

Mating tactics and mating system of an aquatic-mating pinniped: the harbor seal, *Phoca vitulina*

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Abstract Our best understanding of marine mammal mating systems comes from land-mating pinnipeds. Logistical problems of observing behavior at sea have limited our ability to make inferences about species with aquatic-mating systems, which comprise over half the pinnipeds. The mating systems of these species likely involve different mating tactics than land-mating species. We used several methods in combination (e.g., animal-borne cameras, radio telemetry, time-depth recorders, and DNA paternity assessment) to provide a comprehensive study of the aquatic-mating tactics of harbor seal males. Males decreased time offshore (26.0 vs 14.8%) and increased time near shore (33.8 vs 43.7%) between pre-mating and mating periods,

respectively. Concomitantly, males reduced foraging effort and increased activities associated with competition for females (e.g., visual/vocal displays and threats). As females come into estrus near the end of lactation and spend more time at sea, males reduced their near-shore ranges (4.2 vs 1.0 km²), which were clustered within 1–1.5 km of the beach where females attended their pups. Body mass of males was not a major factor affecting their reproductive behavior. From a small number of paternity assignments to study males, it appears that females select males. These combined results are more consistent with a lek-type mating system than with the territorial or female defense systems characteristic of land-mating pinnipeds.

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Introduction

Animal mating systems are influenced by a variety of factors, including phylogeny, distribution of resources, and predation pressure (Wilson 1975; Emlen and Oring 1977; Rubenstein 1986; Clutton-Brock 1989). Among polygynous species, the primary resources affecting female reproductive behavior are food and suitable environments for rearing offspring, whereas the reproductive behavior of males is most influenced by the temporal and spatial distribution of females. In populations where females are clustered and their movements limited or predictable, males generally compete to monopolize females by controlling access to resources used by the females (territoriality or resource defense tactics) or attempt to monopolize females directly (male dominance or female defense tactics). However, when females are dispersed spatially and tempo-

rally, or are highly mobile, so that access to groups of females cannot be controlled, males are more likely to use other tactics, such as, lekking, scramble competition, or sequential defense of single females.

Lekking is a relatively rare mating system reported in less than 0.5% of birds and mammals (Davies 1991; Höglund and Alatalo 1995). Although there is not complete agreement on the critical elements that define a lek, the common criteria are: (1) males aggregate and display to attract females; (2) females and males visit these sites primarily for mating; and (3) females have an opportunity to select a mate (Bradbury 1981; Höglund and Alatalo 1995). The latter criterion is thought to be of lesser importance by Höglund and Alatalo.

The mating systems of many terrestrially breeding pinnipeds and the best-studied terrestrial mammals are similarly well understood. Certain characteristics of such pinnipeds, which are more suitably adapted to life at sea than on land, predispose them to particular mating systems. More specifically, their large body size, extensive subcutaneous blubber layer, and poor mobility on land predispose them to systems in which males usually maximize mating opportunities through territorial defense of resources used by females (i.e., suitable pupping sites) or direct defense of females by males (Bartholomew 1970; Stirling 1983; Boness 1991; Le Boeuf 1991; Boness et al. 2002; Lidgard et al. 2005). Extrapair or extraconsort matings may also occur in these systems (Ambs et al. 1999; Goldsworthy et al. 1999; Hoelzel 1999; Lidgard et al. 2004).

About half of all pinniped species mate at sea rather than on land. The temporal and spatial pattern of females, and hence male mating tactics, in this environment are likely to be different than those for terrestrially mating pinnipeds because of their greater mobility in water and dispersed spatial distribution. Several authors have argued that these conditions should lead to strategies such as lekking or roving than to resource or female defense (Stirling 1983; Le Boeuf 1991; Boness et al. 1993, 2002). For example, certain conditions that lead to lekking, (e.g., high mobility of females, “hot spot” for availability of females, relatively low asynchrony of estrus) (Emlen and Oring 1977; Bradbury 1981; Beehler and Fosters 1988; Davies 1991; Wiley 1991; Höglund and Alatalo 1995; Widemo and Owens 1995; Gjerde et al. 2000) match those of several species of seal that mate at sea shortly after females in colonies on ice or land wean their pups (Boness et al. 1993). However, the evidence to understand the mating system of pinnipeds that mate at sea is much more limited because of logistical difficulties in trying to observe and follow individual animals. Nonetheless, the use of advanced technology and new approaches to studying marine mammals are providing insights into the mating systems of aquatically mating pinnipeds (Bartsh et al. 1992; Perry

1993; Hanggi and Schusterman 1994; Sjare and Stirling 1996; Coltman et al. 1997, 1998a; Nicholson 2000; Van Parijs et al. 2000a,b, 2001, 2003).

Despite the recent increased efforts to study aquatically mating seals, we are still in the early stages of understanding their reproductive behavior and mating system. One species, the harbor seal, *Phoca vitulina*, has been given more attention than most because of its greater accessibility (Perry 1993; Coltman et al. 1997, 1998a,b, 1999; Van Parijs et al. 2000a,b, 2003; Hayes et al. 2004). Unlike most aquatically mating seals, harbor seal females generally give birth and care for their offspring on land rather than on ice, although there are a few locations where harbor seals produce pups on ice floes, too. The nature of harbor seal pupping colonies is diverse, leading to considerable variation in the size of colonies and the structure of the area surrounding colonies (e.g., narrow sand or cobble beaches, small rocky outcroppings affected by tidal cycles, and mud flats with distinct water channels leading to them). Regardless of colony structure or size, females do form small clusters along the shoreline.

Mounting evidence shows that females spend time at sea during the period of maternal care, and that this time at sea involves regular foraging trips away from the colony (Boness et al. 1994; Van Parijs et al. 1997). What appears to be a commonality among studies of male behavior is the use of underwater vocalizations (Van Parijs et al. 2003). Male spatial patterns and movements in relation to the colony and location of females are less clear, but vary considerably among breeding colonies and even within a colony (Perry 1993; Van Parijs et al. 2000a,b; Hayes et al. 2004). In some cases, defense of adjacent discrete territories offshore from female haulout areas has been described, and males may or may not display from such territories (Sullivan 1981; Perry 1993; Hayes et al. 2004). In other cases, males may display from underwater territories that are not adjacent to one another nor near female haulout sites, but be located in known foraging areas or along routes to foraging areas (Van Parijs et al. 2000a,b; Hayes et al. 2004). In still other situations, males may not form discrete territories, but display vocally in the vicinity of female haulouts and engage in combat when they come in close contact with other males (Hanggi and Schusterman 1994). Inferences about the mating system from these varying results range from territorial defense of transit routes or feeding sites to lekking. As noted by Hayes et al. (2004), virtually all of these studies raise the possibility of a lek system. The difficulty with these interpretations is that they generally are based on either a small number of males or on a limited set of behavioral information, or both.

In this study, we used a combination of methods, including an animal-borne video system, time-depth recorders, radio telemetry, and DNA paternity analyses to provide

a more comprehensive assessment of the mating system of the harbor seal at Sable Island, Nova Scotia. Our objectives were to evaluate the likelihood that harbor seal males exhibit a mating system that differs from those exhibited by land-breeding pinnipeds and that some or all males use a lekking-type pattern of behavior to acquire mates.

Methods

Data were collected from 17 to 56 males, depending on data type, off Sable Island, Nova Scotia (43° 55'N; 60° 00'W) between 1993 and 1996. Males in mixed-sex and all-male groups were selected to achieve a full range of body size. We deployed in various combinations on different males, radio transmitters (to obtain locations), time-depth recorders (to obtain diving frequency, depth and duration), and video cameras (to observe behavior) by capturing males when they were resting on land. Each year, males were followed from the beginning of the birthing period (mid-May), about 3 weeks before receptive females became available (pre-mating period), through mid-July when receptive females had been present for 3–4 weeks (mating period) (Coltman et al. 1997).

Spatial analyses

We affixed radio transmitters (Advanced Telemetry Systems, Isanti, MN, USA) on top of the head of seals using 5-min epoxy so that signals could be received when the animals surfaced at sea or were on land. Transmitters remained attached and functioned for 10 males in 1993, 17 males in 1994, 15 males in 1995, and 14 males in 1996. Males were followed from a minimum of 11 days to a maximum of 39 days, with a mean number of days of 25.3, 32.6, 25.3, and 24.7 from 1993 to 1996, respectively.

Markers at 0.5-km intervals provided location references along a 31-km stretch of the north beach where most females gave birth. Twice daily surveys of this area, one in the morning and the other in the late afternoon, listening for radio signals, were made throughout the breeding season to locate males. These surveys involved driving the ATV slowly along the beach looking and listening for radio-tagged males, and obtaining a point sample of their location. When males were seen on land, their locations were recorded to the nearest 0.1 km. If a radio signal was heard off the beach, we obtained bearings from two locations, usually 1–2 km apart, to facilitate triangulation. A 4-element antenna attached to a 4-m pole on an all-terrain vehicle provided a probable receiving range of about 5 km. If a male was neither seen nor heard, we assumed he was beyond the range of our system. A more extensive search, involving circumnavigating the island, was conducted when

a male was not heard for 3 days to be sure that the male was not hauling out outside the study area. On only two occasions was a male located elsewhere during the pre-mating period. Ninety-five percent minimum convex polygon ranges were estimated for 32 of the 56 males that had more than 12 near-shore locations. The number of locations ranged from 13 to 38.

Behavior analyses

We attached to the backs of males the animal-borne video system (Critttercam), which included a built in hydrophone and time-depth recorder so diving data and vocalizations could be associated with behavior (Marshall 1998; Bowen et al. 2002). The total unit weighed about 2 kg or <2% of a male's body mass. A 3-h videotape determined the maximum amount of observation time per 3-day deployment; a saltwater switch ensured maximum filming at sea. The camera was programmed to run for 10 min every hour from 0530 or 0600 to 1400 or 1500, and sampling of dive depth every 7 s. We deployed cameras after 1500 h so they would not begin sampling until the next morning. This provided about 14 h for animals to adjust to the camera before collecting data, although visual observation of animals and video footage did not suggest males were disturbed by the presence of the camera on its back.

In 1995, cameras were deployed on June 6–22, on 10 males. Data were obtained from nine of those deployments. In 1996, deployments occurred on June 2–22 on each of 10 males twice (one each during pre-mating and mating periods). Data were obtained from 15 of these deployments, seven during the pre-mating period, and eight during the mating period. The minimum interval between deployments on a given male was 7 days. Longitudinal analyses were conducted on the seven males for which both deployments yielded data. However, data from all males in 1996 were used once in the cross-sectional analyses, selected randomly for which time of season was used for a given male.

The videotapes were initially examined to determine the behaviors exhibited. From this, behavior categories were established and the tapes scored for the amount of time each male spent in the different categories. The categories were:

- Threat/fight Another male is in view and vocal growls, starting with neck and chest inflated, chasing or biting occurs.
- Display The camera male engages in one of three stereotypical behaviors involving visual and/or vocal signaling and other seals are not in view. Neck-quivering vocalization involves emitting a broadband vocalization during which the head and neck quiver. This is always done underwater, usually near the

bottom, although occasionally it is given during a descent after breathing at the surface. Bubble-blowing vocal display involves the male ascending toward the surface and slowly exhaling a stream of bubbles as he drifts upward, giving a vocalization that ends similarly to that used during neck quivering (Fig. 1). This is often preceded by several neck-quivering vocalizations. For one male in which a camera was allowed to run for 3 h immediately after deployment, neck-quivering and bubble-blowing display occurred the entire time. Surface slapping is done with either one foreflipper or thrashing the rear flippers from side to side. No discernable vocalization is made during slapping although sometimes a male rapidly exhales air creating a cloud of bubbles just before it breaks the surface of the water and slaps.

Patrolling	This is inferred from activity immediately preceding it. It involves a male swimming slowly underwater, usually interspersing active thrusting with the rear flippers and gliding, and is preceded by displaying or threats within a 10-min sampling period. Observations of a few males from elevated dunes near shore in shallow water showed them swimming/gliding underwater repeatedly within a relatively small area.
Foraging	Includes chasing schools or individual fish and rooting in the bottom substrate whether fish are seen in the camera's view.
Searching	This behavior is also defined by the activities preceding it (as in patrolling) and includes

Travelling	This includes swimming with continuous flipper thrusting or alternate thrusting–gliding swimming for which there are no clear foraging or displaying activities during the 10-min sample.
Resting	This includes lying on the bottom or bobbing at the surface.
Other	This includes ascending to the surface to breathe, descending to depth, and hauling out in the surf zone.

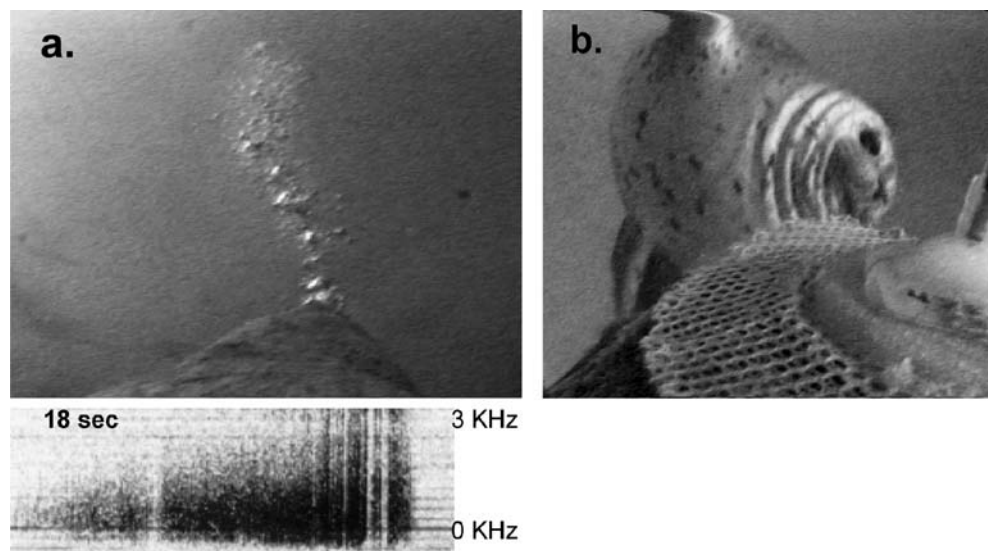
Paternity analysis

The paternity data for this study were a subset of data from a broader study of paternity of harbor seals at Sable Island. Details of analysis methods and broader results can be found in Coltman et al. (1998b). Skin samples were collected from as many females, pups, and males as possible for several simultaneously ongoing studies on Sable Island during this work. Six polymorphic microsatellites were used in the paternity analysis (Coltman et al. 1998b). Paternity assignment was done using a paternity simulation program (CERVUS). The average probability of exclusion was 0.957 and 0.940 (ranging from 0.309 to 0.999) for the 2 years from which data were available for males in this study (Coltman et al. 1998b).

Statistical analyses

Parametric statistical analyses were used when their assumptions were satisfied, otherwise nonparametric tests

Fig. 1 Single frames captured from a Crittercam tape to illustrate a male harbor seal engaged in bubble blowing display and a male with a camera and transmitter attached threatening another male. The radio transmitter and netting glued to the head of the male with the camera are illustrated. The male blowing bubbles is within 5 m of the surface and nearly vertical. He does not surface after completing the bubble blowing. The sonogram represents the vocalization associated with the bubble blowing display



were run. Analyses were conducted using either SigmaStat (Version 2.03) or SPSS (Version 11.0). Rejection of the null hypothesis in tests was set at 0.05.

Results

Interannual variation

As data were collected over several years, we first assessed the impact of interannual variation on our ability to treat the data as a whole. Although within the pre-mating and mating periods there were interannual differences in how often males were either on land, near shore, or offshore during the twice-daily surveys (pre-mating: Chi-square=163.1, $df=6$, $p<0.001$; mating: Chi-square=80.9, $df=6$, $p<0.001$), the pattern of change in the percentage of sightings in each location from pre-mating to mating period was consistent among years. Thus, for comparisons of the percentage of sightings in each location category between the pre-mating and mating periods, we combined data from all years.

A MANOVA of arc-sine transformed percentages of time spent in each behavioral activity (display, patrol, threat, forage, search, travel, and rest) from cross-sectional Crittercam data showed no difference between years in the overall pattern of activity ($F_{7,8}=1.42$, $p=0.315$). Thus, we combined data from the 2 years for an analysis of the difference in proportion of time in each behavior between the pre-mating and mating periods. Since the study design in 1996 was longitudinal, to increase the sample size for the cross-sectional analyses, one deployment for each male from 1996 was randomly chosen to be included in the cross-sectional analysis. A two-way repeated measures ANOVA of the size of near-shore ranges of 32 males to examine differences between years and period failed both normality and variance tests. Hence, we tested differences among years for each season separately using a Kruskal–Wallis ANOVA on ranks and tested for differences between pre-mating and mating periods using a Wilcoxon test. Ranges during the mating period did not differ among years ($H=1.170$, $p=0.557$), but pre-mating ranges did ($H=7.11$, $p=0.029$), so we present the data separately by year.

Daily locations from surveys

Males were not equally sighted onshore, heard at sea near shore (<5 km of shore), or out of range offshore (approximately >5 km) during either the pre-mating or mating periods (Chi-square goodness of fit test: $p<0.0001$ for both periods). Males rested on land during a similar percentage of the surveys (about 40%) in both periods (paired t test: $t=1.66$, $df=55$, $p=0.102$). However, the

percentage of surveys during which males were offshore decreased from the pre-mating to mating periods (26.0 vs 14.8%; paired t test: $t=5.53$, $df=55$, $p<0.001$), whereas the percentage near shore increased (paired t test: 33.8 vs 43.7%; $t=6.35$, $df=55$, $p<0.001$).

Behavior at sea

Based on footage from the animal-borne cameras, males engaged in all recorded activities during both the pre-mating and mating periods. Different deployment procedures for Crittercams in 1995 and 1996 as described in the methods allowed comparison of both cross-sectional and longitudinal data sets between the pre-mating and mating periods. Based on these data, males engaged in display behavior significantly more during the mating period than during pre-mating (Table 1). Small sample sizes and individual variability provided for low power to detect other differences.

Males in this population are known to change their diving behavior between pre-mating and mating periods (Coltman et al. 1997). In the earlier study, males made deep dives (depths >20 m) more frequently during pre-mating, then switched to predominantly shallow (<20 m) diving during the mating period. Deep dives were fairly uniform in shape, having flat and long bottoms and rapid rates of descent and ascent. Shallow dives were more variable in shape. Rates of individual mass loss varied inversely with time spent in deep dives, suggesting that deep diving behavior reflected foraging activity (Coltman et al. 1997). Therefore, using the Crittercam data, we also tested whether behaviors differed between those same depth categories. We found a significant difference between the pattern of behavior exhibited during deep and shallow diving (MANOVA, $F_{7,13}=5.688$, $p=0.004$). Percentage of time spent displaying, patrolling, and foraging clearly differed (i.e., significant in both cross-sectional and longitudinal analyses) with dive depth; displaying and patrolling occurred more during shallow dives and foraging more during deeper dives. Traveling, searching, and threatening males may also have differed, but these differences were significant in only one or the other analysis (Table 2).

Near-shore spatial patterns

Near-shore ranges during the mating period were significantly smaller, about 25% of those during the pre-mating period (Table 3). There was considerable variability among males in the size of near-shore ranges during the mating period, with variability being greatest in 1996 (Table 3; Fig. 2). Male near-shore ranges during the mating period overlapped substantially and in 1994 and 1995 were concentrated in the region off the beach, where the greatest

Table 1 Behavior of male harbor seals at sea

	Cross-sectional data					Longitudinal data				
	Premating (<i>n</i> =9)		Mating (<i>n</i> =9)		<i>T</i> -value (<i>p</i> -value) ^a	Premating (<i>n</i> =7)		Mating (<i>n</i> =7)		<i>T</i> -value (<i>p</i> -value) ^b
	Mean	Standard error	Mean	Standard error		Mean	Standard error	Mean	Standard error	
Threat	0.9	0.51	1.0	0.43	-0.552 (0.589)	0.4	0.23	0.3	0.23	-1.323 (0.234)
Display	2.5	0.84	9.4	2.42	-2.506 (0.023)	3.6	1.38	11.1	4.29	3.692 (0.010)
Patrol	13.1	4.69	25.8	4.70	-2.027 (0.060)	20.1	4.99	22.7	5.72	0.269 (0.797)
Forage	8.2	2.78	5.0	1.53	1.017 (0.324)	3.4	1.11	5.9	1.92	1.133 (0.300)
Search	16.4	3.91	12.6	3.14	0.821 (0.424)	15.6	3.48	15.9	5.01	-0.252 (0.809)
Travel	18.8	3.67	10.8	2.74	1.591 (0.131)	19.0	3.87	8.8	2.20	-2.897 (0.027)
Rest	19.0	2.37	21.3	2.88	-0.628 (0.539)	18.8	2.53	15.1	1.86	-1.261 (0.254)

Mean percentages of time spent in each activity at sea during the premating and mating periods for two data sets, one based on cross-sectional data for 18 males and the other on longitudinal data for seven males. "Other" category is not included so the total is less than 100%

^a *t* tests using arcsine square-root transformation

^b Paired *t* tests using arcsine square-root transformation

number of females with pups was located (Fig. 2). There appeared to be an increase in the number of larger mating ranges in 1996 that coincides with a dramatic reduction in the number of females that produced pups on Sable Island.

Paternity in relation to near-shore range

Paternity analyses were conducted during the same time period as this study, but were published separately (Coltman et al. 1998b, 1999). Each year the entire cohort of pups (and most of the mothers) was sampled. The potential pool of males was estimated to be about 180, 90

of which were sampled (Coltman et al. 1998b). During 1993 and 1994, 12 of 27 males from our study that had radio transmitters attached were assigned one or more paternities: eight sired one pup, two sired two pups, one sired three, and one sired four. In the larger paternity analysis by Coltman, the maximum number of pups sired for a given male was five, and most males sired only one pup or none.

As it has been suggested that harbor seal males hold territories offshore to control travel routes and gain access to estrous females moving from land (Perry 1993), we conducted an analysis to evaluate whether this might be happening at Sable Island. The analysis used the 11

Table 2 Behavior of male harbor seals during diving

	Cross-sectional data					Longitudinal data (<i>n</i> =7)				
	<20 m (<i>n</i> =9)		>20 m (<i>n</i> =9)		<i>P</i> -value ^a	<20 m		>20 m		<i>P</i> -value ^b
	Mean	Standard error	Mean	Standard error		Mean	Standard error	Mean	Standard error	
Threat	1.2	0.47	0.3	0.20	0.049	0.5	0.53	0.8	0.56	0.449
Display	9.0	2.65	3.0	1.91	0.023	4.7	1.26	0.2	0.14	0.006
Patrol	29.9	2.92	6.1	3.11	0.001	21.7	4.25	1.6	0.81	0.001
Forage	1.7	0.43	14.1	2.83	0.001	3.0	1.38	13.4	3.51	0.028
Search	9.8	2.39	24.8	4.11	0.004	13.9	3.12	23.4	4.63	0.196
Travel	15.3	3.1	7.1	2.47	0.059	22.0	4.07	8.65	2.85	0.002
Rest	19.2	2.60	19.4	2.32	0.856	16.8	2.18	26.6	6.59	0.235

Mean percentages of time spent in each activity at sea during dives >20 and <20 m for two data sets, one based on cross-sectional data for 18 males and the other on longitudinal data for seven males. "Other" category is not included so the total is less than 100%

^a *t* tests using arcsine square-root transformation

^b Paired *t* tests using arcsine square-root transformation

Table 3 Near-shore range size of male harbor seals

Year	N	Premating period		Mating period	
		Median	Range	Median	Range
1994	9	1.5	0.4–12.5	0.7	0.2–6.9
1995	10	3.2	0.5–5.3	0.8	0.3–5.6
1996	13	11.3	0.7–19.4	2.2	0.1–15.7
1994–1996	32	4.2		1.0	

Ranges are given in km². A Wilcoxon sign rank test of the median between the premating and mating periods for all years combined is significant ($p < 0.001$)

paternities that could be assigned to one of the males with attached radio transmitters, for which we knew the location of their near-shore ranges. We then asked whether the probability of the female being fertilized by a male adjacent to her location on land was commensurate with the amount of time the male spent in his near-shore range, assuming positioning nearby off the beach gave a male primacy access. We operationally defined “adjacent to a female’s location on land” by determining whether all or part of a male’s range fell within lines perpendicular to the shore one half kilometer on either side of the female’s beach location at the end of lactation. The proportion of surveys males were at their near-shore site was used to calculate the expected frequency of fertilization for an adjacent male. The actual frequency of fertilizations by males that were adjacent to females was compared to this expected frequency. The results showed that females were fertilized less often than expected by a study male that was adjacent to her beach location ($G_{adj}=4.66$; $p < 0.05$); only one of the 11 females was fertilized by an adjacent study male. The average minimum linear distance between a line perpendicular to the closest part of the near-shore range of the male assigned paternity and a line perpendicular to where the female was last located on the beach before weaning was 4.6 ± 3.05 km.

Influence of body mass on male behavior

Previous studies have shown body mass to be a factor in male mating behavior in many polygynous mammals, including some pinniped species. However, body mass may be less important in determining male reproductive behavior of harbor seals (Coltman et al. 1998a,b). To examine the relationship between body mass and behavior of males, we conducted several analyses using male survey, near-shore range, and Crittercam behavioral data. A MANOVA with the percentage (Arcsine Square Root transformed) of surveys observed near shore during the premating period and offshore during the mating period, and near-shore range size during the mating period as dependent variables, and dividing the range of initial body

mass into two groups based on the median mass (106 kg), failed to find an effect of mass on these behaviors ($F_{3,28}=0.695$, $p=0.563$). Consistent with this pattern, a

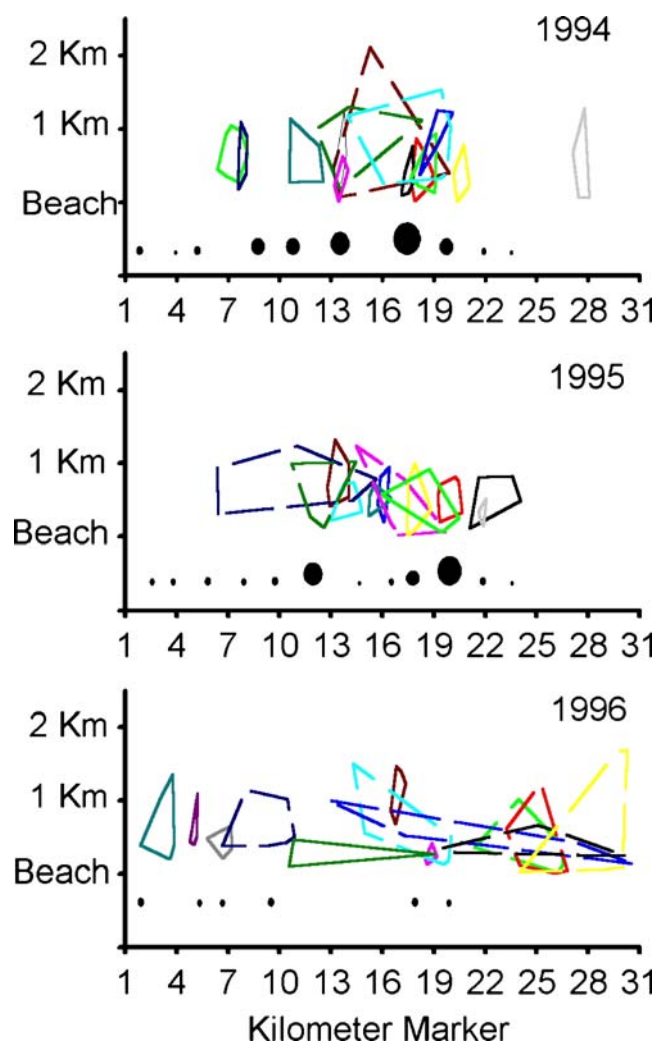


Fig. 2 Schematic of near-shore ranges of male harbor seals during the mating period. Each polygon represents a different male, 17 harbor seal males in 1994, 15 in 1995, and 14 in 1996. The filled circles in the beach area represent relative numbers of females with pups on shore between kilometer marker. The largest filled circle represents 35 females and the smallest one female. There were 130 females in 1994, 116 in 1995, and 39 in 1996

regression analysis of Crittercam behavioral data found a significant negative relationship between percent time spent foraging during the mating period and initial body mass for those Crittercam males for which we had a body mass at the beginning of the breeding season ($R^2=0.545$, $p=0.015$, $n=10$). We failed to find a statistically significant relationship between initial body mass and percent time spent displaying ($R^2=0.208$, $p=0.185$).

Discussion

Male tactics and mating system

The combination of systematic behavioral, spatial, and paternity data used in our study provides the most comprehensive study of an aquatic-mating system of a pinniped population. Yet, even with these more comprehensive data than in previous studies of this species, or any other aquatic-mating pinniped, we are not able to unequivocally describe the mating system in terms of categories used in mating system theory. Nonetheless, our data are more supportive of some male tactics than others. Consistent with several other studies of harbor seals (Walker and Bowen 1993; Hanggi and Schusterman 1994; Van Parijs et al. 1997, 1999, 2000a,b; Coltman et al. 1999; Nicholson 2000; Hayes et al. 2004) and with discussions of alternative mating tactics and plasticity in mating systems (Emlen and Oring 1977; Davies 1991; Lott 1991), our data support the idea that more than one tactic may be used by males to acquire females, and that there may have been a shift in primary tactic in 1996 from 1994 and 1995.

The substantially greater mobility and dispersion of pinniped females at sea compared to on land, should favor male tactics that involve displaying to attract females or those in which males search out or follow individual females than those that involve defense of females or resources that are used by females (Bradbury 1981; Stirling 1983; Clutton-Brock 1989; Boness 1991; Davies 1991; Le Boeuf 1991; Boness et al. 1993, 2002). Moreover, female harbor seals are clustered on land before dispersing at sea, conditions ideal to create a “hotspot” basis for aggregation of males to engage in display competition over females (Beehler and Fosters 1988; Balmford et al. 1993b; Widemo and Owens 1995). We believe our evidence from 1994 and 1995, especially, point to a lek-like tactic as the primary one for harbor seals at Sable Island. The criteria most often used to describe leks include males aggregating and displaying to attract females, both males and females visiting these sites primarily for mating, and females having an opportunity to select males (Bradbury 1981; Höglund and Alatalo 1995). Early descriptions of classical lek

systems in birds also usually reported extremely high levels of mating skew (Wiley 1991; Höglund and Alatalo 1995). Höglund and Alatalo, however, prefer not to use this characteristic in defining a lek system, arguing that mating skew is difficult to define because of variation in determining the number of males in a population, and that other systems also produce high levels of skew. Moreover, the degree of skew appears to be related to the size of the lek, with lower skew found in larger leks (Höglund and Alatalo 1995).

Our spatial analysis shows that harbor seal males increased the amount of time spent near shore during the mating period. Males fitted with radio transmitters aggregated near where females were most abundant on land about the time the females become receptive, which could be considered a “hotspot”. While near shore males did not appear to defend exclusive areas, most maintained relatively small ranges within which they engaged in competitive encounters with other males. Males did not spend their entire time during the mating period on these near shore ranges. They still spent about 40% of their time on land and smaller amounts of time out of range of detection. That male near-shore ranges likely serve a mating function is suggested by changes in behavior from the pre-mating period to the mating period, including the reduction in range size, the increased time spent near shore, and the increased time spent displaying at the expense of time spent foraging.

We were unable to track the pelagic movements of females simultaneously with our observation of males. However, from previous studies of lactation strategies (Boness et al. 1994; Bowen et al. 2001), we know that later in lactation, females make regular foraging trips to sea with typical diving bouts in the range of 15–30 m deep, mixed with time spent in shallower waters of 5–10 m, but return to land daily. The diving and haulout pattern of females changes dramatically soon after weaning their pup. At this time, females begin making dive bouts greater than 45 m in depth continuously for multiple days without returning to shallower water or land. This pattern of behavior before and after weaning provides females with increasing opportunities to sample the quality of males at their near-shore ranges before or immediately after weaning, when females are thought to become receptive. As Höglund and Alatalo (1995) suggest, mating with males that become established at an arena (i.e., location of the aggregation of males) in itself may convey a level of selection by females. In addition, the fact that females at Sable Island were not fertilized by study males in positions opposite to where the female was on land at the end of lactation supports the hypothesis that females are exercising choice among males within the near-shore area, although it is not conclusive evidence of choice.

These results are all consistent with the criteria often used to judge a system as a lek system. Though mating skew in this population was not extreme, it did exist at a low to moderate level (Coltman et al. 1998b), which is consistent with the findings of a negative relationship between level of skew and lek size (Höglund and Alatalo 1995). The area over which male near shore ranges were distributed off the beach at Sable Island stretched along 30 km of beach.

We do not believe our results on behavior in near shore ranges are supportive of either resource defense or female defense systems. Resource defense systems involve defense of discrete territories containing resources used by females. The spatial analysis in this study clearly shows a lack of exclusiveness of the areas used by males. While there may be occasional foraging at the depth of these near-shore ranges, most foraging off Sable Island occurs at deeper depths (Boness et al. 1994; Coltman et al. 1997). We cannot, however, rule out the possibility that some males might have defended exclusive resource territories near foraging areas used by females outside the range of our ability to detect them with radio telemetry (Van Parijs et al. 2000a).

Despite a small sample size, the paternity analysis shows that it is also unlikely that males in their near-shore ranges were simply defending travel lanes of females, where they could control females by capturing them and forcing copulations (Perry 1993; Hayes et al. 2004). Females were not fertilized by males on ranges adjacent to the female's location on the beach, but in addition, the average linear distance between where a female was on the beach and the male that fertilized her was more than 4 km.

If males were defending females directly, we would have expected the video footage to provide relatively frequent views of females in range of the lens, as we saw encounters between males. Yet, we rarely saw females in the videotape analysis. Additionally, from our earlier studies of female diving activity at sea, their daily patterns of movement were to and from the beach and to deeper waters for foraging. It seems unlikely that this pattern of behavior would provide the spatial clustering of females for female defense to be effective.

We cannot so readily rule out male tactics involving roving or scramble competition. Some males in each year had relatively large near-shore ranges during the mating period in contrast to the typical small range. This may reflect the existence of alternative tactics, such as following or searching for departing females in an effort to copulate with them. Such variability in male tactics has been described in terrestrial species that have lek systems (Clutton-Brock et al. 1988; Apollonio et al. 1992; Balmford et al. 1993a; Widemo and Owens 1999) and shifts in reproductive behavior and mating systems associated with changes in female density and distribution are well documented for terrestrial species (Lott 1991). The fact

that there appears to be an increase in the occurrence in large mating ranges in 1996 suggests there might have been a shift away from a primary lekking-type tactic and toward an alternative tactic such as roving. This might not be surprising because the female population at Sable Island, especially in the study area, was dramatically reduced in 1996 compared to the previous 2 years (Bowen et al. 2003), and as a result there was no clear hotspot of females. Plasticity in mating tactics by a few males has also been shown in bearded seals (Van Parijs et al. 2003). It may be that there is a greater degree of flexibility in behavior of aquatic-mating seals than in terrestrially mating species so we may not as yet have adequate descriptions for all mating systems of aquatic-mating species.

Unfortunately, some shortcomings with our study prevent us from understanding the system and potential variation in male tactics within and between years further. As mentioned earlier, we cannot directly link the behavior and location of females with that of males. Nor were we able to collect all data sets on the same individual males because repeated captures necessary for this could have affected the males' behavior. Despite using an animal-borne camera to observe behavior at sea, the view is limited and the total duration of sampling per individual is small.

Body mass and male behavior

The fact that initial body mass of males does not seem to be a major factor affecting the behavior and spatial pattern of harbor seal males is consistent with earlier work at Sable Island that failed to find a clear relationship between large body mass and reproductive behavior or success (Coltman et al. 1998a,b). Indeed Coltman et al. found that the most successful males were the moderate-sized males not the largest ones. Body size was also not related to various behavioral measures of males during the mating period at Elkhorn Slough in California (Hayes et al. 2004). Body size may play a role in extending the length of time engaged in direct sexual activity for male harbor seals (i.e., needing to spend less time foraging during breeding), but it does not appear to confer an advantage through contest or displaying competition (Andersson 1994).

Comparison with other populations

The picture that emerges from the various studies of harbor seal mating behavior at sea is complex. It undoubtedly reflects some real differences, but some apparent differences might be a result of the use of different methodologies. For example, we used signals from radio transmitters when males surfaced to triangulate locations at sea. Others used direct observation, triangulation of vocalizations using a hydrophone array underwater, playback responses to vocalizations to determine

boundaries, or some combination of these methods. Two commonalities that emerge from most studies is an increase in male vocal behavior with the onset of the mating season and a reduction in range size (Hanggi and Schusterman 1994; Van Parijs et al. 1997, 1999, 2000a,b; Nicholson 2000; Hayes et al. 2004). However, in Scotland, range estimates incorporated sampling a much larger area than we could on Sable Island. As a result, the Scottish study found some males frequently located in positions at the feeding grounds used by females during and after lactation, as much as 50 km from the pupping grounds (Van Parijs et al. 1997). As noted above, if we had been able to locate males offshore (i.e., >5 km from the colony), our results might similarly show males defending areas at frequently used feeding sites, if there are distinct and predictable feeding sites around Sable Island. Studies at other colonies, like ours, only followed males close to female pupping sites on land (Perry 1993; Hanggi and Schusterman 1994; Nicholson 2000; Hayes et al. 2004).

We found considerable overlap in the ranges of individual males near Sable Island, whereas most other studies reported at least some males occupying exclusive territories, with clearly defined boundaries, some being adjacent territories (Perry 1993) and others being separated by some distance (Van Parijs et al. 2000b). In California, Hayes et al. (2004) reported some males with large adjacent territories but with smaller nonadjacent display areas within their territories. They also reported males that were highly aggregated and vocalizing from a small area, but do not provide precise data on individual males in such aggregations. While it is possible that our triangulation on radio signals from males at the surface produces a level of error that could spuriously increase the apparent overlap in ranges, it seems unlikely that the error would be great enough to account for the level of overlap we found. The degree of overlap is substantial in many cases (Fig. 2) and we were only defining space use for up to 20 males in a given season. There may have been as many as 150 males engaging in similar mating behavior to those of the males with transmitters we were following off Sable Island in a given season. The size of our ranges and those of males holding clear territories in California were an order of magnitude different, although the territory size of males in Scotland were similar to the ranges at Sable Island.

The apparent differences in exclusive or overlapping areas of use by males from different populations, whether real or artifacts of methodological differences, do not preclude drawing similar inferences about the use of a lek-type tactic. Whether males defend exclusive areas or overlap in space use does not define lekking (Höglund and Alatalo 1995). The order of magnitude of difference in the size of area used by males and difference in location relative to females and female resources is more likely to suggest differences in tactics within or among colonies.

While there is no conclusive evidence from a single study or population of alternative male tactics or annual variation in tactics, the accumulation of circumstantial evidence from our study and those of others supports this hypothesis. Within years, we had males near shore that had ranges differing by an order of magnitude. Moreover, in the last year of our study, when the female population declined dramatically, there was an increase in the number of males exhibiting the pattern of a large near-shore range. In Scotland, those males observed tens of kilometers from pupping sites, stationed at feeding sites are likely engaging in a resource defense tactic (Van Parijs et al. 1997). At Miquelon Island (Perry 1993) some males were observed defending large, adjacent territories in channels off the sand flats where females were hauled out suggesting defense of transit routes of females leaving the beach. Yet, DNA analysis failed to assign paternities to any of these males, suggesting the possibility that males engaged in alternative tactics were likely siring the offspring.

We have provided evidence consistent with an expectation that aquatic-mating seals should exhibit a primary male tactic and a mating system different than those typical of land-mating pinniped species. Our findings add considerably to an accumulating body of evidence that suggests harbor seals may exhibit a lek-type primary mating tactic under certain conditions, but also that this species may show variability in tactics of males within colonies, among colonies, and interannually. To advance our understanding of the mating tactics of harbor seals, and other aquatic-mating pinnipeds, it will be necessary to incorporate measures of mating success along with spatial and behavioral data on both males and females over spatial scales that encompass foraging areas as well as areas near breeding sites.

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