Reproductive behaviour of the Grey seal (Halichoerus grypus) on Sable Island, Nova Scotia

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(With 2 plates and 10 figures in the text)

We describe an unusual mating system, observed in a land-breeding colony of Grey seal, Halichoerus grypus, in the western Atlantic. Males and females begin to visit the breeding beach about a week before the season begins, but none stay ashore for long until the first pup is born. The cows are gregarious, probably return to the same part of the beach to give birth from one year to the next, and tend to remain in the general vicinity of the birth site during their two and a half week sojourn ashore. Within these limits, however, they are quite mobile, and the size, location and composition of the temporary aggregations which they form vary from one day to the next. The cows become thinner and more sedentary as oestrus approaches, but otherwise they give no overt signs of receptivity. The males do not defend territories, nor do they form dominance hierarchies. Instead, they compete for tenure, the right to remain within the shifting population of females. Tenured bulls directly test the receptivity of nearby cows from time to time, and they continually manoeuvre in ways which maximize their chances of being next to cows which are either in oestrus or likely to become so in the near future. Bulls which fail to establish themselves amongst females try to intercept cows as they are leaving for the sea at the end of their season, but their reproductive success, estimated in several ways, is significantly lower than that of bulls with tenure.

The system would be adaptive for seals which breed on the pack ice, but it is unique amongst land-breeding pinnipeds. If, as some circumstantial evidence suggests, Grey seals were originally pack-ice breeders, the persistence of such a system in a land-breeding colony raises some interesting questions about the plasticity of mating behaviour.

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Introduction

The world’s population of Grey seals, *Halichoerus grypus*, is now divided in three reproductively isolated groups. The largest group is found in the eastern Atlantic, mainly on rocky islands, where it breeds between early September and late December. The smallest breeds on the Baltic ice in late February and early March. The third group, in the western Atlantic, is confined to the continental shelf round Nova Scotia, where it breeds from late December until mid-February on the pack ice in George’s Bay and the Northumberland Strait, on rocky ledges off the East coast and on the sandy beaches of Sable Island.

Some circumstantial evidence suggests that at one time the Grey seal may have been an animal of the pack ice (Davies, 1957; McLaren, 1960). First, like almost all the pagophilic phocids, the young are born with a light-coloured coat of lanugo, in contrast to the darker pelage of land-breeding pinnipeds. Then, in common with most seals which now breed on the pack ice, the Grey seal has a relatively short lactation period (17.0 ± 2.4 days for a sample of 38 females observed by us on Sable Island); this contrasts with the longer nursing times of the fast ice and terrestrial breeders (e.g. 23 to 27 days in *Mirounga leonina* and *M. angustirostris* respectively (Laws, 1956; Le Boeuf et al., 1972), about five weeks in *Monachus schauinslandi* (Kenyon & Rice, 1959) and six to eight weeks in *Phoca hispida* (McLaren, 1958; Smith, 1973)). Finally, whereas the males of land-breeding pinnipeds arrive in the vicinity of the traditional breeding grounds well in advance of the females, Grey seal cows are thought to arrive slightly ahead of the bulls (Hewer, 1974). No information is available about the arrival times of species which breed exclusively on the pack ice, but one might guess that in their case it would be maladaptive for the males to arrive before the females.

However, one has to set against this argument the fact that the Grey seal is markedly dimorphic for size, a characteristic which is typical of land-breeding pinnipeds but rare amongst the ice-breeder. If this dimorphism has evolved in the Grey seal as a result of intrasexual competition (as it seems likely to have done in pinnipeds which mate entirely on land (Bartholomew, 1970)), one wonders what kind of polygynous system could possibly develop on a substrate which is as precarious and unpredictable as the pack ice.

Although there is a voluminuous literature on the social behaviour of Grey seal, it provides no answer to this question. The species has variously been described as monogamous (Mansfield, 1967), territorial (Hewer, 1957) and hierarchically organized (Anderson et al., 1975), but the evidence is quite insufficient to justify the use of any of these terms. Hewer, whose studies have provided most of the information we now have about the behaviour of the Grey seal, frequently refers to their territorial behaviour (Hewer, 1974). However, the only facts that he reports are essentially three in number: mature bulls can often be found resting in approximately the same place from one day to the next, they are more widely spaced than the cows, and they may act aggressively when one of them approaches another. He has also identified a territorial display, which he describes as follows: “First the bull comes to a halt, at the end of the pursuit, at the edge of his territory. He usually leans his head forward, opens his mouth and emits an almost silent hiss . . . He then clearly dismisses the intruder and slightly turning his head to one side rolls his whole body over one complete sideways turn. Owing to the tapering shape of the body this brings him round more than half facing back into his territory. He then begins to lumber back to the central position to resume guard.” (Hewer, 1974: 131). While these
facts are obviously consistent with the existence of a territorial system, they fall far short of demonstrating the case for one; and the bulls which roll may simply have found a convenient way of turning round. On the other hand, Anderson and her colleagues, who have published the only quantitative data on the reproductive behaviour of this species, have concluded that males in the colony they observed on North Rona were hierarchically organized (Anderson et al., 1975). They appear to have reached this conclusion solely on the ground that they found a positive correlation between the length of time a bull stayed in the breeding area and the number of copulations he achieved. Again, while this observation is consistent with the existence of a polygynous mating system, it is not sufficient to specify what form of polygyny is involved.

For several years, we have been able to watch a large colony of Grey seals on Sable Island, a sand bar in the western Atlantic. We have seen there a form of polygynous society which differs from the territorial and hierarchical systems of land-breeding pinnipeds—one which is well adapted to the unstable conditions that seals would encounter on pack ice and one in which larger males would be expected to have the greater reproductive success.

**Study area**

Sable Island (43° 55' N; 60° 00' W) is a vegetated sand bar approximately 35 km long and 1.5 km wide, lying 288 km ESE of Halifax, Nova Scotia and about 160 km from the nearest point on the mainland. Boulva (1971), McLaren (1972) and Welsh (1975) have provided detailed accounts of the history, terrain and fauna of the island. In former years, Grey seals bred at both the E and W ends of the island, but when drilling for oil began on the W spit in 1970, they abandoned the area as a breeding site and the herd has

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**Fig. 1.** Sketch map of the Grey seal breeding grounds surrounding the most easterly vegetated dune (Long Dune) on Sable Island. The region marked "A", which contained the study area, is shown on Plate I. See text for further details.
PLATE I. The gully between Long Dune and Steeple Dune (area "A" and its environs in Fig. I). The photograph was taken from the eastern shoulder of Steeple Dune, looking NE.
since concentrated on a 190 hectare neck of land (Fig. 1) nearly 4 km from the main hauling ground at the tip of the E spit.

In each of the three years we have been present from the beginning of the season, the same parts of this area have been occupied in the same progression. Area A (Fig. 1), the first to be occupied, is on the N side of the island and lies in the gully between Long Dune, the most easterly vegetated dune, and the next dune W, Steeple Dune (Plate I). Within a few days of the first landings here, other animals began to haul out and stay ashore at B. Apart from temporary visits by a few subadult males, seals do not begin to occupy area C, the sand flats at the eastern end of Long Dune, until about a week (7 days in 1974 and 1975, 8 days in 1976) after the first animals have colonized area A; then they invade C from both the N and S coasts. As the season progresses, the seals which come ashore at A spread inland through the gully towards area D, up the grass-covered slopes of Long Dune and across the eastern end of Steeple Dune, and along the narrow beach to the N of both these dunes. Those which come ashore on the S coast at B also start to move inland at about the same time. By mid-season, there is a continuous band of seals across the island at the E end of Long Dune, a thin line of animals on the narrow beach to the N of this dune, and another broad band of animals, with a gap in the middle, across the island at the W end of Long Dune. Area E occasionally contains a few scattered adults and pups.

We have concentrated our attention on area A and its environs (Plate I; the NE part of Steeple Dune, the W slope of Long Dune and the NW corner of the sand flats marked as area D in Fig. 1). This region is a natural unit, in the sense that the rest of Steeple Dune and Long Dune, the area immediately to the S of area D, and that part of the sand flats

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**Fig. 2.** Daily census of seals present in area A and its environs (see Plate I) during the first half of the 1973-4 season and during the major part of the 1975-5 and 1975-6 seasons.
labelled E in Fig. 1 were only sparsely used by the seals, and so unoccupied stretches of sand separated area A from the other two breeding beaches labelled B and C. Ideally, that part of the N beach adjacent to area A should have been included, but it was hidden from view by the shoulder of the dune.

**Census of study area**

Our counts of the number of seals present in the study area during three successive breeding seasons are shown in Fig. 2. In 1973–4, the census was taken between 0700 and 0800 hrs and again at 1600 hrs, and the data shown in Fig. 2 for this season are the daily averages of the two counts. In 1974–5 and 1975–6, a single count was made at 0730 hrs, about half an hour after sunrise.

One aspect of the census deserves particular notice: the arrival of males on the breeding ground is synchronized with the arrival of the females (Fig. 2). A few adult males and, very rarely, a pregnant cow will come ashore during the fourth week of December on the sand terrace along the northern margin of area A, but none of them settle until the first pup is born on that beach. The first birth in 1973 occurred during the night of December 26/27 and in both 1974 and 1975 during the night of December 27/28. The second of these pairs of days was the first on which either males or females remained ashore anywhere on the breeding ground continuously throughout the day. This degree of synchrony in the arrival of adults of both sexes at the breeding site is not known to occur in any other land-breeding pinniped.

**Behaviour of females**

*Choice of birth site*

We have been able to record the exact place at which six braded females gave birth ("birth site") in at least two successive seasons. The median distance between birth sites from one season to the next was 18 m (range: 14–51 m). The median difference in birth dates, from one season to the next, for these six cases was one day (range: 0–7 days). In addition, we saw 13 more braded females with their pups in two different seasons but did not see one or both of the births. Seven of these females were found in the same area in successive seasons, two in adjacent areas (in the sense indicated in Fig. 1), and four in non-adjacent areas.

*Spacing*

Before the 1975–6 season began, we marked off the study area with stakes into a grid of 6 m squares covering an area of 3132 m² and then kept a total of 40 cows with pups under almost continuous observation while they were present in the area during daylight. At least nine photographs were taken of this area each day, and from the maps made from these photographs and our field notes we have been able to determine the exact position of these cows at approximately 45-min intervals.

In order to find out whether the females were randomly distributed throughout the study area, we first calculated from the photographs the mean daily distance between each cow and her nearest female neighbour during the interval between parturition and her first copulation. Then, following the procedure described by Clark & Evans (1954), we determined for each day between 3 January and 27 January 1976 (the period when the
number of cows in the study area was greater than nine) the direction in which the pattern of nearest neighbour distances departed from randomness (i.e. whether the cows on a given day were closer to one another ($R < 1$) or further apart ($R > 1$) than one would expect on average). Finally, we used the $G$ test (Sokal & Rohlf, 1969) to estimate the probability that the observed proportion of days on which $R < 1$ would be likely to occur by chance alone.

The results of this analysis are shown in Fig. 3, from which it will be seen that, on most days, the females were closer together ($R < 1$) than one would expect on average if they had been randomly distributed throughout the study area ($G_{adj} = 11.06; df = 1; P < 0.001$).

![Graph showing mean daily distance between nearest female neighbours and mean dispersion index ($R$), as a function of time (1975–6 season).](image)

The mean daily distance, over all days, between each cow and her nearest female neighbour was 4.4 m ($s = 1.3$). Although Anderson et al. (1975) did not make a statistical analysis of the data they obtained on the dispersion of the Grey seal cows during the 1972 breeding season on North Rona, they do provide distributional maps of the animals in their study area, made at approximately weekly intervals. Inspection of these maps suggests that any differences between the Rona and Sable colonies in the way in which the cows distribute themselves over the breeding grounds are likely to be small in relation to the differences in the spacing of males which we shall describe later.

**Movement**

Most accounts of other colonies (except of North Rona (Anderson et al., 1975)), either imply or explicitly state that most, if not all, of the cows move to and from the sea between suckling periods. On Sable Island, we have never seen any signs that suckled cows have been to sea at night and only on the rarest of occasions have we seen one leave her pup and go to the water's edge during the day. Accordingly, we assume that the cows stay
ashore from the time they give birth until they have finished mating, some two and a half weeks later. They are, however, far from sedentary and they frequently move several metres at a time from one place to another. These movements occur for at least two reasons, in addition to the straightforward one of avoiding some local disturbance. First, especially when the pups are young, the mothers move away from them before giving suck, if necessary clearing a space of other seals (particularly of males). Secondly, a pup will often wander away from its mother between one nursing period and the next, and either by going too far or by provoking an outcry from an alien female from which it has tried to nurse, it will cause its mother to close the distance between them. The extent of these movements tends to decline as oestrus approaches. This trend is shown in Fig. 4 where the mean distance between their positions at noon on one day and at the same time on the previous day is shown for the 27 females which gave birth and remained within the confines of the study area grid during the 1975–6 season. The slope of the regression line deviates significantly from zero ($P < 0.001$).

![Graph showing mean distances between a cow's position at noon on a given day and her position at noon on the preceding day, as a function of elapsed time since parturition (1975–6 season).]

Fig. 4. Mean distance ($m$) between a cow's position at noon on a given day and her position at noon on the preceding day, as a function of elapsed time since parturition (1975–6 season).

A cow's movements appear to be anchored to her birth site. Waser's (1976) random-walk model was used to estimate the distance a cow would be expected to cover from the time she gave birth until her first copulation, and this was then compared with the straight-line distance between these two positions. If their movements were random, one would expect that half the cows would have moved further than the predicted distance and that half would have moved a shorter distance. Twenty-six of the 27 cows for which we have the necessary data had moved a shorter distance away from the site of parturition than one would expect on average ($G_{adj} = 32.46; df = 1; P < 0.001$). The noon positions of six typical cows are shown in Fig. 5.

**Oestrus**

On average, in the combined 1974–5 and 1975–6 seasons, tenured (see below) bulls in the study area made their first observed attempt to mount a female 10.5 days after the
birth of her pup and achieved their first observed intromission 4-7 days later. In the same two seasons, two-thirds of the cows in the study area were mounted at least three times before they became receptive.

The frequency with which tenured bulls attempt to copulate with a given cow increases with the approach of the time when she will permit coitus (Fig. 6) and it thus seems very probable that they are able to diagnose the cow's condition before they actually mount her. We are not at all sure how they do so. As in other phocids, the bull does not investigate the cow's perineum, or any other part of her anatomy, before trying to mount her, and the cow gives no active sign of receptivity before the mount leading to the first intromission occurs. Indeed, even on this occasion, she will resist vigorously until the male succeeds in gripping her by the nape of the neck, an act which seems to have the same pacifying effect on Grey seals as it does on other carnivores (Ewer, 1973). The only indications of approaching oestrus that we have been able to discern are those provided incidentally by the emaciation of the female, her relatively sedentary demeanour, and her apparent lack of concern when another seal gets between her and her pup. It is, perhaps, just possible that these are also the only cues available to the bulls, and that this is why so many of their diagnoses are false positives (Fig. 6).

Once mated, some cows appear to solicit further attention from the bull by squirming alongside, placing a foreflipper on his back and gently mouthing his neck (cf. Hickling, 1962; Anderson et al., 1975). This behaviour is strikingly reminiscent of the female courtship one sees in some otariids, but it is unlikely that it serves the same function. A Grey seal bull always responds to "solicitation" of this kind as if it were a low-intensity threat: he either restrains the cow with a fore-flipper, without proceeding with the copulatory sequence of which this movement is also the first step, or he threatens another bull
lying inoffensively nearby in the same way as he might if he were actually being threatened by the cow.

On average 17 days after giving birth, a cow will begin to edge her way very slowly towards the sea. At first, she is usually followed by the male with which she last copulated, and this inevitably brings him into conflicts with other bulls. In the course of the ensuing mêlée, the cow makes a dash for the coast, breaking into a long, sinuous run which is recognizably different from the plodding pace of a female which is still lactating. As soon as she does so, bulls converge on her from all quarters. One of these will usually succeed in climbing on her back, using her as a vantage point from which to threaten the others. If they all become preoccupied with fighting one another, the mounted bull may even be able to achieve intromission. However, when another male comes near, he will almost invariably threaten the intruder, thus relaxing his hold on the female beneath and allowing her to escape. Whereupon the chase to the sea begins all over again. We have occasionally seen a bull apparently in copula while the female was beached in the shallows, but the heavy surf which runs offshore makes it impossible to see whether any mating occurs while the female is afloat.

In summary, different areas of the breeding beach are colonized by the female herd in the same orderly progression from one year to the next, and the general disposition of the cows at any given time during a particular season is predictable in advance. The cows are gregarious and tend to remain within easy reach of the place where they gave birth, but individuals move about haphazardly over distances of several metres in the course of a
day, and so it is impossible to predict where an individual cow will be or where the greatest concentrations of cows will be found within a given area on a particular day. Other than the fact that they are becoming noticeably thinner and somewhat more sedentary, the cows give no signs that oestrus is imminent. Thus, to maximize his reproductive success, a bull must minimize two major sources of uncertainty, one caused by the constantly changing pattern of females around him and the other inherent in the inadequate information that he can obtain at a distance about the receptive states of these females.

**Behaviour of males**

*Tenured and transient males*

At the beginning of the season, adult males lie peaceably cheek by jowl with pregnant females and subadults on the hauling grounds at the tip of the E spit, 4 km from the breeding beach. In contrast, the first males to land on the breeding beach keep an individual distance of several metres, and they chase and threaten one another even when no cows are present. When the first cows pup on the beach, some of the males gather round them and as the latter move further inland with their pups, the bulls begin to move inland too. There is a constant turmoil as animals haul out in increasing numbers, and the beach looks more like a rowdy house than the site of an organized society. The bulls sometimes *appear* to be competing for positions amongst the cows, and many of them move closer to females after they have displaced other males. At other times, however, a bull which has successfully positioned himself amongst a group of females will take off in pursuit of another male and disappear from the beach for the rest of the day. In general, there is a rapid turnover of bulls at the very beginning of the season, and few of the males which dominate the scene on one day are still in sight on the next day. This turnover is reflected by the proportion of all males present on a given day which were present on the previous day.

![Graph showing proportion of males present in area A on a given day who were also there the previous day (1974-5 and 1975-6 seasons).](image)

**Fig. 7.** Proportion of males present in area A on a given day who were also there the previous day (1974-5 and 1975-6 seasons).
(Fig. 7). For the first week of the season, in both 1974–5 and 1975–6, less than 50% of the males present in the study area were the same from one day to the next.

Signs of orderliness become apparent during the second week of the season, when an increasingly greater proportion of the males maintain positions amongst the females for two or more consecutive days. By the time the first females may be expected to come into oestrus (10 January in both 1975 and 1976), 80% or more of the male population in the study area consists of animals which have succeeded in establishing themselves there for two consecutive days or more.

During the combined 1974–5 and 1975–6 seasons, we were able to identify by their markings a total of 52 bulls which spent at least two consecutive days in the study area. Their lengths of stay ranged from two to 30 days, with a mean of 9.7 days. In the following pages, we shall refer to those males as “tenured” or “holding tenure”, terms we have deliberately chosen for their lack of connotation as to the resource or resources (territory, access to females, freedom from interference during the relatively prolonged period required for copulation, etc.) to which these males may have preferential rights.

In addition to these tenured males, a daily average of 3.5 and 2.9 males spent less than two consecutive days in the study area in 1974–5 and 1975–6 respectively. These animals we shall describe as “transients”. Many of them stayed for only a few minutes, too short a time to identify them positively and thus to tell whether or not they returned to the study area at some later date. If one assumes that each of these transients visited only once during the breeding season, this would mean that a maximum of 127 different males spent less than two consecutive days in the study area in the two years combined.

Preliminary evidence suggests that the acquisition of tenure may be related to an animal’s age. Of 125 branded males younger than 8 years old, less than 2% are known to have established tenure, whereas one third of the 15 branded males known to be 11 to 14 years old acquired tenure ($t_s = 3.57; P < 0.001$). No known 9 or 10-year-olds were seen.

**Spacing between tenured males**

In order to find out whether the males which held tenure during the 1975–6 season were randomly distributed over the study area, we followed the same series of steps as we have already described in the account of our analysis of female spacing during the same season. Thirty bulls acquired tenure between 3 January and 27 January, at least seven being present each day during this period. Their mean length of stay was 11.2 days (ranging from two to 30 days), and the mean daily distance between each of these males and his nearest male neighbour was 8.3 m ($s = 1.9$). On a significantly greater proportion of days than one would expect by chance, the index of dispersion ($R$) exceeded the value (1) which would be obtained if these males had been randomly distributed throughout the study area (Fig. 8; $G_{adj} = 18.41; df = 1; P < 0.001$). Only 18 of these males held tenure at a time (10 January until 27 January 1976) when females in oestrus were present in the study area. Their mean length of stay was 16.8 days (ranging from 4 to 30 days) and the mean daily nearest neighbour distance was 7.4 m ($s = 2.1$). On a significant number of days, the bulls in this sub-sample were also more widely dispersed than one would expect on average ($G_{adj} = 22.64; df = 1; P < 0.001$). The pattern of male dispersion thus differs from that of the females: as we have already seen (Fig. 3), the mean daily distance between a cow and her nearest female neighbour was significantly less than one would expect on average.
We determined from our photographs the resting position of each of the above-mentioned 18 bulls at noon on each day of his tenure, and in Fig. 9 the outermost of these positions for each male have been connected together in order to give an approximate idea of the area within which he stationed himself without provoking a serious challenge from his neighbours. The shaded areas in Fig. 9 indicate the overlaps in the use of space by two or more tenured males when at least two of the males concerned were present simultaneously; the striped areas indicate areas of common use when only one of the males concerned was present at that time; the clear areas were used exclusively by the male concerned. It will be clear from an inspection of this map that there is so much overlap in the use of space by tenured males that there would be no virtue in describing them as territorial.*

From the distributional maps published by Anderson et al. (1975), one can obtain a rough estimate of the daily distance between the bulls on North Rona during the 1972 season. The means of these estimates are given in Table I, together with our own data for the corresponding weekly intervals. It is evident that the average distance between male neighbours on North Rona is very much greater than that on Sable. This difference is

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* In the vernacular, which is the sense in which we use the word, the meaning of “territory” is unambiguous: a fixed, geographically defined area within which the individual has exclusive access to one or more limiting resources. However, there have been many advocates of the view that the meaning of the word should be extended to signify “any defended area” (e.g. Noble, 1939; Hinde, 1956; Wilson, 1975). This is done at the price of making the phrase “territorial behaviour” synonymous with “aggressive behaviour”, and thus redundant. One can only know that an animal is defending an area by seeing it engage in aggressive activity, and so there can be no territorial behaviour without aggression; aggressive activity necessarily involves the use of space and so, if territoriality is the defence of any space, there can be no aggression which is not territorial.
associated with another which becomes apparent when one compares the census data of Anderson et al. (1975) with our own (Fig. 2). On Sable, adult numbers in the study area reach their peak between the end of the third and the beginning of the fourth week after the birth of the first pup, and at the time of this peak there are slightly fewer bulls ashore than cows (1 : 1.3). On North Rona, the maximum number of adults ashore is reached at the same time (25 days) in relation to the birth date of the first pup, but the ratio of bulls to cows (1 : 9) is strikingly different ($t_8 = 18.15; P < 0.001$). It is possible that these

\textbf{Table I}

\textit{Mean male–male nearest neighbour distances (m) on North Rona and Sable Island}

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<tr>
<td>Sable Is. (1976)</td>
<td>Mean</td>
<td>11.4</td>
<td>8.5</td>
<td>7.6</td>
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differences reflect a large difference in the amount of intra-sexual competition in the two colonies and that this, in turn, reflects a difference in the ways in which they are organized.

**Aggressive behaviour**

Tenured males become aggressive when one or more of three conditions are satisfied. First, if a transient or neighbouring tenured male heads straight for a female with which a tenured male is consorting, or attempts to pass between her and her consort, the latter will threaten and, if necessary, attack the intruder. Secondly, it frequently happens that a female will threaten her male consort (often as a preliminary move before suckling her pup) and that he will then immediately move towards another male in the vicinity and threaten or attack him. Similarly, if a tenured male is threatened by a male neighbour, the former may, in his turn, threaten a third bull nearby. Finally, two tenured males may be brought into conflict when a female with whom one of them has been consorting moves close to the other male.

By recording all the fights seen in the study area during the 1975–6 season and those threat bouts which occurred when we were not collecting other data, we kept account of the precipitating causes and outcomes of almost 800 disputes between males. When an encounter took place between a tenured and a transient male \((n = 269)\), the latter almost always broke off the engagement first \((H_s \leq 0.50; z = 12.39; \, P < 0.001)\). Thus, transients are generally subordinate to tenured males. When a dispute involved two tenured males, the outcome generally depended upon whether their respective female consorts were involved and, if so, who and where these consorts were. Thus, if a tenured male which had been lying close \((< 5 \text{ m})\) to a female for some time \((> 2 \text{ hr})\) was approached by another tenured male, the former would generally stand his ground \((n = 301; \, z = 8.88; \, P < 0.001)\). However, if the female in question had just joined one of the males, then he was as likely to back away first as was the intruder \((n = 104; \, z = 1.08; \, P < 0.28)\). When neither of the males’ consorts was immediately threatened (that is when both bulls started from positions which were closer to one another than either was to the other’s consort), it seems that one male was as likely to break off the engagement as the other \((n = 124; \, z = 1.88; \, P < 0.06)\). Thus, tenured males behave as if they were equals whose status is not affected by their absolute position on the breeding ground (territory) or by their previous fighting record (rank in a dominance hierarchy). They are, nonetheless, resolute in the defence of their female consorts.

Mature Grey seal bulls possess two distinctive morphological characteristics which one might expect to be displayed prominently if the mating system were either territorial or hierarchical in nature. These characteristics are the nasal rostrum from whose shape their specific name is derived, and the rather massive, rugose neck which, on a smaller scale, resembles that of an elephant seal bull. They also have one call (Plate II) which carries for long distances and which might be suited to advertising either rank or the ownership of property. The facts are quite to the contrary: the aggressive displays of the Grey seal are remarkably inconspicuous and, as the illustrations in Hewer’s (1957) account show, the male which holds his head lower than the other is the one which will usually stand his ground. Likewise, the calls accompanying these postures are scarcely audible above the sound of the surf; the hiss, which accompanies the most frequently given, but lowest intensity, visual threat can only be heard, even when it is dead calm, if one is very close at hand, and the snarl, which sometimes signals an overt attack, does not carry
Plate II. Sonograms of calls ("yodels") made by two males (G and L) on three different occasions. The analysing filter bandwidth for sonograms 1, 2 and 3 was 6 Hz. Calls G1(a) and L1(a) are the same as G1 and L1 respectively, but the analysing filter bandwidth for these was 60 Hz.
Plate II. (continued)
much further. The one call which does carry sounds like the falsetto part of a yodel. It is essentially a pure tone with a gradual onset (Plate II). It is thus difficult to localize at close quarters, but it can be heard several kilometres away. It is made by both tenured and transient males, with the neck outstretched, the muzzle raised dorsally and the chest and neck vibrating, while lying prone, supine or on one side but never, in our experience, while in motion. On Sable Island, the call is made only on the breeding grounds, where it occurs in a wide variety of contexts; often a bull which appears to be fast asleep will rouse himself for long enough to yodel. To some extent, the length, pulse frequency and acoustic pattern of an individual's call are idiosyncratic and we found it easy to identify certain males by their yodels alone (Plate II). However, other seals in the vicinity, whether male or female, do not even open their eyes or turn their heads when one of their neighbours makes this eerie sound. Schneider (1974) has heard the same call during the breeding season on the Basque Island, off the SE coast of Cape Breton, Nova Scotia, but no reference to it is made in any of the descriptions of European colonies.

Finally, as we noticed at the beginning of this paper, Hewer (1974) has claimed that rolling, a behaviour which is commonly seen on Shillay, in the Outer Hebrides, as well as on Sable Island, is a form of boundary display. We have been unable to find any evidence that the bulls on Sable are territorial (cf. Fig. 9) and thus, of necessity, we have not been able to verify Hewer's claim. It seems to us to be much more likely that, as Hewer's (1974) account itself implies, rolling is an alternative method of locomotion.

**Table II**

<table>
<thead>
<tr>
<th>Sexual condition of other females within 5 m of male</th>
<th>Attractive</th>
<th>Unattractive</th>
<th>No other females with 5 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sexual condition of moving female</td>
<td>Attractive</td>
<td>0.21 (N=19)*</td>
<td>0.71 (14)</td>
</tr>
<tr>
<td></td>
<td>Unattractive</td>
<td>0.03 (38)**</td>
<td>0.21 (78)**</td>
</tr>
</tbody>
</table>

_H0: P ≠ 0.50; *P < 0.01, **P < 0.001._

**Movement of tenured males**

The mean daily distance between each of the 18 tenured males referred to above and his nearest female neighbour was 2.9 m (s = 0.3). The daily mean number of females within a 5 m radius of each of these bulls was 1.8, the number ranging between 1.2 and 3.1 cows for individual males.

We noticed that, although almost all tenured males had more than one cow within close reach for most of the day, they tended to focus their activity on some of these cows in preference to the others. In order to analyse this further, we determined for each cow the onset of pro-oestrus, that is to say the four-day period before the first male (not necessarily her nearest male neighbour) was seen to copulate with her successfully. (For the cows in our sample, the median interval elapsing between the first attempted mount and the first intromission was four days.) For want of a better term, we shall describe cows which are either in oestrus (permit a bull to copulate) or pro-oestrus as "attractive". The conditions under which a bull would favour a particular cow, and move with her if she
shifted position, are outlined in Table II. It may be seen that, if all the cows within a 5 m radius of the bull were attractive, and one of them moved away, the bull generally did not follow her. If the female which moved was not attractive but other nearby females were, the bull scarcely ever followed her. If there were two or more cows within reach and the one which moved was the only attractive one, he followed her; if, however, none of the cows within 5 m of the bull was attractive, he tended to stay where he was when one of them moved away. Finally, if the female which moved was the only one within 5 m of the bull, he followed her whether she was attractive or not.

Movement of transient males

We made several attempts to find elsewhere those transient individuals which we had been able to identify during their brief stay in the study area, but we managed to sight only six of them a sufficient number of times to be able to determine whether they had established tenure on another part of the breeding grounds. Two of them finally established themselves amongst females in area C, for at least two weeks in one case and three in the other. The remaining four transients wandered widely over the breeding grounds. However the length of time they spent in any one place increased as the season progressed so that when they were last sighted towards the end of January, all four had occupied that last position for six to eight days. Although this suggests that males which are transient at the beginning of the season may be able to establish tenure when the severity of competition declines at the end of the season, we have no way of telling how representative our very small sample is.

In summary, although tenured bulls are more widely spaced than one would expect on average, three separate lines of evidence point to the conclusion that they are not territorial. This evidence stems from an analysis of the conditions under which they threaten or fight one another and of the conditions which control the outcomes of these disputes, from the absence of any behaviour which would signal an animal's status or intentions at a distance, and from the extensive overlap in the use of space by these males. Similarly, there is no evidence that the bulls on Sable Island are hierarchically organized in a manner which remotely resembles, for instance, that of the Northern elephant seal, *M. angustirostris* (Le Boeuf & Peterson, 1969). Instead, successful bulls manoeuvre their positions within the shifting female herd in ways which increase their chances of being close to attractive females and then, from time to time, they directly test the receptivity of these females by trying to mount them (cf. Anderson et al., 1975: 194).

Reproductive success

During the combined 1974–5 and 1975–6 seasons, a watch was kept on a total of 34 males whose tenure extended into the period when females in oestrus were available in the study area. Records were also taken of the sexual activity of those transient males which entered the study area during the same periods.

On average, undisturbed coitus between Grey seals lasts for 20 min, with times ranging from 5 to 50 min. Thus, it is not surprising to find that interruptions are common and that tenure carries with it some immunity. As may be seen from Table III, tenured males are far more likely to complete coitus without interruption. Moreover, most of the interruptions suffered by tenured males are self-imposed, in the sense that they occur because the bull
Table III
Proportions of attempted copulations by tenured and transient males which were completed without interruption, or which were interrupted either voluntarily or involuntarily

<table>
<thead>
<tr>
<th>Conditions of attempted copulation</th>
<th>Completed without interruption</th>
<th>Voluntary interruption to attack an intruder</th>
<th>Involuntary interruption caused by attack of another male</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tenured males</td>
<td>0.61</td>
<td>0.29</td>
<td>0.10</td>
</tr>
<tr>
<td>Transient males</td>
<td>0.20</td>
<td>0.17</td>
<td>0.63</td>
</tr>
</tbody>
</table>

dismounts in order to threaten or attack another male, whereas the interruptions suffered by transient males generally occur because they themselves are attacked and driven off by another bull while they are trying to copulate.

The median number of uninterrupted copulations achieved by the tenured males in our sample during daylight hours, inclusive of multiple copulations with the same female, was 2.0 per season; the median number of uninterrupted copulations with different females

![Graph](image)

**Fig. 10.** Relation between length of stay and three measures of reproductive success for 34 males during the combined 1974–5 and 1975–6 seasons.
was 1·5; and the median number of uninterrupted copulations with females which had not previously been seen to mate with another male was 1·0.

Figure 10 shows the relation between the length of time that each of the above 34 tenured males held tenure and various measures of reproductive success during a single season (viz., number of uninterrupted copulations, number of different females mated, and number of copulations with females not previously mated). According to all three measures the longer an animal is tenured, the more successful he is likely to be. A similar relationship has been observed on North Rona (Anderson et al., 1975).

Table IV

The relationship between the number of times a female had previously mated and the status of the male presently copulating with her

<table>
<thead>
<tr>
<th>Status of male</th>
<th>Number of times female had previously mated</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Nearest tenured male</td>
<td>0·80</td>
</tr>
<tr>
<td>(N=44)</td>
<td></td>
</tr>
<tr>
<td>Other tenured males</td>
<td>0·15</td>
</tr>
<tr>
<td>(8)</td>
<td></td>
</tr>
<tr>
<td>Transient male</td>
<td>0·05</td>
</tr>
<tr>
<td>(3)</td>
<td></td>
</tr>
<tr>
<td>Total tenured males</td>
<td>0·95</td>
</tr>
<tr>
<td>(52)</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1·00</td>
</tr>
<tr>
<td>(55)</td>
<td></td>
</tr>
</tbody>
</table>

Table IV gives the relation between the status of a male which, at a given instant, is copulating with a particular female and the number of times that female has previously mated. Tenured males account for the greater proportion of copulations, regardless of how many times the female has mated. However, it will be seen from Table IV that while the female's tenured consort at the time when she comes into oestrus is responsible for most of that female's first copulations, his contribution becomes progressively less as the number of times she has previously mated increases. In contrast, the contribution of males which were either transient or, though tenured, were not the nearest neighbour of the female concerned progressively increases as the number of her prior copulations increases, the relative contribution by such tenured males being greater than that by transients.

In sum, tenure very probably confers a selective advantage on those that acquire it.

Discussion

We began by asking why a species which now breeds chiefly on land, but still exhibits some of the characters normally associated with breeding on the ice, should have developed a marked sexual difference in size. We can now suggest a partial solution to this paradox. On Sable Island, Grey seal males are polygynous, but they do not compete for territories or for status in dominance hierarchies in the way that other land-breeding pinnipeds do. Instead, they arrive synchronously on the breeding grounds with females, monitor the
receptive condition of those nearby, consort with the ones which are most likely to become receptive in the immediate future, and rely on face-to-face encounters to prevent other males from infringing on their conjugal rights. This system would be particularly adaptive under the conditions likely to be imposed on a breeding population by the continual movement and breakup of the ice (cf. Hook & Johens, 1972: 42) and it would, at the same time, favour the development of greater size and obesity in the males. Males with heavier fat deposits will have greater endurance, and in the system we have described the males with the greater endurance have the larger reproductive success (Fig. 10).

However, the solution is not entirely straightforward. In recent writing on the evolution of mating systems there has been a consensus that phenotypic variation in the reproductive strategies of a species should be expected from one population to another (Wilson, 1975; Emlen & Oring, 1977). We are thus led to ask: why has the Grey seal male on Sable Island retained a system which may well be ideally adapted to a polygynous existence on the ice but which, in a land-breeding colony, would seem to be less advantageous than a conventional territorial or hierarchical one? In other pinnipeds, the gregariousness of the females during the breeding season (together with a number of other characteristics (Bartholomew, 1970) has made it possible for extreme forms of territorial and hierarchical systems to develop, so that a very small proportion of the adult male population accounts for a very large proportion of all the copulations (e.g., Le Boeuf & Peterson, 1969). If mating systems are as malleable as they are commonly thought to be, why have the same monopolistic tendencies not developed amongst the Grey seals of Sable Island?

There are at least two possible reasons. First, there is some exchange between the Grey seal population which breeds on the ice in the Gulf of St Lawrence and the Sable Island colony (Mansfield & Beck, 1977), and one might argue that the gene flow is sufficient to prevent the development of land-breeding strategies at the latter site. It should be possible to estimate the likelihood of this by comparing the system on Sable with the strategies employed at colonies which are no longer in contact with ice-breeding populations. Do the latter bear a closer resemblance to the typical reproductive behaviour of land-breeding pinnipeds? In fact, this question has no simple answer because, despite the many accounts of such colonies that can be found in the literature, it is impossible to find out from them what a representative sample of animals might actually have been doing while they were being watched. The only study which is immune to this criticism is one by Anderson and her colleagues (Anderson et al., 1975) of the North Rona colony and, as we have already pointed out, the large difference between this colony and the one on Sable Island with respect to the operational sex ratio (Emlen & Oring, 1977) and the spacing between males (Table 1) may indicate stiffer competition between males on North Rona. This, in its turn, might be associated with a difference in mating system between a colony that is still in contact with pack-ice breeders (Sable) and one that is not (North Rona). If this were the case, however, and if the system which had developed on North Rona were akin to an ordinary territorial or hierarchical one, one might legitimately expect the behaviour of the males to be characterized by prominent displays analogous, let us say, to the “upright” posture and clap-threat of the hierarchically organized elephant seal. Grey seals are quite agile on land, but they are not designed for prolonged bouts of locomotion and one would think it essential for territorial or dominant bulls to be able to challenge intruders from a distance. Anderson et al. (1975) make no mention of any such displays. Indeed the yodel of
the Sable Island bulls, which is the one signal in the Grey seal's repertoire which might have been adapted to this purpose, is conspicuous by its absence from colonies in the eastern Atlantic.

The alternative possibility is that mating behaviour is less malleable than it is now generally believed to be. This question of the plasticity of mating systems has two aspects. The first is concerned with the relation between the two classes of system, monogamy and polygamy. Here, both evolutionary theory and observed fact conspire to provide a good understanding of the conditions under which members of a species will make the transition from monogamy to polygamy and, since Grey seals amply satisfy these conditions, there is no difficulty in understanding why they should be polygynous when circumstances permit. The other side of the problem is concerned with the relations between the various forms of polygamy; for instance, with the question of whether a species which is territorial under one set of circumstances can be expected to adopt a hierarchical mode of organization when, let us say, the population density increases beyond some threshold amount. Here there is no theory and very little fact. Although the opinion flourishes that transitions from one form of polygyny to another are not only possible but frequently to be expected (Wilson, 1975; Leuthold, 1977; Emlen & Oring, 1977), most, if not all, of the evidence usually quoted in support of this idea consists either of inadequately controlled experiments or of unpublished observations by a third party. Even in those few cases where the same observer has watched different populations of the same species and has claimed that the form of social organization has varied from one population to another (e.g. Monfort-Braham, 1975), it seems to us that the evidence provided is far from conclusive.

The signalling systems which are available to a species must limit that species' options within the class of polygamous societies (cf. Geist, 1974). The sexual oligarchy practised by the elephant seals on Año Nuevo Island (Le Boeuf & Peterson, 1969) is made possible both by the gregariousness of the females and by the directional, long-distance audiovisual display of the bulls. The opportunities for polygyny which are offered by the behaviour of the Grey seal cows on Sable Island are somewhat less than those presented by their elephant seal counterparts, but the difference between the two species in this respect is less, by an order of magnitude, than the difference between them in the reproductive success of the most successful bulls. It seems probable that an important reason for this difference is that Grey seals lack the ability to compose a prominent and easily localized signal with which they could advertise superior rank or territorial possession.

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