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Limited intra-specific variation in male grey seal dominance relationships in relation to variation in male mating success and female availability

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Synopsis

Inter-male aggressive encounters were examined at three grey seal breeding colonies that differed in topography, adult dispersion patterns and operational sex ratios; North Rona and the Monach Isles (Scotland), and Sable Island (Nova Scotia). At North Rona, known males were observed over three successive breeding seasons, with a total of 275 males being individually identified. A single season's observations at both the Monach Isles and Sable Island provided data on 53 and 80 individual males respectively. Cardinal dominance ranks were computed for 68, 92 and 112 males on North Rona in each season respectively, 37 males on the Monach Isles and 68 males on Sable Island. All sites showed close approximation to dominance hierarchies when considering only interactions resulting in a clear outcome (wins), with less than 10% of interactions resulting in reversals. Measures of variance in male mating success showed no significant differences between colonies. These results show the existence of male dominance hierarchies in colonies from both east and west Atlantic populations and at breeding sites with widely differing habitat structure, seal dispersion patterns and levels of inter-male competition, suggesting limited plasticity in the form of grey seal mating systems and limited variation in the degree of polygyny attained at these sites.

Introduction

Grey seals (*Halichoerus grypus*) generally have a polygynous mating system (Anderson, Burton & Summers, 1975; Boness & James, 1979; Anderson & Fedak, 1985; Twiss, 1991; Amos *et al.*, 1993) but the actual form of polygyny is far from clear. Early authors described the system as territorial (Fraser-Darling, 1939; Cameron, 1967; Hewer, 1957) and even as monogamous (Mansfield, 1967; Hook & Johnels, 1972). These were based primarily upon anecdotal observations and have been refuted by more quantitative studies (Anderson *et al.*, 1975; Anderson & Fedak, 1985; Boness & James, 1979). Boness & James (1979) divided males into tenured and transient, those remaining ashore for at least two days being classed as tenured, those failing to do so as transients. Whilst transient males lost to tenured males in aggressive encounters, they suggested that all tenured males were of equal status. Anderson & Fedak (1985) concluded that males did not form a true linear hierarchy, as reversals of success in dyadic encounters did occur, but stated that some males were "conspicuously unsuccessful, and some seemed invincible", even amongst tenured males. Male pinnipeds do not provide parental care, hence variation in male mating behaviour is dependent upon the means by which males gain access to mates. In polygynous mammals, this is generally determined by female movements and the size and stability of female aggregations, particularly where mating takes place on land (Emlen & Oring, 1977; Clutton-Brock, 1989; Boness, 1991; Le Boeuf, 1991).

Intra-specific variation in mammalian mating systems has been demonstrated in several studies. For example, male fallow deer (*Dama dama*) lek at high population densities, but defend resource based territories at low densities (Clutton-Brock *et al.*, 1988). Similar density related changes in mating pattern have been shown in sika deer, *Cervus nippon* (Balmford, *et al.*, 1993). Amongst pinnipeds, both resource and female defence polygyny are exhibited by *Otaria byronia* (Campagna & Le Boeuf, 1988*a, b*), depending upon the distributional and behavioural responses of females to differing topographies. Thus, intra-specific variation in the form of mating system may be expected where differences occur in breeding colony features, such as sex ratios, densities and dispersion patterns of females. Greater spatial clustering of females and highly skewed operational sex ratios (OSR) suggest more extreme polygyny (Alexander *et al.*, 1979; Anderson & Fedak, 1985; Boness &

James, 1979; Boness, 1991), which is likely to produce more intense inter-male aggression (Emlen & Oring, 1977; Clutton-Brock & Parker, 1992).

Grey seals breed on a wide variety of topographies (Stirling, 1975), and show very different OSRs at different colonies (Bones & James, 1979; Anderson & Fedak, 1985). Therefore, we expect to observe more intense inter-male competition at sites with more skewed sex ratios and greater female clustering, resulting in more clearly defined dominance relationships, with fewer reversals. Here, we examine levels of inter-male aggression and male dominance relationships at three major grey seal breeding colonies. These sites provided contrasting breeding site topographies, with differences in OSRs and male and female dispersion patterns.

Methods

Study sites

Two sites are from the East Atlantic grey seal population, whilst the third is from the West Atlantic population.

(1) North Rona (59°06'N, 05°50'W) is a rocky island lying 75.5 km NNW of Cape Wrath, Scotland. The study area was limited to the most southerly part of the Fianuis peninsula, covering an area of approximately 0.38 km² (Twiss, Pomeroy & Anderson, 1994). The western coast of the study area consists of vertical cliffs 10 to 20m in height with no possible access to or from the sea for seals. Access to the breeding site is restricted largely to three deep and steep walled gullies cutting through the moderately sloping rock slabs of the east coast. The inland breeding area consists of undulating grassy terrain ranging from approximately 2m to 50m above mean sea level, on a slope increasing from 0° immediately above the access points to approximately 40° furthest inland (Twiss, unpubl. data). These grassy slopes are punctuated by irregularly spaced boulders, rocky outcrops and remnants of old stone walls. The breeding season at North Rona extends from late September through to late November. The dispersion pattern of females at the North Rona study site is aggregated with median nearest neighbour distances of 4.36m whilst males are more widely dispersed amongst the female groups, with median nearest neighbour distances of 15.6m (Twiss, unpubl. data). These measurements were made from geo-rectified,

large format colour aerial photographs (Hiby, Thompson & Ward, 1988; Mills, Newton & Twiss, 1997; Twiss & Thomas, 1998) from the 1994 breeding season. Colonisation and dispersion patterns of seals at North Rona have been shown to be consistent between years (Pomeroy *et al.*, 1994). At this study site, females generally remain close to their pups throughout lactation, a period of approximately 17 days (Pomeroy *et al.*, 1994). Towards the end of lactation the female enters oestrus and is mated. She will then return to the sea and the pup is abruptly weaned. Males endeavour to maintain positions amongst the aggregations of females and mating success is correlated with duration of tenure (Anderson & Fedak, 1985; Twiss, 1991).

(2) The Monach Isles ($57^{\circ}31'N$, $07^{\circ}37'W$) are a chain of low lying islands (maximum elevation of 19m above mean sea level), composed of small rocky skerries with large expanses of machair and shell sand dune systems. Seals breed predominantly on the extensive surrounding sandy beaches. The study site was composed of a single, discrete beach and its immediate dune system on the Gortinish peninsula of Ceann Ear (NF 65000, 62600). The entire study area covered 0.049 km^2 at low tide and 0.038 km^2 at high tide. Approximately 80% of the pups were born on the beach with the remaining pups born in the adjacent dune system. These dunes were less than 2m high and well separated by flat areas of sand and marram grass. Access to the breeding sites is largely unrestricted by topography, with individuals able to come ashore at any point along the beach. The timing of the breeding season at the Monach Isles is the same as that for North Rona. The median nearest neighbour distances at this site during in 1994 were 3.28m for females and 22.7m for males. Unlike at North Rona, females breeding at the Monach Isles spend a considerable amount of time away from their pups and in the shallows of the nearby sea but returning regularly to suckle their pups (Anderson & Harwood, 1985; Twiss, unpubl. data). Males maintain positions amongst the female aggregations both on the beach and dune system, and in the shallows.

(3) Sable Island ($43^{\circ} 55' N$, $60^{\circ} 00' W$) is a sand bar 35 km long and up to 1.5 km wide located 288 km ESE of Halifax, Nova Scotia, Canada. The island consists of shifting sand dunes and large areas of flat sand. The only vegetation consists of marram grass, growing on the more stable dunes. The study site was part of a large breeding area known as West 4 and covered approximately 0.045 km^2 . Here, the terrain is mainly comprised of

flat expanses of sand, punctuated by gently sloping, low dunes less than 2m in height. Access to the site is unrestricted from all directions apart from the south-west, where a sheer faced high dune prevented access. The site was located centrally within approximately 500m of the nearest shore. The breeding season at Sable Island extends from the beginning of January through to mid February. Comparable measurements of nearest neighbour distances are not available for Sable Island, however, Boness & James (1979) provided a mean nearest neighbour distance of 4.4 m (s.d. = 1.3) for females at Sable Island, and one would expect the median value to be lower than this. No such data are available for Sable Island males, although Anderson & Fedak (1985) stated that inter-male distances at North Rona were three times greater than at Sable Island. Females at this study site remained with their pups throughout lactation.

Behavioural observations

Data were collected during three breeding seasons at North Rona (1987, 1988 and 1989) and during a single season at Sable Island (1990) and the Monach Isles (1994). Observations were made from hides overlooking the study sites. Data were collected throughout daylight hours during the periods given in Table 1. All males present in the study sites for greater than 1 hour were identified by pelage and scarring patterns and/or brands. The number of individually identified males at each site are given in Table 1.

Sex ratios

Two estimates of sex ratios were derived for each site and breeding season. Firstly, we computed the average of the daily male to female ratio as counted in the field during the observation periods. As individual males and females remain ashore for a number of days this method may not provide a robust estimate of OSR (defined as the ratio of fertilisable females to sexually active males, Emlen & Oring, 1977). Therefore, we plotted the daily number of females present and computed the area under this curve to provide an estimate of the total number of female days for each site and season. We then divided this value by the average length of stay of females (the time from parturition to oestrus) for each site to provide an estimate of the number of females breeding in each

study site and season. The total number of males identified in the study sites during observations (see Table 1) was used in conjunction with this estimate of female numbers to provide a second measure of OSR. This second measure also permitted statistical comparison of sex ratios between sites by Chi-square analyses as we had independent estimates of the number of males and females at each site. It was not possible to statistically compare the average daily sex ratios as these data were not independent given that individual animals were present on more than one day.

Levels of inter-male aggression

All observed inter-male aggressive encounters were recorded *ad libitum* (Altmann, 1974), noting the date and time of occurrence, identities of initiator and participants and the outcome of the interaction. Types of inter-male aggressive encounters were categorised as open mouth threats, fights, chases, aggressive flipping or as single lunges or bites outwith the context of a fight. Only rarely did aggressive encounters involve more than two males. Bouts of open mouth threats between three or four males can occur, but only one fight involving more than two males simultaneously was seen in 7291 observed inter-male aggressive encounters. Individuals retreating from the encounter first were classified as losers. Draws were recorded either where both males retreated simultaneously or neither male retreated. The outcomes of all aggressive interactions were scored equally as either wins, draws or losses, irrespective of the type of encounter.

Daily counts of the number and type of inter-male aggressive encounters were maintained for each identified male. These data provided measures of the average daily rates of aggressive encounters at each site. Note that only those males observed in 10 or more aggressive interactions and present on the study sites for at least one whole day's observations were used for calculation of daily rates of aggression. This excluded biased estimates of daily aggression rates from individuals present for only a few hours. All data sets were natural log transformed to approximate to normality, and comparisons made using one-way analysis of variance (ANOVA) with Scheffe's multiple range test (at a significance level of 0.05).

Calculation of male dominance ranks

To overcome the limitations of assigning males to arbitrary dichotomous classes such as ‘tenured’ or ‘transient’, ‘dominant’ or ‘subordinate’, we used Boyd & Silk’s (1983) FORTRAN program ‘DOMTIES’ for assigning cardinal dominance ranks based on the outcomes of all aggressive interactions. This method allowed us to deal with the incomplete interaction matrices, the occurrence of draws and ambiguous dominance relationships between dyads that occur in such data as these. Draws were assigned equally to both participants in such encounters. Dominance ranks were only computed for males observed in 10 or more aggressive interactions. We used Chi-square tests to compare the relative frequencies of interaction outcomes between the three seasons at North Rona and between sites (using data from a single, randomly selected, season at North Rona). Firstly, we examined the frequencies of reversals in victories, classified as either non-reversals (outcome as predicted by the relative dominance ranks of the participants) or reversals (the opposite outcome to that predicted by the relative dominance ranks of the participants). These analyses excluded all encounters resulting in draws. Secondly, we examined the frequencies of encounters resulting in draws, with all encounters classified as either non-draws (outright victories for one member of the dyad) or draws.

Variation of male mating success and estimation of the intensity of sexual selection (I_s)

All observed copulations were recorded, noting the date and time of occurrence, the identities of both participants and whether the attempt was successful or not. Successful copulations were defined as instances where intromission was clearly achieved and the copulation proceeded, uninterrupted, to completion. During copulation the male uses his jaws to grip the female by the neck and his fore-flippers to grip her body. In the initial stages of intromission the male frequently adjusts position, however, the mating pair soon settle and lie very still for the remainder of the copulation. Towards the end of a successful copulation the female’s ventral pelvic region can be seen pulsating, possibly indicating the time of ejaculation. The female then becomes more agitated and the copulation ends shortly afterwards. Successful copulations have a mean duration of approximately 20 minutes whilst unsuccessful, interrupted copulations last approximately 5 minutes (Twiss,

1991). Mating success for each male was defined as the number of successful copulations with females not observed in copulo previously with either the same or other males. Median values for male mating success were compared between the three seasons at North Rona and between sites using Kruskal-Wallis tests. In order to assess whether there were any significant differences in the relative variation in male mating success between sites and seasons we computed the cumulative percentage of copulations accounted for by each successive 10 % of the identified males (ranked in order of decreasing mating success) in each season. The curves obtained were compared using Kolmogorov-Smirnov two sample tests. The relative variance in male mating success ($I_s = \text{variance}/\text{mean mating success}$; Wade & Arnold, 1980) was computed as an index of the intensity of sexual selection at each site (see Boness, 1991).

Results

Male dominance relationships

Table 2 provides the summary results for the matrices of (i) wins and draws and (ii) wins only, based upon the computed dominance ranks of individuals using Boyd & Silk's (1983) method for each study site and season. The percentage of reversals were relatively high when considering both wins and draws, ranging from 21 to 33%. However, when examining only those interactions resulting in a decisive outcome (wins) the percentage of reversals declined considerably, with maximum values of 10% at Sable Island and the Monach Isles, and a remarkable consistency between the sites. However, Chi-square analyses of victories classified as non-reversals or reversals and of all interactions classified as non-draws or draws revealed some differences between sites and seasons in the makeup of these interaction matrices. There was no significant difference between the three seasons at North Rona in the frequencies of non-reversals and reversals ($\chi^2 = 6.45$, $df = 2$, $p > 0.01$). The inter-site comparison (using data from the 1989 North Rona season) showed that Sable Island exhibited significantly more reversals than expected ($\chi^2 = 10.68$, $df = 2$, $p < 0.01$). Upon removing Sable Island from the analysis and simply comparing North Rona and the Monach Isles, no significant difference was found (χ^2 with Yates'

correction = 2.39, df = 1, $p > 0.01$). Comparison of the frequencies of non-draws and draws between the three seasons at North Rona revealed that there were significantly more draws in the 1989 season than expected ($\chi^2 = 199.31$, df = 2, $p < 0.01$). Removal of the 1989 data from this analysis showed no significant difference between the 1987 and 1988 seasons (χ^2 with Yates' correction = 3.37, df = 1, $p > 0.01$). Comparison between sites revealed considerable deviations from expected values, with North Rona exhibiting more non-draws than expected and Sable Island less non-draws than expected ($\chi^2 = 78.76$, df = 2, $p < 0.01$).

Site differences in sex ratios

These three sites showed considerable differences in the organisation of the breeding colony (Table 3). Average daily sex ratios differed markedly, with up to a five fold difference in the average number of females per male; North Rona exhibiting the most skewed ratio, Sable Island being almost at parity, whilst the Monach Isles were intermediate. Our second estimate of OSR (number of identified males:total number of female days/time from parturition to oestrus) demonstrated a different pattern with up to a nine fold difference between sites. Whilst Sable Island was again the site with the least skewed sex ratio, the ratio for Monach Isles was more skewed than those for any of the North Rona seasons. Our Chi-square analysis of the estimated number of females present and the total number of males identified in each season at North Rona revealed that there were relatively more males present in 1988 than expected ($\chi^2 = 10.21$, df = 2, $p < 0.01$). Upon repeating the analysis without the 1988 data, no significant difference was found between the 1987 and 1989 seasons (χ^2 with Yates' correction = 2.08, df = 1, $p > 0.01$). When comparing between sites, Sable Island was shown to have relatively more males than expected ($\chi^2 = 123.3$, df = 2, $p < 0.01$). When the Sable Island data were removed, no significant difference was found between the North Rona and Monach Isles (χ^2 with Yates' correction = 3.37, df = 1, $p > 0.01$).

Levels of inter-male aggression

Table 3 provides median values for the number of aggressive interactions per day for males involved in 10 or more aggressive interactions and present on the study sites for at least one whole day's observations during each of the study seasons. The daily rates of aggression at North Rona in 1989 were significantly higher than any of the other two North Rona seasons (ANOVA on natural log transformed data: $F_{2,256} = 7.45$, $p < 0.001$).

The daily rates of aggression for Sable Island males were significantly higher than those observed at the Monach Isles and any of the three North Rona seasons, even when comparing against the 1989 North Rona data ($F_{2,207} = 32.63$, $p < 0.0001$). Aggression rates at the Monach Isles were significantly lower than those for Sable Island, but greater than those observed at North Rona in 1987 ($F_{2,170} = 44.17$, $p < 0.0001$) and 1988 ($F_{2,188} = 68.39$, $p < 0.0001$), but showed no significant difference to the 1989 North Rona data. Fig. 1(a) shows a plot of median daily inter-male aggression rates against the sex ratio measured as the average daily number of females per male for each site and season. Fig. 1(b) depicts the same aggression rates plotted against our measure of OSR (number of identified males:total number of female days/time from parturition to oestrus). Whilst the number of sites is limited and prevents statistical comparison of these relationships, it would appear that the negative relationship between aggression and average daily sex ratio is clearer than that with estimated OSR.

Variation of male mating success

The values of I_s for each study season are presented in Table 3. The greatest variation in male mating success was found at the Monach Isles, with North Rona presenting intermediate values and Sable Island the lowest variation. Fig. 2(a) shows a plot of I_s against the sex ratio measured as the average daily number of females per male for each site and season. Fig. 2(b) depicts I_s plotted against our estimate of OSR. Whilst there is no clear relationship between I_s and average daily sex ratio, there does appear to be a positive relationship between I_s and OSR, with the exception of the data for North Rona from 1988. Comparison of the median values of male mating success for the three seasons at North Rona using a Kruskal-Wallis test revealed that the median mating success in 1987 was significantly greater than those for 1988 and 1989 ($\chi^2 = 11.86$, d.f. = 2, $p = 0.003$). Similarly, the North Rona 1987 median mating success was greater than those for Sable Island and the Monach

Isles ($\chi^2 = 17.96$, d.f. = 2, $p = 0.0001$). However, there were no significant differences between Sable Island, the Monach Isles and either North Rona 1988 ($\chi^2 = 1.72$, d.f. = 2, $p = 0.42$) or North Rona 1989 ($\chi^2 = 4.12$, d.f. = 2, $p = 0.13$). Our comparisons of the cumulative percentage of copulations accounted for by each successive 10% of the identified males (ranked in order of decreasing mating success) revealed no significant differences between any of the three seasons at North Rona, nor between any of the seasons at North Rona and either Sable Island or the Monach Isles.

Discussion

Dominance hierarchies

Here we present evidence of dominance hierarchies amongst male grey seals at three major breeding colonies. Male grey seals at these sites are generally widely dispersed, thus giving incomplete interaction matrices. This prevents any reasonable attempt at testing these matrices for linearity or transitivity. However, it is clear that the division of males into simply dominants and subordinates or even tenured and transients (Boness & James, 1979) is an oversimplification. Our data suggest that males at Sable Island did approximate to a hierarchy and, contrary to Boness & James (1979), tenured bulls were not all of equal status. These results support Anderson & Fedak's (1985) suggestion that some males were "conspicuously unsuccessful", whilst others seemed "invincible". Anderson & Fedak (1985) were only able to observe male interactions at North Rona for a two week period during the middle of the breeding season. Here, we present data from studies encompassing the entire breeding season at three study sites, thus providing more complete interaction matrices. These data suggest the existence of dominance hierarchies at each of these colonies, and demonstrate a range of male dominance status between the two extremes identified by Anderson & Fedak (1985). Whilst the occurrence of reversals was high when considering both wins and draws, it is more relevant to consider only interactions resulting in decisive outcomes. Anderson & Fedak (1985) stated that "for an encounter to result in a draw may be as useful as winning because a male's position is not affected". This is clearly true; draws merely result in the

maintenance of the status quo. Only true reversals, where previously victorious males lose an encounter, result in a male being ousted from his position amongst the breeding females. Thus, when we examine only wins, we see relatively low levels of reversal. In a natural system, some reversals are to be expected. For example, dominant males who have just been involved in a strenuous fight may subsequently be defeated by a fresh subordinate male. Also, dominant males approaching the end of their stay, with few remaining females, may defer to other males, perhaps because the potential benefits of fighting have declined.

Males at North Rona show inter-annual site fidelity (Twiss *et al.*, 1994), thus, male dominance relationships at North Rona (and perhaps other colonies) may be established over a number of seasons and/or prior to the breeding season, reducing the number of encounters necessary to re-affirm relationships in any one season.

Topography, daily sex ratios and male aggression levels

The three sites examined here present very different topographies, particularly in terms of access to the site from the sea. Topography influences female dispersion patterns, such that females are less aggregated in more open, uniform terrain (Pomeroy *et al.*, 1994, Twiss & Thomas, 1998). Where females are more widely dispersed and access is unrestricted, relatively more males can gain positions on the breeding colony. Thus, we observe more skewed daily sex ratios at sites with more irregular terrain, aggregated female dispersion patterns and restricted access, such as North Rona, whilst sites such as Sable Island, with unlimited access and relatively flat terrain, show sex ratios closer to parity. Inter-male aggression rates showed a negative relationship with average daily sex ratios. At sites with relatively more males ashore, aggression levels are increased, presumably as there are relatively more opponents for each male to interact with. Sable Island provided the highest levels of inter-male aggression and had significantly more reversals and unclear outcomes to interactions (less non-draws) than expected. This suggests that the dominance hierarchies at the Monach Isles and North Rona were more clearly defined than at Sable Island, despite similar overall levels of reversals. Does this reflect a greater intensity of sexual selection at North Rona and the Monach Isles than at Sable Island?

Intensity of sexual selection

Both our estimate of OSRs and the I_s values (the index of the intensity of sexual selection) suggest a greater intensity of sexual selection at North Rona and the Monach Isles than at Sable Island. Unlike measures of daily sex ratio, our estimate of OSR incorporates the element of individual turnover, and so provides a better indication of the relative numbers of males and females attempting to breed within our study sites during the course of a breeding season. This estimate of OSR demonstrated a reasonable positive relationship with I_s across study sites. No consistent relationship was apparent between either average daily sex ratios or male aggression rates and I_s . This suggests that daily sex ratios may be a poor estimate of OSRs and that observations of high levels of inter-male aggression on the colony do not necessarily indicate high intensity of sexual selection in the form of inter-male competition. Conversely, where OSRs are skewed, more males are excluded from entering the breeding arena indicating greater overall levels of intra-sexual competition. This exclusion appears to be the primary form of inter-male competition, particularly where it is aided by topography and female aggregation. Where OSRs are less skewed, males may adopt higher aggression levels in order to secure access to individual females as they enter oestrus, rather than to defend larger groups of females for longer periods.

Whilst the I_s values were different between colonies, our analyses indicated little or no differences between colonies in the relative variation of male mating success. Median male mating success at North Rona in 1987 was greater than that observed for any other site or season. This is most likely due to the fact that observations in 1987 did not span the entire breeding season, missing both the very early and late parts of the season. It is during these times that most transient males, with little or no mating success, are observed on the breeding colony. This would tend to artificially inflate the median mating success for 1987. Excepting the data for 1987, our analyses of median male mating revealed no significant differences between sites. Similarly, we discovered no significant difference in the relative variation of male mating success between sites. It must be noted that estimates of OSRs and measures of I_s are subject to many potential inaccuracies (Boness, 1991). Sex ratios are estimated from only that portion of the population observed on the study site, and may not truly reflect the ratio of fertilisable females to sexually active males, particularly where transient males may remain offshore (Amos *et*

al., 1993). Estimates of I_s refer to variation in male mating success, which may not accurately reflect variation in male reproductive success, although Amos *et al.* (1993) suggest that variance in male reproductive and mating success were similar in the North Rona study population. Amongst Southern Elephant seals (*Mirounga leonina*), Wainstein *et al.* (1998) have shown that observed mating success provides an accurate predictor of paternity. As suggested by Weatherhead & Boag (1997) such non-genetic estimates of success will therefore provide reasonable estimates for comparisons between populations. Accepting that our measures are at least reasonable comparisons between our study sites, these results suggest that plasticity in the degree of polygyny and the form of grey seal mating pattern may be limited, at least amongst land breeding populations. Whilst the individual behaviour patterns adopted by males at these sites differ, such as in the levels of aggression, males at all three study sites exhibited close approximations to dominance hierarchies, irrespective of other apparent inter-colony differences.

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Figure 1a: Plot of average daily male:female ratio against median daily rates of inter-male aggression for all three study sites.

Figure 1b: Plot of the estimated operational sex ratio (number of identified males:total number of female days/time from parturition to oestrus) against median daily rates of inter-male aggression for all three study sites.

Figure 2a: Plot of average daily male:female ratio against relative variance in male mating success (I_s) for all three study sites.

Figure 2b: Plot of the estimated operational sex ratio (number of identified males:total number of female days/time from parturition to oestrus) against relative variance in male mating success (I_s) for all three study sites.

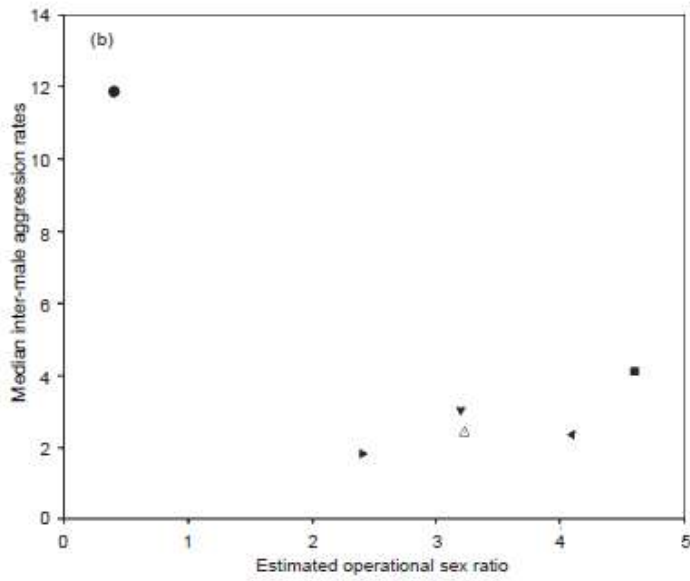
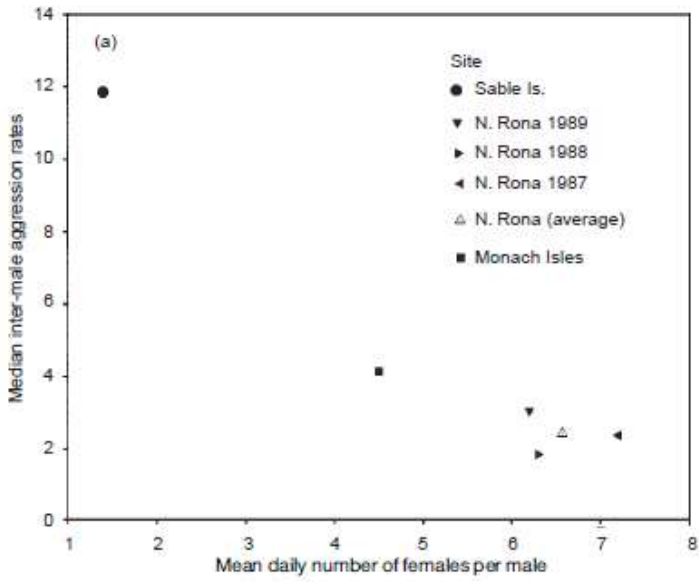


Figure 1a and b

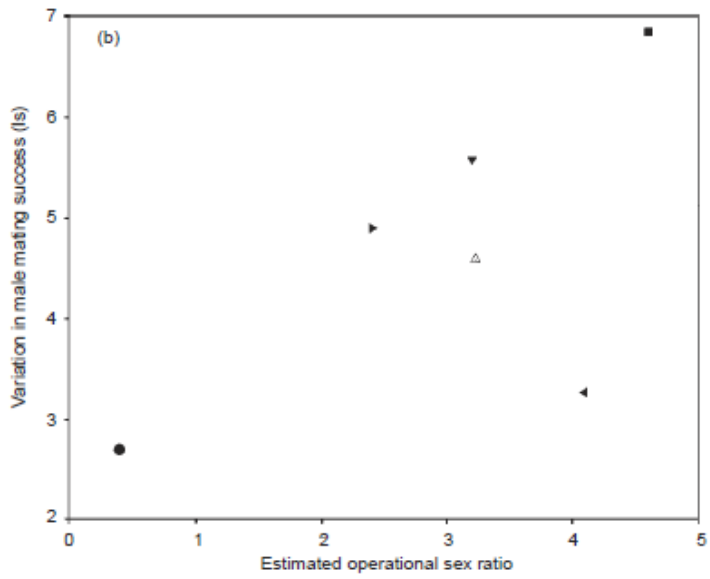
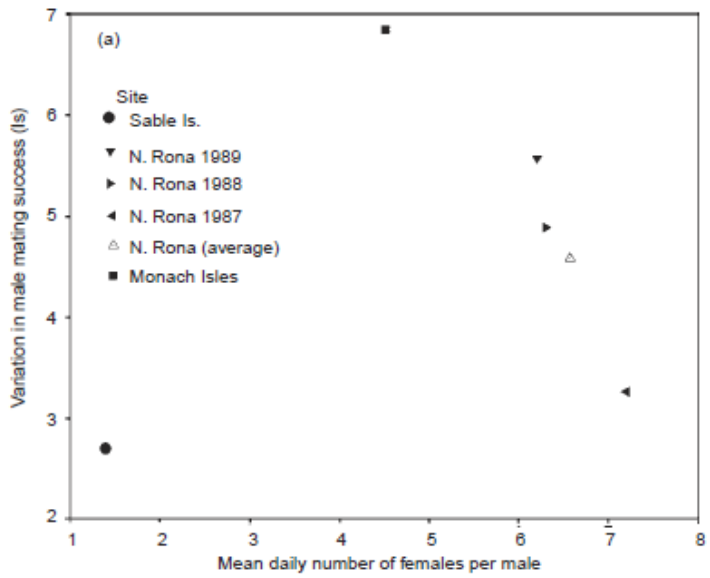


Figure 2a and b

Table 1: Details of observation periods and number of males individually identified for each study site and breeding season.

Site	Year	Date observations commenced	Date observations ceased	No. of males individually identified
North Rona	1987	27/9	12/11	85
North Rona	1988	22/9	16/11	117
North Rona	1989	22/9	23/11	145
Sable Island	1990	11/1	2/2	80
Monach Isles	1994	7/10	25/10	53

Table 2: Summary of the interaction matrices derived from the computed ranks of individuals, showing total number of interactions, number and percentage of reversals for (i) matrices based on wins and draws and (ii) matrices based on wins only. Note: (a) dominance ranks were only computed for males observed in 10 or more aggressive interactions, (b) the total number of interactions denoted here represent the sum of all aggressive interactions recorded for all males except for losses. Thus, for example, a male involved in 10 interactions, all of which he loses will be included in the calculation of dominance ranks, but all of his interactions will be scored as wins for other males.

Site	Year	No. of males	Wins and draws			Wins only		
			Total No. of interactions	No. of reversals	% of reversals	Total No. of interactions	No. of reversals	% of reversals
North Rona	1987	68	1928	403	21	1374	126	9
North Rona	1988	92	1741	358	21	1191	83	7
North Rona	1989	112	2727	743	27	1439	99	7
Sable Island	1990	68	2655	887	33	1111	115	10
Monach Isles	1994	37	240	63	26	144	15	10

Table 3: Summary of seasonal averages for daily sex ratios, estimated operational sex ratio, median daily rates of inter-male aggression and relative variation in male mating success (I_s = variance/mean observed mating success) for each study season and site. Note: sample sizes for median aggression rates differ slightly from those given in Table 2 as individuals present for only a small portion of one day were excluded from the computation of daily aggression rates in addition to those involved in less than 10 aggressive interactions.

Site	Year	Average daily male:female ratio	Estimated operational sex ratio (males:females)	Median daily rate of aggression (n)	Relative variance in male mating success (I_s)
North Rona	1987	1:7.2	1:4.1	2.37 (68)	3.27
North Rona	1988	1:6.3	1:4.2	1.84 (86)	4.89
North Rona	1989	1:6.2	1:3.2	3.05 (105)	5.57
Sable Island	1990	1:1.4	1:0.4	11.86 (68)	2.70
Monach Isles	1994	1:4.5	1:4.6	4.13 (37)	6.84