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The reproductive behavior and energetics of male gray seals (*Halichoerus grypus*) breeding on a land-fast ice substrate

Abstract The reproductive behavior of male gray seals (*Halichoerus grypus*) breeding on land-fast ice at Amet Island, Nova Scotia, was studied. Data on energy expenditure (rate of mass loss over time) were collected. The average time budget of males at Amet Island was comparable to that of land-breeding males. The behavior of males showed seasonal changes, with a decrease in the proportion of time spent in the water and an increase in agonistic behavior during the peak mating period. The estimated amount of body mass lost over the season ranged between 25.6 and 77.1 kg, and the estimated percent of initial body mass lost ranged between 7.7 and 26.5% (n=10). The maximum number of observed copulations for an individual male was nine. Only 15 out of 42 males observed during 1992 and 1993 were seen copulating. The number of observed copulations per male was strongly correlated with success in remaining close to, or attending, females (r=0.91, P<0.001, n=42). The mean duration of attendance was 4.5±5.54 days (n=42). Large size was not an important factor in determining attendance success, but reproductive effort (the estimated proportion of body mass lost over the season) and success in agonistic interactions with other males were both correlated with male success.

Key words *Halichoerus grypus* · Breeding habitat · Male reproductive behavior · Mating system · Energetics

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Introduction

Pinnipeds require a solid substrate for parturition, but morphological adaptations for their life in water have resulted in limited terrestrial mobility and therefore suitable breeding sites represent a limiting resource (Bartholomew 1970). It has been proposed that differences in the availability and stability of parturition habitat, as well as access to it, are largely responsible for differences in pinniped mating systems (Stirling 1983). If this is the case, then colonies of a single species using different breeding habitats should show predictable differences in reproductive behavior and social organization (Stirling 1975). The gray seal is an excellent subject to test this hypothesis because breeding colonies are found in a variety of habitats, including open beaches, grassy island tops and rocky coastlines, as well as land-fast ice and pack ice (Hook and Johnels 1972; Mansfield and Beck 1977; Anderson and Harwood 1985).

A polygynous mating system has been described for land-breeding gray seal colonies in the eastern and western Atlantic (e.g., Hewer 1960; Coulson and Hickling 1964; Cameron 1967; Anderson et al. 1975). It is an unusual system compared to other polygynous pinnipeds in that males do not defend fixed territories or form dominance hierarchies, but instead compete for the right to remain within a shifting population of females (Boness and James 1979; Anderson and Fedak 1985). Males that establish tenure among females are able to achieve high levels of reproductive success by maximizing their chances of being next to females when they come into estrus (Boness and James 1979). While it has been shown that differences in breeding behavior and degree of polygyny among land-breeding gray seal populations are associated with habitat variation (Anderson and Harwood 1985; Boness 1984), little information exists to date on the breeding behavior or energetics of ice-breeding populations.

This study investigated the role of breeding habitat in shaping the mating system of the gray seal. The reproductive behavior of males breeding on land-fast ice was studied and compared with that of land-breeding males, to see if the difference in habitat results in the use of different behavioral strategies.

Two related aspects of mating system theory were addressed. First of all the hypothesis that a relatively unstable land-fast ice substrate, where there is easy access to water and ample space, should limit the potential for polygyny (Stirling 1975, 1983) was tested. A second objective was to investigate the behavioral and energetic factors associated with reproductive success in land-fast ice breeding males. In polygynous mammals there are often relationships between male reproductive success and factors such as large size, aggressiveness and reproductive effort (Le Boeuf 1974; Clutton-Brock et al. 1988; Deutsch et al. 1990), where reproductive effort can be defined as the proportion of available resources that an organism devotes to reproduction over a specified period of time (Gadgil and Bossert 1970; Hirshfield and Tinkle 1975). If the level of polygyny for ice-breeding gray seals is low, however, then these relationships may be less pronounced than for land-breeding colonies (Anderson and Fedak 1985; Godsell 1991).

Methods

Data collection

Amet Island is a small, featureless island with steep, 5-m-high bluffs surrounded by a 2–5 m wide beach, situated in Northumberland Strait, Nova Scotia (Fig. 1). The water around the island is very shallow due to the presence of rocky shoals. During the winter, pack ice moving through the Strait becomes lodged on these shoals and attached to the island, providing a surface for the seals to haul out on. Ice conditions vary from year to year and when there is little ice the seals also crowd onto the beaches around the island (Mansfield and Beck 1977).

A research station was established on the island and data were collected on 18–24 January 1991, 5–23 January 1992 and 2–29 January 1993. Only mass-change data were collected from breeding males in 1991; behavioral and mass-change data were collected in 1992 and 1993. Observation blinds placed on each of the corners of the island provided full visual coverage of the surrounding ice surface (Fig. 1). Three observers, one in each blind, recorded the behavior of almost all seals around the island, except for those very far out on the ice. Blinds were situated so that they could be approached and entered without alerting the seals on the ice below.The number of seals present around the island were counted daily and their positions recorded on maps during censuses taken at 0800, 1200 and 1600 hours. All adult individuals were recognizable by unique pelage markings, scars or dye markings (see below), making it possible to determine from census maps the number of days that individual males were present at Amet.

Observations were made daily from 0800 to 1600 hours (i.e., during all daylight hours) every day, except for afternoons devoted to capturing and weighing animals. Behavioral data were gathered using instantaneous scan sampling (Altmann 1974). All visible seals were scanned at 60-s intervals. The behavior of each seal was classified into one of 20 mutually exclusive categories (Table 1), which included both on-ice and in-water behavior. Inter-observer checks were made at the beginning of the season to ensure that no discrepancies existed between observers in how behavior was classified. Scans were made in blocks of 30 min, separated by 30-min blocks of ad libitum observations when notes were made on the behavior and status of individuals and on the outcome of agonistic encounters. A single scan-block record was obtained by tallying the 30 scans in a block for an individual male.

Mass-change data were obtained by collecting serial mass records for individual males. Because male gray seals fast during the breeding season (Anderson and Fedak 1985; Fedak and Anderson 1987), weight changes were used as an indicator of energy expenditure. Males were captured in sling nets without tranquilization. Each male was tagged using a numbered jumbo roto-tag placed through the webbing of the hind flipper and dye-marked with a unique color pattern to aid in later identification (as in Kovacs 1987a). They were then raised on an aluminum tripod with a chain hoist and weighed using a 500-kg Dillon dynamometer. The accuracy of the weighings was ± 1 kg. The whole capture and weighing process usually took between 10 and 15 min. Males were recaptured and re-weighed whenever possible after 5 or more days.

Standardizing data

For comparisons between years the standardized "stage" of the breeding season was used, rather than the date. The time of peak mating, calculated as the date at which 50% of all observed copulations had occurred each year, was determined. This date and 2 days before and after were designated as the peak mating period. All days before this period were designated as the early mating period and all days after were designated as the late mating period. A 5-day span was chosen for the peak mating period because it
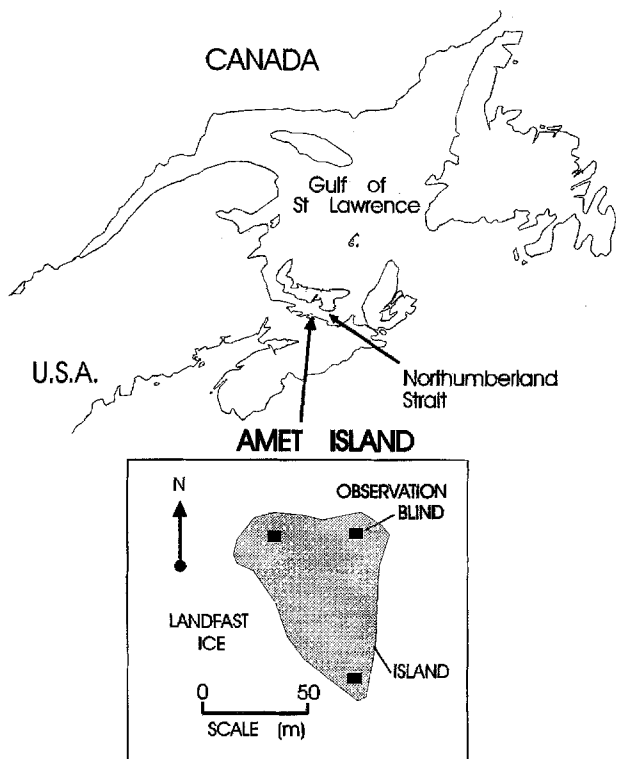

Fig. 1 Map of Eastern Canada showing the location of the study area. The *inset* depicts a schematic map of Amet Island, showing the location of observation blinds (*black squares*)

Table 1 Ethogram used to classify adult male gray seal behavior (based on behavioral categories used by Kovacs (1987b) and Anderson and Harwood (1985), with some modification)

Category	Description
ON ICE SURFACE	
Non-social	
Idle	seal motionless, head down on ice, eyes open or closed
Alert	seal stationary, with head up and eyes open, possibly sniffing
Comfort movement	includes scratching, stretching, and rolling (in one location)
Locomotion	seal changes location, but not obviously to approach another seal
Social: general	
Approach male	seal closing the distance (~5 m or less) between itself and a male seal
Approach female	seal closing the distance (~5 m or less) between itself and a female seal
Social: sexual	
Mount female	seal assumes copulatory position, without intromission
Copulation	seal in copulatory position, with intromission
Social: agonistic	
Directed toward males	
Low threat	seal lying with head elevated, neck extended, often hissing or growling
High threat	seal lying with entire upper body elevated, emitting loud growling sounds
Chase	seal moving quickly towards a male seal, which is apparently fleeing
Flee	seal moving quickly away from a male seal, which is apparently chasing
Fight	seal engaged in agonistic physical contact with a male seal
Directed toward females	
Threat	seal lying with head or upper body elevated, often hissing or growling
Flee	seal moving quickly away from a female, which is apparently chasing
Fight	seal engaged in agonistic physical contact with a female seal
IN WATER	
Beneath surface	seal entirely below surface of water, may or may not be visible
At surface	seal visible at surface of water, may be resting or moving
Agonistic encounter	seal engaged in aquatic threat, chase or fight with another seal
Sexual behavior	seal engaged in aquatic copulation or mounting behavior

included at least 50% of the observed copulations each year (50% in 1992 and 59% in 1993). A pupping curve was constructed for the 1992 and 1993 seasons, to illustrate the relative timing and frequency of births and copulations. For pups born prior to the commencement of observations, pup age was estimated upon first capture from the regression equation of mass versus known pup age and birthdates were estimated from these ages (Haller 1994).

Mass data were compared both within and between years by calculating the estimated mass of each male at the time of peak mating. This date was chosen because it was the date when most of the males were present each year and it was assumed to be the time when males were most actively competing for potential mates. For males whose rate of mass loss was known ($n=17$), this rate was used to interpolate to the peak mating period; for all other males ($n=19$) the average rate of male mass loss was used. Initial mass of males was also estimated by back-calculating to the first date that each male was seen in a given year.

Female distribution

The frequency distribution of nearest-neighbor distances (Krebs 1989) and the average density of females were used to describe female spatial distribution in 1992 and 1993. Nearest-neighbor distances were calculated from the daily census maps (using one census map per day, selected at random) and were accurate to 2 m. Frequency histograms of these values were plotted for early, peak and late mating. The area used by females was determined by drawing a polygon around the outside females, adding a border strip equal to the width of the mean nearest neighbor distance and measuring the resulting area, minus the area of the island. The average density of females on the ice surface was then calculated by dividing the number of females present by the area they occupied.

Reproductive effort, competitive success and attendance success

Reproductive effort was estimated as the total amount of body mass lost over the season and was expressed in both absolute terms and as a percent. Total absolute body mass lost over the season was estimated by multiplying the rate of mass loss by the total number of days a male was observed at Amet. The percent of total body mass lost over the season was calculated by dividing this sum by the estimated initial mass (as in Deutsch et al. 1990). The latter estimate was considered to be a better index of reproductive effort than rate of mass loss per day because it takes into account the total energetic cost to the individual over the breeding season, as well as individual differences in body mass.

For all male-male agonistic encounters observed, the type of encounter and the identity of the winner and loser (except in the case of ties) were recorded. An index of competitive success was calculated (as in Clutton-Brock et al. 1979) for each male (i) using the formula:

$$\text{index}_i = \frac{B + b + 1}{L + l + 1}$$

where B is the number of males that i beat, b is the sum of the numbers of males that the B males beat (excluding i), L is the number of males that i lost to and l is the sum of the numbers of males that the L males lost to (excluding i). The index was converted to its natural logarithm, to obtain a more normal distribution of values, and was calculated only for those males for which five or more encounters were observed.

In most studies of male pinnipeds, the number of observed copulations per male is assumed to be a reasonable measurement of reproductive success (e.g., Le Boeuf 1974; Boness 1984; Anderson and Fedak 1985; Le Boeuf and Reiter 1988; Godsell 1991). The

number of copulations was recorded, but was considered an inadequate measure of reproductive success because copulations often occurred under water and some undoubtedly went unobserved. Because certain males may have preferentially mated in the water rather than on the ice surface, using number of copulations as an index of male success would create a bias favoring those that mated on the ice surface.

To avoid such a bias, "attendance success", calculated as the number of receptive females attended each day summed over the breeding season, was used as an alternate index of male sexual success. A female was considered receptive after day 12 of lactation. A male was considered to be attending if it was the closest male to a female and remained within approximately 10 m of that female for at least 1 h. As an example, if a male attended 1 receptive female for 2 days his attendance success was 2, while if he attended 3 receptive females for 2 days his attendance success was 6 (in both cases the "period of attendance" would have been 2 days).

Data analyses

The proportion of time per day that a male spent in each behavior category was calculated and these daily values were used for all further analyses. The overall activity budget was calculated by taking the mean of individual activity budgets; in this way, the standard deviations for each category represent the variation between males. Differences among males in the amount of time spent in behavioral categories were examined using a Kruskal-Wallis test. Only those males with 5 or more days of behavioral data recorded were used for this analysis, to avoid an overly unbalanced design.

Tide tables were used to determine the tidal cycles during the study period. The tidal level during each scan block was recorded as: (1) low tide, (2) ebb tide, (3) flood tide or (4) high tide. Each state covered 3 h, to make up a full tidal cycle of 12 h (i.e., low, flood, high, ebb). For the purpose of analysis flood tide and ebb tide were grouped together, as both represent an intermediate level of water height between low and high tide. The proportion of time spent in the water at each tidal level was examined. A repeated-measures analysis of variance (Crowder and Hand 1990) was used to account for individual variation in behavior. A repeated-measures design was also used to test for differences in the proportion of time spent in behavioral categories at different stages of the breeding season (early, peak and late mating periods) while accounting for individual variation. The arc sine transformation was applied (Sokal and Rohlf 1981) to satisfy assumptions of normality and homogeneity, based on a graphical examination of residuals. To prevent violations of the assumption of compound symmetry, a Huynh-Feldt adjusted probability level was used to determine significance (Crowder and Hand 1990). If the overall test was significant then a-posteriori pairwise contrasts were used to identify significant differences between effect levels.

Relationships between variables were investigated using Pearson correlation coefficients, except in instances when assumptions of normality or homogeneity of variance were not met, when a Spearman rank correlation test (r_s) was used. Path analysis (Sokal and Rohlf 1981) was used to develop a hypothetical model of how behavioral and energetic factors might affect attendance success and number of copulations.

The SYSTAT statistical package (SYSTAT 1992) was used for all analyses except for the path analysis, which was performed using AmosDraw (Arbuckle 1992). The maximum probability of type I errors was set at $\alpha=0.05$ for all significance tests; non-significant results are accompanied by the minimum effect size that would be detectable at a power of 0.80 (where power is the probability of detecting an effect, if an effect exists; Cohen 1988). Mean values are shown ± 1 SD, unless otherwise stated.

Results

Breeding season summary

Ice conditions around Amet Island were highly variable, both between and within breeding seasons. At times the island was entirely surrounded by ice, while at other times there were large expanses of open water. Access to water for seals hauled out on the ice was correspondingly variable; for some seals open water was only a few meters away, while other seals had their access to water blocked by pressure ridges of ice piled up to 3 m high (Fig. 2).

Except for a few days early in January 1992, there was a lot of ice available to females. However, the distribution of females was clumped (Fig. 3). Most females were within 8 m of another female, although late in the season a fairly high proportion of females (10% in 1992 and over 40% in 1993) were at least 20 m
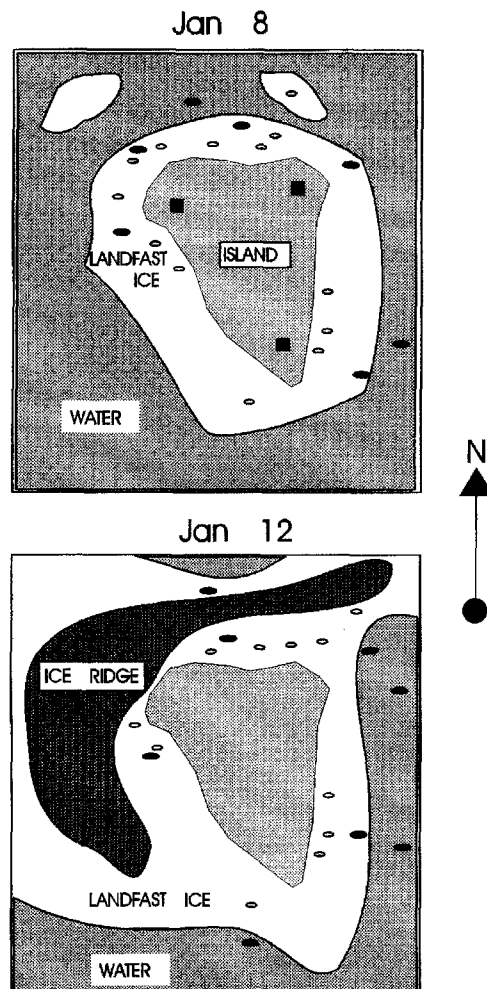

Fig. 2 Ice conditions on 8 January (*top*) and 12 January (*bottom*) 1992. The *solid ovals* indicate the position of males and the *hollow ovals* indicate females. The *unshaded areas* represent land-fast ice, the *light stippled area* represents water and the *dark stippled area* represents ice pressure ridges up to 3 m in height
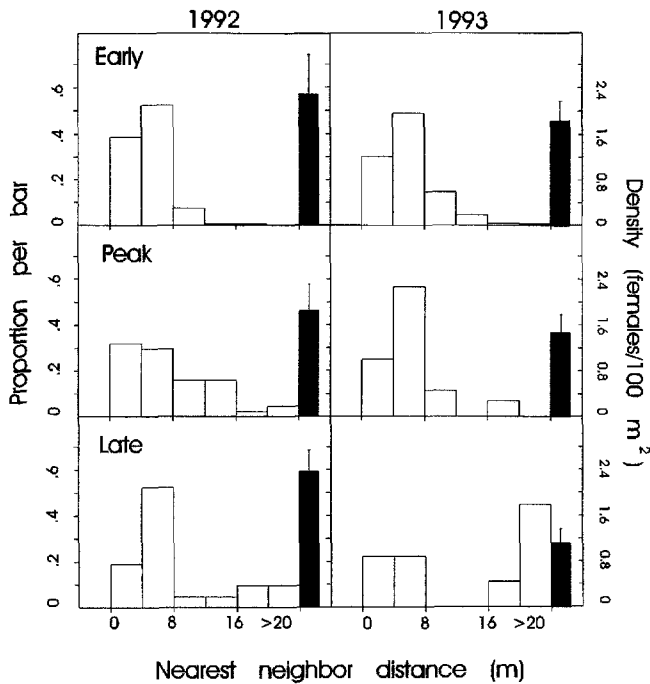
Fig. 3 Frequency histograms of nearest-neighbor distances between females during the early, peak and late mating periods in 1992 and 1993. *Unshaded bars* indicate the relative frequency of 6 distance classes. The *shaded bars* indicate the mean density of females on the ice during each period, expressed as the average number of females in a 10 × 10 m patch of ice
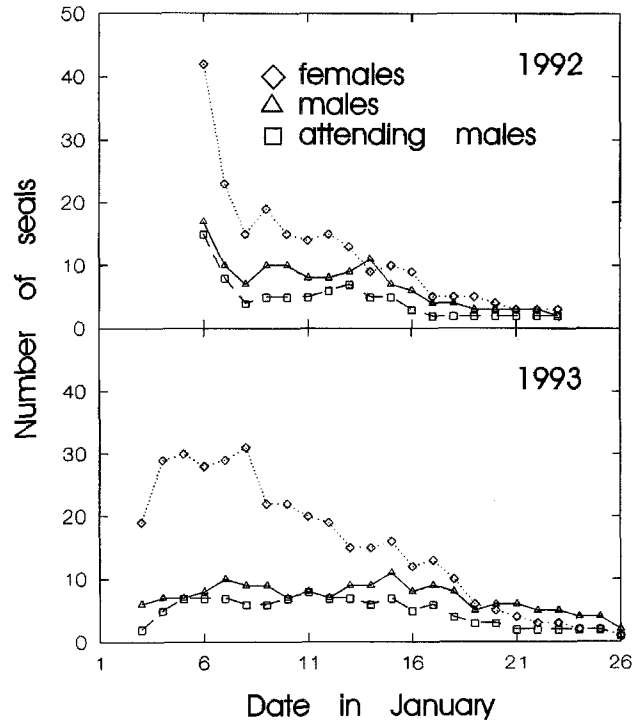

Fig. 4 The number of adult seals present each day around Amet Island during January of 1992 and 1993

from another female. Nearest-neighbor distances in late season had a bimodal distribution, distinguishing between females in groups and solitary females. In 1993, when relatively few females were present, this trend was more pronounced.

More animals were present initially in January 1992 than in January 1993 (Fig. 4) but there was a considerable decrease in numbers early in 1992 due to a storm which caused most of the ice to break up and float away, carrying off many of the mother-pup pairs. The number of adults declined at this time from a peak of 59 on 6 January to only 22 by 8 January. In 1993, the number of females present reached a peak of 31 on 8 January and then began to decline. The number of males present in 1993 reached a peak of 11 on 15 January, which corresponds to the peak mating period. The total number of males present exceeded the number of females on 20 January, although the number of males actually attending females remained below the number of females (Fig. 4).

In January 1992 and 1993, 50% of pup births had occurred by 3 January (Fig. 5). The date at which 50% of copulations had occured was 15 January in 1992 and 16 January in 1993 (Fig. 5).
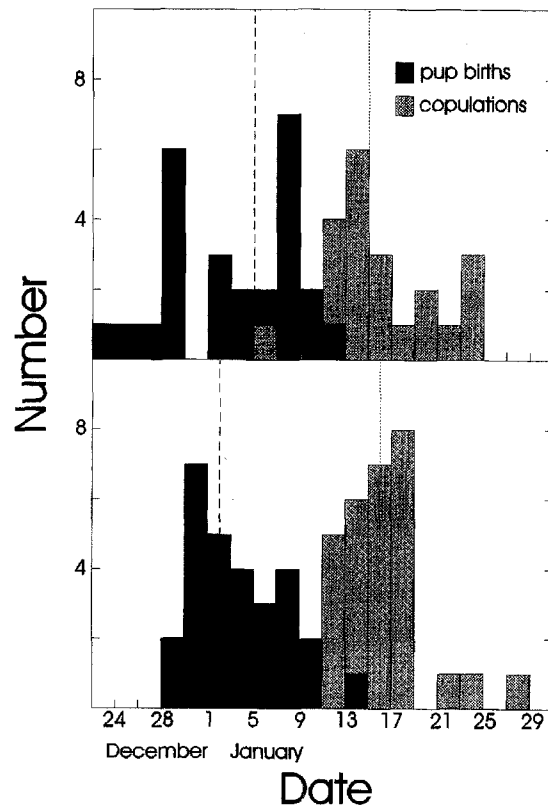

Fig. 5 Frequency distributions of pup births and observed copulations during January 1992 and 1993. The *dashed lines* indicate the commencement of observations each year, while the *dotted lines* indicate the time of peak mating each year

Table 2 Activity budget for male gray seals breeding on land-fast ice at Amet Island, Nova Scotia, during January 1992 and 1993. Means are given as percent of total time budget (± 1 SD) and percent of time on ice. Activity budgets for two land-breeding colonies are provided for comparison

Behavioral Category	Amet Island		Sable Island[a]	Monach Isles[b]
	Mean% Time	% Time on ice	% Time on land	% Time on land
ON ICE SURFACE				
Non-social: inactive				
Idle	38.5 ± 30.5	68.8	75.2	66.0
Alert	10.4 ± 7.4	18.6	12.9	18.0
Comfort movement	1.8 ± 1.9	3.2	0.7	2.6
Inactive: TOTAL		90.6	88.8	86.6
Non-Social: active				
Locomotion	1.5 ± 1.4	2.7	2.1	4.8
Social: locomotion				
Approach male	0.1 ± 0.1	0.2	–	–
Approach female	0.8 ± 1.4	1.4	1.3	–
Locomotion: TOTAL		4.3	3.4	4.8
Social: agonistic				
Threat male	0.7 ± 1.3	1.3	4.9	–
Chase male	0.1 ± 0.2	0.1	1.2	–
Flee from male	0.1 ± 0.4	0.2	–	–
Fight male	0.1 ± 0.2	0.2	0.2	–
Toward male: TOTAL		1.8	6.3	2.4
Threat female	1.1 ± 1.4	2.0	–	–
Flee from female	0.1 ± 0.4	0.1	–	–
Toward female: TOTAL		2.1	–	2.7
Agonistic: TOTAL	2.2 ± 2.0	3.9	6.3	5.1
Social: sexual[c]				
Mount female	0.2 ± 0.5	0.4	0.9	0.8
Copulation	0.5 ± 1.4	0.9	0.6	2.5
Sexual: TOTAL	0.7 ± 1.7	1.3	1.5	3.3
IN WATER				
Beneath surface	32.9 ± 31.2			
At surface	10.5 ± 16.7			
Agonistic encounter	0.5 ± 1.2			
Sexual behavior	0.1 ± 0.5			
Water: TOTAL	44.0 ± 36.9		0.0	63.1

[a] Data from Boness (1984)
[b] Data from Anderson and Harwood (1985)
[c] In Boness (1984), "approach female" was also included in the sexual behavior category

Behavior

In 1992, 77 h of observation were conducted over 19 days. This was equivalent to 118 observer hours for all three blinds and provided 288 scan-block records for males. In 1993, 153 h of observation were conducted during 28 days, which included 321 observer hours and provided 625 scan-block records for males. Over both years a total of 913 scan-block records were obtained for 35 individual males. Five of these males were present in both 1992 and 1993.

The proportion of time males spent idle on the ice and the proportion of time in the water accounted for most of the daily activity budget, but these categories also showed the greatest amount of variation (Table 2). The activity budget was very similar to that found for land-breeding colonies, when only on-ice behavior was considered (Table 2). The proportion of time spent in the water at Amet (44%) was different from both

Sable Island and the Monach Islands. At Sable Island attending males were never observed in the water. At the Monachs, males spent an average of 63% of their time at sea; however, the standard deviation of this mean (3.12%) was considerably lower than at Amet (36.9%).

At Amet Island there were differences among males in the proportion of time per day spent in the water, both for 1992 ($K=9.71$, $P=0.021$, $n=32$) and 1993 ($K=35.56$, $P<0.001$, $n=65$). Some males attended females from the water, while other males attended predominantly from the ice surface. Among individual males there was considerable variability in time budgets over the breeding season. For example, Fig. 6 shows the daily activity budget for male D during January 1993. Male D attended one or more females each day during the 1993 season, but some days were spent mostly in the water and others were spent mostly on the ice surface.
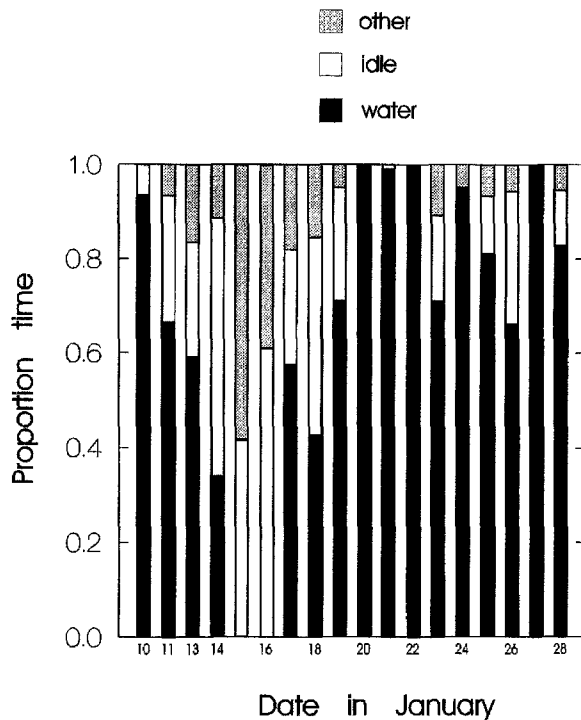
Fig. 6 Daily activity budget for a typical male (*D*) during January of 1993, illustrating the pattern of variation in behavior that occurs over the season

Fig. 7 Rate of mass loss versus date in January for males that were captured three or more times during one breeding season.

Variation in individual attendance strategies was partially explained by three factors: female behavior, tidal fluctuations and stage of the breeding season. The proportion of time spent in the water each day by attending males was correlated to the proportion of time spent in the water by the females they attended (r_s=0.77, P<0.001, n=147). The proportion of time males spent in the water was also related to the level of the tide (repeated-measures F=7.16, P=0.009, n=13 males), with the greatest amount of time in the water at high tide and least amount of time in the water at low tide. High tides tended to shift or dislocate the ice from the rocky shelves beneath and create new cracks or leads, thus increasing the amount of open water. Behavioral data covering early, peak and late mating periods were collected for three males in 1992 and four in 1993. Seasonal differences were observed in the proportion of time these males spent in the water (Table 3), with more time spent in the water in the early mating
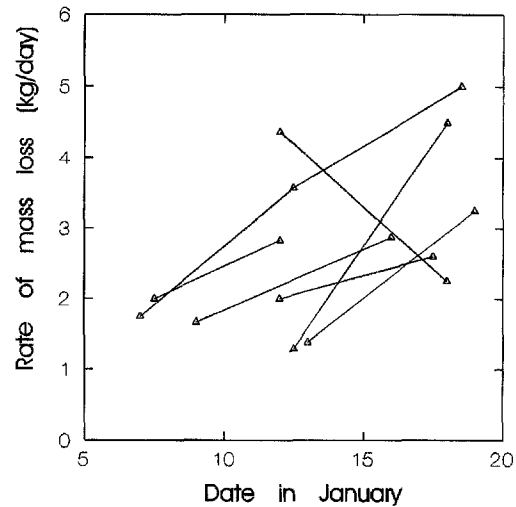
period than in the peak mating period (repeated measures F=5.98, P=0.019, n=7 males). Significantly more time was spent in agonistic behavior (F=5.05, P=0.026, n=7) and sexual behavior (F=3.89, P=0.050, n=7) during the peak mating period compared to the early or late periods.

Mass and mass loss

Mass records were obtained for 27 individual males; 9 of these males were present at Amet in 2 years. Rates of mass loss were obtained for seven males in 1991, six males in 1992 and four males in 1993. No significant differences were found between years in either male mass at peak mating period (F=1.55, P=0.227, n=36) or in the rate of mass loss per day (F=1.57, P=0.243, n=17), so mass data for all 3 years were combined. The mean mass of males at peak mating was 284±31.8 kg and the mean estimated initial mass was 298±29.5 kg (n=36). The mean rate of mass loss was 2.9±0.9 kg/day (n=17). Individual rates of mass loss increased over the season in six out of the seven males for which two or more rates of mass loss were obtained (Fig. 7). The rate of mass loss per day was not correlated with male mass (r=0.30, P=0.238, n=17, minimum detectable r=0.567).

Table 3 Mean percent time (± 1 SD) spent in behavioral categories by males at three stages of the season: early mating period, peak mating period and late mating period. Differences between stages of the season were tested using repeated-measures analysis of variance on seven males which were present in all three stages

Behavior	Early	Peak	Late	Significant differences?
Idle	51.7±22.5	49.8±28.9	61.3±31.4	No
Alert	10.2±4.7	12.8±5.4	10.7±6.0	No
Comfort	2.3±1.9	2.2±1.6	3.0±2.3	No
Movement Locomotion	1.5±0.8	2.6±1.9	1.9±0.14	No
Agonistic	2.3±2.3	3.9±2.6	1.4±1.8	Yes
Sexual	1.3±2.2	4.5±5.2	0.9±2.3	Yes
Water	29.9±24.4	23.7±30.3	20.6±35.2	Yes

The estimated amount of absolute body mass lost over the season (for 1992 and 1993 only) ranged between 25.6 and 77.1 kg, with a mean of 41.9 kg (± 17.7, $n=10$). The estimated percent of initial body mass lost over the season ranged between 7.7 and 26.5%, with a mean of 14.3% (± 5.8, $n=10$). No relationships were found between these indices and any behavioral variables, although because the sample size was limited to ten males the power to detect small or medium effects was very low.

Copulations attendance success and competitive success

The maximum number of copulations recorded in a season for one male was nine, and this male was observed to copulate with six different females. Only 15 of 42 males observed during 1992 and 1993 were seen to copulate. For those males observed to copulate at least once ($n=15$), the mean number of recorded copulations per male was 3.3 ± 2.46 and the mean number of different females mated was 2.1 ± 1.53. When all males were considered ($n=42$), the mean number of copulations per male was 1.2 ± 2.14 and the number of different females mated was 0.7 ± 1.33. The operational sex ratio (the ratio of the number of females known to copulate to the number of males known to copulate) was 1.6 in 1992 and 1.9 in 1993.

The maximum period of attendance for one male was 20 days and the mean period of attendance was 4.5 ± 5.54 ($n=42$). Attendance success was strongly correlated with the number of copulations per male ($r=0.91$, $P<0.001$). Attendance success was not related to either male mass at peak mating ($r=0.02$, $P=0.938$, $n=18$, minimum detectable $r=0.550$) or rate of mass loss per day ($r=0.40$, $P=0.257$, $n=10$, minimum detectable $r=0.706$). In fact, in 1993, the male with the highest attendance success was the second smallest male captured. However, attendance success was found to increase with reproductive effort measured as both the absolute amount of mass lost ($r_s=0.79$, $P=0.007$, $n=10$) and the percent of initial body mass lost over the season ($r_s=0.67$, $P=0.036$, $n=10$). The most successful males in 1992 and in 1993 invested high amounts of energy in reproduction, losing an estimated 20–25% of their initial body mass over the season.

A weak negative relationship was found between the proportion of time spent in the water and attendance success ($r_s=-0.31$, $P=0.046$, $n=40$), while the proportion of time males spent idle on the ice surface was positively correlated with attendance success ($r_s=0.39$, $P=0.013$, $n=40$).

A total of 152 male-male agonistic encounters were observed, of which 58.6% had a clear winner and 41.4% were ties (no clear winner). The types of interaction included low or high threats (44.7%), chases (31.6%) and fights (23.7%). The index of competitive success

was found to be positively related to male attendance success ($r_s=0.57$, $P=0.031$, $n=16$). No relationship was found between this index and either male mass ($r=0.46$, $P=0.179$, $n=10$, minimum detectable $r=0.706$) or the percent of body mass lost over the season ($r=0.21$, $P=0.625$, $n=8$, minimum detectable $r=0.768$) although the power to detect such relationships was very low. The index of competitive success was found to be negatively related to the proportion of time spent in agonistic behavior ($r=-0.52$, $P=0.039$, $n=16$), indicating that those males which win the most interactions were not the males that spent the most time engaged in interactions.

A path diagram was constructed (Fig. 8) which predicted number of copulations in terms of attendance success, competitive success, reproductive effort, the total number of days a male was present at Amet Island, mass at mid-season and rate of mass loss per day. The hypothesized structural model explained approximately 80% of the observed variance in the index of attendance success and 82% of the variance in the number of copulations per male.
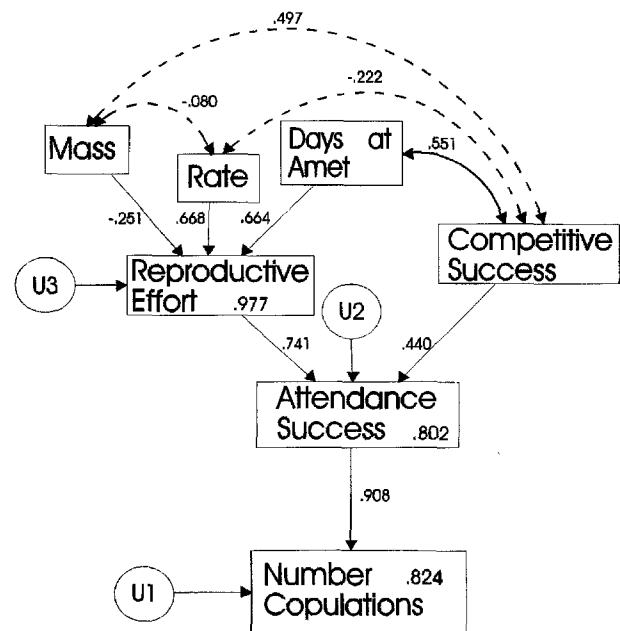

Fig. 8 Path diagram showing hypothesized structural relationships between the number of copulations per male, attendance success, competitive success, reproductive effort, the total number of days at Amet Island, mass at peak mating and rate of mass loss per day. *Two-way arrows* between *predictor variables* indicate correlations and the associated *values* are correlation coefficients. *Two-way arrows with dashed lines* represent correlations which were not found to be significant in independent univariate analyses, but for which insufficient power existed to detect small or medium effects. In these cases the observed correlation coefficients are provided for the interpretation of the hypothesized model. *One-way arrows* connecting *predictor* and *criterion variables* indicate causal relationships and the associated *values* are standard partial regression coefficients, or path coefficients. The unexplained variance components for criterion variables are indicated by U_1, U_2 and U_3, while the variance components explained by predictor variables (r^2 values) are shown as *values* inside the *boxes*

Discussion

The land-fast ice around Amet Island is much less stable than the land substrates used by other gray seal colonies and is also less stable than Arctic or Antarctic land-fast ice, which is usually stationary through the winter (Stirling 1969). The degree of access to open water was variable and unpredictable through time. Such a situation should favor low densities of parturient females and thus restrict the potential for polygyny (Stirling 1983; Emlen and Oring 1977). However, because females aggregated and access to open water was often limited (Fig. 2), it was possible for some males to monopolize more than one female simultaneously, and sometimes as many as five.

The operational sex ratio at Amet (1.6–1.9) was lower than similar female : male ratios found for land-breeding colonies at the Monach Isles (5.0) and North Rona (7.5) in the British Isles (Anderson et al. 1975; Anderson and Harwood 1985), but was approximately the same as Sable Island (1.3–2.6) in Eastern Canada (Boness and James 1979; Godsell 1991). This is consistent with the theory that an ice habitat should limit the degree of polygyny (Stirling 1983). The similarity in degree of polygyny at Amet Island and Sable Island is not surprising, as both sites provide virtually unlimited habitat for females and relatively open access (Boness and James 1979), limiting the extent to which males can monopolize females.

Certain aspects of the activity budget of males breeding on land-fast ice were similar to those of land-breeding males. For example, idle behavior made up approximately 70% of the time out of the water, alert behavior made up over 10% and locomotion, comfort movements and sexual behavior each made up less than 5% of the activity budget (Table 2). The fact that agonistic behavior was less frequent than in land-breeding colonies may be a result of the low density of animals at Amet Island, leading to fewer male-male encounters. The difference in the proportion of time spent in sexual behavior between Amet Island and the Monach Islands reflects the difference in the degree of polygyny between these two sites. Individual males would have been copulating with at least twice as many females at the latter site.

The most notable aspect of the activity budget for males at Amet Island was the high degree of variability in behavior, especially in the percent of time spent idle or in the water. This variation was partially in response to tidal fluctuations, changes in ice conditions and changing access to water. The proportion of time per day that females spent in the water also affected male behavior, although it is likely that female behavior was itself affected by changing ice conditions. Finally, male behavioral patterns appear to have changed as the number of potentially receptive females changed over the season. During the peak mating period, males increased the amount of time spent in agonistic and sexual behavior and decreased the amount of time spent in the water (Table 3). McCann (1981) found a similar increase in agonistic activity associated with increased sexual activity in southern elephant seal males. Gray seals at Sable Island showed just the opposite trend, with agonistic behavior decreasing as sexual behavior increased (Boness 1984). This discrepancy between Amet and Sable Island is difficult to explain, considering the many other similarities between these breeding colonies, but the different statistical analyses used makes direct comparison of results difficult.

The mean rate of mass loss by males at Amet Island (2.9 kg/day) was higher than the mean rate at North Rona (2.1–2.3 kg/day; Anderson and Fedak 1985). However, the estimated mean initial mass at Amet (298 ± 29.5 kg) was higher than mean initial mass at North Rona (235–245 kg), therefore it is to be expected that males at Amet would have higher metabolic costs and thus higher rates of mass loss (Kleiber 1975). Anderson and Fedak (1985) provide two regression equations of rate of mass loss on initial mass, based on data sets collected in 2 consecutive years at North Rona. If these equations are applied to the mean initial mass of males at Amet Island, rates of mass loss of 2.7 and 2.6 kg per day are predicted, only slightly lower than the actual mean of 2.9 kg per day.

The rate of mass loss at Amet was also slightly higher than that found at Sable Island (2.5 kg/day; Godsell 1991), but it is unlikely that the slight difference between these two sites is significant, considering the small sample sizes (Sable Island $n=7$, Godsell 1991) and the variation in rate of mass loss at Amet Island.

An unexpected result was the increase in rate of mass loss per day over the course of the breeding season at Amet (Fig. 7). At North Rona the rate of mass loss was found to be constant, with only one of eight males showing an increase over the season (Anderson and Fedak 1985). In contrast, in the present study only one of seven males did not show an increase in rate of mass loss. One possible explanation for the observed increase in rate of mass loss at Amet is the change in activity over the season (Table 3). The increase in male agonistic and sexual activity at mid-season may correspond to higher energy costs and thus a higher daily rate of mass loss. A second possibility is that there is a decrease over the season in the ratio of fat to protein utilized as fuel, which would require that more tissue be metabolized to provide sufficient energy. However, the available data on protein utilization in fasting seals do not support this explanation (Castellini and Rea 1992).

The high proportion of mass lost by successful males represents a substantial energetic investment in reproduction. In polygynous animals high male

reproductive success is often associated with high levels of reproductive effort (e.g., Farr and Andrews 1978; Gibson and Guinness 1980; Deutsch et al. 1990). In northern elephant seals (*Mirounga angustirostris*), where polygyny reaches extremely high levels (Le Boeuf and Reiter 1988), high-ranking males lost approximately 41% of their body mass, compared to low-ranking adults which lost 34% (Deutsch et al. 1989). This is considerably higher than the estimated 20–25% lost by the two most successful males in this study and is consistent with the hypothesis that higher degrees of polygyny should be associated with greater levels of reproductive effort by males (Trivers 1972). At North Rona, Anderson et al. (1975) found that the five most successful gray seal males remained ashore for over 35 days; assuming a mean rate of mass loss of 2.2 kg/day and a mean initial mass of 245 kg (Anderson and Fedak 1985) these males lost approximately 31% of their body mass, slightly higher than the values estimated for the most successful males at Amet Island. It should be noted, however, that the estimates of total mass loss in the present study may be conservative because they are based on the number of days males were known to be present at Amet. Some males were already present at Amet upon commencement of observations and some males may have gone on to breed on the pack-ice in Northumberland Strait and George Bay after the Amet season. Breeding in these locations continues into mid February. Thus the recorded time males were at Amet may not represent the entire seasonal investment in reproduction.

Large size was not a major factor in determining reproductive success among males at Amet Island. Because only attending males remained on the ice surface and were available for capture, mass data for satellite males (males not attending females) were not obtained. If mass records had have been gathered for these males, then a relationship between mass and reproductive success might have been found. At North Rona there was a strong relationship between initial mass and copulatory success even among males that had won a position within the breeding group (Anderson and Fedak 1985). It is possible that the nature of male-male competition at Amet Island does not favor large size as strongly as on a land-breeding substrate. Although large male size is associated with high rank or competitive success in many polygynous species (e.g. Clutton-Brock et al. 1988; Deutsch et al. 1990), this is not always the case. Male Weddell seals breeding on the Antarctic land-fast ice vigorously defend under water territories in male-male conflicts (Siniff et al. 1977). In this situation smaller size may actually be an advantage (Stirling 1983). At Amet Island, male-male agonistic encounters were observed both on the ice and under water. While large size may give males an advantage in encounters on the ice, it may provide little advantage in under-water encounters.

Generally speaking, male attendance success at Amet seemed to be a function of the ability to win agonistic encounters and the ability to sustain a considerable energetic cost over the breeding season (i.e., reproductive effort). These factors are, of course, interrelated; one hypothesized multivariate model suggests that attendance success was the most important factor affecting number of copulations (Fig. 8). Competitive success and reproductive effort also affected the number of copulations indirectly, through their effect on attendance success. In this model, approximately 80% of the variance in attendance success could be explained by the index of competitive success and reproductive effort.

By definition, virtually all the variance in reproductive effort (98%) was explained by mass, rate of mass loss and number of days at Amet Island, since these were the variables used to estimate reproductive effort. The negative path coefficient between mass and reproductive effort (Fig. 8) demonstrates one advantage of large body size: larger males can lose the same amount of weight as smaller males at less overall cost (Lindstedt and Boyce 1985).

The factors determining male competitive success were not apparent in this study. In a univariate analysis body mass and competitive success were not correlated, although data on both competitive success and body mass were available for only ten males, providing sufficient power to detect only very strong correlations. Age and experience might also be important; Godsell (1991) found that older males initiated and won a greater proportion of fights and chases than younger males at Sable Island.

Anderson et al. (1975) hypothesized that the optimal strategy for gray seal males at North Rona was to remain ashore and maintain a position among females for as long a time as possible. To accomplish this, males would need to conserve energy to enable them to fast over a prolonged period while still maintaining a high level of sexual drive and the ability to defeat (or not be beaten by) other males. The present study supports this model of optimal male reproductive tactics. The negative relationship between competitive success and the proportion of time spent in agonistic interactions suggests that successful males did not spend a great deal of time in costly agonistic encounters, although when they did engage in encounters they usually won.

Variable or unstable habitats are thought to favor flexible social systems (Lott 1984). During recent evolutionary history the gray seal has probably used a variety of ice and land substrates for breeding (Davies 1957) and there may have been strong selective pressure for behavioral plasticity (Anderson and Harwood 1985). Male gray seals at Amet Island show a high degree of variability in reproductive behavior, probably in response to the unstable ice substrate on which they

breed. The most successful males were those that could maintain a position as an attending male for most of the breeding season, but some males attended females from the ice surface while others attended primarily from the water. Attending males altered their behavior in response to changes in ice topography or the behavior of females and day to day changes in individual time budgets were seen over the season. Gray seal males at Amet Island appear to respond to the instability of a land-fast ice habitat in a manner predicted by models of mating system theory, monopolizing access to as many females as environmental conditions will permit.

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