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The Energetics of Male Reproduction in an Aquatically Mating Pinniped, the Harbour Seal

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ABSTRACT

The energy expenditure of breeding male harbour seals, *Phoca vitulina*, on Sable Island, Nova Scotia, was investigated by measuring changes in body mass, body composition, and water flux using isotope dilution. Seals lost 0.47% ± 0.04% ($n = 34$) of their initial mass per day during the breeding season (4 wk), and fat, water, and protein accounted for 64.3% ± 4.8%, 27.8% ± 3.3%, and 6.9% ± 1.4% of this mass loss, respectively ($n = 31$). Total energy expenditure was estimated as 33.3 ± 1.9 MJ d^{-1}, or 3.9 ± 0.2 W kg^{-1} ($n = 17$), similar to rates measured in terrestrially mating pinniped species. However, unlike terrestrially mating pinnipeds, male harbour seals did not fast during the breeding season, and energy intake from foraging accounted for 61.8% ± 4.0% of the total energy expended. Males derived most of their expended energy from food intake early in the breeding season. However, as oestrus females became increasingly available, reduced rates of food intake in males were coupled with increased rates of total energy expenditure. Larger males expended significantly more energy from body stores and more total energy than smaller males. Male harbour seals appeared to balance the energetic costs of reproduction against the constraints of small body size by foraging during

deep-diving trips before the appearance of oestrus females and by opportunistic feeding throughout the breeding season while at sea. We suggest that size dimorphism may be less pronounced in aquatically mating pinnipeds partly because the temporal and spatial separation of foraging and reproduction is less distinct than it is for terrestrially breeding pinnipeds.

Introduction

Studies of the energetics of reproduction in pinnipeds (seals, fur seals, and sea lions) have traditionally focused on females (Fedak and Anderson 1982; Costa and Gentry 1986; Costa et al. 1986, 1989; Bowen et al. 1992; Iverson et al. 1993; Oftedal et al. 1993). Fewer studies have investigated the energetic costs of reproduction in male pinnipeds, and most of these studies have been conducted on polygynous, terrestrially mating species such as grey seals (*Halichoerus grypus;* Anderson and Fedak 1985; Tinker et al. 1995), northern elephant seals (*Mirounga angustirostris;* Deutsch et al. 1990), and Antarctic fur seals (*Arctocephalus gazella;* Boyd and Duck 1991). Males in terrestrially mating species generally fast as they remain onshore throughout the breeding season. Consequently, their energetic investment in reproduction can be measured indirectly by monitoring mass loss (Anderson and Fedak 1985; Deutsch et al. 1990; Tinker et al. 1995) and more accurately by estimating changes in body composition and water flux using isotope dilution (Boyd and Duck 1991). Since male pinnipeds provide no parental care, their reproductive effort is directed solely towards procuring mates (Trivers 1972). Some of these studies have demonstrated a positive correlation between the energetic investment in reproduction and mating success, based on observed copulations (Anderson and Fedak 1985; Deutsch et al. 1990; Tinker et al. 1995).

Few studies have addressed the energetic costs of reproduction for males in aquatically mating pinniped species. Most species of the family Phocidae (the true seals) mate aquatically (Stirling 1983; Le Boeuf 1991); hence, this represents a major gap in our understanding of the energetics of male reproduction among pinnipeds. Since most aquatically mating seal species are relatively small bodied and less size dimorphic than terrestrially mating pinnipeds (Stirling 1983), they generally have smaller absolute energy stores to draw on during the mating season and thus are more limited in their ability to fast

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than are larger terrestrial species (Lindstedt and Boyce 1985). Energetics may therefore play an important role in limiting male reproductive behaviour and shaping the forms of the mating systems exhibited by aquatically copulating pinnipeds. For most species, data on energetics and activity during the breeding season are difficult or impossible to obtain, since males spend a great deal of time in the water where they cannot be directly observed. Also, they are often difficult to recapture, so that the necessary longitudinal measurements of changes in body mass, composition, and water flux have been limited to a few individuals (Reilly and Fedak 1991).

Harbour seals mate in the water, and previous studies monitoring longitudinal changes in mass and circulating chylomicrons (Walker and Bowen 1993b), diving behaviour (Coltman et al. 1997), and locations at sea (Van Parijs et al. 1997) have shown that males reduce feeding during the breeding season. In previous studies (Walker and Bowen 1993b; Coltman et al. 1997), we found that male harbour seals lose mass at a greater rate during the latter portion of the breeding season, when they engage in shallow-diving activity associated with mating, whereas they tend to maintain their mass by foraging during periods of extended deep diving earlier in the breeding season. Male harbour seals thus appear to make a trade-off between time spent foraging and time spent competing for mates while at sea. However, without knowledge of changes in body composition and water flux, changes in body mass provide only minimum estimates of energy expenditure and the extent to which animals are feeding.

The purpose of our study was to quantify changes in body composition and water flux of male harbour seals during the breeding season, using hydrogen isotope dilution, in relation to their activity patterns while at sea. Changes in body mass and body composition provide an accurate assessment of the net energy invested in reproductive effort from initial body stores, and water flux enables an estimate of food intake (FI) during the period of study. Taken together, data on changes in mass, body composition, and water flux can be used to describe the total energy expended (TEE) during the breeding season. We also examined the importance of initial body size and body composition, which reflect the amount of stored energy an individual possessed at the beginning of the breeding season, as factors influencing the reproductive behaviour of male harbour seals.

Material and Methods

Study Site and Animals

The study was conducted during the breeding seasons (mid-May to the end of June) of 1992, 1993, and 1994 on the north beach of Sable Island (43°55′ N; 60°00′ W), a partially vegetated 40-km-long sandbar 160 km east of Nova Scotia. Between 300 and 500 harbour seal females gave birth on Sable Island during each year of the study.

Male harbour seals were captured, individually marked, and weighed as described by Walker and Bowen (1993a, 1993b) near the beginning of each breeding season (range, May 20–30 in each year). Twelve (1992, 1993) or 13 (1994) males were selected for deuterium oxide (D_2O) dilution studies in each season. We designed our study such that our sample represented a broad range of initial body masses (previously reported for adult male harbour seals in this population from 85 to 130 kg; Godsell 1988; Walker and Bowen 1993a, 1993b). We repeated isotope administration near the end of the breeding season (June 15–30) to estimate the total change in body composition. All males in 1993 and 1994 were also recaptured twice at 7–10-d intervals between the initial and final equilibration to monitor changes in the rate of mass loss. We administered sufficient isotope to a subset of these animals ($n = 12$ in 1993; $n = 6$ in 1994) at the initial equilibration to monitor the changes in D_2O concentration throughout the breeding season. A blood sample was taken from these "water-flux" animals during every recapture.

In 1993 and 1994, the first isotope administration and first recapture occurred before the appearance of weaned pups in the colony, while the second and the third recaptures (final isotope administration) occurred following the appearance of weaned pups. Since harbour seals are believed to mate near the time of weaning (Boulva and McLaren 1979; Thompson 1988), we divided the breeding season into a premating period and a mating period. On Sable Island, the first pups were born on May 15, May 13, and May 14 in 1992, 1993, and 1994, respectively. Assuming a mean lactation duration of 24 d (Muelbert and Bowen 1993), oestrus females would have become increasingly numerous after about June 8 in each year (i.e., the median expected date of the appearance of the first weaned pup). We used this date to divide the breeding season into the premating and mating periods. Changes in body mass, composition, and rates of water flux calculated between the first two measurements are referred to as having occurred during the premating period, and those between the last two measurements as having occurred during the mating period.

As part of a concurrent study of diving behaviour described elsewhere (Coltman et al. 1997), each male was also fitted with a Mk3+ time-depth recorder (256K memory, Wildlife Computers, Woodinville, Wash.) at the time of initial isotope administration. We use data describing the proportion of time males spent making deep (to depth > 20 m) and shallow (20 m or less) dives reported in Coltman et al. (1997) to investigate links between FI, gross energy balance, and the activity of individual males while at sea.

Isotope Administration and Analysis

Once secured in nets, seals were sedated with Diazepam (ca. 0.2 mg kg^{-1} body mass) to minimise stress during handling

and isotope administration. A preweighed quantity of D_2O (99.8% purity, Stable Isotopes Division, ICN Biochemicals, Cambridge, Mass.) was administered by syringe with a number 12 French gastric tube, at a dose of approximately 0.6 g kg^{-1} body mass for determining only body composition, or at 2 g kg^{-1} body mass to animals that were in the water-flux study. Syringe and tube were flushed twice with 5-mL quantities of distilled water, followed by 50 mL of air, to ensure complete isotope delivery. Males were held in pens for 2.5–4 h after isotope administration to allow equilibration. Seals were then bled twice from the extradural vein, with 30-min intervals between bleedings to determine whether equilibration of the isotope had occurred. Blood samples were also taken during recaptures of water-flux-study animals to measure D_2O remaining in the animal, and a single blood sample was taken from each animal before the final administration of isotope to determine residual D_2O concentration.

Blood samples (8 cm^3) were collected without anticoagulants and centrifuged to separate sera within 24 h of collection. Sera were transferred to cryovials and stored at −20°C before heat distillation and assay for D_2O concentration with infrared spectrophotometry following the method of Oftedal and Iverson (1987).

Estimation of Body Composition and Water Flux

All concentrations of D_2O were corrected by subtracting the natural background concentration of D_2O found in male harbour seals on Sable Island (0.011% ± 0.001%, $n = 6$). We considered an animal to have equilibrated the administered isotope if the concentration of D_2O in the second sample did not exceed the first by more than 0.01%. At equilibration, body water pool was then estimated as: body water pool (kg) = $M_d/(10S_d)$, where M_d is the amount of D_2O administered (g) and S_d is the average percentage of D_2O at equilibration. Since the dilution space of D_2O has been found to overestimate total body water (TBW), we corrected body water pool by 2.8% to estimate TBW (Reilly and Fedak 1990). Given that data are not available for harbour seals, body composition was calculated from TBW and total body mass (TM) using regression equations derived by Reilly and Fedak (1990) for grey seals to give total body fat (TBF), total body protein (TBP), and total body energy (TBE). The equations used were: TBE (MJ) = (40.8TM) − (48.5TBW) − 0.4, %TBP = (0.42 × %TBW) − 4.75, and %TBF = 105.1 − (1.465 × %TBW), where %TBP, %TBW, and %TBF are total body protein, total body water, and total body fat, respectively, each calculated as a percentage of total body mass.

We calculated the fractional daily water flux from changes in D_2O concentration over time (Fig. 1) using calculations described by Oftedal and Iverson (1987). The concentration of D_2O in a given sample was corrected for changes in pool
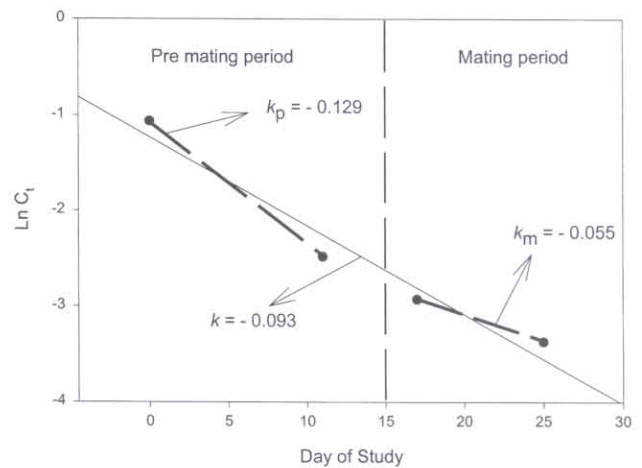

Figure 1. Changes in the concentration of D_2O (C_t) corrected for changes in TBW over time in a single male harbour seal during the breeding season. Fractional rate of water flux (k) for the entire season is estimated by the slope of the line fit to all four data points. The fractional rates of water flux during the premating (k_p) and mating periods (k_m) are estimated from the rate of change in D_2O concentration between the first two measurements, and between the third and the final measurements, respectively. The vertical dashed line marks the separation of the premating and mating periods of the breeding season.

size by assuming that changes in TBW were linear during the study period, to give a concentration of D_2O corrected for the change in TBW at time t. Regression of the natural logarithm of the corrected D_2O concentration over time gave an estimate of fractional daily water flux over the entire breeding season (Fig. 1). To determine whether fractional daily water flux changed as the breeding season progressed, independent two-point estimates were also made for the premating period (the rate of change between the initial equilibration and the first recapture) and for the mating period (the rate of change between the third and the final recapture; Fig. 1).

Estimates of total daily water flux for the entire breeding season (TWF) and the premating and mating periods were made for each seal from the appropriate fractional daily water flux and the mean daily change in TBW (ΔTBW) as: TWF = k TBW$_{1/2}$ + ΔTBW, here TBW$_{1/2}$ represents the estimated TBW at the midpoint of the period in question and k is the fractional daily water flux.

Estimation of FI and Gross Energy Expended

We estimated the rate of FI for males from TWF assuming the following relationship (Oftedal and Iverson 1987):

$$FI = \frac{100 \times [TWF + (1.071\ \Delta F) + (0.396\ \Delta P)]}{\%W_{food} + ME \times [(1.071\ \%F_{food}) + (0.396\ \%P_{food})]},$$

where ΔF is the daily change in body fat content, ΔP is the

daily change in body protein content, $\%W_{food}$ is the percent water content of food, ME is metabolization efficiency, $\%F_{food}$ is the percent fat content of food, and $\%P_{food}$ is the percent protein content of food. We assumed a diet of sandlance (*Ammodytes* sp.), the major prey at this time of year (Walker and Bowen 1993*b*; W. D. Bowen, unpublished data), which is composed of 78.44% H_2O, 5.14% fat, and 15.47% protein (S. J. Iverson, unpublished data). Based on published estimates of metabolization efficiency of grey and harp seals fed herring that range from 82.7% to 88.7% of food-energy content (Keiver et al. 1984; Ronald et al. 1984; Worthy 1990), we assumed metabolization efficiency to be 85%. FI was then converted to total food energy ingested (FEI) as 85% of FI at 39.3 kJ g^{-1} fat and 23.6 kJ g^{-1} protein (Schmidt-Nielson 1979). TEE was then calculated as the sum of the negative change in daily body energy (ΔTBE) plus FEI: TEE = $-\Delta$TBE + FEI. We calculated the daily TEE for the entire breeding season using the change in daily body energy and food water intake, and also for both the premating and mating periods using the independently derived two-point estimates of total water intake and changes in TBE for the respective periods.

Data Analysis

All data are presented as the mean plus or minus one standard error. The probability of type I error was set at $\alpha = 0.05$ for all statistical tests. Before statistical tests, all data were checked for normality and transformed if necessary. Arcsine square-root transformation was used on proportions before statistical testing, but regression equations and means are presented for the untransformed data. ANCOVA models were used to account for body size effects when testing hypotheses using energetic variables. Initial mass was used as a covariate. To examine the influence of body size on reproductive energetics, we divided our sample into two groups based on body mass. Males with initial mass greater than the median were considered large, and males equal to or less than the median were classified as small. Regression analyses involving energetic parameters that may scale allometrically, such as relations between morphometric variables, were fitted using a reduced major axis regression model to account for measurement error in both variates (Rayner 1985). Statistical analyses were performed with Minitab for Windows (version 10, Minitab Inc.), except for repeated measures ANOVA models, which were tested in SPSS (version 6.13, SPSS Inc.).

Results

Changes in Body Mass and Composition

Initial TBW could not be calculated for two of the 37 study animals (one in 1992, one in 1993), since the isotope was not equilibrated. One of these seals was a subject in the water-flux study and was omitted from those analyses. We obtained four captures on all other water-flux-study animals ($n = 17$). Final equilibrations were not performed on three males in 1992 and on one male in 1994. In total, we obtained mass change data from 34 individuals, body composition change data from 31 individuals, and water-flux data from 17 individual males (Table 1). Time-depth records were recovered from 30 animals, 14 of which were in the water-flux study.

TBW was strongly correlated with mass at both the initial and final equilibrations (Fig. 2). Following standardisation of both variates to a mean of zero and standard deviation of one, the 95% confidence interval of the slope estimated by reduced major axis regression included one (95% confidence interval = [0.81, 1.235] and [0.679, 1.48] for initial and final equilibrations, respectively). Body composition was therefore independent of body mass. ANCOVA indicated that there were significant differences in both initial and final TBW between years after the influence of body size was accounted for (initial or final mass included as covariate, $F_{2, 31} = 10.01$ and $F_{2, 27} = 4.39$; $P < 0.05$ for both). Males in the 1993 sample had significantly higher average percent fat and lower protein content than in the 1992 or 1994 samples (Table 1) at the beginning of the breeding season. This difference can be partly attributed to the influence of the two largest males; however, several other animals in the 1993 sample also had low TBW content relative to their initial mass (Fig. 2). There were no significant differences in initial percent fat or protein body composition between years if the data from the two largest animals were removed (one-factor ANOVA, $F_{2, 30} = 2.18$, $P = 0.13$ and $F_{2, 30} = 2.19$, $P = 0.13$, respectively). Neither average initial mass nor initial TBE varied significantly between years (one-factor ANOVA, $F_{2, 32} = 1.15$, $P = 0.33$ and $F_{2, 32} = 0.91$, $P = 0.41$, respectively).

Final equilibrations were performed significantly later in each successive season (22.4 ± 0.2, 27.6 ± 3.3, and 33.8 ± 0.7 d after the initial equilibration in 1992, 1993, and 1994, respectively; one-factor ANOVA, $F_{2, 31} = 29.8$; $P < 0.001$); thus, final body mass and composition data were not statistically compared between years. Males sampled in 1994 had higher TBW content relative to their body mass at the final equilibration, and therefore lower percentage fat content (Table 1), but final equilibrations occurred later in the season in 1994 than in previous years; thus, this is not surprising. Rates of change in mass, fat, protein, and TBE did not differ significantly between years; therefore, data from all years were pooled for all subsequent analyses.

Initial masses ranged from 85.0 to 131.5 kg. Initial fat and protein content ranged from 14.1% to 32.9% and 15.9% to 21.3%, respectively. Fat content was more variable than was protein (coefficient of variation [CV] = 15.7% vs. 5.7% for fat and protein, respectively). Initial TBE ranged from 1,022 to 2,233 MJ and was more variable than was initial mass (CV

Table 1: Changes in mass, body composition, and total body energy of male harbour seals during the breeding season

	Initial Measurement		Final Measurement		Rate of change (d^{-1})	
n:						
1992	11		8 (11 for mass)			
1993	11		11			
1994	13		12			
Total	35		31 (34 for mass)			
Mass (kg):						
1992	111.1 ±	1.7	102.3 ±	1.8	−.36 ±	.07
1993	105.0 ±	4.4	92.0 ±	3.9	−.45 ±	.07
1994	106.7 ±	2.2	89.5 ±	1.8	−.53 ±	.08
Mean	107.5 ±	1.7	94.7 ±	1.8	−.47 ±	.04[a]
Fat (%):						
1992	22.9 ±	.9	20.0 ±	2.0	−.16 ±	.06
1993	26.1 ±	1.2	20.4 ±	1.7	−.20 ±	.05
1994	22.1 ±	.9	13.2 ±	1.7	−.26 ±	.05
Mean	23.6 ±	.6[b]	17.5 ±	1.2	−.21 ±	.03[a]
Protein (%):						
1992	18.7 ±	.2	19.6 ±	.6	+.05 ±	.02
1993	17.8 ±	.3	19.4 ±	.5	+.06 ±	.01
1994	19.0 ±	.3	21.5 ±	.5	+.08 ±	.01
Mean	18.5 ±	.2[b]	20.3 ±	.3	+.06 ±	.01[a]
Total body energy (MJ):						
1992	1,518 ±	27	1,305 ±	78	−10.6 ±	3.1
1993	1,559 ±	103	1,193 ±	93	−13.0 ±	2.4
1994	1,435 ±	54	944 ±	66	−14.8 ±	2.4
Mean	1,500 ±	39	1,126 ±	53	−13.1 ±	1.5[a]

Note. Final measurements were made 22.4 ± 0.2, 27.6 ± 3.3, and 33.8 ± .7 d after the initial measurement in 1992, 1993, and 1949, respectively.

[a] Indicates rate of change significantly different from zero (one-sample t-test; $P < .001$ for all).

[b] Indicates significantly difference between years (one-factor ANOVA; df 2, 32; $P < .05$).

= 15.3% vs. 9.3%). The heaviest animal had the highest TBE content (2,233 MJ). Rates of mass loss varied greatly among males, ranging between 0 and 1.0 kg d^{-1} (CV = 50.6%), with a maximum rate relative to initial body mass of 0.90% d^{-1}. Males lost up to 33.5 kg over the entire breeding season, and the maximum percent of initial mass lost was 28.8% by a male in the 1994 sample over 32 d. Changes in TBE were even more variable, ranging from −28.3 to +4.2 MJ d^{-1} (CV = 59.4%). Changes in TBE were correlated with initial body mass ($r = -0.589$, $P = 0.003$). One individual in the 1992 sample gained TBE during the study period (4.2 MJ d^{-1}) and maintained constant mass; however, all others were in negative net-energy balance during the study period. Fat, protein, and water accounted for 64.3% ± 4.8%, 6.9% ± 1.4%, and 27.8% ± 3.3% of mass loss, respectively ($n = 31$). Assuming an energy density of 39.3 MJ kg^{-1} for the energy content of fat, fat catabolism

accounted for 89.4% ± 3.4% of the change in TBE. Expressed in relative terms, male harbour seals lost on average 0.41% ± 0.04% of their initial body mass per day over the entire breeding season.

The rate of change in TBE was closely correlated with daily percent mass change (Fig. 3; daily change in TBE = 2.15 + 35.3 × [rate of % mass change]). If we assumed that a harbour seal losing 1.0% of its initial mass per day was fasting, implying that all energy expended came from the catabolism of stored energy, then the field metabolic rate could be estimated as 33.2 MJ d^{-1} from this relationship (Fig. 3). Fasting juvenile harbour seals and other breeding adult male pinnipeds of similar body size lose mass at approximately 1.0% d^{-1}: harbour seals, 1.06% d^{-1} (Markussen and Ryg 1992); male grey seals, 0.97% d^{-1} (Anderson and Fedak 1985) and 0.92% d^{-1} (Tinker et al. 1995); male Antarctic fur seals, 0.81% d^{-1} (Boyd and Duck 1991).
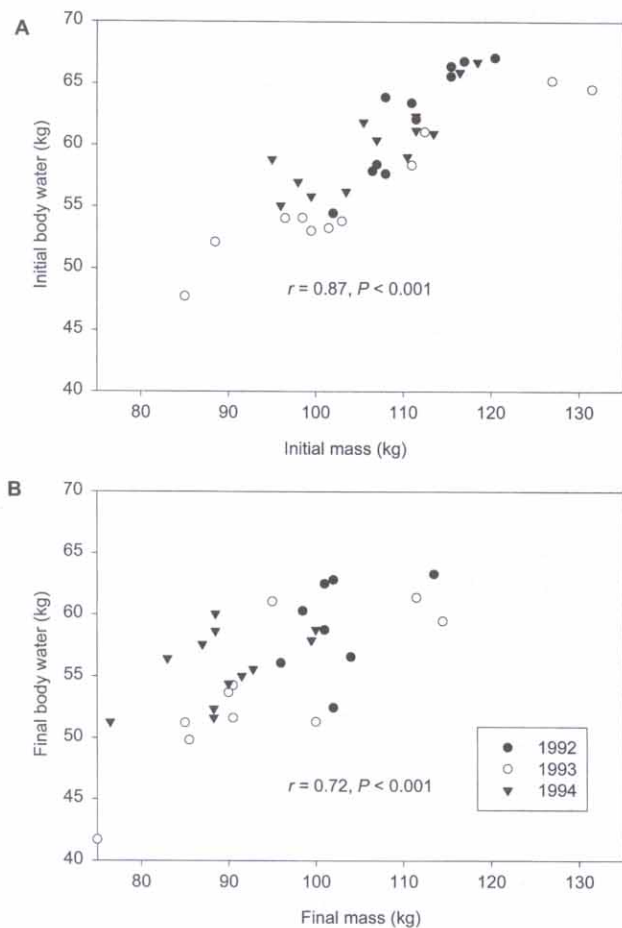
Figure 2. TBW estimated from D_2O dilution of male harbour seals at the beginning of the breeding season versus initial body mass (A) and at the end of the breeding season versus final body mass (B).

Figure 3. The rate of change in TBE (ΔTBE) as a function of the percent rate of mass change during the breeding season. Field metabolic rate can be estimated from the -1.0% mass-change intercept (33.2 MJ d^{-1}), assuming that a male losing 1.0% mass per day would be fasting. Zero intercepts are shown as dotted lines.

daily change in TBE, water flux, FEI, and TEE between the premating and mating periods of the breeding season (Table 3). Males lost on average 5.3 times as much mass and TBE per day during the mating period as they did in the premating period. TWF was significantly higher during the premating period than during the mating period, which suggests that the males were feeding more intensely before most females became sexually receptive. We estimate that the FEI accounted for more than three-quarters of TEE during the premating period, whereas it accounted for less than one-half of TEE during the mating period. Males had a significantly higher mean rate of

Water Flux, Activity, and Total Energy Balance

The daily change in TBE was positively correlated with deep-diving effort (Fig. 4) and negatively correlated with shallow-diving effort ($r = -0.346$, data not shown). Following arcsine square-root transformation of deep and shallow-dive effort, only the relationship between daily change in TBE and deep-dive effort was statistically significant ($F_{1, 25} = 10.7$; $P = 0.003$), indicating that males that spent relatively more time diving deeply lost less TBE over the breeding season.

Estimates of FEI ranged between 12.2 and 30.2 MJ d^{-1} (CV $= 23.6\%$), giving a mean TEE of 33.3 ± 1.9 MJ d^{-1} (Table 2). TEE ranged between 19.2 and 51.2 MJ d^{-1} (CV $= 23.7\%$). FEI was not related to initial body mass ($r = -0.10$, $P > 0.05$, $n = 17$), but initial mass and TEE were positively correlated ($r = 0.49$, $P = 0.045$, $n = 17$). Expressed in terms of mass-specific power, the average TEE was 3.9 ± 0.2 W kg^{-1} (calculated from the arithmetic mean mass of the water-flux-study animals).

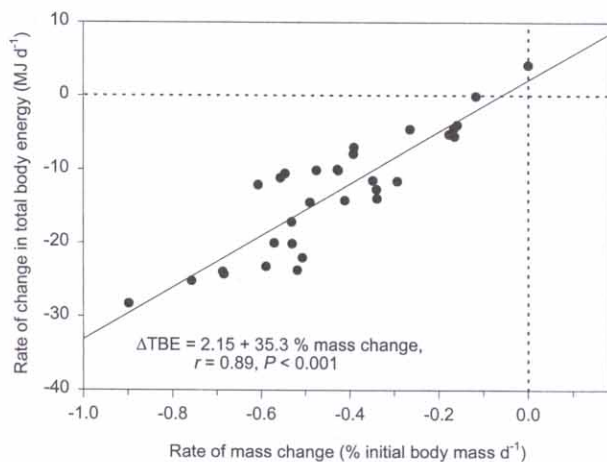There were clear differences in the rates of mass change,
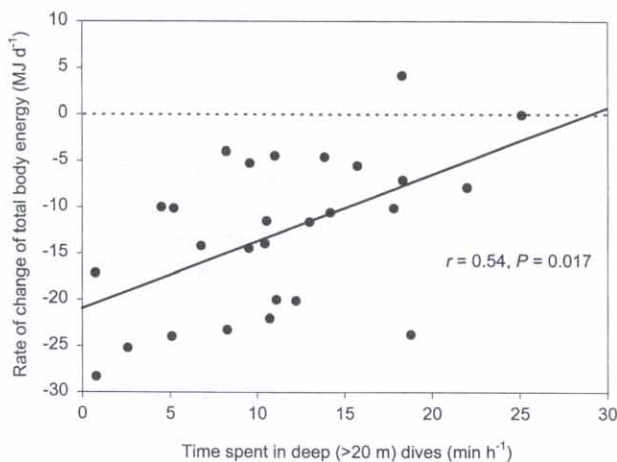

Figure 4. Variation in the rate of change of TBE in relation to deep-diving activity of male harbour seals during the breeding season. The zero change in TBE intercept is shown as a dotted line.

Table 2: Body water flux and energy expenditure of male harbour seals during the breeding season

	n	Mean	Range	CV (%)
Total water flux (L d^{-1})	17	4.3 ± .2	3.0–6.1	20.3
Metabolizable energy from feeding (MJ d^{-1})	17	19.9 ± 1.1	12.2–30.2	23.6
Rate of change in body energy (MJ d^{-1})	31	−13.1 ± 1.5	−28.3–4.2	61.9
Total energy expenditure (MJ d^{-1})	17	33.3 ± 1.9	19.2–51.2	23.7
Percent of energy from feeding	17	61.8 ± 4.0	35.7–99.8	26.4

Note. Total energy expenditure does not equal the sum of energy from feeding and change in total body energy shown in this table, because the average change in total body energy shown here was estimated from a larger sample of males.

TEE during the mating period than they did during the premating period. On average, males also spent more than twice as much time in deep dives (15.6 min h^{-1}) during the premating period than they did in the mating period of the breeding season (6.4 min h^{-1}), which is consistent with a reduction in time spent foraging in deeper water (Coltman et al. 1997). Conversely, males spent significantly more time making dives to depths of less than 20 m during the mating period than they did during the premating period (Coltman et al. 1997).

During the premating period, FEI was significantly positively correlated with time spent deep diving (Fig. 5) but not with shallow-dive effort (following arcsine square-root transformation of the diving variables, $r = 0.55$ and 0.02, $P = 0.034$ and 0.94 for deep- and shallow-dive effort, respectively). During the premating period, 30% of the variation in FEI among male harbour seals could be attributed to variation in the time they spent diving deeply (Fig. 5); however, during the mating period, FEI was not significantly correlated with either measure of diving activity ($r = 0.275$ and $−0.098$ for deep- and shallow-dive effort, respectively).

Large males, with initial mass greater than the median (108 kg), had similar rates of FEI to those of small males during the premating and mating periods (two-factor repeated measures

ANCOVA, initial mass included as covariate, $F_{1, 14} = 0.25$, $P = 0.628$), but lost significantly more TBE (two-factor repeated measures ANCOVA, initial mass included as covariate, $F_{1, 20} = 4.65$, $P = 0.043$), particularly during the premating period (Fig. 6). Both large and small males exhibited lower rates of FEI and greater rates of change in TBE during the mating period than during the premating period ($F_{1, 15} = 8.56$ and $F_{1, 21} = 22.79$ for FEI and change in TBE, respectively; $P < 0.01$ for both). Overall, relatively large males had higher TEE than did smaller males over the entire breeding season (two-factor repeated measures ANCOVA, initial mass included as covariate, $F_{1, 14} = 4.59$, $P = 0.05$).

Discussion

Sources of Error

The methods used to estimate body composition and food energy make several assumptions. With respect to estimating TBW and body composition, hydrogen-isotope-dilution methods have been verified by carcass analysis for adults of two pinniped species, grey seals (Reilly and Fedak 1990) and Antarctic fur seals (Arnould et al. 1996). We used the predictive

Table 3: Comparison of water flux, energy balance, and diving behaviour of male harbour seals during the premating and mating periods of the breeding season

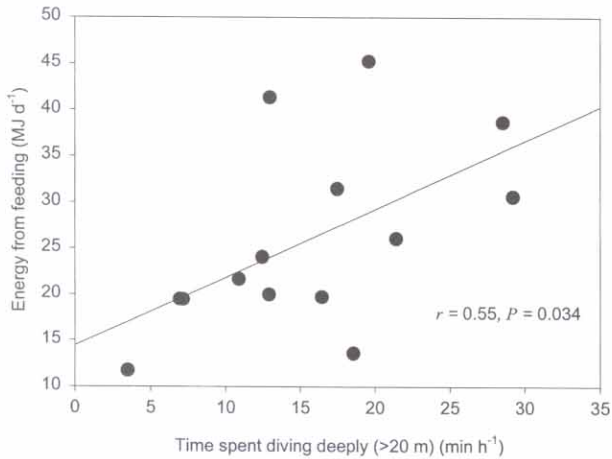|	Premating Period	Mating Period	t^{a}	n	P
Mass change (kg d^{-1})	−.15 ± .02	−.88 ± .02	5.53	23	<.001
Change in total body energy (MJ d^{-1})	4.7 ± 2.4	−24.7 ± 2.8	4.97	23	<.001
Total water reflux (L d^{-1})	5.3 ± .4	3.6 ± .3	3.21	17	.003
Food energy ingested (MJ d^{-1})	25.6 ± 2.4	15.6 ± 1.9	3.02	17	.008
Total energy from ingested (%)	88.5 ± 9.0	43.0 ± 6.1	3.70	17	.002
Total energy expenditure (MJ d^{-1})	30.8 ± 2.2	39.2 ± 2.3	2.56	17	.02
Deep (>20 m) dive effort (min h^{-1})[b]	15.6 ± 2.0	6.4 ± 1.6	2.93	14	.010
Shallow (<20 m) dive effort (min h^{-1})[b]	13.6 ± 1.9	21.0 ± 3.5	2.15	14	.046

[a] Paired t-test.
[b] Data from Coltman et al. (1997).

Figure 5. Metabolizable energy derived from feeding versus time spent diving deeply for breeding male harbour seals during the premating period of the breeding season.

equations of Reilly and Fedak (1990) for grey seals because they were empirically derived from a more closely related phocid seal species, and the range of body sizes included in their analyses spanned the range of our study animals.

The assumption of a diet of only sandlance would cause a downward bias to our estimate of FEI if harbour seals fed on a significant amount of higher-energy prey, as sandlance has a relatively low energy content (about 5% fat). If we assumed a diet of herring, which contains about twice as much fat as sandlance (68.2% H_2O, 9.9% fat, 17.5% protein; Worthy 1990), the estimated food-energy intake would be approximately 50% higher (29.5 MJ d^{-1}, assuming a herring diet, vs. 19.9 MJ d^{-1}, assuming a diet of sandlance). In turn, the assumption of such a higher-energy diet would increase the estimated TEE by 28.9% to 42.9 MJ d^{-1}. Although our estimates of FEI and TEE are sensitive to the exact composition of diet, to our knowledge sandlance is the primary prey consumed during the breeding season at Sable Island, based on stomach lavage and faecal analysis (Walker and Bowen 1993b; W. D. Bowen, unpublished data).

A different approach to calculating food-energy intake and TEE could also have been used by assuming an average rate of metabolic water production from field metabolic rate and then taking the difference between TWF and this figure as pre-formed dietary water intake (method described in Costa [1987]). Field metabolic rate, and thus metabolic water production, is normally estimated using doubly labelled water (e.g., Costa et al. 1989) or from TWF in fasting animals (e.g., Boyd and Duck 1991). If we used 33.2 MJ d^{-1} as an estimate of average field metabolic rate from Figure 3 (i.e., assuming that a harbour seal losing 1.0% body mass per day was effectively fasting), metabolic water production would be 0.90 kg d^{-1}, assuming that energy was derived from lipid catabolism

(0.0272 kg H_2O MJ^{-1}; Schmidt-Nielson 1979). Mean FEI estimated this way would be 21.0 ± 1.3 MJ d^{-1}, assuming a sandlance diet. This is slightly higher (10.5%) than the estimate calculated by the method of Oftedal and Iverson (1987; Table 2). The method of Costa (1987) is more sensitive to the assumed exact composition of diet, however. Assuming a diet of herring, it would predict a rate of FEI 62.9% higher than that from a sandlance diet. It also introduces an additional source of error, as it requires the assumption of some rate of metabolic water production if doubly labelled water is not used for each study animal.

The Energetics of Aquatic versus Terrestrial Mating

Male harbour seals lose mass and expend energy from initial body stores at a rate similar to male northern elephant seals. This is approximately one-half the rates estimated for males
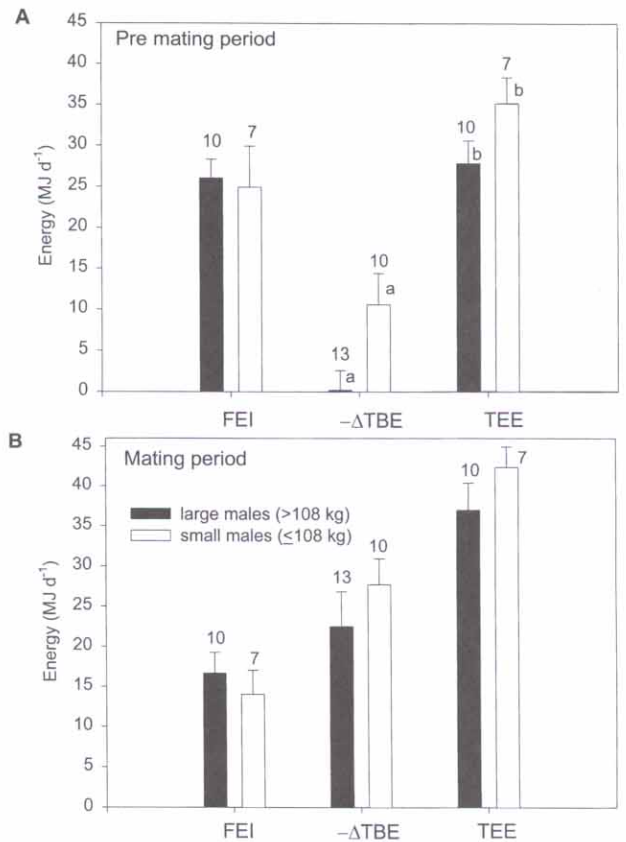

Figure 6. Rates of energy intake from feeding (*FEI*), change in TBE ($-\Delta TBE$), and total energy expenditure (*TEE*) of relatively large and small male harbour seals during the premating (*A*) and mating (*B*) periods of the breeding season. Bars represent one standard error, and numbers are sample sizes. Letters denote pairs of values that differ significantly (Student-Newman-Keuls multiple comparisons, $P < 0.05$)

Table 4: Body size and energy expenditure of breeding male pinnipeds

Species (n)	Body Mass (kg)	Mass Loss (% d^{-1})	Loss of Body Energy (MJ kg^{-1} d^{-1})	Total Energy Expenditure (W kg^{-1})	Duration of Breeding Season
Harbour seal (17)	107.5	.44	.12	3.9[a]	4 wk
Antarctic fur seal (1)	188	.81	.30	3.2[a]	4 wk
Grey seal (33)	257	.86	.32[b]	3.7[b]	4 wk
Hooded seal (19)	312	.80	.29[b]	3.4[b]	2 wk
Weddell seal (7)	372	.81	.30[b]	3.5[b]	5 wk
Northern elephant seal (17) ...	1,704	.42	.16[b]	1.8[b]	2 mo

Sources. Harbour seal, this study; Antarctic fur seal, Boyd and Duck 1991; grey seal, Anderson and Fedak 1985; hooded seal, Bartsh et al. 1992; Weddell seal, Kovacs et al. 1996; northern elephant seal, Deutsch et al. 1990.

[a] Total energy expenditure estimated from isotope dilution.

[b] Estimated from mass loss, assuming a caloric density of 36.7 MJ kg^{-1} (Fedak and Anderson 1987) and no energy intake from feeding.

of other species of pinnipeds for which there are comparable longitudinal data (Table 4). However, when energy intake from feeding is added, our data suggest that breeding male harbour seals expend total energy at a rate similar to terrestrially breeding grey and Antarctic fur seals and aquatically mating Weddell seals (*Leptonychotes weddelli*) and hooded seals (*Cystophora cristata*), which breed on fast and pack ice (Table 4). The energetic cost of reproduction per unit of time among males of aquatically mating species is therefore similar to that of species in which males compete for mates on land. Based on the measurement of metabolic rate in one animal, and the observation of higher relative rates of water flux for male harbour seals than for male grey seals, Reilly and Fedak (1991) suggested that male harbour seals expend energy at a much greater rate than do terrestrially mating pinnipeds, the equivalent of six times the basal rate predicted by Kleiber (1975). Reilly and Fedak (1991) postulated that this was due to the relatively high cost of aquatic displays and aggressive encounters with other males at sea. Our data suggest that a higher rate of water flux in male harbour seals can largely be attributed to water intake from feeding during the breeding season. Although Reilly and Fedak's (1991) estimate of TEE from doubly labelled water (52.5 MJ d^{-1} for a 109-kg male) is significantly higher than that presented here (33.3 ± 1.9 MJ d^{-1}; one-sample *t*-test, $t_{17} = 10.0$, $P < 0.001$) and falls just outside of the range of our estimates (17.7–51.2 MJ d^{-1}), it was based on a single observation and may not be generally representative.

Body Size, Cost of Reproduction, and Fasting Endurance in Male Pinnipeds

The scaling of body size accounts for almost 87% of the variation in the rate of TEE among breeding male pinnipeds for which there are longitudinal data (Fig. 7). There were no sig-

nificant differences in TEE between males of aquatically and terrestrially breeding species when the influence of body size is accounted for (ANCOVA, mass included as covariate, $F_{1, 102} = 0.14$, $P = 0.70$). The slope of the regression line (0.77 ± 0.03) is not significantly different from the coefficient of Kleiber (1975) for the scaling of basal metabolic rate to body mass (0.75: $t_{104} = 0.67$, $P > 0.05$), and the regression line falls only slightly above three times the basal metabolic rate predicted by Kleiber's equation (1975; Fig. 7). This suggests that male pinnipeds expend approximately 50% more mass-specific energy during the breeding season than they do at other times of the year, as the average realized metabolic rate for homeotherms including marine mammals, based on maintenance metabolic requirement, is about twice the basal metabolic rate (Peters 1983; Lavigne et al. 1987).

The consistency in energy expenditure relative to body size among males across species is remarkable given the different levels of polygyny, reproductive strategies, and mating environments represented (Fig. 7). Given the range of body size in this regression, available data suggest that average rates of energy expenditure can be estimated for breeding males of all pinniped species. There is, however, a great amount of variation in TEE among individuals within each species. The allometric relation indicates that males of smaller-bodied pinniped species, such as the harbour seal, expend more mass-specific energy and are likely to have less fasting endurance than males of larger species. Fasting endurance for a breeding male pinniped can be estimated by dividing usable body-energy stores by the rate of energy expenditure (Lindstedt and Boyce 1985). Assuming the mass of body fat an individual possesses represents usable energy stores (E_s), then E_s scales allometrically to body mass (M; Lindstedt and Boyce 1985) as: $E_s(MJ) = 2.948 M^{1.19}$. Breeding male pinnipeds expend energy (TEE) at the rate of: log TEE(W) $= 1.09 + 0.77$ log M (Fig. 7), or TEE(MJ d^{-1}) $= 1.063 M^{0.77}$. Thus, fasting endurance (F) for a breeding male can be esti-
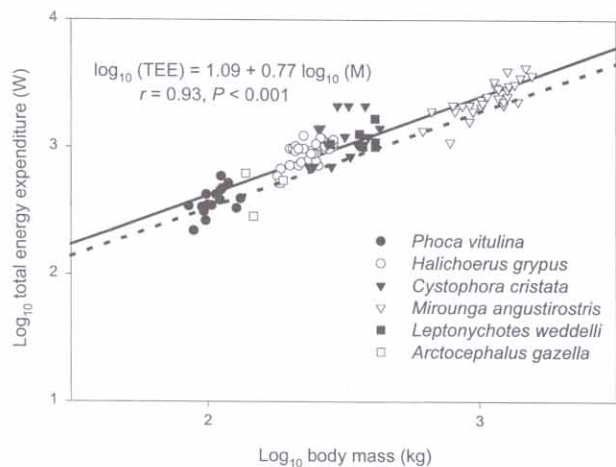
Figure 7. Rates of energy expenditure (*TEE*) of breeding male pinnipeds as a function of body mass (*M*). The dotted line represents three times the basal metabolic rate predicted by the equation of Kleiber (1975). Data were either taken directly from sources given or calculated from individual rates of mass loss assuming an energy density of 36.7 MJ kg^{-1} (Fedak and Anderson 1987). Individuals of aquatically mating species are represented by filled symbols; individuals of terrestrially mating species are indicated by open symbols. Sources of data were as follows: *Phoca vitulina*, this study; *Halichoerus grypus*, Anderson and Fedak (1985); *Cystophora cristata*, Kovacs et al. (1996); *Mirounga angustirostris*, Deutsch et al. (1990); *Leptonychotes weddelli*, Bartsh et al. (1992); and *Arctocephalus gazella*, Boyd and Duck (1991).

mated as: F(d) = E_s/TEE = 2.948 $M^{1.19}$/1.063 $M^{0.77}$, or 2.773 $M^{0.42}$, assuming a thermoneutral environment (Lindstedt and Boyce 1985). A 100-kg male harbour seal can thus afford to fast for approximately 19 d, whereas a 300-kg male pinniped such as a grey, hooded, or Weddell seal can afford to fast for about 30 d, and a 1,500-kg northern elephant seal can fast for 60 d. Thus males of small-bodied species may need to forage and/or to economize their energy expenditure such that they can afford levels of activity that may cost three times the basal metabolism during the mating period, if oestrus is asynchronous to the extent that the period of female receptivity exceeds male fasting endurance. Most males of the species shown in Table 4 other than the harbour seal are capable of fasting for the duration of their mating seasons due to their larger body size, and thus may not need to forage.

Body Size, Foraging Activity, and Reproductive Effort of Male Harbour Seals

For male harbour seals, the temporal and spatial separation of foraging and reproduction remains somewhat unclear. As only about 30% of the variation in FEI and in the rate of TBE expenditure among males can be attributed to variation in

deep-dive effort (Figs. 4, 5), foraging probably does not occur exclusively in deeper water. Male harbour seals may also be feeding during periods of shallow-diving activity and on dedicated foraging trips. Also, our measure of foraging effort, which is based solely on dive depth, may not be very accurate if males spend a considerable amount of time competing for mates in deeper water offshore, perhaps on the foraging grounds or on transit routes used by females. Data presented in this study indicate that male harbour seals derive more than one-third of their energy from feeding during the mating period, yet at the same time most males had ceased to make trips consisting of predominately deeper dives (Coltman et al. 1997). Opportunistic feeding, occurring within bouts of shallow-diving activity or while patrolling home ranges near the shore, may therefore provide an additional source of energy to maintain their reproductive effort.

Studies have previously shown that male harbour seals feed during the early breeding season and have suggested that the energetic constraints of small body size may have played a role in shaping male reproductive strategies (Thompson et al. 1989; Walker and Bowen 1993b). On Sable Island, males tend to maintain their body mass during periods of deep diving before the time when females enter oestrus (Coltman et al. 1997). Data presented here and in Coltman et al. (1997) indicate that male harbour seals foraged more intensely and made fewer shallow dives early in the breeding season when relatively few oestrus females were available. At the same time, males also expended total energy at a lower rate during the premating period of the season (Table 3). If males were to rely entirely on their initial energy stores and fast throughout the breeding season, yet maintain an average rate of TEE of 33.2 MJ d^{-1}, an average male harbour seal (with 1,500 MJ of stored body energy and 23.6% fat at the beginning of the breeding season) would deplete 50% of its TBE in less than 3 wk. As most of this energy comes from fat catabolism, an average male would fall below 5% body fat during the breeding season if fasting. It is therefore likely that only the largest males can afford to fast throughout the entire breeding season, yet maintain their reproductive effort.

We previously hypothesized that larger males may have a mating advantage since they spend less time foraging and more time making shallow dives, which are more likely to be associated with aggressive behaviours and displays associated with acquiring mates (Coltman et al. 1997). The results of this study show that larger males depleted their body-energy stores during the premating period to a significantly greater extent than smaller males (Fig. 6), and they spent significantly more total energy during the breeding season. Males that are relatively large at the beginning of the breeding season therefore invested more total energy in reproduction. This may translate into a mating advantage, as reproductive effort is a strong predictor of dominance status and mating success in other pinniped

species such as grey seals (Anderson and Fedak 1985; Tinker et al. 1995) and northern elephant seals (Deutsch et al. 1990). Larger males made more shallow dives earlier in the season, at a cost in terms of energy expended from body-energy stores (Fig. 6). This may provide them with a mating advantage if increased shallow-diving activity improves their encounter rates with, or effective advertisement to, potentially receptive females. Males with large initial mass may also represent relatively older animals, or males that are in better overall condition. The latter may be less likely, however, as large and small males had similar body composition (Fig. 2). Differences in the activity of large and small males may therefore also reflect the effects of previous breeding experience in addition to general body size and energy stores.

Harbour seals have limited size dimorphism; on Sable Island, adult males are approximately 6% longer (McLaren 1993) and 18% heavier than postpartum females (W. D. Bowen, D. J. Boness, and S. J. Iverson, unpublished data). This suggests that large size may be advantageous for males, yet less strongly selected for in the harbour seal than it may be in more dimorphic, terrestrially breeding pinniped species. Since mating and feeding both occur at sea in aquatically mating pinnipeds, relatively smaller males, or males in inferior condition at the beginning of the breeding season, may be at less of an energetic disadvantage if they can feed during the mating season. Furthermore, large size is less likely to confer a direct competitive advantage in the aquatic environment where agility may be more important in mate competition (Le Boeuf 1991). Clearly, knowledge of male mating success is required to evaluate the selective advantage of body size and the importance of energetics to male fitness.

For male harbour seals, and perhaps other pinnipeds that mate at sea, the classic paradigm, that complete temporal and spatial separation of feeding and reproduction acts as a dominant factor in the evolution of pinniped mating systems and size dimorphism (Bartholomew 1970), may be less applicable than it is for terrestrially mating species. For aquatically mating pinnipeds, reproductive behaviour and size dimorphism have evolved subject to a different set of ecological variables, such as the local distribution of prey at sea, from that of pinnipeds that mate on land. For male harbour seals on Sable Island, relatively large size may not greatly enhance mating success if foraging can effectively supplement initial energy reserves to cover the energetic costs of reproduction during the breeding season. Alternately, smaller, energetically challenged males may be making the best of their situation by feeding until the time when most females are receptive. For aquatically mating pinnipeds, male reproductive strategies may therefore be influenced by the distribution of food as well as the by availability and the economic defensibility of oestrus females in time and space (Emlen and Oring 1977; Stirling 1983; Boness 1991).

Literature Cited

Anderson S.S. and M.A. Fedak. 1985. Grey seal males: energetic and behavioural links between size and sexual success. Anim. Behav. 33:829–838.

Arnould J., I.L. Boyd, and J.R. Speakman. 1996. Measuring the body composition of Antarctic fur seals (*Arctocephalus gazella*): validation of hydrogen isotope dilution. Physiol. Zool. 69:93–116.

Bartholomew G.A. 1970. A model for the evolution of pinniped polygyny. Evolution 4:546–559.

Bartsh S.S., S.D. Johnston, and D.B. Siniff. 1992. Territorial behaviour and breeding frequency of male Weddell seals (*Leptonychotes weddelli*) in relation to age, size, and concentrations of serum testosterone and cortisol. Can. J. Zool. 70:680–692.

Boness D.J. 1991. Determinants of mating systems in the Otariidae (Pinnipedia). Pp. 1–44 in D. Renouf, ed. Behaviour of Pinnipeds. Chapman & Hall, London.

Boulva J. and I.A. McLaren. 1979. Biology of the harbour seal (*Phoca vitulina*) in eastern Canada. Bull. Fish. Res. Board Can. 200:1–24.

Bowen W.D., O.T. Oftedal, and D.J. Boness. 1992. Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). Physiol. Zool. 65:844–866.

Boyd I.L. and C.D. Duck. 1991. Mass changes and metabolism in territorial male Antarctic fur seals (*Arctocephalus gazella*). Physiol. Zool. 64:375–392.

Coltman D.W., W.D. Bowen, D.J. Boness, and S.J. Iverson. 1997. Balancing foraging and reproduction in male harbour seals: an aquatically mating pinniped. Anim. Behav. 54:663–678.

Costa D.P. 1987. Isotopic methods for quantifying material and energy balance of free-ranging marine mammals. Pp. 43–66 in A.C. Huntley, D.P. Costa, G.A. Worthy, and M.A. Castellini, eds. Marine Mammal Energetics. Society for Ma-

rine Mammalogy Special Publication no. 1. Allen, Lawrence, Kans.

Costa D.P., J.P. Croxall, and C.D. Duck. 1989. Foraging energetics of Antarctic fur seals in relation to changes in prey availability. Ecology 70:596–606.

Costa D.P. and R.L. Gentry. 1986. Free-ranging energetics of northern fur seals. Pp. 79–101 in R.L. Gentry and G.L. Kooyman, eds. Fur Seals: Maternal Strategies on Land and at Sea. Princeton University Press, Princeton, N.J.

Costa D.P., B.J. Le Boeuf, C.L. Ortiz, and A.C. Huntley. 1986. The energetics of lactation in the northern elephant seal. J. Zool. (Lond.) 209:21–33.

Deutsch C.J., M.P. Haley, and B.J. Le Boeuf. 1990. Reproductive effort of male northern elephant seals: estimates from mass loss. Can. J. Zool. 68:2580–2593.

Emlen S.T. and L.W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215–223.

Fedak M.A. and S.S. Anderson. 1982. The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). J. Zool. (Lond.) 198:473–479.

———. 1987. Estimating the energy requirements of seals from weight changes. Pp. 205–223 in A.C. Huntley, D.P. Costa, G.A.J. Worthy, and M.A. Castellini, eds. Marine Mammal Energetics. Society for Marine Mammalogy Special Publication no. 1. Allen, Lawrence, Kans.

Godsell J. 1988. Herd formation and haul-out behaviour in harbour seals (*Phoca vitulina*). J. Zool. (Lond.). 215:83–98.

Iverson S.J., W.D. Bowen, D.J. Boness, and O.T. Oftedal. 1993. The effect of maternal size and maternal milk energy output on pup growth in grey seals (*Halichoerus grypus*). Physiol. Zool. 66:61–88.

Keiver K.M., K. Ronald, and F. Beamish. 1984. Metabolizable energy requirements for maintenance and faecal and urinary losses of juvenile harp seals (*Phoca groenlandica*). Can. J. Zool. 62:769–776.

Kleiber M. 1975. The Fire of Life: An Introduction to Animal Energetics. Kreiger, Huntington, N.Y.

Kovacs K.M., C. Lydersen, M. Hammill, and D.M. Lavigne. 1996. Reproductive effort of male hooded seals (*Cystophora cristata*): estimates from mass loss. Can. J. Zool. 74:1521–1530.

Lavigne D.M., G.A. Worthy, K.M. Kovacs, O.J. Schmidt, and J.P. Hickie. 1987. Metabolic rates of seals and whales. Can. J. Zool. 64:279–284.

Le Boeuf B.J. 1991. Pinniped mating systems on land, ice, and in the water: emphasis on the Phocidae. Pp. 45–65 in D. Renouf, ed. Behaviour of Pinnipeds. Chapman & Hall, London.

Lindstedt S.L. and M.S. Boyce. 1985. Seasonality, fasting endurance, and body size in mammals. Am. Nat. 125:873–878.

Markussen N.H. and M. Ryg. 1992. Metabolic rate and body composition of harbour seals, *Phoca vitulina*, during starvation and refeeding. Can. J. Zool. 70:220–224.

McLaren I.A. 1993. Growth in pinnipeds. Biol. Rev. 68:1–79.

Muelbert M.M. and W.D. Bowen. 1993. Duration of lactation and postweaning changes in mass and body composition of harbour seal, *Phoca vitulina*, pups. Can. J. Zool. 71:1405–1414.

Oftedal O.T., D.J. Boness, and W.D. Bowen. 1993. Energy transfer by lactating hooded seals and nutrient deposition in their pups during the four days from birth to weaning. Physiol. Zool. 66:412–436.

Oftedal O.T. and S.J. Iverson. 1987. Hydrogen isotope methodology for measurement of milk intakes and energetics of growth in suckling young. Pp. 67–89 in A.C. Huntley, D.P. Costa, G.A. Worthy, and M.A. Castellini, eds. Marine Mammal Energetics. Society for Marine Mammalogy Special Publication no. 1. Allen, Lawrence, Kans.

Peters H.R. 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge.

Rayner J.M.V. 1985. Linear relations in biomechanics: the statistics of scaling functions. J. Zool. (Lond.) 206:415–439.

Reilly J.J. and M.A. Fedak. 1990. Measurement of the body composition of living grey seals by hydrogen isotope dilution. J. Appl. Physiol. 69:885–891.

———. 1991. Rates of water turnover and energy expenditure of free-living male common seals (*Phoca vitulina*). J. Zool. (Lond.) 223:461–468.

Ronald K., K.M. Keiver, W.H. Beamish, and R. Frank. 1984. Energy requirements and faecal and urinary losses of the grey seal (Halichoerus grypus). Can. J. Zool. 62:1101–1105.

Schmidt-Nielson K. 1979. Animal Physiology: Adaptations and Environment. Cambridge University Press, Cambridge.

Stirling I.A. 1983. The evolution of mating systems in pinnipeds. Pp. 489–527 in J.F. Eisenberg and D.G. Kleiman, eds. Advances in the Study of Mammalian Behaviour. American Society of Mammalogists, Shippensburg, Pa.

Thompson P.M. 1988. Timing of mating in the common seal (*Phoca vitulina*). Mammal Rev. 18:105–112.

Thompson P.M., M.A. Fedak, B.J. McConnell, and K.S. Nicholas. 1989. Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). J. Appl. Ecol. 26:521–535.

Tinker M.T., K.M. Kovacs, and M.O. Hammill. 1995. The reproductive behavior and energetics of male gray seals (*Halichoerus grypus*) breeding on a land-fast ice substrate. Behav. Ecol. Sociobiol. 36:159–170.

Trivers R.L. 1972. Parental investment and sexual selection. Pp. 136–179 in B. Campbell, ed. Sexual Selection and the Descent of Man, 1871–1971. Aldine, Chicago.

Van Parijs S.M, P.M. Thompson, D.J. Tollit, and A. MacKay. 1997. Changes in the distribution and activity of male harbour seals during the breeding season. Anim. Behav. 54:35–43.

Walker B.G. and W.D. Bowen. 1993a. Behavioural differences among adult male harbour seals during the breeding season may provide evidence of reproductive strategies. Can. J. Zool. 71:1585–1591.

———. 1993b. Changes in body mass and feeding behaviour in male harbour seals, *Phoca vitulina*, in relation to female reproductive status. J. Zool. (Lond.) 231:423–436.

Worthy G.A. 1990. Nutritional energetics of marine mammals. Pp. 489–520 in L.A. Dierauf, ed. CRC Handbook of Marine Mammal Medicine: Health, Disease, and Rehabilitation. CRC, Boca Raton, Fla.