

Diving behaviour during the breeding season in the terrestrially breeding male grey seal: implications for alternative mating tactics

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Abstract: We examined the diving behaviour of breeding male grey seals (*Halichoerus grypus*) at Sable Island, Nova Scotia, from 1997 to 2001. The proportion of time spent at sea varied between 0 and 78% ($N = 30$). Males engaged in deep (43.4 ± 3.3 m (mean \pm SE), $N = 27$) diving, and these dives were clustered into bouts, which mostly occurred during long trips (62.2 ± 14.7 h). We suggest that males spent time foraging during deep dives. Shallow diving (5.9 ± 0.1 m, $N = 27$) accounted for 40.8% of dives, which were also clustered into bouts that mostly occurred during short trips (2.1 ± 0.37 h). We suggest that shallow diving comprised a suite of behaviours, but included little foraging behaviour. Phenotypic traits had little influence on diving behaviour. Further work is required to understand the extent to which foraging behaviour enhances reproductive success, and whether shallow diving is a component of the mating tactics of male grey seals at Sable Island.

Résumé : Nous avons étudié le comportement de plongée de mâles du phoque gris (*Halichoerus grypus*) en période de reproduction à l'île de Sable, Nouvelle-Écosse, de 1997 à 2001. La fraction du temps passé en mer varie de 0 à 78 % ($N = 30$). Les mâles entreprennent des plongées profondes ($43,4 \pm 3,3$ m (moyenne \pm erreur type), $N = 27$) qui sont regroupées en épisodes, surtout durant les voyages prolongés ($62,2 \pm 14,7$ h). Nous croyons que les mâles passent une partie du temps de ces plongées profondes à la recherche de nourriture. Les plongées moins profondes ($5,9 \pm 0,1$ m, $N = 27$) représentent 40,8 % des plongées et elles se font aussi par épisodes, principalement durant les voyages courts ($2,1 \pm 0,37$ h). Nous pensons que les plongées peu profondes consistent en une suite de comportements, mais avec peu de recherche de nourriture. Les caractéristiques phénotypiques influencent peu le comportement de plongée. Seules des études additionnelles permettront de comprendre comment le comportement de recherche de nourriture contribue à améliorer le succès de la reproduction et de savoir si les plongées de faible profondeur font partie des tactiques d'accouplement chez les phoques gris de l'île de Sable.

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Introduction

The determinants of a polygynous mating system and the extent of polygyny include the spatial and temporal distribution of females or resources critical to female reproduction, and the ability of the male to exploit this potential for polygyny (Emlen and Oring 1977). In pinnipeds, dependence on limited terrestrial sites for parturition has favoured the evolution of a polygynous mating system (Bartholomew

1970; Stirling 1975; Boness 1991). Polygyny is most extreme in terrestrially breeding species in which females are highly gregarious and provide the opportunity for males to defend multiple females at one time (female-defence polygyny), e.g., the southern elephant seal, *Mirounga leonina* (Modig 1996), or defend territories within which females give birth and nurse young (resource-defence polygyny), e.g., the Antarctic fur seal, *Arctocephalus gazella* (McCann 1980). Males are able to exploit this high potential for polygyny because they provide no paternal care and have large body energy reserves that enable them to fast during the breeding season, thereby maximizing their time spent onshore defending females (Boness 1991). Thus, it has been assumed that terrestrially breeding male pinnipeds concentrate their time on land during the breeding season to maximize reproductive success.

The grey seal (*Halichoerus grypus*) is primarily a terrestrially breeding pinniped, although pagophilic (Haller et al. 1996) and aquatic (Hewer and Backhouse 1960; Caudron 1998) breeding occurs in some parts of the species' range. Males arrive at the breeding colony with large quantities of stored energy and compete for access to females. Studies have divided reproductively active males into two behavioural categories: dominant or "tenured" and subordinate or "transient". Males in the first category are considered to be the most successful and adopt a tactic whereby they main-

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tain a position within a loose group of females throughout the season (Anderson et al. 1975; Boness and James 1979; Anderson and Fedak 1985; Godsell 1991; Twiss et al. 1998). Several studies have shown a positive correlation between length of tenure and mating success (Boness and James 1979; Twiss et al. 1994; Tinker et al. 1995). Males in the second behavioural category are usually younger, smaller, and more mobile than tenured males and have lower mating success (Anderson et al. 1975; Boness and James 1979; Anderson and Fedak 1985; Godsell 1991; Twiss 1991). However, these studies have largely focused on individuals that remained at one site, thus the full behavioural repertoire of males may not be known. Although studies have shown that grey seal males go to sea during the breeding season (Davies 1949, 1956; Hewer 1957; Anderson and Harwood 1985), it has been assumed that they spend their time close to the colony and therefore do not forage.

In a recent study of male grey seals at Sable Island, Canada, Lidgard et al. (2001) found that they exhibited much greater variability in mating tactics than was previously believed. The majority of males visited several sites during the breeding season and, surprisingly, 9 of the 11 males studied went to sea and undertook a series of shallow and deep dives.

Several studies have associated bouts of relatively deep diving by male phocids during the breeding season with foraging behaviour (Coltman et al. 1997; Lesage et al. 1999). Given the positive correlation between length of tenure and mating success in grey seals, males may forage during the breeding season to increase their length of tenure at the breeding colony either by accumulating additional energy reserves or by decreasing the loss of stored reserves. Energetic constraints on breeding behaviour have been found in male harbour seals, *Phoca vitulina* (Coltman et al. 1998). If the capacity for tenure in the grey seal is constrained by body size, we may expect small males to spend more time at sea deep diving. Thus, behaviour at sea may have important implications for the mating success of male grey seals and be important to an understanding of intraspecific variation in the grey seal mating system.

The objectives of this study were to determine whether males are likely to forage during the breeding season. We did this by studying the characteristics of diving behaviour known to be associated with foraging in other pinniped species (e.g., Lesage et al. 1999; Baechler et al. 2002). Secondly, as male age and size are often implicated in alternative male mating tactics and may play a role in energy constraints (Le Boeuf 1974; Clutton-Brock et al. 1982; Dunbar 1982; Caro and Bateson 1986; Coltman et al. 1997), we examined the effects of male phenotype on diving behaviour.

Materials and methods

Study site, study animals, and instrument attachment

The study was conducted from late December to early February during the breeding seasons of 1997–2001 at Sable Island (43°55'N, 60°00'W), a crescent-shaped partially vegetated sandbar approximately 54 km long and 1.2 km wide, situated 288 km east-southeast of Halifax, Nova Scotia. Over the past several decades, grey seals have been periodically

branded at weaning, thus providing a pool of individually identifiable known-age adults.

Forty-two branded males were selected for the study and each male was studied in 1 of the 5 study years. Their ages (10–31 years) covered the reproductive life-span of this species (W.D. Bowen, D.J. Boness, S.J. Iverson, and J.I. McMillan, unpublished data) and a wide range of body masses were represented. In selecting males, priority was given to those that were fitted with a VHF transmitter the previous summer or autumn to allow us to determine when they first arrived on the island. Other males were selected as close to arrival on the island as possible, based on the results of weekly brand-resighting surveys of males on the entire island.

Males were captured at the start of the season using a hinged pole net and weighed using tandem 300 (± 1) kg Salter spring balances. For those males with a VHF transmitter upon arrival ($N = 25$), the median number of days between arrival and capture was 2. Males were then immobilized with an intramuscular injection of the chemical anaesthetic Telazol (0.45 mg·kg⁻¹) to allow attachment of telemetry and data-logging devices and to obtain an accurate measure of standard dorsal length (McLaren 1993). The length of two males was predicted from the regression of length on mass at initial capture: length (cm) = 163.7 + 0.17 × initial mass. Each male was fitted with a VHF transmitter (164–165 MHz; Advanced Telemetry Systems, Isanti, Minn.) to determine locations on land, and either a Mk3, Mk5, or Mk7 timed-data recorder (TDR; Wildlife Computers, Woodinville, Wash.) to measure overall activity and diving behaviour. The TDR and VHF transmitter were attached to the hair of the seal using a 5-min epoxy as described in Boness et al. (1994). The entire instrument package weighed approximately 350 g, about 0.12% (0.09–0.17%) of the mean body mass of males. The TDRs were programmed to sample every 10 s, recording depth when submerged in seawater and counting the 10-s periods when dry. Depth was measured to 1 m accuracy. Each male was relocated two or three times a day using a R2000 VHF receiver (164–165 MHz; Advanced Telemetry Systems) and a dipole antenna secured to an all-terrain vehicle. Males were recaptured at the end of the season to determine final body mass and recover instruments.

Data analysis

To allow for disturbance effects of capture on male behaviour, the first dive analysed was that recorded after the first land sighting the day after capture. To examine the influence of age on diving behaviour, males were divided into three age classes (young (10–14 years); intermediate (15–23 years); and old (24–31 years)) based on the 33rd and 66th percentiles, which represent increasing levels of breeding experience and decreasing adult growth rates (McLaren 1993). The 33rd and 66th percentiles were used to define three groups based on body mass (small (212–276 kg); medium-sized (277–302 kg); large (303–381 kg)) and length (small (183–208 cm); medium-sized (209–217 cm); large (218–229 cm)) at capture. When examining the effects of age on diving behaviour we used analysis of covariance (ANCOVA) to remove the effects of size (i.e., mass and length at capture), and likewise when examining the effects of size.

Dive analysis

Data from each TDR were analysed using software from the manufacturer (Wildlife Computers). Prior to analysis, depth values were adjusted for drift in the zero-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 Dive Analysis program to provide estimates of dive parameters (defined according to definitions in the Dive Analysis program) for each record. Based on the inspection of a histogram of dive depths, dives were split into shallow (<10 m) and deep. Dives were clustered into bouts of diving following Beck et al. (2003). Briefly, a bout began when three dives occurred consecutively within a 35-min period and terminated when the time to the next dive was significantly greater (t test, $p < 0.05$) than the mean time elapsed between dives currently included in a bout. The time spent at sea was further divided into trips. The start of a trip had the same definition as the start of a bout. A trip terminated when the TDR recorded a mean dry period of ≥ 15 min and the seal was assumed to have hauled out. Dry periods were confirmed, wherever possible, by sightings on land.

To gain a reasonable measure of foraging effort, we assumed that most foraging in this study occurred during the time when a male was at the bottom of a deep dive. This assumption was based on dietary (Bowen and Harrison 1994; Hammond et al. 1994) and telemetry (Thompson et al. 1991; Thompson and Fedak 1993) studies suggesting that grey seals are benthic foragers, and studies on the foraging behaviour of harbour seals (Coltman et al. 1997; Bowen et al. 2002) suggesting that most foraging occurs during deep rather than shallow dives. We therefore calculated diving effort separately for shallow and deep dives as the total time spent at the bottom of the dive per day as an estimator of foraging effort (after Beck et al. 2003):

$$[1] \quad \text{Diving effort} = \left[\left(\sum_{j=1}^i b \right) / 60 \right] / n$$

where b is bottom time (min), i is the total number of dives recorded, j is the dive number, and n is the number of days of sampling.

Dive-shape analysis

Given that we are primarily concerned with foraging behaviour, and that the function of the majority of dive shapes in pinniped species remains vague, we focused our interest on square dives, since they have been assigned to foraging behaviour in several pinniped species (Thompson et al. 1991; Lesage et al. 1999; Schreer et al. 2001; Baechler et al. 2002). Other dive shapes were categorized for descriptive purposes. As discussed earlier, foraging likely occurred during deep dives, therefore shallow dives were not included in the dive-shape analysis. A random sample of approximately 10% of dives deeper than 10 m ($N = 1344$) were manually classified into four shape classes based on the following parameters: duration, bottom time, bottom time / duration, average rate of descent, average rate of ascent, and average rate of descent / average rate of ascent. Discriminant function analysis (DFA) was used to determine discriminant functions for each shape,

which in turn were used to classify the entire dataset. Dive depth lowered the performance of the DFA and was removed. Ninety-four percent of dives were correctly classified. The presence of wiggles (i.e., vertical movements) at the bottom of the dive was used to form a fifth dive shape.

All analyses were performed using SPSS version 10.0 for Windows (SPSS Inc., Chicago), and the probability level for significance was $\alpha = 0.05$. Mean values of each variable for each individual were transformed where appropriate to meet the assumptions of parametric statistics. The standard error is given to describe variation about the mean.

Results

Of the 42 males initially captured and outfitted with TDRs, 40 were recaptured. No data were recovered from seven of the TDRs; thus, data from 33 males were used in this analysis. Three young males did not go to sea. Data for three males were not collected for the entire deployment period. Of these, two TDRs failed 12 days prior to recapture and only recorded 43 and 50% of the sampling period. Thus, the data from these two units were only included in the dive-shape analysis. Another male, given a TDR 12 days after the initial capture, was only included in the dive-shape analysis. The ages of the 30 males used in all analyses varied between 11 and 31 years (Table 1). Capture masses varied between 252 and 380.5 kg and lengths varied between 1.83 and 2.29 m. A total of 22 217 dives were recorded during a median deployment period of 20 days, with a mean of 823 ± 119 (CV = 75.3%) dives per male ($N = 27$). There were too few males in each year to examine year effects, so data from all years were pooled.

Given that males were captured and recaptured in different periods during the season, and the need for a representative sample of data for statistical analyses, the breeding season was divided into three periods: from the first recorded dive to the date when the greatest number of pups were born (estimated as 1 January in 1997 and assumed to be the same for all years; W.D. Bowen, R. Mohn, and J.I. McMillan, unpublished data); from the peak pupping date to the date when males began to leave the colony (approximately 28 January; Godsell 1991); and from the male departure date to the last recorded dive (Fig. 1). During the early and late periods, a median of only three males dived each day compared with eight males during the mid-season period. Further, only five males in total dived during the early period and four during the late period, and of these only three males in each of these periods dived on more than 1 day. Statistical analyses were therefore conducted on the mid-season data only. We found no significant temporal changes in diving behaviour during the mid-season period, so all data were pooled.

Characteristics of individual dives

Of the 27 males that dived during the sampling period, only 1 did not dive during the mid-season period. During this period, a total of 19 721 dives occurred, of which 41% were to a depth of less than 10 m. Males had significantly fewer shallow dives than deep dives per day (log-transformed data, repeated-measures ANOVA, $F_{[1,25]} = 4.79$, $p = 0.038$). All

Table 1. Age, body size, mass loss, and duration of record for 30 TDR-equipped male grey seals (*Halichoerus grypus*) and their diving characteristics during the mid-breeding season (1–28 January) at Sable Island, 1997–2001.

Male ID No.	Year of study	Age (years)	Body length (m)	Capture mass (kg)	Mass loss (kg/day)	Duration of record (days)	No. of dives	No. of bouts	No. of trips	Deep-diving effort (h/day)
M669	1997	11	1.96	252.0	2.70	20	0	0	0	0
M85	1997	12	2.03	289.0	2.65	20	38	5	1	0.14
7C8	1997	23	2.12	351.5	3.02	23	165	11	4	0.15
9C6	1997	23	1.91	262.0	1.75	28	709	44	1	1.13
E84	1998	11	2.28	337.0	2.91	22	138	20	8	0.10
E120	1998	11	2.21	318.0	2.58	19	0	0	0	0
M538	1998	12	2.04	288.0	2.54	23	265	12	2	0.52
M656	1998	12	1.83	264.0	2.05	20	1053	58	8	2.71
S	1998	20	2.07	302.5	2.48	23	241	17	1	0.46
C42	1998	24	2.15	288.0	2.64	25	288	17	2	0.33
B448	1998	25	2.21	280.0	2.23	24	33	3	1	0.16
S_3024	1999	21	2.11	316.0	3.18	20	719	54	6	1.72
S_H8491	1999	21	2.08	305.0	2.93	15	1637	88	8	3.56
B239	1999	26	2.11	291.5	2.42	18	440	33	2	0.82
522	1999	29	2.02	279.0	2.18	17	1457	109	1	1.92
861	1999	29	2.16	277.0	2.00	20	1534	96	7	3.14
E142	2000	13	2.17	303.5	2.40	26	705	82	21	0.94
E81	2000	13	2.20	315.0	2.15	27	323	43	15	0.10
M34	2000	15	2.27	311.5	2.37	30	103	8	2	0.13
M731	2000	14	2.20	316.0	2.83	22	0	0	0	0
S_053	2000	22	2.22	275.0	2.07	14	1298	96	2	3.28
P90	2000	26	2.16	302.0	2.50	20	733	53	5	1.58
F416	2001	15	2.12	302.5	2.26	31	1273	86	7	1.72
S_151	2001	23	2.29	287.0	2.26	19	440	19	5	0.72
S_152	2001	23	2.20 ^a	335.5	2.88	17	1023	67	4	1.0
S_154	2001	23	2.09	274.0	1.94	31	1779	130	1	2.07
B423	2001	28	2.15	283.0	2.19	27	980	92	7	1.01
B511	2001	28	2.28	380.5	3.23	23	1109	88	1	1.18
753	2001	31	2.20 ^a	335.5	2.50	29	0	0	0	0
837	2001	31	2.21	287.5	1.90	25	1238	72	2	1.77

^aLength was predicted from the following regression: length (cm) = 163.7 + 0.17 × initial mass.

characteristics of shallow and deep dives were significantly different ($p < 0.0001$ for all comparisons; Table 2). The characteristics of shallow dives were generally more variable than those of deep dives.

Square dives, with similar rates of descent and ascent, accounted for 27% of dives greater than 10 m in depth (Table 3). This dive type had greater mean depth and variation in depth, and a longer bottom time, than all other dive types. Right-skewed dives, where the rate of descent was greater than the rate of ascent, were the most common (54%) during the mid-season period.

The number of shallow and deep dives per day per male did not differ with age (log-transformed data, repeated-measures ANCOVA, $F_{[2,21]} = 1.25$, $p = 0.307$) or size (length: $F_{[2,16]} = 2.98$, $p = 0.080$; capture mass: $F_{[2,16]} = 3.60$, $p = 0.051$). The proportion of each of the five dive shapes did not vary among the phenotypic traits (arcsine-transformed data, repeated-measures ANCOVA, age: $F_{[4,37]} = 1.29$, $p = 0.291$; length: $F_{[4,30]} = 0.278$, $p = 0.880$; capture mass: $F_{[4,30]} = 1.00$, $p = 0.418$).

To investigate whether there were diurnal changes in diving behaviour during the mid-season period, eight 3-h periods were defined according to the times of sunrise and

sunset. For those males that dived in each of the eight periods ($N = 20$), the proportion of shallow and deep dives in each period was calculated. The proportion of shallow and deep dives did not differ significantly with time of day (arcsine-transformed data, two-factor repeated-measures ANOVA, $F_{[7,13]} = 2.47$, $p = 0.076$).

Characteristics of dive bouts

All 27 males exhibited diving behaviour that could be grouped into diving bouts. Over the entire season, 1552 bouts were identified. Only 3% of dives were not included in bouts. Bouts were categorized into three groups according to depth. Shallow bouts were defined as those in which all dives were less than 10 m in depth. The other two groups were defined according to the median depth of those dives greater than 10 m in depth: intermediate, i.e., those with a median depth of less than 23 m, and deep, i.e., those with a median depth greater than 23 m. Of the 1552 bouts, 1403 occurred during the mid-season period; of these, 30% were defined as shallow, 35% as intermediate, and 35% as deep. The number of bouts per day per male did not vary among the three types (log-transformed data, repeated-measures ANOVA, $F_{[2,24]} = 0.068$, $p = 0.935$; Table 4). Other than the

Fig. 1. Seasonal changes in mean number of dives per day made by male grey seals (*Halichoerus grypus*) during the breeding season at Sable Island, 1997–2001. Data represent the mean (with standard error bars) of means calculated for each male. The non-hatched area represents the mid-season period.

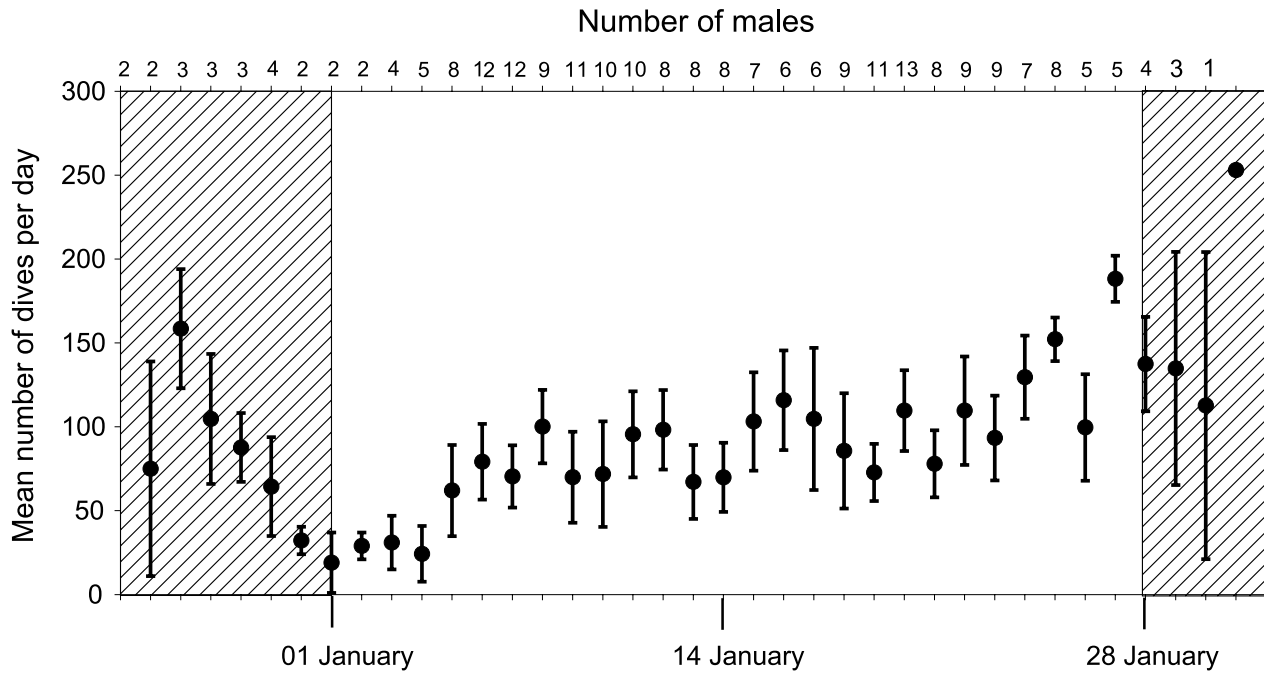







Table 2. Characteristics of individual shallow dives (<10 m depth) and deep dives (>10 m depth) made by male grey seals (*N* = 26) at Sable Island during the mid-breeding season (1–28 January), 1997–2001.

	Shallow dives			Deep dives		
	Mean ± SE	CV (%)	Range	Mean ± SE	CV (%)	Range
No. of dives/day	17.8 ± 3.25	93.5	0.2–56.7	24.2 ± 3.90	82.9	1.6–76.8
Depth (m)	5.9 ± 0.11	9.4	5.1–7.4	43.4 ± 3.30	38.7	16.5–80.8
Duration (min)	2.2 ± 0.10	22.1	1.4–3.7	5.3 ± 0.17	16.9	3.7–7.7
Time spent at bottom (min)	0.9 ± 0.06	34.0	0.3–1.7	3.3 ± 0.16	25.1	2.5–6.3
Rate of descent (m/s)	0.3 ± 0.02	27.8	0.2–0.6	0.9 ± 0.04	21.0	0.6–1.5
Rate of ascent (m/s)	0.2 ± 0.01	30.8	0.1–0.5	0.7 ± 0.03	23.0	0.4–1.1

Note: The mean ± standard error and range of means calculated for each individual male are given.

Table 3. Characteristics of the shapes of deep dives (>10 m depth) made by 26 male grey seals at Sable Island during the mid-breeding season (1–28 January), 1997–2001.

Description of dive shape	 Square	 Right-skewed	 Left-skewed	 V	 Wiggle
Percentage of dives	27	54	7	5	7
Depth (m)	67.8 ± 0.80	46.7 ± 0.46	40.7 ± 1.13	20.7 ± 0.47	42.4 ± 1.14
Duration (min)	5.9 ± 0.03	5.1 ± 0.02	5.9 ± 0.09	2.4 ± 0.05	5.4 ± 0.05
Bottom time (min)	3.8 ± 0.02	2.9 ± 0.02	3.3 ± 0.09	0.3 ± 0.02	3.4 ± 0.05
Rate of descent (m/s)	1.0 ± 0.01	0.9 ± 0.01	0.4 ± 0.01	0.8 ± 0.04	1.1 ± 0.02
Rate of ascent (m/s)	1.0 ± 0.01	0.6 ± 0.004	0.8 ± 0.01	0.5 ± 0.02	0.8 ± 0.02
Rate of descent / rate of ascent	1.0 ± 0.002	1.9 ± 0.01	0.6 ± 0.01	2.6 ± 0.16	1.5 ± 0.05

Note: The mean ± standard error and range of means calculated for each individual male are given.

time since the last bout, the characteristics of dives within bouts and the characteristics of bouts varied significantly among the three bout groups (time since last bout: $F_{[2,42]} = 3.46, p = 0.053$; all other p values < 0.0001). Mean duration and time spent at the bottom of dives were greater in deep bouts and less in shallow bouts. Shallow bouts were shorter and the time between bouts was longer. In contrast, deep

bouts were longer and the time between bouts was shorter. Square dives were more frequent during deep bouts.

Phenotypic traits did not influence the number of bouts of each type per day per male (log-transformed data, repeated-measures ANCOVA, age: $F_{[4,40]} = 1.96, p = 0.119$; length: $F_{[4,30]} = 0.890, p = 0.482$; capture mass: $F_{[4,30]} = 0.505, p = 0.732$). However, medium-sized males had fewer bouts in to-

Table 4. Characteristics of shallow (all dives <10 m depth), intermediate (median depth <23 m depth), and deep (median depth >23 m depth) dive bouts for 26 male grey seals during the mid-breeding season (1–28 January) at Sable Island, 1997–2001.

	Shallow bouts			Intermediate bouts			Deep bouts		
	Mean ± SE	CV (%)	Range	Mean ± SE	CV (%)	Range	Mean ± SE	CV (%)	Range
No. of bouts per day	0.9 ± 0.15	86.8	0–2.7	1.0 ± 0.2	99.0	0.9–3.9	1.0 ± 0.17	89.0	0–2.9
Dive depth (m)	5.2 ± 0.05	21.0	4.0–8.9	19.5 ± 0.65	74.4	4.8–92.3	60.0 ± 1.56	57.6	17.3–202
Dive duration (m)	2.0 ± 0.05	48.9	0.3–7.4	3.3 ± 0.06	40.3	0.3–10.3	5.3 ± 0.05	22.2	2.3–9.0
Time spent at bottom (min)	0.7 ± 0.03	86.1	0–4.2	1.5 ± 0.04	63.4	0–6.8	3.1 ± 0.04	31.5	0.6–6.5
Bout duration (min)	23.5 ± 0.93	81.5	1.7–126	81.8 ± 4.70	128	4.7–934	117 ± 5.26	100	12.8–811
Time since last bout (h)	13.7 ± 2.17	317	0.02–453	10.9 ± 1.92	387	0.02–376	8.9 ± 1.96	490	0.02–458
Proportion of shallow dives	1.0	—	—	0.5 ± 0.01	48.4	0–1.0	0.1 ± 0.01	117	0–0.5
Proportion of square dives	0	—	—	0.1 ± 0.01	174	0–1.0	0.3 ± 0.01	84.6	0–1.0

Note: The mean ± standard error and range of means calculated for each individual male are given.

Table 5. Characteristics of short (median duration <4.9 h) and long trips to sea made by 26 male grey seals during the mid-breeding season (1–28 January) at Sable Island, 1997–2001.

	Short trips			Long trips		
	Mean ± SE	CV (%)	Range	Mean ± SE	CV (%)	Range
No. of trips per day	0.1 ± 0.04	154	0–0.8	0.1 ± 0.02	83.6	0–0.4
No. of bouts	2.5 ± 0.22	69.9	1–10	20.7 ± 3.36	126	1–130
Trip duration (h)	2.1 ± 0.37	69.7	0.2–4.8	62.2 ± 14.7	118	5.1–272
Intertrip interval (days)	3.6 ± 1.12	103	0.6–11.3	5.3 ± 1.24	94	0.6–15.9
Proportion of shallow bouts	0.7 ± 0.08	43.2	0–1.0	0.3 ± 0.04	62.5	0–0.8
Proportion of intermediate bouts	0.2 ± 0.06	110	0–0.8	0.4 ± 0.03	45.7	0.1–0.8
Proportion of deep bouts	0.1 ± 0.04	283	0–0.7	0.3 ± 0.04	56.3	0–0.7

Note: The mean ± standard error and range of means calculated for each individual male are given.

tal per day than males in the smallest or largest mass class ($F_{[2,16]} = 3.68, p = 0.048$).

Characteristics of diving trips

During the entire season, 142 trips to sea were made by 30 males. The median trip duration was 4.9 h and the longest trip lasted for 11 days, which suggests that there is potentially more than one type of trip. Thus, trips were divided into short (less than the median) and long (greater than the median). Of the 142 trips, 124 occurred during the mid-season period, and of these, 49% were short. The mean numbers of short and long trips per day per male did not differ significantly (log-transformed data, repeated-measures ANOVA, $F_{[1,29]} = 0.315, p = 0.579$; Table 5). Other than the proportion of intermediate bouts in a trip, the characteristics of short and long trips differed significantly (proportion of intermediate bouts, arcsine-transformed data, $F_{[1,14]} = 0.842, p = 0.374$; all other characteristics, $p < 0.05$; Table 5).

To better understand the behaviour of males during short and long trips to sea, we examined the sequence of bout types during short and long trips. Short trips comprised mostly shallow bouts, with 66% of the 61 short trips containing shallow bouts exclusively. Only 7% of short trips contained deep bouts. During short trips, the general pattern was for shallow bouts to precede other shallow bouts (80% of cases). Intermediate bouts were preceded by shallow bouts in 30% of cases and by other intermediate bouts in 50% of cases. Long trips consisted of approximately equal proportions of the three bout types, although there was substantial variation among trips (Table 5). During long trips,

shallow bouts were mostly preceded by other shallow bouts (64% of cases) and only occasionally by deep bouts (8% of cases). Intermediate bouts were mostly preceded by other intermediate bouts (54% of cases) or by deep bouts (29% of cases). Deep bouts showed a strong tendency to cluster, with 73% of deep bouts preceded by other deep bouts. Thus, within short and long trips, shallow bouts showed a strong tendency to cluster and also preceded both intermediate and deep bouts during long trips to sea. Deep bouts showed a strong tendency to cluster during long trips.

For the males that went to sea, the number of short and long trips to sea per day during the mid-season period varied greatly (Table 5). Seven males made only one trip, of which six trips were long. If one includes the four males that did not go to sea during the mid-season period, phenotypic traits did not influence the number of each type of trip per day per male (log-transformed data, repeated-measures ANCOVA, age: $F_{[2,25]} = 1.30, p = 0.290$; length: $F_{[2,20]} = 2.02, p = 0.159$; capture mass: $F_{[2,20]} = 1.96, p = 0.167$). However, males in the largest mass class made more trips in total per day than those in the smaller mass classes ($F_{[2,20]} = 3.65, p = 0.045$).

Diving effort and mass loss

During the mid-season period, the mean proportion of time males spent at sea showed large variation (0.21 ± 0.04 , CV = 96%, $N = 30$), with four males spending no time at sea and one male spending 78% of his time at sea. For those males that dived during the mid-season period, diving effort during deep dives (1.2 ± 0.2 h/day, CV = 84.1%, $N = 26$) was greater

than diving effort during shallow dives (0.3 ± 0.06 h/day, CV = 105%, $N = 26$; log-transformed data, repeated-measures ANOVA, $F_{[1,25]} = 53.2$, $p < 0.0001$). During deep dives, one male spent as much as 3.6 h/day at the bottom of deep dives (Table 1).

During the whole season, males lost between 1.8 and 3.2 kg of their body mass per day (2.5 ± 0.1 kg/day, CV = 15.7%, $N = 30$; Table 1). To determine whether diving reduced mass loss, we compared mass loss per day with diving effort during deep dives per day for the entire season. Deep-diving effort was not correlated with absolute mass loss per day (Pearson's correlation, $r_s = -0.32$, $N = 30$, $p = 0.081$), suggesting that males were not reducing mass loss during diving. Deep-diving effort and the proportion of the breeding season spent at sea on long trips did not vary among the three mass classes (ANCOVA, $F_{[2,26]} = 1.36$, $p = 0.275$, and $F_{[2,26]} = 1.51$, $p = 0.241$, respectively), indicating that putative foraging effort was not related to male body mass.

Discussion

Although studies have reported that male grey seals spend considerable time during the breeding season at sea but close to shore (Davies 1949, 1956; Hewer 1957; Anderson and Harwood 1985), this study is the first to document the extent of diving and the behaviours that may occur at sea in terrestrially breeding grey seals. We have shown that diving is a substantial component of the behavioural repertoire of many male grey seals on Sable Island during the breeding season.

Males engaged in both deep and shallow diving. Deep dives had a mean depth of 43.4 m and were of long duration, and more than half of the dive was spent at the bottom. Grey seals appear to be mostly benthic foragers (Thompson et al. 1991; Thompson and Fedak 1993; Bowen and Harrison 1994; Hammond et al. 1994) and during the winter months at Sable Island their primary prey is northern sand lance (*Ammodytes dubius*) (Bowen and Harrison 1994). Bowen et al. (2002) have shown that harbour seals feed on sand lance during the breeding season at Sable Island, and do so at a depth of 29.9 ± 2.2 m (mean \pm SE). Given that male grey seals in this study dived to similar depths as breeding male harbour seals (Coltman et al. 1997), it is likely that intermediate and deep diving by male grey seals in this study involved periods of foraging. Further, square dives were relatively common and several studies have equated this dive type with foraging in several pinniped species (Thompson et al. 1991; Lesage et al. 1999; Schreer et al. 2001; Baechler et al. 2002). Deep-dive bouts showed a strong tendency to cluster during long trips to sea, suggesting that males spent most of their trip involved in foraging behaviour.

However, we found no relationship between deep-diving effort and mass loss, and no evidence that males were acquiring energy to alleviate energetic constraints. Overall, this suggests that males were gaining little net energy. Using the same measure of diving effort as in this study, Beck et al. (2003) have shown that during the 7-month period prior to the breeding season, when grey seals are accumulating fat stores, males spend an average of 6.47 h/day at the bottom of dives. The mean deep-diving effort in this study was 1.24 h/day, supporting the view that male grey seals con-

sume relatively little food during the breeding season. Komers et al. (1992) found that male wood bison (*Bison bison athabasca*) spent time away from the breeding colony resting and feeding before rejoining female groups, and it was suggested that this is to regain condition. Of 11 male grey seals studied, Lidgard et al. (2001) found that 10 spent time at several sites rather than at a single site. Thus, although males likely foraged while at sea, the ingestion of food may simply be incidental to spending time at sea recuperating before reestablishing tenure.

Whereas deep diving is likely associated with foraging, shallow diving, which accounted for a large proportion of the diving behaviour, may have other functions. Shallow dives had a mean depth of 5.9 m, were short in duration relative to deep dives, and mostly occurred during short trips to sea. Given that neither behaviour nor location relative to the shore was known, it is difficult to predict the type of behaviours that would be exhibited during shallow diving. However, given that depths of 20 m or more can only be reached approximately 4 km or more offshore, it is likely that some bouts of shallow diving occurred close to shore. D.J. Boness and W.D. Bowen (unpublished data), using underwater video cameras, found that male harbour seals engaged in more agonistic and display behaviours during shallow diving than during deep diving. Thus, if male grey seals adopt searching or displaying tactics for mating with females at sea, they are more likely to do so close to shore, since the concentration of females, and thus the chances of intercepting females, are likely to be higher. Thus, shallow diving by male grey seals at Sable Island might also represent sexual activity. Kelly and Wartzok (1996) suggest that shallow diving by adult male ringed seals (*Phoca hispida*) is associated with guarding territories or mates near the ice surface. Recent genetic studies support the notion that terrestrially breeding male grey seals may copulate at sea. The strongest support comes from studies at the terrestrial breeding sites of North Rona and the Isle of May in the U.K., where a large proportion of pups born are not sired by males sampled onshore (Worthington Wilmer et al. 1999). Ambs et al. (1999) have also shown that on Sable Island, 43% of pups are not sired by the consort male. Although some extra-consort fertilizations are likely to occur on land, others may occur at sea.

Another possible explanation for shallow diving is that it is related to male movement. Lidgard et al. (2001) found that male grey seals changed location during the breeding season. The distances between consecutive sites (the range of mean distances per male is 0.3–10.9 km) indicates that some of this movement must have occurred during short trips to sea rather than across land. Bengtson and Stewart (1992) and Jay et al. (2001) suggest that travelling is associated with shallow diving in the crabeater seal (*Lobodon carcinophagus*) and the Pacific walrus (*Odobenus rosmarus divergens*), respectively.

We have shown that there is considerable variation in the extent of diving by male grey seals at a major terrestrial breeding colony. Phenotypic traits appeared to have little influence on diving behaviour. The characteristics of dives and the pattern of dive bouts suggest that some of the diving is associated with foraging. A substantial proportion of diving was composed of shallow dives and this warrants further

study to ascertain whether shallow diving is a component of the mating tactics of male grey seals on Sable Island.

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References

- Ambs, S., Boness, D.J., Bowen, W.D., Perry, E.A., and Fleischer, R.C. 1999. Proximate factors associated with high levels of extra-consort fertilizations in polygynous grey seals. *Anim. Behav.* **58**: 527–535.
- Anderson, S.S., and Fedak, M.A. 1985. Grey seal males: energetic and behavioural links between size and sexual success. *Anim. Behav.* **33**: 829–838.
- Anderson, S.S., and Harwood, J. 1985. Time budgets and topography: how energy reserves and terrain determine the breeding behaviour of grey seals. *Anim. Behav.* **33**: 1343–1348.
- Anderson, S.S., Burton, R.W., and Summers, C.F. 1975. Behaviour of grey seals (*Halichoerus grypus*) during a breeding season at North Rona. *J. Zool.* (1965–1984), **177**: 179–195.
- Baechler, J., Beck, C.A., and Bowen, W.D. 2002. Dive shapes reveal temporal changes in the foraging behaviour of different age and sex classes of harbour seals (*Phoca vitulina*). *Can. J. Zool.* **80**: 1569–1577.
- Bartholomew, G.A. 1970. A model for the evolution of pinniped polygyny. *Evolution*, **24**: 546–559.
- Beck, C.A., Bowen, W.D., McMillan, J.I., and Iverson, S.J. 2003. Sex differences in the diving behaviour of a size dimorphic capital breeder: the grey seal. *Anim. Behav.* In press.
- Bengston, J.L., and Stewart, B.S. 1992. Diving and haulout behavior of crabeater seals in the Weddell Sea, Antarctica, during March 1986. *Polar Biol.* **12**: 635–644.
- Boness, D.J. 1991. Determinants of mating systems in the Otariidae (Pinnipedia). In *The behaviour of pinnipeds*. Edited by D. Renouf. Chapman and Hall, London. pp. 1–44.
- Boness, D.J., and James, H. 1979. Reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. *J. Zool.* (1965–1984), **188**: 477–500.
- Boness, D.J., Bowen, W.D., and 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.
- Bowen, W.D., and Harrison, G.D. 1994. Offshore diet of grey seals *Halichoerus grypus* near Sable Island, Canada. *Mar. Ecol. Prog. Ser.* **112**: 1–11.
- Bowen, W.D., Tully, D., Boness, D.J., Bulheier, B.M., and Marshall, G.J. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. *Mar. Ecol. Prog. Ser.* **244**: 235–245.
- Caro, T.M., and 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*. Doctoral dissertation, University of Liège, Liège, Belgium.
- Clutton-Brock, T.H., Guinness, F.E., and Albon, S.D. 1982. Red deer, behavior and ecology of two sexes. The University of Chicago Press, Chicago.
- Coltman, D.W., Bowen, W.D., Boness, D.J., and 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., and Boness, D.J. 1998. The energetics of male reproduction in an aquatically mating pinniped; the harbour seal. *Physiol. Zool.* **71**: 387–399.
- 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*. Edited by P.P.G. Bateson and P.H. Klopfer. Plenum Press, New York. pp. 385–431.
- Emlen, S.T., and Oring, L.W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science (Wash., D.C.)*, **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.
- Haller, M.A., Kovacs, K.M., and Hammill, M.O. 1996. Maternal behaviour and energy investment by grey seals (*Halichoerus grypus*) breeding on land fast-ice. *Can. J. Zool.* **74**: 1531–1541.
- Hammond, P.S., Hall, A.J., and Prime, J.H. 1994. The diet of grey seals around Orkney and other island and mainland sites in north-eastern Scotland. *J. Appl. Ecol.* **31**: 340–350.
- 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. R. Soc. Lond. B Biol. Sci.* **128**: 23–68.
- Hewer, H.R., and 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.
- Jay, C.V., Farley, S.D., and Garner, G.W. 2001. Summer diving behavior of male walrus in Bristol Bay, Alaska. *Mar. Mamm. Sci.* **17**: 617–631.
- Kelly, B.P., and Wartzok, D. 1996. Ringed seal diving behavior in the breeding season. *Can. J. Zool.* **74**: 1547–1555.
- Komers, P.E., Messier, F., and Gates, C.C. 1992. Search or relax: the case of bachelor wood bison. *Behav. Ecol. Sociobiol.* **31**: 195–203.
- Le Boeuf, B.J. 1974. Male–male competition and reproductive success in elephant seals. *Am. Zool.* **14**: 163–176.
- Lesage, V., Hammill, M.O., and Kovacs, K.M. 1999. Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Can. J. Zool.* **77**: 74–87.
- Lidgard, D.C., Boness, D.J., and Bowen, W.D. 2001. A novel mobile approach to investigating mating tactics in male grey seals (*Halichoerus grypus*). *J. Zool. (Lond.)*, **255**: 313–320.
- McCann, T.S. 1980. Territoriality and breeding behaviour of adult male Antarctic fur seal, *Arctocephalus gazella*. *J. Zool.* (1965–1984), **192**: 295–310.

- McLaren, I.A. 1993. Growth in pinnipeds. *Biol. Rev. Camb. Philos. Soc.* **68**: 1–79.
- Modig, A.O. 1996. Effects of body size and harem size on male reproductive behaviour in the southern elephant seal. *Anim. Behav.* **51**: 1295–1306.
- Schreer, J.F., Kovacs, K.M., and O’Hara, H.R.J. 2001. Comparative diving patterns of pinnipeds and seabirds. *Ecol. Monogr.* **71**: 137–162.
- Stirling, I. 1975. Factors affecting the evolution of social behaviour in the pinnipedia. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer*, **169**: 205–212.
- Thompson, D., and Fedak, M.A. 1993. Cardiac responses of grey seals during diving at sea. *J. Exp. Biol.* **174**: 139–164.
- Thompson, D., Hammond, P.S., Nicholas, K.S., and Fedak, M.A. 1991. Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*). *J. Zool. (Lond.)*, **224**: 223–232.
- Tinker, M.T., Kovacs, K.M., and 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. 1991. Behavioural and energetic determinants of individual mating success in male grey seals (*Halichoerus grypus*, Fabricius 1791). Ph.D. dissertation, University of Glasgow, Glasgow, Scotland.
- Twiss, S.D., Pomeroy, P.P., and 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., Anderson, S.S., and 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.
- Worthington Wilmer, J., Allen, P.J., Pomeroy, P.P., Twiss, S.D., and Amos, W. 1999. Where have all the fathers gone? An extensive microsatellite analysis of paternity in the grey seal (*Halichoerus grypus*). *Mol. Ecol.* **8**: 1417–1429.