

Measures of breeding inequality: a case study in southern elephant seals

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Abstract: Inequality in distribution of resources is a key aspect of evolutionary biology particularly in relation to distribution of mates and copulations. Notwithstanding its important role, inequality is not easily defined, and its measurement is complicated by theoretical and methodological issues. Although the formal treatment of inequality has been mostly limited to the evolution of lek mating system, a methodologically correct approach to measurement of inequality is generally valid for the study of any kind of mating system. In this paper, we analyze inequality in a large set of southern elephant seal (*Mirounga leonina*) harems. The observed distribution of fertilizations was significantly different from both the expected distribution with equal shares of resources and the expected distribution with equal propensities to acquire resources. We calculate and compare various measures of inequality, observing a wide variation particularly among unbounded and bounded indices. We check the effect of choosing a specific measure of inequality by considering the effect of two aspects of harem sociometry, the number of females in the harem (i.e., the total amount of resources to be shared) and the number of males associated with the harem (i.e., the number of competitors). The choice of a specific measure of inequality had a strong impact on the results obtained and should be considered a critical step in every study of functional and evolutionary correlates of inequality. Unbounded indices showed a strong relationship with both harem size and number of males, while no effect was evident in the analysis of bounded indices. This demonstrates that, in this species, the despotism of the mating system remains high even in large harems and with many competitors, i.e., the worst conditions for monopolization.

Résumé : L'inégalité dans la répartition des ressources, particulièrement la répartition des partenaires sexuels et des accouplements, est l'un des facteurs clés de la biologie évolutive. Malgré son rôle important, l'inégalité est difficile à définir et à mesurer à cause de problèmes théoriques et méthodologiques. À ce jour, l'inégalité a été étudiée surtout dans le contexte de l'évolution du système d'accouplement sur leks; une approche méthodologiquement correcte de la mesure de l'inégalité devrait être valide pour l'étude de n'importe quel système d'accouplement. Nous analysons ici l'inégalité au sein d'une grande série de harems d'éléphants de mer (*Mirounga leonina*). La répartition observée des fécondations diffère significativement de la répartition théorique prévue lorsque les ressources sont réparties également et diffère aussi de la répartition à laquelle on peut s'attendre lorsque les animaux ont tous la même propension à chercher à obtenir la ressource. Nous calculons et comparons diverses mesures de l'inégalité et obtenons une grande variation, particulièrement entre les indices non bornés et les indices bornés. Nous vérifions les effets du choix d'une mesure spécifique de l'inégalité en tenant compte de deux aspects de la sociométrie des harems, le nombre de femelles dans le harem (i.e., la quantité totale de la ressource à partager) et le nombre de mâles dans le harem (i.e., le nombre de compétiteurs). Le choix d'une mesure spécifique de l'inégalité a un impact important sur les résultats obtenus et doit être considéré comme une étape critique dans toute étude des facteurs fonctionnels et évolutifs liés à l'inégalité. Les indices non bornés mettent en lumière une forte relation avec la taille du harem et le nombre de mâles, alors que l'analyse des indices bornés ne révèle aucun effet particulier. Nos résultats démontrent que, chez cette espèce, le despotisme du système d'accouplement demeure élevé même dans les grands harems et même en présence de plusieurs compétiteurs, i.e., dans les pires conditions pour la monopolisation.

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Introduction

The variation of breeding success among individuals is a key aspect of evolutionary biology (Darwin 1871) and behavioral ecology (Dunbar 1984). The whole study of breed-

ing strategies, mating tactics, and sexual selection has its first motivation in the presence of differences between individuals in their share of breeding resources acquired (Andersson 1994). Selection requires the presence of a nonrandom variation in the distribution of resources. Therefore, the study of

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selection and evolution of phenotypic traits does not make sense if the distribution of reproduction is even (Kokko et al. 1999).

The presence of observed inequality in the distribution of breeding success is not, per se, a sufficient indication of the presence of a true, nonrandom, inequality (Sutherland 1987). Even in an egalitarian social system, where all individuals have the same propensities to acquire resources, purely random processes may produce inequality in the observed distribution of resources. In this case, the expected distribution of resources is a Poisson distribution, with an expected variance of resource shares equal to the mean (Sutherland 1985). Hence, the first step in the analysis of potential phenotypic targets of selection is to establish if the observed variation in resource distribution is greater than the one expected from a random process. Notwithstanding the crucial role of inequality, the definition of inequality is not very clear, and there is much debate about how to measure inequality and how to test its significance in relation to random, even, or despotic processes of resource acquisition (Kokko et al. 1999). Moreover, the temporal and spatial scales of calculation strongly affect the observed inequality and its relationships with both sociometry (social group structure, i.e., the distribution of individuals of a social group among social classes, where a social class is defined by a combination of factors like sex, age, dominance rank, breeding status, and kinship) and individual phenotype (Galimberti et al. 2002). The formal analysis of inequality has been mostly limited to the study of reproductive skew in eusocial systems (Keller and Reeve 1994) and to the study of evolution of leks in birds (Mackenzie et al. 1995; Widemo and Owens 1995a).

Elephant seals are a classic textbook example of sexual selection (e.g., Andersson 1994). They are the most dimorphic land-breeding mammals, and they have a clearly polygynous mating system based on the formation of harems of up to hundreds of females. Moreover, the distribution of fertilizations of females among males associated with harems is apparently very uneven (Le Boeuf and Laws 1994). Notwithstanding this, rigorous quantification and tests of inequality are lacking, even in the northern species (*Mirounga angustirostris*), which is probably one of the most studied polygynous mammals. In this paper, we analyze a large sample of harems of southern elephant seals (*Mirounga leonina*) for which good estimates of the number of females fertilized are available. We calculate a wide range of inequality measures and test deviations from randomness. We compare the observed inequality with the expected values at the extremes of the evenness–monopolization spectrum. We evaluate the effect of total resources (harem size) and number of competitors on inequality, and the role of the choice of a specific inequality measure.

Materials and methods

Data collection was carried out during two breeding seasons (1993 and 1994) at Punta Delgada (Valdés Peninsula, Argentina, hereinafter DEL; for details on the population see Campagna et al. 1993) and during five breeding seasons (1995–1999) at Sea Lion Island (hereinafter SLI), the main breeding colony of southern elephant seals in the Falkland

Islands (for details on the population see Galimberti and Boitani 1999).

Here, “harem” is a group of two or more females, with or without a male (Baldi et al. 1996). The dataset comprises 74 harems (23 at DEL, 51 at SLI). “Harem size” is the total number of females that breed in the harem during the whole breeding season. Harem size was 55.6 ± 35.2 (mean \pm SD) females. “Harem holder” is the male that resides within the female group. Very rarely a second male was observed within the female group. In these cases, the harem holder is defined as the one male that is more inside the females’ group. The “associated male” of a specific harem is each male that was observed in the harem or within 10 standard body lengths from the nearest female of the harem (Deutsch et al. 1990; Baldi et al. 1996), during daily counts, for the majority of days that the male was on land. The number of associated males was 6.5 ± 4.4 . The whole sample comprises 485 males (55–104 per year) and 4104 females (512–753 per year). Some males are represented in the dataset for more than 1 year (22.1% for 2 years, 11.0% for 3 years, 3.9% for 4 years, 1.7% for 5 years), raising a concern about pseudoreplication. This should not be a problem for the present study because (i) it involves a harem-level analysis, which is not directly related to individual phenotype; (ii) the social habitat, and hence the competition and resource-acquisition processes, changes among consecutive seasons; and (iii) the phenotypic quality of males changes among seasons, owing to growth and increase in experience. In general, inequality will always be measured in the context of season-specific competition, hence the effect of pseudoreplication should be slight.

Our measure of acquired breeding resources is the estimated number of females inseminated (ENFI, Le Boeuf 1974; see also Deutsch et al. 1990). ENFI is calculated from the proportion of copulations achieved by each male in or around the harem and harem’s size. The proportion of copulations achieved by each male in each harem was estimated from a total of 6634 h of systematic observations (the observation protocol is described in Galimberti et al. 2000). We observed a total of 3090 copulations. We trust the quality of our estimates of the proportion of copulations because of the continuous monitoring of the breeding beaches for the whole length of the breeding season and the conspicuousness of elephant seal copulations (e.g., Le Boeuf 1972). Frequently, copulations of males of low social rank are more difficult to observe than copulations of males of high social rank, resulting in biased estimates of mating success (Drickamer 1974). This effect is unlikely in elephant seals, where females are grouped, the breeding habitat is open, and copulations are easy to spot. We carried out observations almost exclusively during the day, but we also did a small sample of observations with night-vision equipment (32 h in all). Activity was equal between day and night (F. Galimberti, A. Fabiani, and S. Sanvito, unpublished data; see also Baldi et al. 1996). The number of females breeding in each harem was estimated from individual records of marked females. Each year, about 99% of the females were marked by cattle tags. Moreover, 70–85% of the females were also marked by hair dye. Details of the marking protocol can be found in Galimberti and Boitani (1999).

The reliability of the estimated number of inseminated fe-

Table 1. Descriptive statistics of inequality measures.

	Mean	<i>s</i>	CV	Min	Max	<i>g</i> ₁	<i>g</i> ₂	<i>r</i>
Unbounded inequality index								
Sample variance (<i>s</i> ²)	413.3874	484.6038	1.1723	0	2081.3669	1.7519	2.6971	0.4391
Standard deviation (<i>s</i>)	17.257	10.8297	0.6276	0	45.6220	0.7899	-0.054	0.4949
Coefficient of variation (CV)	1.9133	0.7760	0.4056	0	3.7801	0.1946	-0.0626	0.6740
Opportunity for selection (<i>I</i>)	4.2543	3.1939	0.7508	0	14.2889	1.1487	0.8127	0.5773
Index of dispersion (<i>I</i> _d)	36.0054	27.5491	0.7651	0	119.6716	0.9852	0.5214	0.5952
Morisita coefficient (<i>I</i> _δ)	4.5900	3.0736	0.6696	0.9286	14.3840	1.2274	0.9211	0.4828
Poissonian deviance (<i>δ</i>)	403.7762	479.2332	1.1869	-12	2054.0000	1.7498	2.6939	0.4880
Lloyd's mean crowding (<i>m</i> [*])	44.6155	30.6077	0.6860	3.5000	127.0466	0.8203	-0.1674	0.5076
Bounded inequality index								
Standardized Morisita coefficient (<i>I</i> _p)	0.7602	0.2654	0.3491	-0.5000	1	-2.5739	8.6234	0.7595
Simpson's (<i>S</i>)	0.6991	0.2223	0.3180	0.2448	1	-0.0937	-1.0845	0.6669
Bradbury's bounded skew (<i>B</i>)	0.6190	0.2884	0.4660	0	1	-0.2014	-0.9895	0.7542
Keller's skew (<i>W</i>)	0.7045	0.2764	0.3924	0	1	-0.8378	-0.1607	0.7681
Kokko's iterative skew (<i>K</i>)	0.7805	0.2024	0.2594	0	1	-1.1516	1.7434	0.6885
Hovi's mean error skew (<i>M</i>)	0.7823	0.2055	0.2627	0	1	-1.3606	2.3183	0.7177
Pietra ratio (<i>P</i>)	0.5454	0.2100	0.3850	0	0.8889	-0.2576	-0.5899	0.5965
Pamilo's linear skew (<i>L</i>)	0.8464	0.2110	0.2492	0	1	-2.3585	5.7458	0.6236
Green's coefficient (<i>F</i>)	0.6074	0.3010	0.4956	-0.0714	1	-0.2735	-0.8511	0.5436
Gini coefficient (<i>G</i>)	0.6777	0.1952	0.2881	0	0.9282	-1.2947	1.9334	0.6126

Note: *g*₁, coefficient of skewness; *g*₂, coefficient of kurtosis; *r*, mean correlation of the measure with all other measures (Pearson's correlation coefficient).

males, as an estimate of the effective share of offspring, is supported by evidence from genetic parentage studies. In the DEL population, estimates of paternity from behavioral observations show good agreement with genetic estimates (Hoelzel et al. 1999; Wainstein 2000). For the SLI population, there is no published information on genetic paternity yet, but the results of a recently completed analysis using microsatellite markers demonstrated a very good agreement (A. Fabiani, unpublished results).

The measurement of inequality presents significant methodological problems because each one of the many measures proposed has drawbacks (for a summary of inequality measures see Table 1 and Kokko et al. 1999). To test deviations from randomness and to compare observed inequality with expected inequalities under various null hypotheses, we used the sample variance (*s*²). This is the simplest measure of inequality (Mackenzie et al. 1995); its statistical distribution is known (e.g., Zar 1984); and it has the obvious advantage of being directly related to evolutionary theory (Arnold and Wade 1984). If the propensities for acquisition of resources are equal, the observed distribution of resources follows a Poisson distribution, for which the variance equals the mean. This null hypothesis may be tested using the χ^2 distribution because $(n \times s^2)/\sigma^2$ follows the χ^2 distribution with *n* - 1 degrees of freedom (Zar 1984). Using the χ^2 distribution, it is possible to set confidence limits on the observed variance, to test the two extreme hypothesis of even distribution ($E(s^2) = 0$) and complete monopolization ($E(s^2) = n \times \text{mean}$), and to estimate the post-hoc power of tests. As an additional test of the randomness hypothesis we compared the observed distribution of ENFI with a Poisson distribution (with the mean equal to the mean of observed distribution) using the Kolmogorov-Smirnov test with exact estimation of probability. Although routinely used for comparing observed and theoretical distributions, the Kolmogorov-Smirnov test assumes that the pa-

rameters of the theoretical distribution (in our case the mean of the Poisson distribution) are known. In contrast, in most situations and in our study, the parameters are estimated from data, and the test becomes conservative (Conover 1980). The first test, based on the comparison of *s*², and the second one, based on the comparison of observed frequencies with expected Poisson frequencies, may produce different results (Zar 1984). Therefore, the use of both methods increases confidence in the significance of deviations from randomness.

Although effective in testing hypotheses within each social group, the variance becomes a problematic measure of inequality if groups of different sizes are compared, because it is algebraically dependent on the total size of resources (Mackenzie and Reynolds 1995). Hence, harems with different numbers of females are, in principle, nondirectly comparable using variance as a measure of inequality. All measures based on the distribution of the actual number of copulations or fertilizations depend more or less on the number of females or males. They are, therefore, "unbounded measures", with a variable expected value in the case of evenness or monopolization. To avoid this sensitivity to total resources and number of competitors, and to simplify the comparison between social units, various indices based on the proportion of resources have been proposed (Kokko et al. 1999). These indices are "bounded measures", formulated to vary between -1 or 0 (even distribution of resources) and +1 (complete monopolization of resources). All of them have drawbacks and they tend to be sensitive to different aspects of inequality and to different components of the distribution of resources (Downhower et al. 1987; Kokko et al. 1999). Hence, the only robust solution in comparing inequalities, when size of resources and number of competitors are variable, is to calculate a wide array of measures and verify the concordance of the results. We calculated for each harem of the dataset

the measures summarized in Kokko et al. (1999); for a list of indices, symbols, and classification as bounded or unbounded see Table 1; for formulas and theoretical expectations of the indices see Kokko et al. 1999. We excluded four indices: (1) the Theil index, because it is not defined when an individual acquires zero resources; (2) the cumulative skew index, because it is somehow arbitrary in the choice of the proportion of top males to be included in the calculation; (3) the two skewness statistics (moment and L -moment), because they are not a direct measure of inequality (and often perform poorly in this role; see Kokko et al. 1999). We added the standard deviation (s), which is the most common measure of relative variation, and the opportunity for selection (equal to the standardized variance, s^2/mean^2), for its relevance to phenotypic selection theory (Arnold and Wade 1984).

We evaluated the effects of two key factors of sociometry, the number of females that breed in the harem and the number of males associated with the harem, using linear regression with robust errors calculated using the Huber–White sandwich method. We checked residuals after regression fitting with standard procedures (scatterplots, Shapiro–Wilk test of normality of residuals, Cook–Weisberg test of homogeneity of variances of residuals). To validate results of the ordinary least squares (OLS) regression, we ran least absolute deviation (LAD) regressions (Birkes and Dodge 1993), estimating standard errors of parameters by the bootstrap (1000 samples) method. LAD regression is more resistant to the effect of outliers than OLS regression (Cade and Richards 1996). We plotted two-dimensional scatterplots with LOWESS lines (Trexler and Travis 1993) and three-dimensional plots with distance-weighted least-squares surfaces (McLain 1974) to check for systematic deviations in linearity of the relationships. Inequality measures and tests against the null hypothesis using s^2 were calculated using custom scripts developed in HyperCard (Apple Computers Inc., Cupertino, Calif.). Procedures for power analysis are available for very few nonparametric tests. Therefore, we calculated power for equivalent parametric tests, as they were the best approximation that we can offer. Nonparametric tests with Monte Carlo estimation of probability (100 000 samples in all cases) were run in StatXact 4.0 (Cytel Software Corp., Cambridge, Mass.). The remaining tests were run using STATA 5.0 (Stata Corp., College Station, Tex.).

Results

Randomness

Five SLI harems with just one male, the harem holder, were excluded from this analysis, and we tested randomness of the ENFI distribution on a reduced set of 69 harems. Deviation from the expected (Poisson) distribution when resource acquisition propensities are equal was not significant at $p = 0.05$ in four cases (in one case, $p < 0.10$). In the remaining 94.2% of harems, deviation from randomness was significant ($p = 0.001 \pm 0.006$), and in 88.4% very significant ($p < 0.0001$). The power of these tests was high, notwithstanding the rather small number of males per harem ($1 - \beta = 0.899 \pm 0.202$). We compared the observed ENFI distribution with the Poisson distribution using exact Kolmogorov–

Smirnov tests for 44 harems with five or more associated males, and we obtained a qualitative confirmation of the χ^2 tests on variance. Only 1 of 44 tests revealed a nonsignificant deviation from the Poisson distribution at $p = 0.05$, and 70.5% of tests were significant at $p = 0.0001$ or lower.

Evenness and monopolization

Deviations from a uniform distribution (expected variance = 0) was significant at $p = 0.001$ or lower in all harems except one, a small harem with two associated males that had the same observed ENFI. In contrast, deviations from perfect monopolization were not significant in all cases except the one described above ($p = 0.670 \pm 0.211$). The problem here is the very low power of these tests ($1 - \beta < 0.10$ in all cases), owing to the very large share of fertilizations acquired by the harem holder in most harems. In the majority of the harems, copulations were not completely monopolized by the harem holder, with 1–10 (3.243 ± 2.232) males having an estimated ENFI of at least one. Notwithstanding this, the harem holder did the vast majority of fertilizations, with a mean percentage of fertilizations of $80.4 \pm 18.1\%$. In 24.3% of harems, the harem holder did 100% of the fertilizations.

Measures of inequality

Statistics for the various measures of inequality are reported in Table 1. Inequality measures had different distributions (Fig. 1). Unbounded measures had a positive skewness (g_1 from 0.7899 to 1.7519), while bounded indices had a negative skewness (g_1 from -0.0937 to -2.5739). The whole set of measures was highly correlated (Bartlett's test of sphericity: $\chi^2 = 6109.6$, $df = 170$, $p < 0.0001$), but the value of each pairwise correlation was variable. All correlations were positive, with values ranging from 0.165 to 1 (0.606 ± 0.236 , $n = 153$ pairs of variables). Seventy percent of correlations were ≥ 0.50 and 27.6% were ≥ 0.80 . The uncorrected probability of the null hypothesis of zero correlation was ≤ 0.05 in 97.1% of pairs and ≤ 0.0001 in 74.3%. Probabilities corrected for multiple comparisons using a sequential method (Holm's or Hochberg's procedure gave equivalent results) demonstrated a correlation significantly greater than zero at $p = 0.05$ in 92.4% of pairs of measures of inequality. The measure with the greater mean correlation was Keller's skew index (W) (mean $r = 0.7681$) and the measure with the lower mean correlation was s^2 (mean $r = 0.4391$). Parametric measures of correlation are suspect when variables are skewed. Hence, we ran a nonparametric concordance analysis on the whole set of measures. Concordance among inequality measures was high and significant (Kendall's coefficient of concordance, with 10 000 randomizations: $W = 0.918$, $p = 0.0000$). Concordance was lower among the bounded indices ($W = 0.551$) than among unbounded ones ($W = 0.959$).

We ran a principal-component analysis (PCA) to verify if the set of inequality measures could be grouped in clusters and summarized by one or a few synthetic indices. The first component of the PCA explained 63.9% of the variance of the original measures, the second 16.8% (cumulative 80.7%), and the third 13.0% (cumulative 93.7%). All the variables had large positive loadings on component 1. All the unbounded indices had negative loadings on component 2 or component 3 or both, while all the bounded indices had pos-

Fig. 1. Box plots of the inequality measures (see Table 1 for index abbreviations).

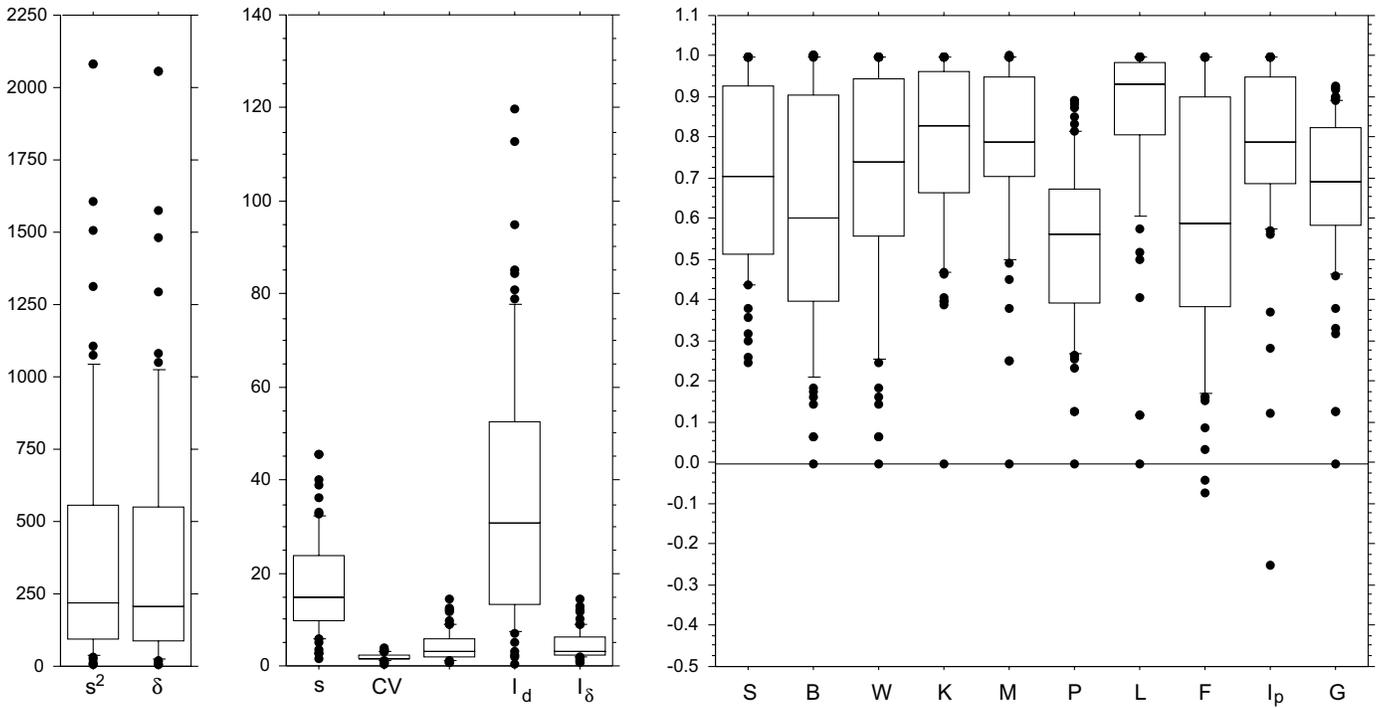
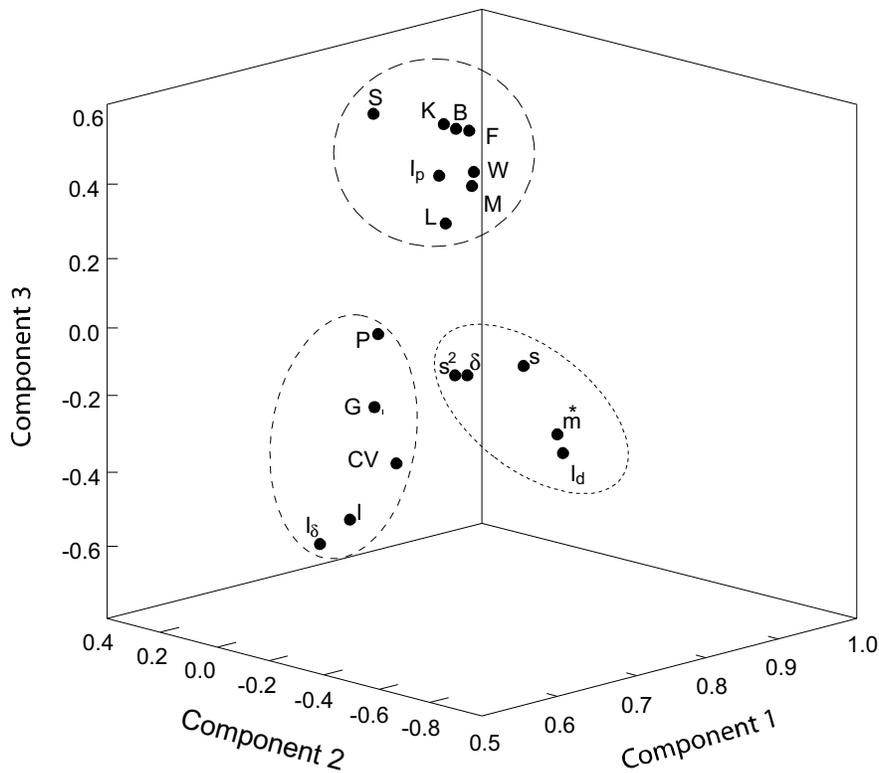


Fig. 2. Plots of loadings of inequality measures on the first three principal components. The loadings define the relative positions of the inequality measures in the three-dimensional space set up by the first three principal components (which explain almost all variance in the original measures). Therefore, proximity in the principal-components space means that the inequality measures are similar.



itive loadings on all three components. Therefore, cluster separation was clearer in the component 3 versus component 2 space (Fig. 2). Three clusters were identified. The first cluster comprised the s^2 and four unbounded measures (Poissonian

deviance (δ), s , Lloyd's mean crowding index (m^*), index of dispersion (I_d)). The second cluster comprised three unbounded indices (Morisita coefficient index (I_δ), opportunity for selection (I), coefficient of variation (CV)) related to standard-

Table 2. Descriptive statistics and results of Mann–Whitney tests for comparing inequality measures between the two study populations.

Index	DEL (mean \pm SD)	SLI (mean \pm SD)	<i>U</i>	<i>p</i>	99% LCI	99% UCI
s^2	276.4 \pm 273.5	481.9 \pm 551.3	477.0	0.518	0.514	0.523
<i>s</i>	14.91 \pm 7.524	18.43 \pm 12.06	477.0	0.518	0.514	0.523
CV	1.894 \pm 0.6936	1.923 \pm 0.8213	521.0	0.925	0.923	0.927
<i>I</i>	4.048 \pm 2.493	4.358 \pm 3.514	521.0	0.925	0.923	0.927
I_d	29.85 \pm 17.21	39.08 \pm 31.19	480.0	0.543	0.539	0.547
I_δ	4.4456 \pm 2.363	4.662 \pm 3.395	488.0	0.607	0.603	0.611
I_p	0.7226 \pm 0.3023	0.7790 \pm 0.2463	438.0	0.250	0.246	0.253
<i>S</i>	0.6194 \pm 0.2478	0.7390 \pm 0.1995	381.5	0.060	0.058	0.062
<i>B</i>	0.5487 \pm 0.3012	0.6542 \pm 0.2785	429.0	0.206	0.203	0.209
<i>W</i>	0.6425 \pm 0.2972	0.7355 \pm 0.2634	437.0	0.243	0.239	0.246
<i>K</i>	0.7067 \pm 0.2484	0.8175 \pm 0.1661	397.0	0.093	0.091	0.095
<i>M</i>	0.7420 \pm 0.2247	0.8025 \pm 0.1947	429.0	0.206	0.203	0.209
<i>P</i>	0.5263 \pm 0.1871	0.5550 \pm 0.2219	485.0	0.577	0.573	0.581
<i>L</i>	0.8403 \pm 0.2171	0.8495 \pm 0.2102	499.0	0.705	0.701	0.709
δ	267.9 \pm 270.0	471.7 \pm 545.2	478.0	0.522	0.518	0.526
<i>F</i>	0.5399 \pm 0.3077	0.6411 \pm 0.2952	426.0	0.191	0.188	0.194
\bar{m}^*	37.38 \pm 18.99	48.23 \pm 34.63	467.0	0.439	0.435	0.443
<i>G</i>	0.6819 \pm 0.1955	0.6756 \pm 0.1972	522.0	0.932	0.930	0.934

Note: DEL, Punta Delgada; SLI, Sea Lion Island; *p*, probability obtained by Monte Carlo resampling (100 000 samples); LCI and UCI, lower and upper confidence limits of the probability, respectively. See Table 1 for index abbreviations.

ized variance, and two bounded indices (Pietra ratio (*P*) and Gini coefficient (*G*)). The last cluster comprised all bounded indices.

Comparison of inequality among populations

The number of males that fertilized at least one female was significantly greater at DEL than at SLI (4.83 ± 2.81 vs. 2.53 ± 1.46 ; Mann–Whitney test with randomization: $U_{[23,51]} = 300.5$, $p = 0.001$), but the proportion of these males relative to the total number of associated males was only slightly greater, and the difference was not significant ($U_{[23,51]} = 562.5$, $p = 0.50$). The proportion of fertilizations by the harem holder was significantly greater at SLI ($83.8 \pm 16.1\%$ of the fertilizations by the harem holder versus $73.0 \pm 20.2\%$; Mann–Whitney test with randomization: $U_{[23,51]} = 407.5$, $p = 0.036$). All the 18 inequality measures had higher values at SLI than at DEL, but none of the differences was significant at $p = 0.05$ in a series of Mann–Whitney tests with randomization (Table 2). There are currently no established procedures to calculate the power of the Mann–Whitney test. Therefore, we calculated the power of equivalent parametric tests, finding low values in all cases ($1 - \beta$ ranged from 0.0565 to 0.5006, 72.2% of tests had $1 - \beta < 0.20$). The power of a Mann–Whitney test is about 95% of the power of the equivalent *t* test (Siegel and Castellan 1988). Inequality measures were correlated, but not multicollinear on the whole. Therefore, to test their joint difference among populations, we ran a MANOVA. Most measures of inequality had a non-normal distribution (Shapiro–Wilk test, $p < 0.05$, except for CV, Simpson’s index (*S*), and *P*). Therefore, to improve normality and homoscedasticity, we employed a maximum-likelihood Box–Cox transformation on all variables. After transformation, Shapiro–Wilk tests on most variables were not significant ($p > 0.05$ in all cases except Hovi’s mean error skew index (*M*) and Bradbury’s bounded skew index (*B*)). The univariate

F ratios confirmed the results of the nonparametric tests ($p > 0.05$ for all measures, except *S* with $p = 0.0472$; 83.3% of tests with $p > 0.20$). In contrast, the multivariate test revealed a significant difference between the two populations (Wilks’ $\lambda = 0.5228$, $F_{[18,48]} = 2.4342$, $p = 0.0073$).

The effect of harem sociometry

The two main factors of harem sociometry, harem size and number of associated males, were related. The linear regression of the number of males on harem size explained 47.5% of the variation in the former ($b = 0.0875$, $SE = 0.01068$, $t = 8.194$, $p < 0.0001$). However, the correlation between these two variables was not strong enough to produce multicollinearity problems in the following regression models (variance inflation factor = 1.93, tolerance = 0.5174).

The number of males with at least one fertilization increased with both harem size and number of males associated with the harem (linear regression: $R^2 = 0.3378$; $\beta_{\text{harem size}} = 0.3142$, $t = 2.373$, $p = 0.0203$; $\beta_{\text{no. of males}} = 0.3339$, $t = 2.5217$, $p = 0.0139$). To evaluate the effect of harem sociometry on the proportion of males that achieved at least one fertilization, we ran a generalized linear model with binomial distribution of errors and a logit link. We calculated robust SEs of parameters and asymptotic *z* test of null hypothesis (odds ratio = 1). At DEL, the proportion of males that fertilized at least one female slightly increased with an increase in harem size (odds ratio = 1.028, $SE = 0.0095$, $z = 2.926$, $p = 0.003$) and decreased with an increase in number of males (odds ratio = 0.784, $SE = 0.0630$, $z = -3.026$, $p = 0.002$). In contrast at SLI, only the number of males had a significant negative effect (odds ratio = 0.841, $SE = 0.0313$, $z = -4.652$, $p < 0.001$), while the odds ratio for harem size was not significantly different from 1 (odds ratio = 1.004, $SE = 0.0050$, $z = 0.829$, $p = 0.407$).

To evaluate the effect of harem size and number of males

Table 3. Parameters of multiple linear regression of inequality measures versus harem size and number of males.

Index	R^2	Harem size			Number of males				
		b	SE(b)	p	β	b	SE(b)	p	β
s^2	0.7107	0.1139	0.0099	0.000	1.0999	-0.4570	0.0749	0.000	-0.5441
δ	0.7016	0.1031	0.0090	0.000	1.0864	-0.4150	0.0694	0.000	-0.5422
s	0.7107	0.0570	0.0049	0.000	1.0999	-0.2285	0.0374	0.000	-0.5441
\hat{m}	0.6701	0.0728	0.0075	0.000	0.9653	-0.1532	0.0491	0.003	-0.2513
I_d	0.6170	0.0850	0.0106	0.000	0.8345	-0.0635	0.0700	0.368	-0.0769
I_δ	0.6320	0.0009	0.0018	0.632	0.0482	0.1109	0.0151	0.000	0.7619
I	0.5610	0.0015	0.0038	0.689	0.0434	0.2055	0.0304	0.000	0.7194
CV	0.5610	0.0008	0.0019	0.688	0.0435	0.1027	0.0152	0.000	0.7194
G	0.5938	0.0001	0.0003	0.957	-0.0057	0.0156	0.0019	0.000	0.7744
P	0.2443	-0.0007	0.0007	0.295	-0.1444	0.0239	0.0046	0.000	0.5782
L	0.0353	0.0001	0.0002	0.874	-0.0250	0.0022	0.0014	0.131	0.2035
M	0.0054	0.0001	0.0005	0.967	0.0066	0.0016	0.0031	0.599	0.0689
W	0.0178	-0.0003	0.0006	0.623	-0.0762	0.0056	0.0042	0.186	0.1711
I_p	0.0097	0.0002	0.0005	0.688	0.0619	-0.0032	0.0033	0.323	-0.1272
F	0.0156	0.0002	0.0011	0.843	0.0303	-0.0083	0.0075	0.270	-0.1427
B	0.0110	0.0003	0.0011	0.755	0.0482	-0.0075	0.0074	0.316	-0.1305
K	0.0420	0.0002	0.0005	0.713	0.0555	-0.0059	0.0031	0.064	-0.2375
S	0.0581	0.0002	0.0009	0.821	0.0345	-0.0125	0.0059	0.039	-0.2627

Note: R^2 , adjusted coefficient of determination; b , regression coefficient; SE, robust standard error of the coefficient; p , probability of the t test ($H_0: b = 0$); β , standardized regression coefficient.

on inequality we ran multiple regressions with each Box-Cox-transformed measure of inequality as the dependent variable (Table 3). To check the robustness of OLS regressions for the presence of outliers we ran LAD regressions. The latter gave similar results to the former, hence we present results only from OLS regressions. Sample variance and measures of the same cluster (δ , s , \hat{m} , I_d) had a strong positive relationship with harem size ($\beta > 0.83$). Variance and the first three measures of this cluster had a strongly negative relationship to the number of males ($\beta < -0.25$). For this cluster, 60–71% of the variance in the inequality measures was explained by the joint variation of harem size and number of males. The CV and the related measures (I_δ , I , G , P) had a strong positive relationship with number of males ($\beta > 0.58$), but they were not related to harem size. For this cluster 46–66% of the variance in inequality was explained by the variation in the number of males. All measures of the main cluster of the bounded indices (Pamilo's linear skew index (L), M , W , standardized Morisita coefficient (I_p), F , B , Kokko's iterative skew index (K), S) were not related to either harem size or number of males, with less than 6% of the variation in inequality explained by the regression. We also ran a regression using the first principal component as the dependent variable and found no effect of harem size or number of associated males ($R^2 = 0.0051$).

To evaluate the effect of sociometry on the capability of the harem holder to monopolize females, we ran a generalized linear model (with binomial distribution off errors and logit link) on the proportion of fertilizations achieved by the holder of each harem. At DEL, monopolization decreased with harem size (odds ratio = 0.989, SE = 0.0024, $z = -4.667$, $p < 0.001$), but number of males had no statistically significant effect (odds ratio = 0.979, SE = 0.0.205, $z = -0.995$, $p = 0.320$). At SLI, the increase in harem size, contrary to ex-

pectations, increased the likelihood of monopolization (odds ratio = 1.010, SE = 0.0020, $z = 4.978$, $p < 0.0001$), while the increase in number of males decreased it (odds ratio = 0.9185, SE = 0.119, $z = -6.557$, $p < 0.0001$).

Inequality within and among harems

We compared the expected variance with even, random, and monopolized fertilizations at population level using the seven yearly datasets, and we were able to confirm the results obtained at the harem level. The observed variance of ENFI was significantly different from the expected distribution, with equal propensities for resource acquisition, i.e., variance equal to mean ($p < 0.0001$ in all years). It was also significantly different from a uniform distribution of resources, i.e., variance equal to 0 ($p < 0.0001$ in all years). Comparison of yearly distribution of ENFI with the Poisson distribution by exact Kolmogorov-Smirnov tests revealed significant deviations (exact $p = 0.0000$ in all cases).

We then calculated, from yearly ENFI distributions, the within-harem and among-harem variance components and the intraclass correlation coefficients, i.e., the proportion of among-harem variance (Lessels and Boag 1987). In 6 out of 7 years, the among-harem variance was much lower than the within-harem variance, producing a negative value of the intraclass correlation (ranging from -0.052 to -0.182). In 1997, the intraclass correlation was slightly greater than 0. In all, most of the variance observed at the population level was due to inequality of distribution of resources inside each harem.

Comparison of inequality with lek species

We compared the inequality measures (s^2 , I_δ , I_p , B , W , K , L , P) reported in Table 2 of Kokko et al. (1999) (71 leks, including 2 mammal species with 7 leks and 15 bird species

with 64 leks) with measures calculated for our sample of harems. In the full dataset, all measures of inequality were greater in southern elephant seals, and the difference was significant for all of them (Mann–Whitney test with randomization, $p < 0.02$ in all cases), except I_8 ($p = 0.50$). The lek datasets had a greater mean number of males than our dataset (15.9 vs. 7.0). Therefore, we repeated the analysis using only leks with a number of males in the range observed for elephant seal harems ($n = 20$) and were able to confirm the results from the full dataset.

Discussion

Formal analysis of breeding inequality in vertebrates has been concentrated on the study of leks. The aim was to quantify the effect of lek size (i.e., the number of males on the lek) on the distribution of matings and to test hypotheses about the evolution of clumping of males (Widemo and Owens 1995a, 1999). A formal approach to the analysis of inequality can be fruitful in all research areas involving the study of phenotypic and socioeconomic effects on reproductive success (Kokko et al. 1999). This paper is a first attempt to study inequality in a non-lekking species, using a sample of social units large enough to permit an intraspecific analysis of inequality measures. This considerably improves the effectiveness of the analysis because the processes that lead to monopolization and inequality are likely to present significant across-species variation (Widemo and Owens 1995b). Moreover, the random component of inequality, which generates the baseline variance in resource distributions, is likely to be different in different species (Sutherland 1987).

Our study demonstrated that the distribution of fertilizations in southern elephant seals is not compatible with a random process generated by equal propensities and equal capability of males to acquire access to females. Notwithstanding the small number of males associated with each harem, which may lead to low power of tests, the results of the analysis pointed very clearly in this direction. Moreover, the observed distribution of ENFI was not only different from a uniform distribution of resources, but also tended towards a full monopolization by the harem holder. This monopolization at the harem level was mirrored by inequality at the population level, with most of the observed population variance resulting from the variation within each harem. Compared with the inequality in other species, the level of inequality shown by southern elephant seal harems is very high as the comparison with lek species demonstrated. Lek mating systems are usually considered the most “extreme” mating systems in terms of the variance of reproductive success and the opportunity for the action of sexual selection (Clutton-Brock 1989). In the literature on elephant seals, it is customary to consider this very high level of monopolization as “expected” and to express surprise when genetic studies reveal a lower capability of holders to monopolize females (Hoelzel et al. 1999). We believe that, on the contrary, such a level of monopolization should be considered far from expected because of the size of elephant seal harems, which are at least one order of magnitude larger than harems of other polygynous mammals (Clutton-Brock 1989). The structured social behavior of elephant seals (McCann 1981), the large size of female groups, the concentration of the breeding sea-

son in a short time-span (Galimberti and Boitani 1999), and the persistence of non-harem holders in trying to interact with females produce a complex social network. Harem holders show an amazing capability to manage a such a complex situation.

Harem holders at SLI seem to be able to monopolize matings better, acquiring a larger share of copulations carried out in each harem. This result was recently confirmed by a comparison of genetic paternity monopolization (for DEL see Hoelzel et al. 1999; for SLI see A. Fabiani, unpublished data). Notwithstanding this, none of the inequality measures revealed a significant difference between the populations in univariate tests. This result, although due in part to the low power of these tests, suggests that none of the measures is completely effective when the degree of monopolization is high. Inequality measures are formulated to capture the variance in the full distribution of resources, and hence, they may lack sensitivity when the inequality is due mostly to a high degree of monopolization by a single male, with small and almost equal shares for with the rest of the males. This was confirmed by the results of the multivariate test. The joint variation of all inequality measures revealed a difference between populations that the single univariate tests were not able to detect.

The effect of the size of resources to be shared and the number of competitors on inequality is a hot topic in the study of mating systems and sexual selection. We would expect inequality to decrease when the total quantity of resources and the number of competitors increase. This happens in lek mating systems (Widemo and Owens 1995a), where the presence of a negative relationship between inequality and lek size, which was initially criticized on methodological grounds (Mackenzie and Reynolds 1995), has been recently confirmed (Kokko et al. 1999). In southern elephant seals, harem size interacts with individual phenotype to determine reproductive behavior of males (Modig 1996). We expected to find a decrease in inequality with an increase in the number of females and the number of competitors. In our study populations, inequality measures based on actual number of females fertilized showed a strong relationship with both harem size and number of associated males. In contrast, bounded indices, which are based on proportion of resources instead of actual shares, showed no relationship with either factor. This is strong evidence that the relationship with sociology shown by the former set of measures is mostly an artifact of their mathematical formulation. Bounded indices demonstrated that in this species inequality is not related to the size of resources or the number of competitors. Contrary to expectations, at SLI monopolization by harem holders increased with harem size. This result is mostly due to the large difference in resource-holding potential between the harem holders of the larger harems and the rest of the males. Variation in resource holding potential (structural and behavioral) is greater at SLI than at DEL (F. Galimberti, unpublished data). In the SLI population, some males are able to acquire uncontested control of the largest harems, with more than 100 females. These harem holders are capable of effectively managing the complexity of a social system that comprises hundreds of individuals, maintaining access to females, even when sociology presents the worst conditions for monopolization.

The two populations considered in this study are at the bottom end of the variation in harem size and density recorded for elephant seals. Harems size is larger at South Georgia (mean = 74.2, 6–232; McCann 1980), Macquarie Island (mean = 277, up to 1000; Carrick et al. 1962), and the Kerguelen Islands (mean = 102, 5–1350; Van Aarde 1980). Hence, the general validity of our conclusions for populations with larger harems and greater crowding is questionable. The distribution of ENFI in a single large harem at South Georgia (251 females (McCann 1981); data are proportions of copulations from Fig. 4) shows less inequality than the distribution at the largest harem observed at DEL (132 females) and SLI (134 females; likelihood-ratio test on ENFI with randomization, $G = 147.1$, $p = 0.0000$). Unfortunately, the lack of precise quantification of the distribution of matings and fertilizations in the southern elephant seal literature prevents further interpopulation comparisons. The northern elephant seal, which breeds at greater density and forms larger harems with more males, shows a decrease in the percentage of copulations monopolized by the harem holder with the increase harem size (Le Boeuf 1974; Le Boeuf and Reiter 1988). Genetic studies confirmed that the share of paternity monopolized by harem holders is lower than in the southern species (Hoelzel et al. 1999).

From a methodological point of view, our analysis confirms the previous concern about the general applicability of inequality indices (Kokko et al. 1999). Although all measures were correlated and showed no negative correlations, their distributions and correlations were variable. Simple measures, like s^2 , are effective and powerful when comparing observed inequality with randomness and uniformity within social units. In contrast, they may strongly bias conclusions on the relationship between inequality and descriptors of sociometry. Bounded indices are much better in this role, but they have drawbacks. Their expectation in the case of randomness is not clear, and the test of their significance requires the adoption of resampling techniques. Overall, the operational suggestion to use many different measures of inequality (Kokko et al. 1999) should to be endorsed. The comparison of observed distribution of ENFI with the expected distribution with full monopolization (propensity to acquire resources equal to 1 for one male and 0 for all the others) illustrates another problem of inequality analysis: the lack of power of tests (Kokko et al. 1998, 1999). Although the null hypothesis of full monopolization was not rejected in the vast majority of elephant seal harems, the power of these tests was low. Owing to the high variance shown in most elephant seal harems, unreasonably large samples will be required to obtain enough power to statistically reject the null hypothesis. Therefore, in studies of natural populations with a very unequal distribution of resources, it should be quite difficult to discriminate between an observed tendency towards high monopolization and true full monopolization.

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