State-dependent male mating tactics in the grey seal: the importance of body size

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The purpose of this study was to examine the importance of body size and body composition as determinants of conditional mating tactics exhibited in male grey seals. We combined behavioral observations with measures of energy expenditure and success on 42 known-age individuals during the breeding seasons of 1997–2001 at Sable Island, Canada. Males with a large body mass arrived at the breeding grounds with more body fat and body energy and catabolized less body protein than smaller males. Males consumed 1.9 ± 0.2 MJ day^{-1}, and those with a smaller percentage of body fat had higher rates of food energy intake. The amount of body energy on arrival was positively correlated with the duration of the breeding period. Males that exhibited the primary mating tactic of consortship were heavier, had absolutely more body fat and body energy, and sustained breeding longer than those males that did not exhibit the primary tactic. Amongst all males, body mass showed a quadratic relationship with the number of female consorts mated and the estimated number of pups sired. Thus, intermediate-sized males mated with the most consorts and achieved the highest success. Intermediate body size may be optimal during breeding due to greater agility in male combat. Body size was an important determinant of mating tactics used by male grey seals. A large body size provided an energetic advantage of greater endurance while an intermediate body size may provide greater competitive ability in acquiring consortships. *Key words:* body size, conditional mating tactics, endurance rivalry, energetics, *Halichoerus grypus*, pinnipeds, reproductive behavior. *[Behav Ecol 16:541–549 (2005)]*

Much of the variation in some polygynous mating systems may be due to the differential ability of males to defend females (Clutton-Brock, 1989). Males will differ in their competitive ability due to differences in their state. Variations in state among individuals may occur due to genetic variation, ontogeny, environmental fluctuations during growth, and hormonal action (Dunbar, 1982; Festa-Bianchet et al., 2004; Lindström, 1999; Moore, 1991; Moore et al., 1998). Conditional reproductive strategies comprise a primary tactic that yields average high success and several alternative tactics that yield lower average success. State is thought to be an important determinant of tactics such that individuals exhibit the tactic or tactics that provide the highest success according to their state (Dunbar, 1982; Gross, 1996).

There are many traits that represent an individual's state, and all will contribute toward shaping the life history (McNamara and Houston, 1996). In some polygynous mating systems, body size and body composition are likely to be important components of state in breeding adult males. Here, the primary mating tactic typically involves an extended period of attendance that is often correlated with success (Boness, 1991; Halliday and Tejedo, 1995; Thornhill, 1981; Wiley, 1974). Such tactics can be costly due to the risks of being injured or killed during male combat (Bartsh et al., 1992; Clutton-Brock et al., 1979; Thornhill, 1981) and high energy expenditure (Deutsch et al., 1990; Judge and Brooks, 2001; Vehrencamp et al., 1989; Yoccoz et al., 2002). In many species, large body size can provide a male that engages in the primary mating tactic with an advantage in male-male competition (Andersson, 1994; Enders, 1993; Howard, 1978; McElligott et al., 2001). Among mammals that store energy for breeding, stored fat becomes a greater fraction of body mass as size increases (Lindstedt and Boyce, 1985). Large individuals may therefore have both absolutely and relatively more stored energy for breeding (e.g., Coltman et al., 1998) and an advantage in endurance rivalry (Andersson, 1994; Arnould and Duck, 1997; Judge and Brooks, 2001; Murphy, 1998). We may therefore expect individuals of a large body size and with large energy stores to exhibit the primary mating tactic.

Small individuals or those in poor condition (i.e., low body fat per unit body mass) might either fail to become reproductive and not appear at the breeding grounds or might engage in alternative tactics (Dunbar, 1982; Gross, 1996). Several molecular studies have shown that alternative mating tactics yield success (e.g., Coltman et al., 1999, 2002). Nevertheless, few studies have examined the consequences of expressing alternative tactics on energy expenditure. In addition to their lower ability to compete, individuals exhibiting alternative tactics may also have high energy expenditure, which presumably could further reduce their endurance ability at the breeding grounds. Coltman et al. (1998) and Judge and Brooks (2001) have demonstrated energetic constraints in male harbor seals (*Phoca vitulina*) and male bullfrogs (*Rana catesbeiana*), respectively.

The grey seal (*Halichoerus grypus*) is a sexually dimorphic pinniped with a polygynous mating system (Anderson et al., 1975; Boness and James, 1979). Males arrive at the breeding colony with large quantities of stored energy and compete for access to females. The primary mating tactic is prolonged female defense whereby a male defends a position among

a group of females that may change in membership over time (Anderson et al., 1975; Boness and James, 1979). Studies have demonstrated a positive correlation between male size and mating success (Anderson and Fedak, 1985) and length of stay and mating success (Anderson et al., 1975; Boness and James, 1979; Tinker et al., 1995; Twiss et al., 1994). Three alternative mating tactics have been defined (Lidgard, 2003): the first involves a male mating with a female that has weaned her pup and is departing the colony; the second involves a male that is in defense of females mating with a neighboring lactating female; and the third involves a male that is not in defense of females mating with a lactating female that is either alone or is a consort of another male. Males that exhibit alternative tactics have been shown to achieve some success (Ambs et al., 1999; Amos et al., 1993; Lidgard et al., 2004; Worthington Wilmer et al., 1999). Lidgard (2003) categorized males according to whether they exhibited the primary tactic of consortship (consort males) or only expressed alternative tactics (nonconsort males). Nonconsort males were mostly young, made more moves and spent shorter periods of time at a site, were less competitive, and had a lower body condition index (body mass/standard length) than consort males. These differences remained after controlling for age, suggesting that other components of state such as body size may be important determinants of mating tactics.

We combined detailed behavioral observations with measures of energy expenditure and success to test the hypothesis that body size and body composition are important determinants of the mating tactics exhibited by male grey seals. We predicted that energy expenditure would be the same for males of all body sizes but that breeding endurance would be positively correlated with total body energy (TBE) of the male on arrival. We also predicted that only large males would exhibit the primary tactic of consortship and that the number of consorts mated would increase with body size.

METHODS

Study site and study animals

The study was conducted during the breeding seasons of 1997 to 2001 at Sable Island (43° 55′ N, 60° 00′ W) situated 288 km ESE of Halifax, Nova Scotia. The island is approximately 54 km long and 1.2 km wide, with vegetated sand dunes along its length and both wide and narrow beaches around its perimeter. The breeding season extends from mid December to early February, and the estimated pup production in 1997 was 25,400; the annual rate of increase is 13% (Bowen et al., 2003). A proportion of both male and female grey seals are branded and are of known age. We studied 42 branded males whose age range (10–31 years) approximates the reproductive life span of this species on Sable Island (Bowen WD, Boness DJ, Iverson SJ, and McMillan JI, unpublished data). A wide range of body masses and lengths were represented. The study design was cross-sectional such that each male was studied in only 1 year.

Field procedures

Males were captured at the start and toward the end of the breeding season using a nylon net fastened between two aluminum poles. At each capture males were injected intramuscularly with a preweighed dose of tritium oxide (HTO; 18.5 MBq ml^{-1}; approximately 0.02 g kg^{-1} body mass). The isotope was delivered using a 10-ml syringe fitted with a three-way tap valve and another 10-ml syringe filled with ~5 ml of distilled water. This configuration allowed us to remove any residual tritium and ensured complete administration (Beck et al., 2003). Males were then weighed using tandem

300-kg (±1 kg) Salter spring balances and thereafter held in the net to allow the tritium to equilibrate. Ninety minutes after the HTO was administered, approximately 10 ml of blood was taken from the extradural vein; this was repeated 15 min later to determine if the isotope was equilibrated in body fluids. To determine water flux, a blood sample was taken at the final capture prior to HTO administration to measure the residual isotope level. Blood samples were collected in 10-ml Vacutainers (with no additives) and centrifuged for 15–20 min. Serum was removed and stored frozen at −20°C in cryovials.

Prior to release, each male was fitted with a radio transmitter (164–165 MHz, Advanced Telemetry Systems, http://www.atstrack.com) to relocate them on the island and a timed-depth recorder (TDR; Wildlife Computers, http://www.wildlifecomputers.com) to record overall activity and diving behavior and a length was taken (Lidgard et al., 2003). In 1997 and 1998, both radio transmitter and TDR were removed at final capture late in the season. From 1999 to 2001, males wore the radio transmitter until they left the breeding colony ($N=27$) or until the research team departed the island ($N=4$).

Estimation of body composition, water flux, and energy expenditure

The specific activity of ^{3}H in each serum sample was measured in triplicate and distilled using the evaporated-freeze-capture method of Ortiz et al. (1978). For each replicate, 50 µl of serum was transferred to a preweighed (±0.1 mg) scintillation vial, distilled, reweighed to obtain the weight of the distillate, and 10 ml of Scintiverse II was added. A Beckman LS 5000CE scintillation counter was used to measure the activity of ^{3}H. The activity of the standard from which the injectant was taken was measured in triplicate at the same time as the serum samples. Mean specific activity was calculated from triplicates where the coefficient of variation (CV%) among replicates was <2% (most samples). Otherwise, the two closest samples were used. Dilution space was calculated according to the equation given in Bowen et al. (1999). We used the equation in Bowen and Iverson (1998) to calculate total body water (TBW) and the equations given in Reilly and Fedak (1990) to calculate total body protein (TBP), total body fat (TPF), and TBE. Daily water flux was calculated according to Oftedal and Iverson (1987).

To estimate food intake, we used the following winter diet estimated from the recovery of hard parts from grey seal feces on Sable Island; northern sandlance (Ammodytes dubius) 60%, capelin (Mallotus villosus) 6%, winter flounder (Pseudopleuronectes americanus) 14%, cod (Gadus morhua) 11%, and silver hake (Merluccius bilinearus) 8% (Bowen WD, unpublished data). The mean composition of this diet was 77.7% TBW, 15.7% TBP, and 5.6% TBF (Budge SM, Iverson SJ, and Bowen WD, unpublished data). We used the equation in Bowen et al. (2001) to estimate daily food intake and assumed an assimilation efficiency of 93% (Lawson et al., 1997; Ronald et al., 1984). Daily food intake was converted into daily food energy intake (FEI) by assuming a calorific density of fat of 39.3 MJ kg^{-1} and a calorific density of protein of 23.6 MJ kg^{-1} (Schmidt-Nielsen, 1990). Daily FEI was converted to daily metabolizable energy intake (MEI) assuming that 15% of the ingested food energy was lost as fecal and urinary matter (Lawson et al., 1997; Ronald et al., 1984). Daily energy expenditure (DEE) was given as the sum of daily TBE expended and daily MEI gained.

Behavior on land and at sea

Each male was located between one and three times a day using a R2000 radio receiver (164–165 MHz, Advanced

Telemetry Systems) and dipole and yaggi antennae according to the protocol described in Lidgard et al. (2001). At each sighting, a description of the location and a global positioning system (GPS) reading (Garmin 45 & 48, http://www.garmin.com) was recorded. To account for the error associated with GPS locations prior to the removal of selective availability (May 2000), a move from one site to another was recorded when the distance was ≥100 m. To minimize the influence of capture on behavioral data, the first location used in the analysis was the first land location the day after capture or final capture. TDR records were used to estimate deep-diving effort (see Lidgard et al., 2003, for the definition and the dive effort for each male). We used the operational sex ratio (OSR; Kvarnemo and Ahnesjo, 1996) as a proxy for the level of competition to test if the level of male-male competition around a male influenced daily expenditure. The OSR has a range of 0–1.0 as the number of males relative to receptive females increases. The number of males and the number of females in estrus within a 10 m radius the male was recorded at each location. We assumed that females came into estrus when their pup was at least 14 days of age (Boness and James, 1979; see Kovacs and Lavigne, 1986, for the age-classification scheme).

Measures of success

We defined four mating tactics. Males were deemed as exhibiting the primary tactic of consortship (referred to as consort males) if they defended at least one estrous female for ≥2 days. A period of 2 days was chosen because a visit to a male on any one day may occur when the consort male is temporarily away from the consort female; thus, a visit on a second day increases the chance of observing the male in defense of the consort female. Three alternative tactics have been described (Lidgard, 2003) and are (1) male mating with a female that has weaned her pup and is departing the colony, (2) male that is in defense of females mating with a neighboring lactating female, and (3) male that is not in defense of females mating with a lactating female that is either alone or is a consort of another male.

Extraconsort fertilizations occur in grey seals (Ambs et al., 1999), thus we were unable to use the number of females mated as a measure of success. Rather, we used rates of fertilization success for the primary tactic of consortship (0.27) and the alternative tactic of mating with departing females (0.10; Lidgard et al., 2004) and the number of females mated to estimate the number of pups sired. In Lidgard et al. (2004), the rate of fertilization success was estimated by grouping paternity data from a sample of focal males and by estimating the proportion of offspring sired for the primary tactic and the alternative tactic of males mating with departing females. To provide an estimate of the number of pups sired in this study, the number of females mated through exhibiting the primary tactic or an alternative tactic was multiplied by the appropriate rate of fertilization success. Lidgard et al. (2004) only provided a measure of fertilization success for one of the three alternative tactics. However, given that the remaining two alternative tactics also do not involve a period of defense, we have assumed that the rate of fertilization success of these two tactics was similar to that of the departing female tactic.

Data analysis

We assumed that capture mass was a good estimate of mass on arrival at the breeding grounds based on the following observations. Twenty-five of the 42 males in this study were tagged with a radio transmitter in the months previous to the

study season, and the median number of days between their first sighting on the island and capture was two. Eight other males were sighted prior to capture, and the median number of days between their first sighting and capture was also two. Although the remaining nine males were first sighted on the day of capture, given that the entire colony was surveyed for brands at least twice before the date of the last capture (7 January), only a few days could have passed between their first sighting and their arrival.

Given our small sample in each year and the fact that the age structure of the males studied differed by year, the effects of year were not addressed in this study. All analyses were performed using SPSS version 11.5 for Windows, and the probability level for significance was $\alpha = 0.05$. Energetic and behavioral variables were transformed as necessary to meet assumptions of parametric statistics. Standard errors are given with means.

RESULTS

Of the 42 males captured at the start of the season, only 40 were reweighed near the end of the breeding season because in 1999 two males departed the breeding colony early (see Appendix). At the beginning of the season, TBW was measured in 37 of the 42 males. Near the end of the breeding season, 8 of those 37 males (including the two males that departed the breeding colony early) did not receive final TBW measurements, and the tritium apparently did not equilibrate in three of those males. Thus, 40 males were used to estimate mass loss, 37 males were used to estimate initial body composition, and 26 males were used to estimate changes in body composition, water flux, and food intake. All males had complete behavioral records on land, and 30 males had complete TDR records. The mean number of days between the initial and final capture was 22 ± 1 days. From a subset of males ($N = 27$) that were followed from their arrival to their departure from the breeding colony, the duration of the breeding season was 29 ± 1 days and the final capture occurred on day 21 ± 1.

Body size, body composition, and changes over the breeding season

The mean mass of males at capture was 290.6 ± 5.4 kg, and their mean length was 2.1 ± 0.02 m ($N = 42$; Table 1). Capture mass comprised an average of 53.0 ± 0.5% TBW, 17.5 ± 0.2% TBP, 27.2 ± 0.8% TBF, and 4396 ± 129 MJ TBE ($N = 37$). There was little variation among individuals in percentage TBP and TBF at capture (CV = 7.6% and 17.1%, respectively). Smaller males had absolutely less TBF and TBE at capture than larger males (Pearson $r = .734$, $N = 37$, $p < .0001$ and $r = .848$, $p < .0001$, respectively). There was a negative relationship between percentage TBF at capture and age (partial [controlling for mass] $r = -.449$, df $= 34$, $p = .006$). When controlling for age, larger males had a greater percentage TBF at capture than smaller males (partial $r = .448$, df $= 34$, $p = .005$), suggesting that large males arrived at the breeding colony in better condition.

During the sampling period, males lost 18.1 ± 0.5% ($N = 40$) of their capture mass, which was equivalent to an average loss of 2.4 ± 0.1 kg day^{-1} (CV = 15.6%) or a loss of 0.8 ± 0.02% of their capture mass per day. Although all males lost a similar proportion of their capture mass per day, larger males lost absolutely more of their capture mass per day than smaller males (partial [controlling for number of days] $r = .69$, $N = 40$, $p < .001$). Protein accounted for 10.8 ± 1.6% (CV = 73.1%; $N = 26$) of mass loss and body fat accounted for 50.7 ± 5.5% (CV = 55.0%). Males with a greater percentage

Table 1

Body mass, length, mass loss, and body composition for breeding grey seal males on arrival at Sable Island, 1997–2001: for all males and by male type

	All males		Consort males		Nonconsort males		
	Mean ± SE	CV%	Mean ± SE	CV%	Mean ± SE	CV%	p^a (ANOVA)
Body mass (kg)	290.6 ± 5.4 (42)	12.1	302.9 ± 5.5 (29)	9.7	263.2 ± 9.0 (13)	12.4	<.001
Length (m)	2.1 ± 0.02 (42)	4.7	2.2 ± 0.02 (29)	4.7	2.1 ± 0.03 (13)	5.3	.077
Loss (kg day^{-1})	2.4 ± 0.1 (40)	15.6	2.5 ± 0.08 (29)	16.8	2.3 ± 0.06 (11)	8.4	.064
Body water (kg)	153.4 ± 3.0 (37)	11.7	161.9 ± 3.9 (18)	10.2	146.6 ± 6.8 (8)	13.2	.006
Body protein (kg)	50.7 ± 1.0 (37)	12.1	53.4 ± 1.4 (18)	10.8	48.8 ± 2.3 (8)	13.3	.016
Body fat (kg)	79.4 ± 3.0 (37)	23.3	84.1 ± 3.7 (18)	18.6	68.4 ± 6.2 (8)	25.7	.002
Body energy (MJ)	4396 ± 129 (37)	17.8	4651 ± 153 (18)	13.9	3909 ± 276 (8)	20.0	<.001

[a] *p*-value refers to comparison between consort and nonconsort males.

Numbers in parentheses are sample sizes.

TBF on capture expended less TBP per day (Pearson $r = -.735$, $N = 26$, $p < .0001$; Figure 1). All males lost TBE throughout the sampling period with a mean loss of 56.3 ± 5.0 MJ day^{-1} (Table 2). Assuming an energy density of 39.3 MJ kg^{-1} for fat and 23.6 MJ kg^{-1} for protein (Schmidt-Nielsen, 1990), fat and protein catabolism accounted for 79.9 ± 4.2% and 18.2 ± 4.1%, respectively, of the daily change in TBE. All of the 26 males with body composition data also had estimates of water flux (Table 2). All males apart from one visited the sea and fed. The mean daily food intake was 0.4 ± 0.04 kg day^{-1} ($N = 26$), which gave a mean daily MEI of 1.9 ± 0.2 MJ day^{-1} (CV = 49.5%). Mean DEE was 58.2 ± 4.9 MJ day^{-1}. The percentage DEE that was gained from food varied between 0% and 21% (4.5 ± 0.8%). There was no relationship between DEE and capture mass (Pearson $r = .159$, $N = 26$, $p = .439$). There was a strong negative relationship between percentage TBF at capture and percentage DEE gained from feeding (arcsine transformed data, Pearson $r = -.661$, $p < .001$; Figure 2).

Body size, body composition, and male mating tactics

Twenty-nine of the 42 males exhibited the primary tactic of consortship and mated with consort females. The number of consorts mated per male varied from 0 to 12 (see Appendix).
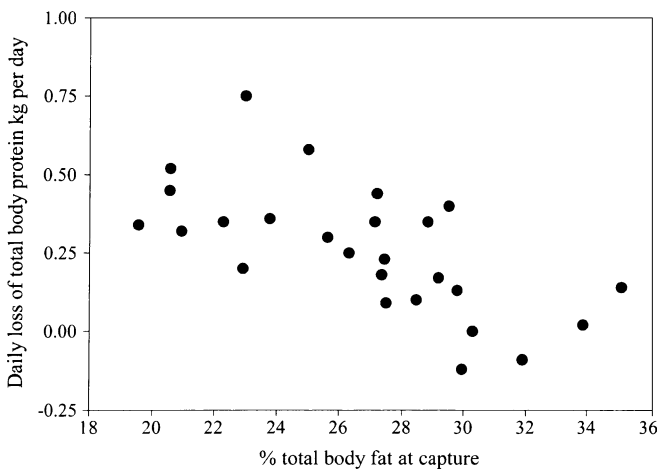

Figure 1
Daily loss of total body protein kg day^{-1} and the percentage total body fat at capture for male grey seals ($N = 26$) on Sable Island, Nova Scotia, 1997–2001.

Males that exhibited the primary tactic were heavier at capture than males that did not (ANOVA, $F_{1,40} = 15.3$, $p < .0001$; Table 1) and had absolutely more of each body component (MANOVA, $F_{3,33} = 5.74$, $p = .003$) and TBE (ANOVA, $F_{1,35} = 15.2$, $p < .001$). However, the proportion of each body component did not differ between consort and nonconsort males (MANOVA, $F_{3,22} = 0.611$, $p = .615$), indicating that they arrived in similar relative condition. Mass-specific mass loss per day and DEE also did not differ between consort and nonconsort males (ANOVA, $F_{1,38} = 0.565$, $p = .457$ and $F_{1,24} = 0.187$, $p = .669$, respectively).

For all males, the estimated number of pups sired per male through exhibiting the primary and alternative tactics varied between 0 and 3.2 (see Appendix). The estimated number of pups sired was correlated with the maximum duration of stay at a site (Pearson $r = .606$, $N = 42$, $p < .001$; Figure 3). To determine the relative importance of body size on the maximum duration of stay, a stepwise linear regression model was developed with body mass at capture, length, and age as predictor variables. The model with length and age excluded explained the greatest variation in duration of stay ($F_{2,39} = 5.01$, $p = .031$). Body mass at capture also showed a quadratic relationship with the number of consorts mated ($F_{2,39} = 4.91$, $p = .013$) and the estimated number of pups sired ($F_{2,39} = 5.40$, $p = .009$; Figure 4). To determine whether these relationships were driven by age with smaller, younger, and less experienced males being constrained by their low competitive ability and older, larger males suffering from the effects of senescence, stepwise linear regression models were developed with the linear and quadratic terms for body mass and age included. The original quadratic models with

Table 2

Daily water flux, energy intake, and expenditure for breeding grey seal males ($N = 26$) on Sable Island, 1999–2001

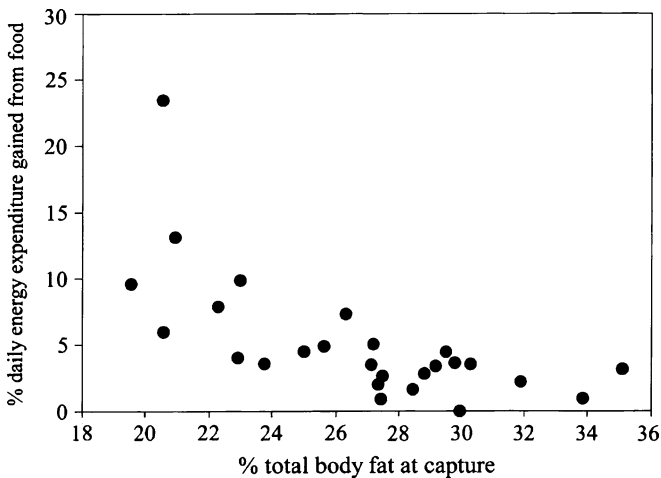|	Mean ± SE	CV%
Fractional daily water flux (k)	0.04 ± 0.003	25.0
Total body water flux (l day^{-1})	5.2 ± 0.4	35.6
Metabolizable food energy intake (MEI) (MJ day^{-1})	1.9 ± 0.2	49.5
Body energy expenditure (TBE) (MJ day^{-1})	56.3 ± 5.0	44.8
Daily energy expenditure (DEE) (MJ day^{-1})	58.2 ± 4.9	42.7
Percentage of DEE from MEI	4.5 ± 0.8	95.1

Figure 2
Percentage daily energy expenditure gained from food and percentage total body fat at capture for male grey seals ($N = 26$) on Sable Island, Nova Scotia, 1997–2001.

Figure 4
Estimated number of pups sired and the mass of males at capture for male grey seals ($N = 42$) on Sable Island, Nova Scotia, 1997–2001.

age excluded explained the greatest variation in success. Thus, the maximum duration of stay at a site increased with body mass, but intermediate-sized males mated with more consorts and achieved the highest success. Figure 4 also suggests there is a threshold body size for achieving success; males below 260 kg achieved zero or low success.

The DEE was not correlated with the maximum duration of stay at a site (partial [controlling for mass] $r = -.031$, df = 23, $p = .882$) or with the OSR (partial $r = -.068$, df = 23, $p = .745$). Thus, there appear to be no differential costs associated with components of a mating tactic. Of the 30 males that had complete TDR records, 27 males went to sea during the sampling period. The mean proportion of time spent at sea was 0.23 ± 0.04, and the mean deep-dive effort was 1.2 ± 0.2 h day^{-1}. Deep-dive effort was strongly correlated with the maximum duration of stay (partial $r = -0.559$, df = 27, $p = .002$) and the MEI (partial $r = .731$, df = 14, $p = .001$). Thus, males that had short periods of stay at a site and therefore mated with few consorts spent more time at sea deep diving, and males that dove deep acquired more energy from food.
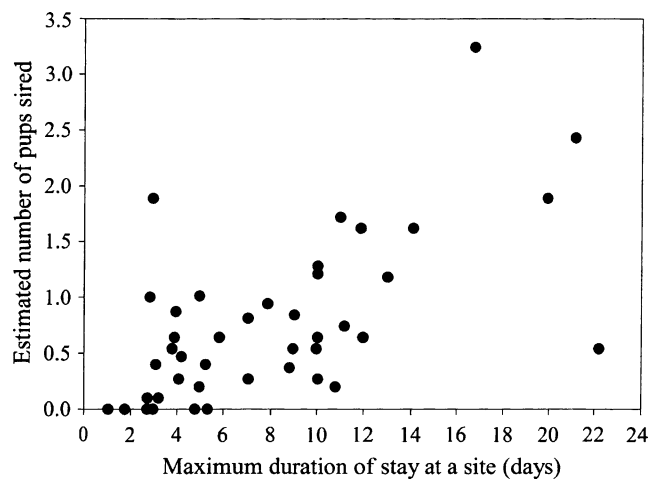
For the subset of males that was studied until they left the breeding colony ($N = 27$), the amount of TBE at capture was positively correlated with the duration of the breeding period (Pearson $r = .625$, $N = 22$, $p = .002$; Figure 5), and males that had a longer breeding period lost a greater proportion of their mass (Pearson $r = .472$, $N = 25$, $p = .017$). Consort males had a significantly longer breeding period (32 ± 1.4 days, $N = 17$) than nonconsort males (23 ± 2.2 days, $N = 10$; ANOVA, $F_{1,25} = 13.5$, $p = .001$). The duration of the breeding period was strongly correlated with the estimated number of pups sired (Pearson $r = .464$, $N = 27$, $p = .015$), but there was no relationship when capture mass was controlled for (partial $r = .012$, df = 24, $p = .953$).

DISCUSSION

Mating systems are typically conditional, and individuals are expected to exhibit the tactic that yields the greatest success relative to their state (Gross, 1996; McNamara and Houston,

Figure 3
Estimated number of pups sired and the maximum duration of stay at a site for male grey seals ($N = 42$) on Sable Island, Nova Scotia, 1997–2001.
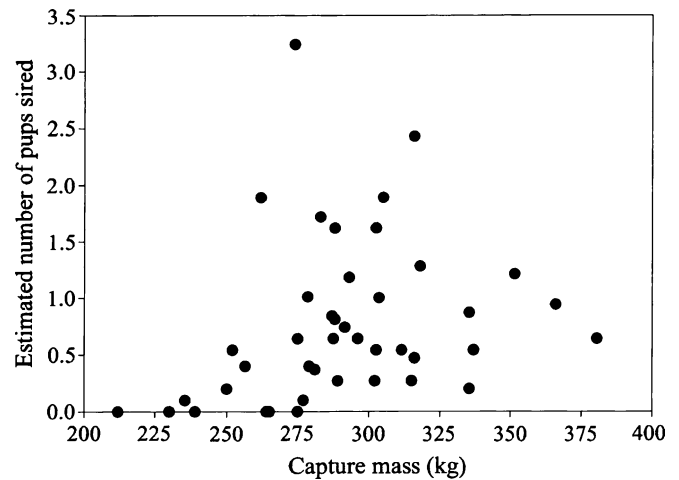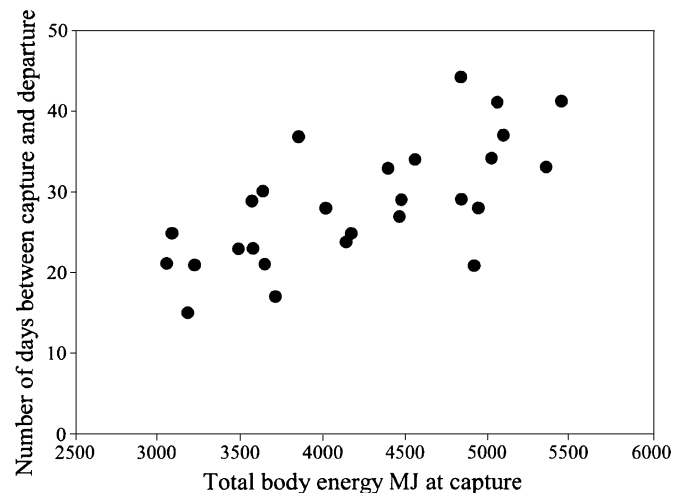

Figure 5
Number of days between capture and departure and total body energy at capture for male grey seals ($N = 27$) on Sable Island, Nova Scotia, 1997–2001.

1996). This study has shown that body size on arrival at the breeding grounds was an important determinant of the mating tactics exhibited by male grey seals and of their success. Males that exhibited the primary mating tactic of consortship were heavier, arrived with absolutely more body fat and energy reserves, and sustained breeding longer than those males that did not exhibit the primary tactic. Amongst all males, body fat, energy reserves, and the duration of the breeding period increased with body mass; however, intermediate-sized males mated with the most consorts and achieved the highest success. Many other studies have demonstrated relationships between size and success across several taxa (Enders, 1993; Fleming and Gross, 1994; Howard, 1978; McElligott et al., 2001).

Given that extraconsort fertilizations occur in grey seals (Ambs et al., 1999), we used the rates of fertilization success given in Lidgard et al. (2004) to estimate the number of pups sired by males. However, without a measure of success for the other alternative tactics and a better understanding of the frequency by which males exhibit alternative tactics, our measures of success should be treated as minimum estimates. Further, we have also assumed that the tactic of consortship yields the highest per capita success and is therefore the primary tactic (Gross, 1996), but we acknowledge that the two alternative tactics of which we have no estimates of fertilization success may achieve a higher success. However, we consider this unlikely. The order and timing of mating relative to ovulation has been shown to be important in determining fertilization success in some mammals (Huck et al. 1985, 1989; Preston et al., 2003). Thus, males that defend females and copulate on several occasions likely increase their chances of siring the offspring. Because alternative tactics do not involve a period of defense and may involve a single copulation, we consider it unlikely that their per capita success is higher than that of the primary tactic.

Large body size confers two advantages to a male: greater competitive ability in male combat and greater endurance (Andersson, 1994; Murphy, 1998). This study has shown that although the duration of stay at a site was correlated with body mass and success, intermediate-sized males achieved the highest success. Lidgard (2003) suggested that grey seal males on Sable Island might suffer from high male-male competition and high male turnover due to strongly male-biased OSRs. Thus, the ability of a male to engage in an extended period of consortship at a site might depend more on the male's competitive ability and less on the amount of body energy available for an extended period of stay. However, this will differ according to local variations in the degree of male-male competition.

Several previous studies on the grey seal have failed to find a relationship between size and success (Godsell, 1991; Tinker et al., 1995; Twiss, 1991). This might be due to excluding males that failed to establish consortships or a small sample size. In this study, the number of consortships varied among males, and body mass at capture was both a determinant of the primary tactic of consortship and a predictor of the number of consortships and success. However, the relationship between body mass and success was not linear but rather quadratic, suggesting that intermediate-sized males achieved the highest success. We found no evidence to suggest that this relationship was driven by male age, thus body mass rather than age appears to be an important determinant for exhibiting the primary tactic of consortship and achieving success in male grey seals. In ungulates, male combat typically involves clashes, butts, and pushing behaviors (e.g., Clutton-Brock et al., 1979); thus, larger, heavier males with larger horns or antlers achieve the highest success (Coltman et al., 2002; McElligott et al., 2001; Preston et al., 2003). Similar

forms of male combat occur in elephant seals (*Mirounga* spp.; Le Boeuf and Petersen, 1969), where male size determines rank, which, in turn, determines success (Fabiani et al., 2004; Haley et al., 1994). However, the behavior of male grey seals during combat is quite different. Although pushing and clashing behaviors do occur, wrestling appears to be more important, and the winner in aggressive encounters is often the male that bites the opponents' hind flippers, which requires a certain degree of agility (Twiss, 1991). Males also need to move quickly to chase opponents away from the area of defense. Thus, large males may simply be too large and lack the required agility to be successful in male combat and defend multiple females. This study also suggests there is a threshold body mass for exhibiting the primary tactic of consortship and for achieving success. Body mass is likely important during male combat in pushing and clashing events. An intermediate body size may therefore provide the necessary strength and agility to be successful in defending multiple females from male competitors. This suggests that stabilizing selection may be operating on body size in male grey seals.

Thirteen males did not exhibit the primary tactic of consortship and achieved low success. Of these, seven were 14 years old or less and are thus likely to increase in body size with concomitant increases in success (McLaren, 1993). While young and small, these males may express alternative mating tactics as a means to maximize their age-specific reproductive output (Dunbar, 1982). However, the remaining older males are likely to be at a disadvantage as a result of their smaller body size for the remainder of their reproductive life. Differences in size at adulthood among males may be partly attributed to genetic variation, maternal effects on weaning mass (Mellish et al., 1999), and environmental influences on growth (Festa-Bianchet et al., 2004; Lindström, 1999). If small males are never able to exhibit the primary mating tactic and experience a lower lifetime reproductive success as a result, they may exhibit alternative mating tactics as means to 'make the best of a bad job' (Dunbar, 1982). Although alternative tactics have a lower probability of fertilization success than the primary tactic (Lidgard et al., 2004), within a single breeding season small males may be able to achieve at least some success through exhibiting alternative tactics. Indeed, if male grey seals mate at sea, as suggested by Worthington Wilmer et al. (1999), small size may provide an advantage through greater agility in aquatic male combat (Andersson, 1994). Further, other components of state, in addition to body mass, such as experience, and sex and stress hormones are likely to influence success. Alexander and Irvine (1998) and Abott et al. (2003) have shown that in horses and some species of primate, subdominant individuals have higher basal levels of the stress hormone cortisol. High levels of cortisol contribute to lower levels of testosterone and inhibition of dominant or territorial behaviors (Boonstra and Singleton, 1993; Moore, 1991; Sapolsky, 1985).

Large males arrived with relatively and absolutely more body fat and body energy than smaller males and were able to sustain breeding for longer. Judge and Brooks (2001) have demonstrated that male bullfrogs that arrive at the breeding grounds in better condition (i.e., greater body mass per unit length) have longer periods of tenure. In this study, large males were also able to minimize protein catabolism, whereas smaller males with absolutely less fat expended more of their body protein as energy and acquired more energy through food intake. In penguins where both the male and female sustain long periods of fasting during the breeding season, critically low fat stores (20–30% of initial fat stores expended) may be part of a stimulus that initiates feeding trips (Groscolas and Robin, 2001). A similar refeeding stimulus

may occur in those male grey seals that remain at a site in defense of females for extended periods of time. In this study, one male stayed at the same location for a period of 24 days. At day 21, percentage TBF was 12%, and he had expended 32% of initial fat reserves. Two days after leaving this site he went to sea for 2 days. Deutsch et al. (1994) suggested that a similar stimulus for feeding may operate in northern elephant seals (*Mirounga angustirostris*).

Coltman et al. (1998) have shown that small harbor seal males forage prior to and during the availability of estrous females to overcome the energetic constraints of small size. Judge and Brooks (2001) have demonstrated energetic constraints on the breeding behavior of male bullfrogs. We found that males that had short maximum periods of stay, and therefore more likely to exhibit only alternative tactics, spent more time engaged in deep diving, and deep-dive effort was strongly correlated with food intake. However, we found no evidence to suggest that spending short periods of time at a site was more energetically demanding than remaining at a site for long periods. Thus, we are unable to conclude whether small grey seal males suffer from energetic constraints. Further, although the size of body fat reserves and the extent of protein catabolism may be involved in stimulating feeding, trips to sea may also occur in response to failing to establish consortship, losing consortship, or simply taking a break in between periods of consortship. Male wood bison (*Bison bison athabascae*) have been shown to take breaks in between periods of defending female groups, and this is thought to allow them to regain condition (Komers et al., 1992).

Despite differences in mating tactic, consort and non-consort males arrived at the breeding grounds in similar condition and expended the same relative amount of energy. Initial percentage TBF in four species of pinniped representing different mating systems is very similar to the initial percentage TBF reported in this study (22–29%; Boyd and Duck, 1991; Coltman et al., 1998; Kovacs et al., 1996; Crocker DE, Webb PM, and Houser DS, unpublished data). If there are costs associated with energy storage (Beck et al., 2003; Jönsson, 1997), this comparison suggests that males may optimize the size of their stored energy but ultimately are limited by their body size. Coltman et al. (1998) found no significant differences in the daily specific energy loss among species of pinniped representing aquatic and terrestrial mating systems. If there are reproductive costs associated with energy expenditure (Clutton-Brock, 1984), males may optimize the trade-off between the energy expended in one season and the subsequent reproductive costs such that males of all body sizes, regardless of the mating system, expend the same relative amount of body energy during the breeding season. This highlights the advantages of a large body size for endurance rivalry in breeding male pinnipeds.

APPENDIX

Table A1

Phenotypic characteristics, initial body composition, record duration, maximum duration of stay, and mating and reproductive success for breeding grey seal males on Sable Island, 1997–2001 (see text for explanation of abbreviations)

Male	Age (years)	Initial mass (kg)	Length (m)	TBW (kg)	TBF (kg)	TBP (kg)	TBE (MJ)	Record (days)	Max. duration of stay (days)	Consort matings	Nonconsort matings	Number of pups sired[a]
1997												
6	11	252.0	2.0					10.0	19.9	2	0	0.5
2	23	262.0	1.9					20.0	27.9	7	0	1.9
7	12	289.0	2.0					10.0	19.8	1	0	0.3
1	23	351.5	2.1					10.0	22.8	3	4	1.2
1998												
8	12	264.0	1.8	121.7	98.6	38.6	4868	3.0	20.0	0	0	0
4	24	288.0	2.2	141.1	95.2	45.6	4906	7.0	25.0	3	0	0.8
9	12	288.0	2.0	140.8	95.7	45.5	4920	14.1	23.1	6	0	1.6
5	25	293.0	2.2	155.0	80.1	51.2	4437	13.0	24.0	4	1	1.2
3	20	302.5	2.1	149.1	98.7	48.3	5109	11.9	23.3	6	0	1.6
11	11	318.0	2.2					10.0	19.1	4	2	1.3
10	11	337.0	2.3	165.1	111.4	53.3	5740	3.8	21.9	2	0	0.5
1999												
16	13	212.0	2.0	111.9	58.3	36.9	3220	2.7	15.2	0	0	0
13	12	230.0	2.1	127.9	53.7	42.8	3181	1.8	15.0	0	0	0
12	10	239.0	2.1	137.4	49.2	46.4	3086	5.3	16.9	0	0	0
14	12	256.5	2.1	139.3	64.8	46.3	3710	3.1	17.0	0	4	0.4
21	29	277.0	2.2	161.2	54.1	54.6	3482	2.7	20.0	0	1	0.1
20	29	279.0	2.0	149.5	73.4	49.6	4130	5.2	17.1	0	4	0.4
19	26	291.5	2.1	154.2	79.7	50.9	4414	11.2	17.9	2	2	0.7
15	14	296.0	2.0	156.9	80.5	51.8	4468	5.8	19.0	2	1	0.6
18	21	305.0	2.1	155.2	92.3	50.7	4914	2.9	15.1	7	0	1.9
17	21	316.0	2.1	164.0	91.0	53.9	4938	4.2	19.8	1	2	0.5

Table A1, Continued

Male	Age (years)	Initial mass (kg)	Length (m)	Initial body composition				Record (days)	Max. duration of stay (days)	Number of females mated		Number of pups sired[a]
				TBW (kg)	TBF (kg)	TBP (kg)	TBE (MJ)			Consort matings	Nonconsort matings	
2000												
131	14	265.0	2.1	149.3	59.0	50.1	3571	4.8	16.0	0	0	0
128	22	275.0	2.2	157.9	56.9	53.2	3563	1.0	13.9	0	0	0
124	27	278.5	2.2	159.4	58.3	53.7	3630	5.0	17.8	3	2	1.0
115	22	281.0	2.2	157.1	64.4	52.6	3845	8.8	27.0	1	1	0.4
122	26	302.0	2.2	160.2	81.9	52.9	4551	4.1	19.9	1	0	0.3
117	13	303.5	2.2	151.1	96.8	49.1	5052	2.8	26.3	0	10	1.0
114	15	311.5	2.3	162.4	88.6	53.4	4830	22.2	30.2	2	0	0.5
118	13	315.0	2.2	152.6	106.7	49.2	5448	7.1	27.1	1	0	0.3
119	14	316.0	2.2	161.6	94.6	52.8	5056	21.2	22.1	9	0	2.4
120	26	366.0	2.3	204.4	84.1	68.5	5017	7.9	21.2	2	4	0.9
2001												
197	16	235.5	2.1	135.1	48.9	45.6	3055	3.2	21.2	0	1	0.1
195	28	250.0	2.2	135.2	64.0	44.9	3644	5.0	19.0	0	2	0.2
188	23	274.0	2.1	157.6	56.3	53.2	3537	16.8	31.0	12	0	3.2
194	16	275.0	2.1	140.9	81.9	46.1	4386	3.9	25.9	2	1	0.6
189	28	283.0	2.2	146.2	82.6	47.9	4457	11.0	27.0	6	1	1.7
198	23	287.0	2.3	158.8	68.2	53.1	4008	9.0	19.1	2	3	0.8
206	31	287.5	2.2	156.1	72.8	51.9	4161	12.0	24.9	2	1	0.6
191	15	302.5	2.1	144.0	106.2	46.1	5356	9.0	31.1	2	0	0.5
192	31	335.5	2.2	177.3	92.0	58.5	5090	10.8	28.8	0	2	0.2
196	23	335.5	2.2	182.5	83.9	60.8	4835	3.9	17.0	1	6	0.9
208	28	380.5	2.3	195.7	112.2	64.1	6033	10.0	22.8	2	1	0.6

[a] Number of pups sired estimated according to the following correction factors: number of consorts × 0.27; number of nonconsorts × 0.10 (Lidgard et al., 2004).

Males are listed according to the year and in ascending order of body mass.

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