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Opportunity for selection in southern elephant seals (*Mirounga leonina*): the effect of spatial scale of analysis

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Abstract

The opportunity for selection, *I*, calculated as the variance in relative fitness, sets an upper limit to the amount of adaptive change that selection may produce. Therefore, it is a potentially valuable, and frequently used, measure of the potential of action of phenotypic selection. Although many different aspects of *I* calculation and analysis have been explored, the effect of the spatial scale chosen for calculation received little attention, notwithstanding the growing evidence that natural populations are not homogeneous and present a hierarchical spatial structure. The effect of scale on the estimation of *I* was examined from data collected in two populations of southern elephant seals (*Mirounga leonina*), an easily observable and strongly polygynous species. A significant effect of spatial scale on three important aspects of *I* calculation and analysis was found: dependence of *I* on mean fitness, between population variation of *I*, and effect of local demography on *I*.

Key words: opportunity for selection, spatial scale, southern elephant seals, *Mirounga leonina*

INTRODUCTION

The study of phenotypic selection in natural populations has grown exponentially in recent years (Brodie, Moore & Janzen, 1995). The first, preliminary step in selection analysis is often the calculation of opportunity for selection (*I*), i.e. the standardized variance in fitness (Arnold & Wade, 1984). This measure represents the upper limit of the potential for the action of phenotypic selection in each specific system (group, population, species), because no component of covariance between fitness and phenotypic traits may be higher than the covariance of fitness with itself. Therefore, *I* may be used as guidance, although a rough one, in the choice of populations and sites for selection analysis. *I* has also been used frequently to improve the quality of comparisons between mating systems, and, because of the wide availability of fitness measures from natural populations, values of *I* are now frequently calculated and compared between populations and species. Notwithstanding this, the use of *I* has many potential drawbacks, many of which have already been identified (e.g. dependence to mean fitness, Downhower, Blumer & Brown, 1987; mixing of random and deterministic components, Sutherland, 1987; lack of direct links to selection mechanisms, Grafen, 1988). One potential problem of the method has received little attention; although the effect of the temporal scale of measurement has been examined (e.g. Nishida, 1989), the role of spatial scale has not. This effect may be relevant because most natural populations are not homogeneous; they present a more or less pronounced hierarchical structure, which in turn may have a significant effect on the action of selection (Heisler & Damuth, 1987).

In structured populations, different local demography may produce a spatial variation in operational sex ratio (Ims, 1988), and OSR is often the main source of variation of *I* on a temporal scale (McLain *et al.*, 1993; Madsen & Shine, 1993). In the present study, the effect of spatial scale on estimation of opportunity for selection in two populations of southern elephant seals *Mirounga leonina* is examined. Southern elephant seals are a good subject for calculation of *I* from field-derived measures of fitness; they are easy to mark and observe (e.g. Galimberti & Boitani, 1999), copulation rate can be estimated (McCann, 1981), and their mating success, which is an important component of total fitness, is closely related to paternity (Hoelzel *et al.*, 1999; Wainstein *et al.*, 1999). Using measures of copulation frequencies for a large number of male elephant seals, our objective was to evaluate the effect of spatial

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structure on: (1) the effect of mean fitness on I values; (2) the detection of differences between populations; (3) the relationships between I and local demography.

METHODS

Observation of copulations were carried out during 2 breeding seasons (August–October 1993 and 1994) at Punta Delgada, Valdés Peninsula, Argentina (DEL), and during 4 breeding seasons (September–November 1995–98) at Sea Lion Island, Falkland Islands (SLI). At DEL, 521 mature females and 76 breeding males were monitored in 1993, and 613 mature females and 92 breeding males in 1994. At SLI, the whole population was monitored. During the study, the population increased from 517 breeding females in 1995 to 567 in 1998, with 55–70 breeding males. Additional information about the demography of the study populations may be found elsewhere (DEL: Campagna, Lewis & Baldi, 1993; SLI: Galimberti & Boitani, 1999).

At SLI, all breeding males and females were marked by putting nylon cattle tags (Jumbo Rototags, Dalton Supplies Ltd) in the interdigital membrane of the hind flippers; all males and the majority of females (70–85%) were marked with commercial black hair dye. At DEL females were not tagged and were dye marked only in 1994; males were tagged and dye marked as on SLI. During a total of 4586 h of observation (periods 2 h long; see Galimberti, Boitani & Marzetti, 2000 for observational protocol), 2590 copulations were recorded (1218 at DEL, 1372 at SLI). To collect data in different breeding situations, all harems of our study areas (4–5 km of coast at DEL; 4.4 km of coast at SLI) were observed; almost the same observational effort was spent on each harem (9–12 harems per breeding season; 3–168 females per harem), except for small harems that formed for only short periods. Copulation success was estimated for a total of 394 males (168 from DEL, and 226 from SLI). Some males were represented more than once in the data set, because they were observed breeding in more than 1 year. This raises a concern that there may have been risk of pseudoreplication (Bartz, Fligner & Notz, 1998). To check the effect of this partial non-independence, the analysis was repeated using each male for 1 year only (with random selection of the year), obtaining small differences in size (and no differences in direction) of statistical effects between the full and the reduced set. Therefore, results only of the former are presented.

Four levels of spatial structure are considered. This included the whole population plus 3 intrapopulation levels. The lower level was the *harem*, defined as a group of 2 or more females with or without a male in attendance; a harem is both a social and a spatial unit, because elephant seal harems tend to occupy the same position during the whole breeding season. The other 2 levels were: the *breeding area*, which is a continuous stretch of beach separated from other areas by evident landmarks, but without any solution of continuity in terrain suitable for elephant seals reproduction, and the *breeding zone*, which is the area of the beach separated from other zones by stretches of habitat not suitable for elephant seals and not used for breeding. Each area may comprise 1 or more harems, and each zone comprises 2 or more areas.

The estimated number of females which had been mated was chosen as a fitness measure (ENFI, Le Boeuf, 1974). The calculation of ENFI requires an estimate of the proportion of copulations realized in each harem by each male that copulates in or around the harem (as estimated by the number of copulations observed during standard periods), and an estimate of the total number of females that breed in the harem (as calculated from individual records of marked females, or from corrected census values for 1993, when females were not marked). For each male in each harem, the number of females mated is the proportion of his copulations multiplied by the number of females that breed in the harem, rounded to nearest integer. Total ENFI is the sum of his harem specific ENFI for all harems in which he was observed to copulate. ENFI is a common index of reproductive success in elephant seals (e.g. Deutsch, Haley & Le Boeuf, 1990), and it is well related to actual paternity, in particular in the southern species (Wainstein *et al.*, 1999). Mean ENFI was not significantly different between the 2 study populations (DEL: mean ± SD = 7.613 ± 17.565, $n = 168$ males; SLI: 9.243 ± 23.558, $n = 226$; t-test: mean difference = −1.630, $t_{392} = -0.754$, $P = 0.4510$), but variance in ENFI was much lower at DEL (DEL: 308.5; SLI: 554.9; F-test: variance ratio = 0.556, $F_{167,225} = 0.556$, $P < 0.0001$). Mean ENFI was also homogeneous among years both at DEL (1993 *vs* 1994: mean difference = 0.394, $t_{166} = 0.144$, $P = 0.89$) and SLI (1995–98: $F_{3,222} = 0.044$, $P = 0.99$). The opportunity for selection was calculated as the ratio of variance of ENFI to the square of the mean ENFI. In this study, the main disadvantage of using I as measure of potential for selection was overcome (Trail, 1985; Downhower *et al.*, 1987) because: (1) the fitness measure was consistent between populations and years; (2) I was based on data collected with the same methods and effort in both populations, using eqivalent criteria for estimation of mating success and harem size; (3) mean fitness was the same in both populations, and mean fitness was also homogeneous between years. To reduce potential bias in the estimation of I, calculations only included harems/areas/zones with 5 or more breeding males (the analysis was also repeated with the full data set and obtained the same results but with larger standard errors of parameters). Estimates of I are sensitive to the set of males included in the analysis (Grafen, 1988). Our estimates included all males hauled out during the part of the breeding season in which at least 1 female was in oestrus (Galimberti & Boitani, 1999).

Exploratory data analysis and calculation of descriptive statistics tests were run in StatView 5.0 (Abacus Concepts Inc.), non-parametric test (exact and Monte Carlo) were run in StatXact 4.0 for Windows (Cytel

Table 1. Statistics (mean ± SD; sample size = number of zones/areas/harems in parentheses) and tests of the differences between populations (*t*-test, with randomization)

Spatial level	SLI	DEL	Mean difference	P_{20K}
Zones	4.859 ± 1.601 (4)	8.641 ± 3.982 (8)	–3.782	0.1057
Areas	4.696 ± 1.530 (10)	8.293 ± 4.477 (18)	–3.597	0.0210
Harems	4.874 ± 2.278 (12)	7.811 ± 3.873 (15)	–2.937	0.0281

Table 2. Correlation between *I* and demographic variables at different spatial levels; Spearman's rank correlation plus the test probability are given in parentheses derived from exact test for whole populations and randomization tests with 20000 resampling for the remaining spatial levels

Spatial level	No. of females	No. of males	BSR
Whole populations	–0.200 (0.7139)	–0.486 (0.3556)	0.430 (0.4194)
Zones	–0.147 (0.6500)	0.357 (0.2610)	–0.706 (0.0124)
Areas	–0.098 (0.6251)	0.411 (0.0319)	–0.490 (0.0097)
Harems	0.149 (0.4531)	0.672 (0.0001)	–0.421 (0.0314)

Software Corporation), and randomization equivalent of parametric test were run in RT 2.1 (Manly, 1996). When using randomization tests, the number of resamplings is reported as a subscript (e.g. P_{20K} = probability obtained by 20000 resamplings).

RESULTS

Relationship between *I* and mean fitness

One of the problems of *I* as a measure of potential for sexual selection is its dependence on mean fitness. A negative relationship between *I* and mean fitness is expected (Downhower *et al.*, 1987). However, at the level of the population, we found that *I* was positive (Spearman's rank correlation, with exact test, $\tau_2 = 0.600$, $n = 6$ breeding seasons, $P_{exact} = 0.2417$). Conversely, when considering the spatial structure of populations, we found significant negative correlations at all spatial scales, although with different magnitude (breeding zone: Spearman's rank correlation, with randomization test, $\tau_2 = -0.742$, $n = 13$, $P_{20K} = 0.0102$; breeding areas: $\tau_2 = -0.473$, $n = 28$, $P_{20K} = 0.0139$; harems: $\tau =_2 -0.508$, $n = 27$ harems, $P_{20K} = 0.0096$).

Opportunity for selection variation between populations

First *I* was compared between populations without considering spatial structure, and then the comparison was repeated at breeding zone, breeding area, and harem level, by using mean values of males breeding in each specific harem/area/zone. *I* was lower at DEL 222 than at SLI, whatever the spatial scale used for calculation, but size and statistical significance of the difference varied at different scales. Ignoring the intra-population structure, *I* was lower at DEL than at SLI (5.323, $n = 168$ *vs* 6.496, $n = 226$ males), but the 22% difference was non-statistically significant (randomization test on difference in *I* values, as obtained by randomly allocating individual males to the two populations: $P_{20K} = 0.2131$). Differences between populations when the spatial structure of each population was accounted for was always larger than when not accounted for, but significance of the difference varied depending on the spatial scale of calculation of *I* (Table 1).

Effect of breeding sex ratio on opportunity for selection

The sex ratio between breeders (breeding sex ratio, BSR; Galimberti & Boitani, 1999) was considered as a simple demographic measure that may affect opportunity for selection, and the effect of the scale of calculation was evaluated on the strength of this relationship (Table 2). The two populations were first compared using breeding seasons as data points, and a positive non-significant correlation was found between *I* and the sex ratio. Then these calculations were repeated taking into account the spatial structure of the population. There were negative correlations between *I* and the sex ratio although the correlations had variable magnitude and statistical significance (Table 2). Although the power of the population level test was very low, as a result of the small number of breeding seasons considered, the sign of the correlation was opposite to the one found for every intrapopulation spatial level. Correlation analyses were also carried out for the two components of BSR (Table 2), the number of mature females and the number of breeding males (note that these three series of tests are not independent). The correlations between the number of females or males and *I* were not significant at all levels.

DISCUSSION

I is a valuable measure in selection analysis because even considering its disadvantages (Koenig & Albano, 1986; Downhover *et al.*, 1987), it may indicate the potential action of phenotypic selection in different observational/experimental systems (Wade, 1987). Therefore, *I* may be used to inform the choice of the observational or experimental system to be used for selection analysis even for demographic data (Barrowclough & Rockwell, 1993). Moreover, *I* may be used as a quantitative index of a mating system (e.g. Struhsaker & Pope, 1991), and it may be used to compare populations (e.g. Twiss, Anderson & Monaghan, 1998) and species (e.g. Boness, 1991). A main advantage of *I* compared with other measures of inequality in fitness distribution is its direct link with the equations describing selection on quantitative traits (Arnold & Wade, 1984).

From a methodological point of view, our main result is a cautionary tale: even when methods of data collection and measures of fitness are homogeneous, and when basic requirements of *I* calculation are met, correct estimation of the potential for selection requires the choice of the right spatial scale. Our paper shows the effect of spatial scale on some aspects of calculating and analysing *I* that were crucial in past criticisms of the suitability of *I* as a measure of potential for selection. One of the main practical criticisms was dependence between *I* and mean fitness, that may prevent comparison of *I* between groups/populations/sexes with different mean fitness (Downhover *et al.*, 1987). When examined at population level, elephant seals showed a pattern of dependence of *I* on mean fitness contrary to prediction, but this was not true when calculations were done on a smaller spatial scale.

The comparison of *I* values among mating systems could be a valuable improvement on pure description, but this requires congruent spatial measures of mating (Trail, 1985). The hierarchical spatial structure found in many natural populations requires the calculation of *I* in such a way as to cope with spatial effects. In elephant seals, different spatial scales of analysis revealed different magnitude of variation between populations. The optimal scale at which calculations should be carried out could be different in different populations of the same species. At DEL and SLI, we observed different propensities of males to move between zones/areas/harems (unpublished data), and this was in part because SLI is an isolated population (Galimberti & Boitani, 1999) while DEL is not (Campagna *et al.*, 1993). In the Falkland Islands, males have very few opportunities to breed outside SLI (Galimberti *et al.*, 2000), while in the Valdés Peninsula there are plenty of alternative breeding sites. Therefore, the spatial scale at which selection operates could differ between the two populations. From a functional point of view, tests of hypothesis about correlates and determinants of opportunity for selection may be affected by spatial scale, as demonstrated by the results of the relationship between *I* and sex ratio in elephant seals. It is unlikely that an a priori assessment of the right level of analysis will normally be possible and subtle differences in breeding behaviour and local breeding situation may potentially produce a significant variation of the level at which selection operates most effectively. When the lack of cues based on biological information precludes a choice of spatial scale for experimentation, the best approach should be to evaluate the effect of spatial scale by repeating the analysis at various scales, or including the spatial scale as an additional factor (e.g. using a nested design). For southern elephant seals, evidence about the movements of males during the breeding season may help in the choice of the spatial level of analysis. Although males frequently move among harems of the same area, they almost never change breeding zone, and, when females start coming into oestrus, they rarely change breeding area. Therefore, competition between males for access to females is concentrated at area level, at least during the phase of the breeding season in which fertile females are available. Hence, the analysis of the fitness consequences of male competition should be carried out at this level, and the opportunity for selection should be calculated accordingly.

It could be suggested that because of its disadvantages the use of *I* as measure of sexual selection should be abandoned altogether. However, we think that the opportunity for selection is a valuable measure because of its relationships with theoretical equations describing selection on phenotypic traits, and that partitioning of the opportunity for selection is a valuable tool in the study of selection episodes (Wade, 1987). Moreover, most alternative measures of inequality also present drawbacks (Kokko *et al.*, 1999), including sensitivity to the spatial scale of calculation. The spatial structure of populations may interfere with the operation of phenotypic selection. This is reflected in the method for calculating *I* suggested in the present study.

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