both the amount and composition of mass spent by females during lactation was similar to that gained over the entire 7-month, pre-breeding foraging period (Fig. 5). These results suggest that females are willing to pay the costs of long-term storage of body mass and energy for reproduction because the risk of storing insufficient energy is more critical to successful pregnancy and weaning of offspring. The higher energy content in females throughout the year (Fig. 3) may be another reflection of this. The cross-sectional data (Fig. 2) suggest that females gain a greater proportion of the mass stored prior to reproduction during the last three

months of the pre-breeding season than was indicated by the longitudinal data (Fig. 5). This apparent inconsistency presumably results from the small longitudinal sample used to estimate mass gain, as the cross-sectional and longitudinal estimates are consistent at other sampling points. Nevertheless, females accumulate the mass and energy used during lactation over the entire pre-breeding foraging period. In contrast, the magnitude and composition of body mass expended by males during the breeding season was similar to that gained in only the last 3-months of this foraging period (Fig. 5). This result is also evident in both the longitudinal and cross-sectional analysis (Fig. 5 and Table 1). Since reproductive success in grey seal males is not so tightly linked to stored body mass and energy (Anderson & Fedak 1987; Godsell 1991; Lidgard *et al.* 2001), males may not benefit from early storage to the same degree as females, such that the costs associated with long-term storage are not worth supporting until the 3 months prior to breeding.

The costs of long-term mass and energy storage in pinnipeds are unclear. As in other taxa, these costs could include an increased risk of predation, decreased mobility and increased metabolic costs associated with maintaining and transporting additional body mass (Witter & Cuthill 1993; Gosler *et al.* 1995; Gentle & Gosler 2000). Recent studies indicate that marine mammals employ sophisticated patterns of swim and glide to reduce the energetic cost of diving (Williams *et al.* 2000). Changes in buoyancy associated with energy storage decrease rates of descent during diving, thereby increasing both the time and potentially the cost of foraging (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 significant given that a grey seal will make more than 60 000 dives in the course of a year (Beck 2002). Understanding the costs associated with long-term storage and maintenance of body mass for reproduction would improve our understanding of the different seasonal patterns of fat and protein storage in pinnipeds and other mammals, as well as elucidate how each sex balances the costs and benefits of storing energy for reproduction.

Sex differences in the seasonal patterns of change in body mass or fat content also have been found in herbivores. Hewison *et al.* (1996) found that female roe deer, *Capreolus capreolus*, recovered from the reproductive period earlier than males. Early recovery of body condition in females has been shown to increase the probability of subsequent pregnancy in several ungulate species (Mitchell, McCowen & Nicholson 1976; Thomas 1982; White *et al.* 1997). In contrast, male roe deer continue to lose body condition for several months after the rutting period. As in our study, this suggests that subsequent reproductive success in males is less dependent on body condition at this time of year and therefore males delay increasing body mass in order to forgo the associated costs of carrying and maintaining extra body mass. Muskrats, *Ondatra zibethicus*,

also show asynchronous patterns of seasonal changes in fat mass with females increasing fat mass earlier following the breeding season than males (Virgl & Messier 1992).

We have interpreted our findings in the context of sex-specific differences in costs and benefits of energy storage for reproduction. However, the different seasonal patterns of energy storage in grey seals might result from differences in the ecology (i.e. diet and prey availability) of males and females in this population. Among herbivore species, seasonal changes in body mass and composition are known to generally coincide with the seasonal changes in food availability (Adamczewski *et al.* 1987; Worden & Pekins 1995; Chan-McLeod *et al.* 1999) and sex-specific patterns of body mass or fat content may reflect sex differences in diet composition. We believe there are several reasons why such ecological explanations are unlikely to account for our results. First, data from satellite tags and geolocation time-depth recorders show that there is a broad overlap in the at-sea distribution of adult male and female grey seals in this study population during the pre-breeding period (Beck 2002). Second, the depths of dives used by both sexes during foraging are similar (mean difference of 8 m; Beck 2002), suggesting that males and females are generally using the same type of habitat to make their living. Finally, based on an analysis of fatty acid signatures from blubber biopsies, there is a substantial overlap in the diet composition of adult males and females in this population (Beck 2002). As a result, males and females should be affected by the same seasonal changes in environmental conditions and prey availability. The variance in TBE of males and females also supports our conclusion that ecological factors are unlikely to account for our findings. If males and females are influenced differently by environmental stochasticity, we might expect the sex that is most affected to show a higher degree of variability among individuals. However, the coefficient of variance (CV) of total body energy of males and females is similar in both the cross-sectional and longitudinal data, which suggests that males and females are similarly effected by environmental variability.

If our interpretation is correct, we would expect to find similar sex-specific patterns of energy storage and expenditure in other pinniped species, particularly among other capital breeders. Although body mass and condition have been examined in several other phocid species (e.g. Pitcher 1986; Deutsch, Haley & Le Boeuf 1990; Ryg, Smith & Oritsland 1990), we were unable to find comparable annual data to that presented here. In our study, males and females were sampled explicitly at the beginning and end points of key events in the annual cycle (breeding and moulting) and mid-way through the pre-breeding foraging period. In other studies, samples were taken on a monthly basis without specific reference to moult or lactation stage (Chabot, Stenson & Cadigan 1996), did not sample all key times throughout the annual cycle (e.g. Ryg *et al.*

1990; Worthy *et al.* 1992), or investigated only one sex (Carlini *et al.* 1999). Nevertheless, like grey seals, female elephant seals, *Mirounga angustirostris* and *M. leonine*, appear to gain mass after both periods of terrestrial fasting (Boyd, Arnbohm & Fedak 1993; Carlini *et al.* 1999; Le Boeuf *et al.* 2000). Male northern elephant seals also appeared to gain mass after both periods of terrestrial fasting, although only two males were studied over the post-moult period (Le Boeuf *et al.* 2000). Ryg *et al.* (1990) and Chabot *et al.* (1996) examined changes in body mass in various age-sex groups in ringed seals, *Phoca hispida*, and harp seals, *Phoca groenlandica*, respectively. While not directly comparable to the present study, both studies found sex-specific seasonal changes in carcass mass among adults, but not in immature animals. Juveniles do not have reproductive costs and so would not be expected to show sex-specific seasonal patterns. Similar studies on terrestrial carnivores have not found differences in the seasonal patterns of body condition in males and females (*Canis latrans*, Poulle *et al.* 1995; *Alopex lagopus*, Prestrud & Nilssen 1992; *Martes americana*, Buskirk & Harlow 1989). However, these terrestrial carnivore species are income breeders, acquiring the energy used for reproduction at the time it is required (Jönsson 1997). As individuals are not relying on stored body energy for reproduction, we would not expect to see marked sex-specific seasonal patterns in energy storage. Both this and the data on juveniles lend support to our hypothesis that seasonal patterns of energy storage and expenditure by male and female grey seals are likely to reflect differences in the costs and benefits of energy storage for reproduction.

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