

A novel mobile approach to investigating mating tactics in male grey seals (*Halichoerus grypus*)

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Abstract

Studies of the grey seal *Halichoerus grypus* mating system, using focal animal sampling constrained by study site location and size, limit the measurement of variation in male mating tactics and success. Using this method, the mating tactics of grey seal males have been classified as either 'tenured' or 'transient'. Preliminary evidence is presented of wider variation in male mating tactics and success using mobile focal-animal techniques that are not constrained by site, and of the effects of age on behaviour when accounting for body mass. The study was conducted during the breeding seasons of 1997 and 1998 at Sable Island, Nova Scotia. Six young (11–12 years) and five old (20–25 years) males were captured at the beginning of the breeding season, weighed and fitted with a VHF transmitter and time-depth recorder. Each male was located daily, and a count of late-lactating females within a 10 m radius recorded as a measure of mating potential. Female guarding and observed copulatory attempts were used as a measure of mating success. Mean initial body mass of young males and old males was similar, 291 ± 13 kg and 298 ± 14 kg, respectively. All males changed location during the study period. Young males changed sites more often and moved shorter distances between sites than old males. Estimated mating success varied from probably no matings to a minimum of seven; there were no differences between young and old males. Maximum duration of stay at a site and the number of late-lactating females at a site significantly influenced mating success. All the males except for two young males departed on diving excursions during the breeding season and engaged in deep diving behaviour. Diving behaviour did not differ between the age classes. Our results indicate that the current classification of mating tactics in grey seal males is an oversimplification. Preliminary data show that age may account for some of the variation in male behaviour on land and mating success, but not for behaviour at sea.

Key words: *Halichoerus grypus*, mating systems, alternative mating tactics, reproductive ecology

INTRODUCTION

Variation in the genotype and phenotype of individuals and in their responses to changes in the social and ecological environment may be the major proximate causes of intraspecific variation in mating systems (Emlen & Oring, 1977; Dunbar, 1982). This variation may lead to a mixed evolutionary stable strategy where a set of alternative strategies yielding equal fitness are maintained through frequency-dependence (e.g. the ruff *Philomachus pugnax*; Widemo, 1998). However, it is becoming apparent that a more common situation is for conditional stable strategies in which a primary tactic is

pursued by most males but, owing to ontogenetic, historical or social constraints, subordinate males pursue alternative tactics that yield lower fitness (Dunbar, 1982; Caro & Bateson, 1986; Gross, 1996). The mating system of the grey seal *Halichoerus grypus* has been described as polygynous (Anderson, Burton & Summers, 1975; Boness & James, 1979; Anderson & Fedak, 1985; Tinker, Kovacs & Hammill, 1995). Behavioural studies have identified two male tactics, the most successful of which has been termed the 'dominant' or 'tenured' tactic. In this tactic, a mature male arrives at the breeding colony with stored energy reserves and maximizes his mating success by defending and maintaining his position within a group of females throughout the season (Anderson *et al.*, 1975; Boness & James, 1979; Anderson & Fedak, 1985). Several studies have shown a positive correlation between length of

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tenure and mating success and have suggested that younger males adopt a transient pattern of behaviour and are the least successful (Anderson *et al.*, 1975; Boness & James, 1979; Godsell, 1991; Twiss, Pomeroy & Anderson, 1994; Tinker *et al.*, 1995).

Most of these studies of male mating behaviour in grey seals used focal-animal techniques at a fixed site representing only a small portion of the breeding colony. This methodology potentially limits our understanding of the mobility and opportunistic nature of alternative mating tactics. Thus, the view that young, small male grey seals adopt alternative tactics which yield low rates of mating success and are overall classed as sub-optimal, may be an outcome of inappropriate methodology.

One of the more recent studies (Godsell, 1991), which highlighted variation in grey seal male tactics, investigated the role of age and size on behaviour of males that remained in a given area and for those that did not. Based on this study it seems that young sexually mature males (>7 years; Hammill & Gosselin, 1995) were unable to compete for tenure until 13 years of age or older. By attempting to relocate both young and older males that moved from the main study area, Godsell found that younger males seemed to adopt a tactic that was more mobile than that of older males. However, Godsell also found that some older, larger males occupied more than one site, either as a tenured male or as a transient. Although Godsell (1991) searched part of the colony for males that had moved from the study site, her ability to relocate males was limited by the large colony and because males were only identifiable by paint marks. Moreover, she ignored movements of <250 m.

The objectives of this study were to demonstrate that a mobile approach to studying the mating tactics of grey seal males is likely to reveal greater variation than has previously been shown, and to provide a preliminary analysis of the effects of age on mating behaviour.

METHODS

The study was conducted from early January to early February, during the breeding seasons of 1997 and 1998 at Sable Island (45°55'N, 60°00'W); a crescent-shaped partially vegetated sand-bar *c.* 40 km long, 1.5 km wide and 288 km east-south-east of Halifax, Nova Scotia. The island supports a large breeding colony of grey seals from late December to mid-February. A small number of seals were branded at weaning and thus were of known age. A total of 6 young (11–12 years) and 5 old (20–25 years) branded males was captured at the start of the season using a nylon net fastened between 2 aluminium poles. Males were weighed using tandem 300 kg (± 1 kg) Salter spring balances and were then immobilized, by giving an intramuscular injection of the chemical anaesthetic Telazol (dose 0.45 mg/kg), to allow attachment of telemetry and data-logging devices. Each male was fitted with a VHF transmitter (164–165 MHz, Advanced Telemetry Systems, Isanti, MN) to assist with

relocating them on the island and a Mk3 (100 g, 15 cm long * 2.5 cm diameter) or Mk5 (45 g, 6.5 cm long, 3.5 cm wide, 1.5 cm deep) Time-Depth Recorder (TDR; Wildlife Computers, Woodinville, WA) to record overall activity and diving behaviour at sea. The TDR and VHF transmitter were attached to the hair of the seal using a 5-min epoxy as described in Boness, Bowen & Oftedal (1994). The entire instrument package weighed 350 g, *c.* 0.12% of the mean initial mass of males. The TDR units were programmed to sample every 10 s, recording depth when submerged in seawater and counting the number of periods when dry. Depth was measured to an accuracy of 1 m. Males were recaptured at the end of the season to remove their devices. Males were restrained for 15–40 min at each capture.

Each male was relocated 2 or 3 times/day using a R2000 VHF receiver (Advanced Telemetry Systems) and a dipole and Yagi antenna secured to an all-terrain vehicle. A GPS (Garmin 75) reading was taken for each new location to measure the distance moved between sites. Given the inherent error in GPS positional data, a male was recorded as being in a new location if he had moved >100 m from his previous location. To determine whether the density of males and females in oestrus had an influence on the movement and mating success of a male, the number of males, females and age-classified pups within a 10 m radius of the male was recorded at each sighting of the male. We assumed that females came into oestrus when their pup was in the late stage-class III (see Kovacs & Lavigne, 1986 for description of the classification scheme), i.e. about 14 days of age (Boness & James, 1979). Thus the number of late-lactating females, i.e. those that had either weaned their pup or had a pup of stage III, IV or V, was used as a measure of the number of oestrous females.

Using DNA typing, Amos *et al.* (1993) and Ambs *et al.* (1999) have shown that proximity to a female during perioestrus is a reasonable indicator of relative reproductive success in male grey seals although not an assurance of paternity. In this study, given that copulations are rarely observed, female attendance in addition to copulatory behaviour, were used as an index of mating success. Females and pups of age class III in proximity to the male were marked for individual identification using either Rodamine dye or an oil-based paint. For each sighting, as a measure of female defence, the identity of those marked females that had the focal male as their nearest male neighbour were recorded. An index of mating success was then derived by assuming success: (1) if a focal male maintained a nearest-neighbour position to a marked female for 2 days; or (2) was observed attempting to copulate or copulating with a female.

Dive analysis

Data from each TDR were analysed using software from the manufacturer (Wildlife Computers). Before

analysis depth values were adjusted for drift in the 0-depth reading, which may have occurred during data collection, using the Zero-Offset-Calibration program and converted into a binary file. Each binary file was then analysed using the program Dive Analysis to provide estimates of dive parameters (defined according to definitions in the Dive Analysis program) for each record.

Dive duration: the duration between the time of the surface readings immediately preceding and following the dive, minus 1 sampling interval.

Dive depth: the maximum depth reading that was taken during the dive.

Bottom time: the time between the first and last depth reading $\geq 85\%$ of the maximum depth.

Dive effort: number of min of dives ≥ 10 m per hour of TDR deployment (Boness *et al.*, 1994).

Based on previous studies (Boness *et al.*, 1994; Coltman *et al.*, 1997) and the inspection of data from this study, dives were analysed as bouts defined according to shallow or deep. Shallow dive bouts were operationally defined as those that began with 4 consecutive dives of < 10 m but > 4 m, and terminated with 4 consecutive dives of ≥ 10 m, or a dry or submerged (dives < 4 m) period > 15 min. Deep dive bouts were defined as those that began with 4 consecutive dives > 10 m and terminated with 4 consecutive dives of < 10 m or a dry or submerged period > 15 min.

Data analysis

To allow for disturbance effects of capture on male behaviour, the first datum used was the male's position at the earliest time the day after capture. Data collection ended on the day of re-capture. A search-protocol was used to ensure equal searching effort among males. To confirm the location of a male, a sighting was required. If a male had moved from his previous location and no VHF signal was heard, a VHF search was conducted for 3 km west and east of the previous location. If no signal or an intermittent signal was heard, the male was assumed to be at sea and this was later confirmed by comparing VHF data with TDR records. Garmin Map Source software was used to measure the distance between locations. It was assumed that if a male was at the same location, he had not moved in between any 2 sampling times. If a male returned from a trip to sea and his location on land was recorded within 24 h of his arrival, it was assumed that he had been at that location since his arrival on land. Time of arrival and departure were determined from TDR records. If the location was not recorded within 24 h of his arrival, it was described as unknown until a sighting was recorded. If a male hauled out between trips to sea for a period of < 24 h and was not sighted, his location was also described as unknown and the amount of time spent on land was determined from the number of 10-s dry periods recorded by the TDR.

As several studies have shown that initial body mass

influences male reproductive behaviour (Godsell, 1991) and mating success (grey seal, Anderson & Fedak, 1985; Godsell, 1991; northern elephant seal, Haley, 1994; Haley, Deutsch & Le Boeuf, 1994), to examine possible age effects, male mass was used as a covariate in all analyses (ANCOVA). Behavioural data were transformed for the ANCOVA except for counts and dive measures, for which we could not find a suitable transformation. Thus, for these data we applied both non-parametric and parametric tests and found that both tests yielded the same result in all analyses. Thus, in the text we will refer to results from the parametric analyses. Statistical analyses were performed using SPSS version 9.0 for Windows, and the probability level for significance was $\alpha = 0.05$. Standard error is given to describe variation about the mean.

RESULTS

One 11-, one 12- and two 23-year-old males were captured in 1997, and four 11- and 12-year-old males and one 20-, 24- and 25-year-old males were captured in 1998. All males were re-captured at the end of the season. Data were collected from 4 January to 1 February 1997 and from 3 to 27 January 1998. Because of the small sample sizes in each year, year effects were not examined and data from both years were pooled. Young and old males did not differ in mean initial body mass (291 ± 13 kg vs 298 ± 14 kg, respectively; *t*-test: $t_9 = -0.38$, $P = 0.71$).

Behaviour on land: movement and associations with males and females

Behavioural characteristics of mating tactics on land differed among males. Only one male exhibited behaviour typical of the tenured tactic, described in previous studies as staying at the same site for the entire time on the island. Although this male changed location late in the season, subsequent data could not be collected because we had to depart from the island. All other males changed location more than once during the study period. The number of sites visited for all males varied between two and 11 (Table 1). Young males visited more sites than old males (ANCOVA: $F_{1,9} = 5.54$, $P = 0.046$; Table 2). Five males re-visited previous locations either after going to sea or moving directly from another location in the colony. The distance travelled between consecutive sites could only be calculated for 10 of the 11 males because of insufficient GPS data for one male. Distance travelled varied from 0.1 km to *c.* 22 km. The mean distance between sites was significantly shorter for young males (1.9 km) than for old males (4.8 km) (ANCOVA: $F_{1,8} = 10.03$, $P = 0.016$), but there was wide variation for both age classes as shown by the high coefficients of variation in Table 2.

The duration of time spent at each site also varied

Table 1. Descriptive statistics of components of the mating tactics of male grey seals *Halichoerus grypus* for 11 males on Sable Island, Nova Scotia 1997–1998

Age (years)	Initial mass (kg)	No. of sites visited	Distance between sites, range (km)	Duration of stay at a site, range (days)	Median date of dive trips	No. of dive bouts	No. of dives	Dive effort ^a (min/h)	Mating success ^b
11	252	3	0.2–0.3	4.9–9.1	—	—	—	—	2
11	337	11	0.1–7.2	0.2–3.7	18	13	110	0.4	2
11	318	5	0.1–0.5	0.9–10.0	—	—	—	—	6
12	289	5	0.2–1.3	0.1–10.1	10	1	37	0.5	1
12	264	9	0.8–20.0	0.2–3.2	16	27	946	9.7	0
12	288	8	0.1–5.3	0.2–13.8	7.5	9	251	2.2	6
20	303	2	2.0	8.1–10.6	15	8	231	2.0	6
23	346	5	0.7–1.9	0.2–10.1	8	8	141	0.5	6
23	262	2	5.1	19.8	25	22	711	3.9	7
24	288	5	4.3–21.8	0.2–6.7	—	11	279	1.4	4
25	293	5	—	0.1–7.0	24	2	32	0.5	5

^a No. of min of deep diving (> 10m) per h of TDR deployment.

^b No. of females likely to have been mated by focal male (see description in Methods).

Table 2. Characteristics of the mating tactics of male grey seals *Halichoerus grypus* on Sable Island, Nova Scotia 1997–1998; movement, association with males and females and mating success. Data are given as the mean, and range, of means calculated from each individual male

	All			Young			Old			<i>P</i> ^d
	Mean	Range	CV%	Mean	Range	CV%	Mean	Range	CV%	
No. of sites visited	5.5	2–11	52.1	6.8	3–11	43.8	3.8	2–5	43.2	0.046
Mean distance between sites (km)	3.0	0.3–10.9	114	1.9	0.3–6.5	127	4.8	1.2–10.9	92.2	0.016
Mean duration at a site (days)	5.2	1.1–19.8	103	3.1	1.1–6.3	64.8	7.9	2.3–19.8	91.3	NS
Maximum duration at a site (days)	9.5	3.2–19.8	48.9	8.3	3.2–13.8	49.3	10.9	6.7–19.8	48.9	NS
Minimum duration at a site (days)	3.2	0.1–19.8	192	1.1	0.1–4.9	177	5.7	0.1–19.8	151	NS
% of total time spent at unknown sites	3.5	0–19.1	176	3.4	0–19.1	224	3.6	0–7.3	108	NS
Mean no. of:										
Males	1.5	0.2–2.6	56.7	1.4	0.2–2.6	75.8	1.7	0.8–2.6	38.8	NS
Early-lactating females ^a	0.9	0.2–2.0	72.1	0.6	0.2–1.2	55.9	1.2	0.3–2.0	64.9	NS
Late-lactating females ^b	1.7	0.5–3.2	59.3	1.0	0.5–1.6	45.2	2.5	1.8–3.2	22.3	0.001
Mating success ^c	4.1	0–7	59.3	2.8	0–6	90.5	5.6	4–7	20.4	NS

^a Early-lactating females are classed as either pregnant females, or females with a pup of stage I or II.

^b Late-lactating females are classed as either females that have weaned their pup, or females with a pup of stage III, IV or V.

^c No. of females likely to have been mated by focal male (see description in Methods).

^d *P* value refers to result of ANCOVA between young and old males.

considerably from *c.* 2 h to 20 days with a mean of 5 days. There were no significant differences between the two age classes in the amount of time males spent at each site, although old males had higher coefficients of variation in the amount of time they spent at each site (Table 2).

The mean daily number of males within 10 m of the focal male was 1.5 and the mean daily number of early- and late-lactating females within 10 m of the focal male were 0.9 and 1.7, respectively (Table 2). Young and old males were in proximity to a similar number of males and early-lactating females. Young males associated with significantly fewer late-lactating females (ANCOVA: $F_{1,9} = 25.21$, $P = 0.001$) than old males and showed almost twice as much variation as old males in the number of males and late-lactating females within a 10 m radius.

Behaviour at sea: characteristics of dive bouts

Nine of the 11 males had diving trips during the study period (Table 1). Considerable variation was observed in diving behaviour among males, although we did not find differences between males of the two age classes (Table 3). Diving behaviour occurred throughout the breeding season, with the median date of dive trips for each male ranging between 7 and 25 January. The total number of dive bouts for each male varied from one to 27 and eight of the 11 males had eight dive bouts or more. The mean interval between dive bouts showed substantial variation (range 3 h to 3 days; $CV = 119\%$), with older males showing almost twice as much variation as younger ones (Table 3). Dive effort varied between 0.4 and 9.7 min/h. Dive effort was not significantly correlated with the mean (Spearman correlation:

Table 3. Characteristics of the mating tactics of male grey seals *Halichoerus grypus* on Sable Island, Nova Scotia 1997 to 1998 diving behaviour for all, shallow (< 10 m) and deep (> 10 m) bouts. Data are given as the mean, and range, of means calculated from each individual male

	All			Young			Old			<i>P</i> ^b
	Mean	Range	CV%	Mean	Range	CV%	Mean	Range	CV%	
All bouts										
Interval between dive bouts (h)	28.9	3.0–78.0	95.0	30.2	17.6–53.8	68.0	27.9	3.0–78.0	125	NS
Dive effort (min/h) ^a	2.3	0.4–9.7	127	3.2	0.4–9.7	138	1.7	0.5–3.9	84.1	NS
Shallow bouts										
No. of bouts	7.6	0–18	78.6	8.3	0–18	90.9	7	1–14	74.9	NS
Mean depth of bouts (m)	5.8	4.8–7.8	17.0	5.5	4.5–6.0	11.6	6.0	4.8–7.8	20.0	NS
Mean duration of bouts (min)	31.6	10.2–54.6	41.2	28.2	24.3–34.3	18.9	33.7	10.2–54.6	48.7	NS
Mean bottom time per dive (min)	0.7	0.2–1.5	52.8	0.8	0.5–1.5	68.6	0.7	0.2–1.0	44.0	NS
Deep bouts										
No. of bouts	3.7	1–9	85.0	4.3	1–9	80.0	3.2	1–8	99.7	NS
Mean depth of bouts (m)	34.3	17.1–49.7	34.9	31.9	17.1–49.7	48.9	36.2	26.6–49.5	26.7	NS
Mean duration of bouts (min)	387	51.6–737	52.5	362	51.6–616	67.0	408	266–737	47.5	NS
Mean bottom time per dive (min)	3.6	2.5–6.3	32.9	3.7	3.3–4.4	13.6	3.5	2.5–6.3	45.9	NS

^a No. of min of deep diving (> 10m) per h of TDR deployment.

^b *P* value refers to result of ANCOVA between young and old males.

$r_9 = 0.21$, $P = 0.59$) or maximum duration of stay at a site ($r_9 = 0.28$, $P = 0.46$).

Considerable variation in the pattern of shallow (< 10 m) and deep (> 10 m) diving behaviour was also observed (Table 3). Shallow diving was more frequent than deep diving (paired *t*-test: $t_8 = 2.82$, $P = 0.022$). The greatest number of shallow bouts for one male was 18 whereas the greatest number of deep bouts was nine. All males engaged in deep diving. The mean depth of deep dives was 34 m and the greatest depth to which a male dived was 96 m. The duration of deep bouts was significantly greater than the duration of shallow bouts ($t_7 = -4.96$, $P = 0.002$). The duration of shallow bouts varied from *c.* 10 to 55 min while the duration of deep bouts varied from *c.* 52 min to 12 h. The mean duration of bottom time was also greater in deep bouts ($t_7 = < 5.31$, $P = 0.001$). Except for the mean bottom time, coefficients of variation were higher for deep dive characteristics than for shallow. The number of bouts and bottom time showed the greatest variation (CV = 78.6% and 52.8%, respectively) in shallow diving, while the number of bouts and duration of bouts showed the greatest variation (CV = 85.0% and 52.5%, respectively) in deep diving.

Relationships between mating success and male tactic

Mating success varied from one male being entirely unsuccessful to a male that probably mated with seven females. Five males had a mating success of at least six females and the median was five. Young and old males did not differ significantly in their mating success (ANCOVA: $F_{1,9} = 3.80$, $P = 0.09$), but younger males showed much more variation (Table 2). Indeed, among old males, mating success showed the least variation of all the behavioural parameters measured, while among

young males, other than distance between sites, variation in mating success showed the greatest variation. Four of the five old males achieved success equal to or higher than the median for all males, and four of the six young males had a mating success lower than the median with one male being entirely unsuccessful.

The number of sites visited and the distance travelled between sites had no influence on mating success. The maximum duration of stay at a site was positively correlated with mating success (Spearman correlation: $r_{11} = 0.78$, $P = 0.004$), but there was no correlation for mean duration of stay ($r_{11} = 0.56$, $P = 0.08$). The duration of stay at a site was not dependent on the density of males, early- or late-lactating females at the site. Likewise, the density of males or early-lactating females at a site had no influence on mating success. However, there was a significant positive correlation between the mean number of late-lactating females within a 10 m radius of the male and mating success (Spearman correlation: $r_{11} = 0.72$, $P = 0.013$). Initial body mass did not correlate with mating success when age groups were pooled or treated separately.

DISCUSSION

Variation in male mating behaviour and methodology of study

Over the past three to four decades the numerous studies of the mating behaviour of male grey seals have revealed what seems to be substantial variation in male tactics across populations but little variation within them (Hewer, 1957; Hewer & Backhouse, 1960; Boyd & Laws, 1962; Darling & Boyd, 1964; Mansfield, 1967; Cameron, 1971; Hook & Johnels, 1972; Anderson *et al.*, 1975; Boness & James, 1979; Anderson & Fedak, 1985;

Tinker *et al.*, 1995; Twiss, Anderson & Monaghan, 1998). Grey seals breed in qualitatively different habitats (ice, expansive sand-flats, cliff-bound beaches, restricted-access island tops and caves), thus some of this variation is a product of habitat type and topography (Caudron, 1998; Twiss & Thomas, 1998; Twiss, Anderson *et al.*, 1998; Twiss, Caudron *et al.*, 2000). However, some of this variation is probably the result of misinterpretation of limited data. Our study shows that the limited within-colony variation in male mating tactics is an oversimplification and further that it may be largely a product of the methodology used. By locating focal males several times daily throughout the colony we have shown that males establish tenure at multiple locations within the colony. Indeed, of the 11 males, only one held a position at a single site throughout the season, behaviour typical of the tenured male tactic previously described (Boness & James, 1979). Moreover, this male departed on a 5-day trip to sea before returning to the breeding colony. The greater number of sites visited by males in the present study, compared to Godsell's (1991) study on Sable Island, probably occurred because Godsell confined her observations to only a portion of the island. It is clear that males travel considerable distances to find mating opportunities.

Although we found high within-colony variability in the length of stay at a site (the duration of stay at each site varied between 2.5 h and 20 days), the length of tenure for those males that stayed at least 2 days at a site, the threshold value defining tenure in the earlier studies, ranged from 3 to 20 days. This range is similar to that reported by Godsell (1991), Boness & James (1979) and Anderson *et al.* (1975).

Diving behaviour and potential foraging activity

Previous to this study there was little evidence to suggest that male grey seals at Sable Island or at other sites foraged during the breeding season (Sable Island: Boness & James, 1979; Godsell, 1991; North Rona: Anderson *et al.*, 1975; Anderson & Harwood, 1985; Ramsey Island: Davies, 1949; Isles of Scilly: Davies, 1956; Monach Islands: Anderson & Harwood, 1985; Twiss *et al.*, 1998; Cornwall: Caudron, 1998). Thus we were surprised to find that nine of the 11 study males went to sea and exhibited deep diving. Several lines of evidence suggest that males forage during these deep dives. The greatest mean depth that a male dived was 50 m. To reach this depth, bathymetry charts indicate that a male must travel 12 km from Sable Island. At this distance, it is unlikely that a male would intercept a sexually receptive female although it is possible that the male might follow a departing female. Second, several studies have associated deep diving behaviour in phocids during the breeding season with foraging behaviour (Testa, Hill & Siniff, 1989; Lydersen & Kovacs, 1993; Boness *et al.*, 1994; Coltman, Bowen, Boness *et al.*, 1997). Walker & Bowen (1993) found that the serum

of male harbour seals that have returned from sea, particularly early during the breeding season, had high concentrations of chylomicrons, indicative of recent feeding. Using isotope dilution methods to estimate food intake, Coltman, Bowen, Iverson *et al.* (1998) showed that deep diving harbour seal males derived about over half of their daily energy expenditure from feeding.

Effect of male age on mating behaviour

Our preliminary analysis of the effects of age on mating behaviour suggests that age may be a factor contributing to the mating tactic exhibited by individual male grey seals but we express caution here because our sample sizes are small. Young males changed locations more frequently and moved shorter distances between sites. They also showed much greater variability in most behavioural measures than old males. These results are consistent with the less detailed findings and anecdotal reports of Godsell (1991) and Boness & James (1979), who also found that young males on Sable Island were more transient than older males. Differences in age did not account for much of the variation observed in behaviour at sea. Shallow and deep diving behaviour was similar in both age groups with similar degrees of variation. All of the young and old males that visited the sea engaged in deep diving behaviour and thus it is probable that both young and old males engaged in foraging to some extent.

Mating success and male mating tactic

Estimated mating success varied considerably in our study, ranging from probably no matings to a minimum of seven. While our estimate of mating success is not directly comparable to that reported by Boness & James (1979), the range of success is of a similar magnitude. The maximum duration of stay at a site had important consequences for mating success. For Sable Island and North Rona, respectively, Ambs *et al.* (1999) and Amos *et al.* (1993) have shown that *c.* 60–70% of females are fertilized by the male that guards and defends them against approaches by other males during late lactation. Several studies have found a positive correlation between length of tenure and mating success (Anderson *et al.*, 1975; Boness & James, 1979; Godsell, 1991; Twiss *et al.*, 1994; Tinker *et al.*, 1995). This study also showed that a high mating success might be a result of residing in areas with a high number of oestrous females. Twiss *et al.* (1994) found that males with the highest mating success were those that held tenure in areas with the highest female density. Thus, a high mating success was achieved when a male remained tenured at a site that had a high proportion of late-lactating females and had the ability to remain associated with those females long enough to copulate.

By following males throughout the colony we have

shown that there is greater variation in the mating behaviour of grey seals than previously recognized, including apparent foraging behaviour, which has not previously been reported. Preliminary data show that male age may account for some of the variation in male behaviour on land and mating success, but not for behaviour at sea; further studies are required to confirm these trends. Our results do indicate that the current classification of the mating tactics of male grey seals is oversimplified.

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REFERENCES

- Ambs, S., Boness, D. J., Bowen, W. D., Perry, E. A. & Fleischer, R. C. (1999). Proximate factors associated with high-levels of extra-consort fertilizations in polygynous grey seals. *Anim. Behav.* **58**: 527–535.
- Amos, W., Twiss, S. D., Pomeroy, P. P. & Anderson, S. S. (1993). Male mating success and paternity in the grey seal, *Halichoerus grypus*: a study using DNA fingerprinting. *Proc. R. Soc. Lond. B Biol. Sci.* **252**: 199–207.
- Anderson, S. S., Burton, R. W. & Summers, C. F. (1975). Behaviour of grey seals (*Halichoerus grypus*) during a breeding season at North Rona. *J. Zool. (Lond.)* **177**: 179–195.
- Anderson, S. S. & Fedak, M. A. (1985). Grey seal males: energetic and behavioural links between size and sexual success. *Anim. Behav.* **33**: 829–838.
- Anderson, S. S. & Harwood, J. (1985). Time budgets and topography: how energy reserves and terrain determine the breeding behaviour of grey seals. *Anim. Behav.* **33**: 1343–1348.
- Boness, D. J., Bowen, W. D. & Oftedal, O. T. (1994). Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. *Behav. Ecol. Sociobiol.* **34**: 95–104.
- Boness, D. J. & James, H. (1979). Reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. *J. Zool. (Lond.)* **188**: 477–500.
- Boyd, J. M. & Laws, R. M. (1962). Observations on the grey seal (*Halichoerus grypus*) at North Rona in 1960. *J. Zool. (Lond.)* **139**: 249–260.
- Cameron, A. W. (1971). Territorial behaviour in the Western Atlantic grey seal (*Halichoerus grypus*). *J. Zool. (Lond.)* **164**: 433–449.
- Caro, T. M. & Bateson, P. (1986). Organization and ontogeny of alternative tactics. *Anim. Behav.* **34**: 1483–1499.
- Caudron, A. K. (1998). *Behavioural plasticity in function of the breeding environment in a marine mammal, the grey seal Halichoerus grypus*. PhD thesis, University of Liege, Belgium.
- Coltman, D. W., Bowen, W. D., Boness, D. J. & Iverson, S. J. (1997). Balancing foraging and reproduction in the male harbour seal, an aquatically mating pinniped. *Anim. Behav.* **54**: 663–678.
- Coltman, D. W., Bowen, W. D., Iverson, S. J. & Boness, D. J. (1998). The energetics of male reproduction in an aquatically mating pinniped, the harbour seal. *Phys. Zool.* **71**(4): 387–399.
- Darling, F. F. & Boyd, J. M. (1964). The life of the grey seal. In *The Highlands and Islands*: 239–254. Fisher, J., Gilmour, J., Huxley, J. & Stamp, L. D. (Eds). London: Collins.
- Davies, J. L. (1949). Observations on the grey seal (*Halichoerus grypus*) at Ramsey Is., Pembrokeshire. *Proc. zool. Soc. Lond.* **119**: 673–694.
- Davies, J. L. (1956). The grey seal at the Isles of Scilly. *Proc. zool. Soc. Lond.* **127**: 161–166.
- Dunbar, R. I. M. (1982). Intraspecific variations in mating strategy. In *Perspectives in ethology*: 385–431. Bateson, P. P. G. & Klopfer, P. H. (Eds). New York: Plenum.
- Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection and the evolution of mating systems. *Science* **197**: 215–223.
- Godsell, J. (1991). The relative influence of age and weight on the reproductive behaviour of male grey seals *Halichoerus grypus*. *J. Zool. (Lond.)* **224**: 537–551.
- Gross, M. R. (1996). Alternative reproductive strategies and tactics: diversity within sexes. *TREE* **11**: 92–97.
- Haley, M. P. (1994). Resource-holding power asymmetries, the prior residence effect, and reproductive payoffs in male northern elephant seal fights. *Behav. Ecol. Sociobiol.* **34**: 427–434.
- Haley, M. P., Deutsch, C. J. & Le Boeuf, B. J. (1994). Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Anim. Behav.* **48**: 1249–1260.
- Hammill, M. O. & Gosselin, J. F. (1995). Grey seal (*Halichoerus grypus*) from the northwest Atlantic: female reproductive rates, age at first birth, and age of maturity in males. *Can. J. Fish. Aquat. Sci.* **52**: 2757–2761.
- Hewer, H. R. (1957). A Hebridean breeding colony of grey seals, *Halichoerus grypus* (Fab.), with comparative notes on the grey seal of Ramsey Island, Pembrokeshire. *Proc. zool. Soc. Lond.* **128**: 23–68.
- Hewer, H. R. & Backhouse, K. M. (1960). A preliminary account of a colony of grey seals *Halichoerus grypus* (Fab.) in the southern Inner Hebrides. *Proc. zool. Soc. Lond.* **134**: 157–195.
- Hook, O. & Johnels, A. G. (1972). The breeding and distribution of the grey seal (*Halichoerus grypus* Fab.) in the Baltic Sea, with observations on other seals of the area. *Proc. R. Soc. Lond. B Biol. Sci.* **182**: 37–58.
- Kovacs, K. M. & Lavigne, D. M. (1986). Growth of grey seal neonates: differential maternal investment. *Can. J. Zool.* **64**: 1937–1943.
- Lydersen, C. & Kovacs, K. M. (1993). Diving behavior of lactating harp seals, *Phoca groenlandica*, females from the Gulf of St Lawrence, Canada. *Anim. Behav.* **46**: 1213–1221.
- Mansfield, A. W. (1967). The mammals of Sable Island. *Can. Field-Nat.* **81**: 40–49.
- Testa, J. W., Hill, S. E. B. & Siniff, D. B. (1989). Diving behavior and maternal investment in Weddell seals (*Leptonychotes weddelli*). *Mar. Mamm. Sci.* **5**: 399–406.
- Tinker, M. T., Kovacs, K. M. & Hammill, M. O. (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.
- Twiss, S. D., Anderson, S. S. & Monaghan, P. (1998). Limited intra-specific variation in male grey seal (*Halichoerus grypus*) dominance relationships in relation to variation in male mating success and female availability. *J. Zool. (Lond.)* **246**: 259–267.
- Twiss, S. D., Caudron, A. K., Pomeroy, P. P., Thomas, C. J. & Mills, J. P. (2000). Fine scale topographical correlates of

- behavioral investment in offspring by female grey seals (*Halichoerus grypus*). *Anim. Behav.* **59**: 327–338.
- Twiss, S. D., Pomeroy, P. P. & Anderson, S. S. (1994). Dispersion and site fidelity of breeding male grey seals (*Halichoerus grypus*) on North Rona, Scotland. *J. Zool. (Lond.)* **233**: 683–693.
- Twiss, S. D. & Thomas, C. J. (1998). Fine scale topographic influences on environmental potential for polygamy (EPP) in grey seals. In *European research on cetaceans-12*: 191–195. *Proceedings 12th Annual Conference ECS, Monaco, 20–24 January 1998*. Evans, P. G. H. & Parsons, E. C. M. (Eds). Valencia, Spain: European Cetacean Society.
- Walker, B. G. & Bowen, W. D. (1993). 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.
- Widemo, F. (1998). Alternative reproductive strategies in the ruff, *Philomachus pugnax*: a mixed ESS? *Anim. Behav.* **56**: 329–336.