Evidence of polygyny from spatial patterns of hooded seals (*Cystophora cristata*)

DARYL J. BONESS
Department of Zoological Research, National Zoological Park, Washington, DC, U.S.A. 20008
W. DON BOWEN[1]
Northwest Atlantic Fisheries Center, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Nfld., Canada A1C 5X1
AND
OLAV T. OFTEDAL
Department of Zoological Research, National Zoological Park, Washington, DC, U.S.A. 20008

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Based on scant empirical data, the mating system of the hooded seal (*Cystophora cristata*) has been variously characterized as monogamous or polygynous. To evaluate the hypothesis that female hooded seals are clustered to a degree that would facilitate polygyny, we collected data on the spatial dispersion of female and male seals on the ice floes off the Labrador coast. While flying from a ship at the edge of the seal herd to a study site within the herd, we recorded each sighting of female seals as a "solitary female" or a "cluster of females" (using an approximate 10 body length radius to differentiate these conditions). The numbers of males near females were also recorded. Nearest-neighbor distances were obtained during on-ice transects. The frequency of nearest-female-neighbor distance classes peaked at 6–10 seal body lengths (one body length = 1.9–2.6 m) and then declined to distances of greater than 25 body lengths. About 40% of 357 females with pups (or 22% of 279 sightings of seals) were in clusters consisting of two or more mother–pup pairs; the maximal cluster size observed was five. The majority of females or clusters of females had a single male in attendance (54% of 245 sightings). Females in the central part of the herd were both clustered and attended by males more often than were females at the periphery. Observations of a few marked males suggested that some took up positions near additional females when their original female companions departed. These results are consistent with the hypothesis that the spatial pattern of hooded seals should facilitate polygyny.

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D'après des données empiriques assez éparses, la stratégie du choix d'un partenaire chez le Phoque à capuchon est considérée tantôt comme un système monogame, tantôt comme un système polygyne. L'hypothèse selon laquelle les phoques femelles se regroupent jusqu'à un point qui facilite la polygynie a été éprouvée par l'accumulation de données sur la dispersion spatiale des phoques femelles et des phoques mâles sur les glaces flottantes, au large des côtes du Labrador. Des déplacements par air à partir d'un bâteau ancré aux abords du troupeau jusqu'à un site au sein du troupeau ont permis d'identifier les femelles comme des «femelles solitaires» ou comme des «femelles d'un groupe» (un rayon égal à environ 10 fois la longueur du corps a servi de critère de différenciation entre les femelles des deux types). Le nombre de mâles entourant les femelles, de même que la distance entre chaque phoque et son plus proche voisin le long d'un transect sur la glace, ont également été enregistrés. Sur l'histogramme des fréquences, la classe à fréquence la plus élevée est celle qui regroupe les distances de 6–10 longueurs de corps (une longueur = 1,9–2,6 m) et les fréquences diminuent graduellement jusqu'aux distances supérieures à 25 longueurs. Environ 40% des 357 femelles avec des petits (ou 22% des 279 observations) étaient des femelles de groupes formés de deux paires ou plus de mère–petit; le groupe le plus nombreux contenait cinq de ces paires. La majorité des femelles ou des groupes de femelles étaient accompagnés d'un mâle solitaire (54% des 245 observations). Les femelles de la portion centrale du troupeau étaient plus souvent des femelles de groupes que les femelles de la périphérie, et elles étaient aussi plus souvent accompagnées d'un mâle. L'observation de quelques mâles marqués indique que quelques mâles viennent s'installer près de nouvelles femelles lorsque leur propre partenaire femelle s'en va. Ces résultats confirment l'hypothèse selon laquelle la répartition spatiale des Phoques à capuchon favorise la polygynie.

[Traduit par la revue]

Introduction

The mating system of the hooded seal (*Cystophora cristata*) was originally described as monogamous because casual observations revealed "family groups" (male, female, and pup) spaced relatively far apart (Bartlett 1927; Olds 1950). More recent observations of aggressive behavior among males near females (Ognev 1935; Øritsland 1964; Øritsland and Benjaminsen 1975; Frank and Ronald 1982) and sexual dimorphism in size and head structure (Berland 1966; Miller and Boness 1979) suggest a polygynous mating system. Based on these scant observations, comparative analyses of mammalian mating systems have variously treated the hooded seal as monogamous (Stirling 1975; Kleiman 1977; Alexander et al. 1979) or polygynous (Stirling 1983). During a study of postnatal growth and lactation in this species (Bowen et al. 1985, 1987*a*; Oftedal et al. 1988), we collected data on the spacing of male and female hooded seals to evaluate the hypothesis that females cluster to a degree that would permit polygyny.

Two reasons for the lack of information on the hooded seal are its inaccessibility and extremely short breeding period. Breeding takes place on the pack ice of the northern Atlantic Ocean (Sergeant 1974), and the time between birth of the first pups and departure of the last females from the breeding areas

[1]Present address: Marine Fish Division, Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, N.S., Canada B2Y 4A2.

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TABLE 1. Distribution of nearest-neighbor distances among female hooded seals

	Distance class (body lengths)					
	0–5	6–10	11–15	16–20	21–25	>25
% of total observations	14	28	13	3	3	39
No. of observations	11	22	13	2	2	30

is approximately 2 weeks (Bowen et al. 1987*b*). Individual females wean their pups abruptly by leaving them on the ice about 4 days postpartum (Bowen et al. 1985). Females apparently attain oestrus about this time and copulations occur in the water (Øritsland 1964).

Methods

Between 17 and 26 March 1984 we studied hooded seals approximately 180 km off the southeast coast of Labrador (52° N, 54° W). The Canadian Scientific Ship (*CSS*) Baffin was positioned in the pack ice at the edge of a herd of seals. The herd was estimated to number about 55 000 animals, with a mean density of 56 pups/km² (range: 4 pups/km² at the periphery to 120/km² in the densest regions) (Bowen et al. 1987*b*).

We collected spacing data while flying between the ship and our study sites and during transects walked on the ice. From the helicopter, we noted the sex of adult seals, whether females were solitary or in a cluster, and the number of females and males within a radius of approximately 10 body lengths (BL) of the "middle" of each cluster of seals. A female was considered solitary if there was not another female within approximately 10 BL. Although there are no data available to provide an empirical basis for defining clusters, we selected 10 BL because preliminary observations suggested that this distance would encompass most animals within a cluster but would not include other clusters. Adult hooded seals range in length from about 1.9 to 2.6 m (Reeves and Ling 1981; Kovacs and Lavigne 1986; Bowen et al. 1987*a*). As the density of seals obviously differed between the periphery and the main part of the herd, we divided the herd into central and peripheral areas and recorded data separately for each area.

Data were also collected on distances (in BL) between each female and her nearest female neighbor during on-ice transects. A value of greater than 25 BL was assigned to any female around which no other female could be seen. Ice hummocks often prevented us from seeing further than that.

On 20 March, nine males attending females were marked with paint pellets and an identifying dye mark was placed on the ice near them. Our intention was to search for these males each day, but inclement weather, shifting ice conditions, and time constraints due to participation in the other studies permitted only occasional searches.

Results

The choice of approximately 10 BL as a criterion for estimating the degree of clustering of females appears to have been reasonable. The frequency of nearest-neighbor distances reached a peak at 6–10 BL and then declined; for nearly 40% of the observations the nearest neighbor could not be seen (i.e., greater than 25 BL) (Table 1). Descriptive statistics were not calculated for these data because it was not possible to determine quantitative distances between animals that were greater than 25 BL apart.

From the aerial transects, 39% of 357 individual females with pups (or 22% of 279 sightings of seals) were in clusters of two or more females. Most clusters had only two females and the maximal number of females recorded was five (Fig. 1A). Females in the main part of the herd had a greater tendency to be clustered than did females that were located peripherally: 44% of 273 individual females (or 26% of 205 sightings) in the main herd had at least one other female within 10 BL as compared with 21% of 84 females (or 11% of 74 sightings) at the periphery (Fisher's exact test, $p < 0.002$ for individual females and $p < 0.008$ for sightings).

Females did not always have males near them on the ice (Fig. 1B). They were more likely to be attended by one or more males in the main part of the herd than on the periphery (71% of 175 sightings vs. 57% of 70; Fisher's exact test, $p < 0.040$). When individual females or clusters were attended by males, there was usually only one male (54% of 245 sightings). In the main part of the herd, 23% (of 124 sightings of females or clusters) had more than one male present compared with 7% (of 40) at the periphery (Fisher's exact test, $p < 0.020$). As many as six males were seen in close proximity to a female or cluster of females. The distribution of the number of males in close proximity to one or more females was skewed to the right (Fig. 1B).

On the day after marking, we resighted only one male (No. 9). He was about 60 m from where he had been marked, attending a different female with a pup. His female companion of the previous day was absent from the area although her unattended pup was still present. The females that had been closest to three of the marked males had departed, as had these males. The females previously near another marked male were still at the same location, but this male was not relocated. Because of weather conditions, we were unable to visit the previous locations of the remaining four marked males.

On two occasions we observed females wean their pups by departing the ice. In both instances, the attending males left the ice with the females, and on subsequent resightings of the pups there was no sign of either the females or males.

After 21 March, we could not systematically search the area where males were marked, but during other work we subsequently observed two of the males (Nos. 1 and 9) several kilometres from their previous locations. The resightings were on 24 and 25 March, respectively, and, although we do not know precisely how the ice shifted during the intervals between sightings, there was no sign of our dye marks on the ice. In both instances the males had female companions with pups that were too young for the females to be the same as those previously seen with the males.

Discussion

Contrary to the earlier belief that the social structure of the hooded seal is characterized by "family groups," females with pups were frequently seen within a few body lengths of other female–pup pairs during this study off the coast of Labrador, creating a spatial pattern in which several females could be defended simultaneously by a single male. Analysis of hooded seal reproductive tracts suggests that ovulation occurs about the time of weaning (Øritsland 1964), although systematic

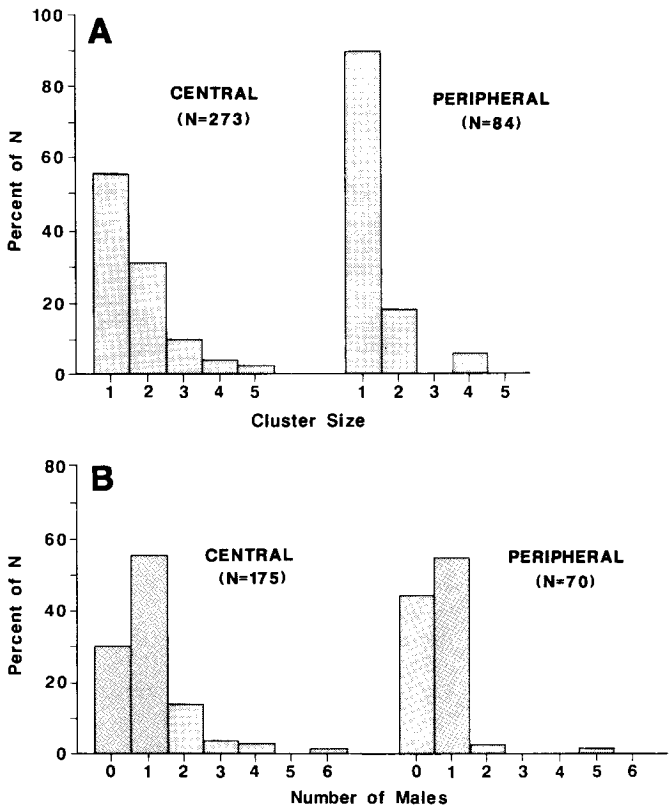

FIG. 1. (A) Relative frequency distribution of hooded seal females among clusters of various sizes. A solitary female is indicated by a cluster size of 1. (B) The number of males within a radius of approximately 10 body lengths of each cluster or solitary female. Data are presented separately for seals in the central and peripheral areas of the breeding herd.

observations of individually identifiable animals are needed for confirmation. If there is indeed a close correlation between the timing of weaning and oestrus in individual females, the spacing observed in this study would facilitate a higher level of polygyny than that suggested by Stirling (1983), who argued that male hooded seals only have access to one female at a time.

The extremely short lactation period of 4 days in this species (Bowen et al. 1985) would also enhance the opportunity for males to mate with several females within a short period of time, especially if the females are clustered. In contrast, the marked synchronization of births (i.e., virtually all pups are born over a 2-week period; Bowen et al. 1987*b*) and the consequent brief period over which females attain oestrus will place a limit on polygyny. A male is not likely to acquire sequential access to large numbers of widely dispersed females because many females will become receptive while the male is attending others.

Competition between males has been described both on ice and underwater (Ognev 1935; Øritsland 1964; Øritsland and Benjaminsen 1975; Frank and Ronald 1982). The fact that several males occur in close proximity to a female or a group of females more frequently in the main herd than at the periphery may simply reflect a greater proportion of oestrus females in this region during our observations. The data may also indicate that there is a premium related to position within the main herd and that this premium is access to a greater number of potential mates. It is well documented that the reproductive success of centrally located males in "colonial" breeding species is higher than that of peripheral ones (Buechner and Schloeth 1965; Gentry 1970; Kruijet et al. 1972; Emlen 1976; Boness 1979).

There may be several explanations for the differences between the spatial distribution we observed and those observed by earlier researchers (Bartlett 1927; Olds 1950; Frank and Ronald 1982). The previous studies may have involved animals at the periphery of a main herd (where the degree of clustering was significantly less in our study). A second explanation may be that spatial patterns of females may differ from one population to another and (or) from year to year. For example, the study by Frank and Ronald (1982) was carried out in the Gulf of St. Lawrence while ours was performed off the coast of Labrador. The density of female–pup pairs in the gulf appears to be about 1/12 that observed during our study (G. Stenson, Department of Fisheries, St. John's, Newfoundland, personal communication). Good data are not available for both locations from any given year. There is annual variation in the number and density of whelping concentrations even in the same population. Furthermore, in 1984, approximately 9% of females gave birth outside of the whelping concentration, over vast areas of ice at a density of 0.12 animals/ km^2 (Bowen et al. 1987*b*). At this density it is likely that individual males would mate with only one female. If mating systems exhibit plasticity as postulated, the degree to which food resources or females are clumped may be important in determining the mating system observed at a given location or point in time (Orians 1969; Wilson 1975; Emlen and Oring 1977).

The limited data on location and movements of the paint-marked males do not yield firm conclusions, but are the first direct evidence that individual males attend more than one female within a breeding season. Males not resighted in a given area may have been in the vicinity under the ice, but in at least some circumstances males departed when females weaned their pups by leaving them on the ice. The reproductive strategies of two other phocids, the grey seal (*Halichoerus grypus*) (Boness and James 1979; Anderson and Fedak 1985) and the crabeater seal (*Lobodon carcinophagus*) (Siniff et al. 1979), are characterized by males focusing attention on one female in or near oestrus at a time and shifting attention to a new female after mating, regardless of female clustering. As pointed out by Boness and James (1979), such a strategy seems ideally suited for pack-ice species, for which ice conditions make the spatial arrangement of the breeding group unpredictable over time. It is also consistent with theoretical arguments about the form of polygyny that would be expected given a spatial distribution of females that is only moderately defendable and a relatively high synchrony of oestrus (Emlen and Oring 1977; Bradbury and Vehrencamp 1977).

The spatial pattern of females and movement of males described by our results suggest that some males could defend more than one female simultaneously and that males may move sequentially from one female or cluster of females to another to acquire additional matings. These findings, combined with the inductive arguments of sexual dimorphism in size and head adornments (Berland 1966; Miller and Boness 1979), support the hypothesis that a polygynous mating system is common in the hooded seal, as suggested by Miller and Boness (1979).

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