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Socio-spatial levels in linearity analysis of dominance hierarchies: a case study on elephant seals

Abstract The analysis of linearity is a key aspect of the study of dominance hierarchies. To study the effect of the choice of socio-spatial level of analysis, we calculated linearity in a large set of southern elephant seal (*Mirounga leonina*) hierarchies from two populations (Valdés Peninsula and Falkland Islands). The socio-spatial level of analysis affects the observational effort, the completeness of matrices, and the frequency of unknown relationships. These factors, in turn, have a notable effect on linearity. We conclude that dominance should be studied at the local level, where the absence of structural zeros and the low incidence of observational zeros produce complete matrices, well rooted in the true spatial and social structure of the population. Depending on the specific social system, the extrapolation of dominance from the local level to higher levels may result in sparse matrices, and in biased estimates of linearity. The variation of the socio-spatial level of analysis may in part explain the contrasting results obtained in different studies of linearity of dominance hierarchies.

Key words Dominance hierarchies · Linearity · Socio-spatial structure · Observational effort · Southern elephant seals · *Mirounga leonina* · Falkland Islands

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Introduction

Dominance hierarchies are an important target of ethological research (see, for example, review in Drews 1993), and the analysis of hierarchy structure has always been a central issue, beginning with the work of Landau (1951a, b, 1953). The analysis of dominance hierarchies has been the subject of much theoretical effort, largely directed towards the estimation and test of linearity (Appleby 1983). A linear hierarchy is a hierarchy in which all dyadic relationships, between all individuals, are transitive; that is, if a first individual dominates a second one, he also dominates all the individuals dominated by the second. A hierarchy with non-transitive relationships is not fully linear and presents a variable degree of circularity. Linearity has a significant theoretical role, since it implies specific models of hierarchy formation, and maintenance. For example, the formation and maintenance of linear hierarchies in groups larger than seven to eight individuals is mostly unlikely in the absence of assessment of resource-holding potential (Mesterton-Gibbons and Dugatkin 1995). A problem of linearity estimation is the presence of unknown dominance relationships, which are frequent in studies of large social groups in natural populations. The search for new methodological approaches to analyse the resulting sparse matrices has recently produced a spurt of theoretical work (De Vries 1995, 1998; Tufto et al. 1998). These new methods are often complex, and their assumptions are sometimes not very realistic (Jameson et al. 1999). Therefore, most observational and experimental studies are still based on older models, indices, and tests, due to their simplicity.

During an ongoing study of male hierarchies in elephant seals, we were confronted with some unexplored methodological issues that may have a significant impact on the study of hierarchy structure. In this article, we present results of the analysis of a large set of dominance hierarchies of southern elephant seals (*Mirounga leonina*), collected during six breeding seasons in two local populations, Punta Delgada (Valdés Peninsula) and Sea Lion Island (Falkland Islands). We examine the effect of choice of socio-

spatial level on social interactions coverage, variability in observational effort, and differences in interaction rate. We evaluate the effects of these factors on the estimation of linearity, and on its comparison between social groups and populations. We concentrated on linearity, but most of our considerations have a general relevance for the study of dominance, because they concern basic aspects of the data collection and analysis protocol.

Materials and methods

We carried out observations of agonistic interactions between southern elephant seal males during two breeding seasons (August–October 1993 and 1994) at Punta Delgada (Valdés Peninsula, Argentina; hereafter DEL), and during four breeding seasons (September–November 1995–1998) at Sea Lion Island (Falkland Islands; hereafter SLI). At DEL, the number of breeding males in the local population was 76 in 1993 and 92 in 1994. At SLI, the number of breeding males ranged from 55 to 62. In all, we monitored 168 males/seasons at DEL and 226 males/seasons at SLI. Some males were represented more than once in the data set, because they were breeding males in more than 1 year. Due to the large variation of resource-holding potential of each male in different years (Clinton 1994), and to the equally large variation in the social habitat, each individual/year was considered as an independent data point in the analysis. Additional information about the study populations may be found elsewhere (DEL: Campagna et al. 1993; SLI: Galimberti and Boitani 1999).

We marked all breeding males by putting nylon cattle tags (Jumbo Rototags, Dalton Supplies Ltd) in the inter-digital membrane of the rear flippers, and by writing names or codes on back and flanks using commercial black hair dye. Both males were recognised in more than 99% of social interactions. To collect data in different breeding situations, we observed all harems of our study areas (4–5 km of coast at DEL; 4.4 km of coast at SLI), trying to spend the same observational effort on each harem (9–12 harems per breeding season).

We considered four levels of socio-spatial structure, the whole local population plus three intra-population levels. The lower level was the *harem* (H), defined as a group of two or more females with a male in attendance. A harem is both a social and a spatial unit, because in elephant seals harems tend to occupy the same position during the whole breeding season. Then, we considered two more levels: the *breeding area* (BA), 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 seal reproduction; and the *breeding zone* (BZ), which is, on the contrary, separated from other zones by stretches of habitat not suitable for elephant seals and not used for breeding. Each area may comprise one or more harems, and each zone comprises two or more areas.

We observed dyadic interactions between males for a total of 2,886 2-h periods, evenly distributed during the day-light hours (456 at DEL, 2,430 at SLI). In all, we recorded a total of 24,252 male–male interactions (8,334 at DEL, 15,918 at SLI). Ad libitum recordings of interactions, collected outside standard observation periods, were not used in hierarchy estimation to avoid sampling bias. From all agonistic interaction records (including vocal threats, chases, fights), we built up two kinds of matrices: symmetric interaction matrices, and asymmetric dominance matrices, with wins above the diagonal and losses below; both matrices obviously have undefined diagonals. Dominance matrices were rearranged to minimise entries below the diagonals using a two-stages algorithm (similar to the algorithm implemented in MatMan software, De Vries et al. 1993). Interaction matrices were then rearranged using the males' order of the corresponding dominance matrix. For each dominance hierarchy, we calculated structure statistics after van Hooff and Wensing (1987), including mean number of interactions per male, percentage of unknown relationships, number of non-transitive relationships, and linearity.

Linearity was calculated with the Landau index (h) for complete dominance matrices, in which all dominance relationships were known, and with De Vries' (1995) corrected index (h') for matrices with unknown relationships, which were due to observational zeros only. A dominance matrix may contain two different kinds of zeros: (1) *observational zeros*, in which the two individuals of the dyad are never observed to interact due to biased sampling, inadequate observational effort, or stochastic factors; and (2) *structural zeros*, in which the two individuals cannot interact because they have no chance to meet due to low mobility, belonging to different and isolated local populations, or being associated with different and non-overlapping social groups. Structural zeros may produce a bias in linearity estimation and tests, and there is currently no fully accepted measure of linearity for matrices with structural zeros (De Vries 1995). Our data set comprises only local hierarchies of a social system where males move among social units and, therefore, does not include any structural zeros. We tested significance of linearity using a randomisation test based on 10,000 permutations of the dominance matrix. Since the probability of having a linear dominance hierarchy by pure effect of chance is higher than 0.05 for groups comprising up to five individuals (Appleby 1983), we included in the analysis only hierarchies with six or more individuals.

Due to the unknown distributional properties of linearity, we analysed data by non-parametric tests, with exact calculation of probabilities when possible, and Monte Carlo simulation (number of re-samplings written as P subscripts) when exact calculation was not feasible. Recently, Kasuya (2001) showed that the Mann–Whitney test type I error rates are inflated when variances among the samples are not equal and suggested checking heteroscedasticity using the Siegel–Tukey test. Therefore, before running a Mann–Whitney test on small samples, we checked homogeneity of variances. We used the Klotz test, instead of the Siegel–Tukey, because it is more powerful (Metha and Pathel 1998). Before calculating correlations, we examined scatterplots

and fitted LOWESS smoothers to data (Trexler and Travis 1993) to check for signs of non-linearity. Manipulation of dominance matrices and calculation of hierarchy structure measures, including linearity, were carried out using custom scripts written in HyperTalk (Apple Computer Inc.). Exploratory data analysis and calculation of descriptive statistics were run in StatView 5.0 (Abacus Concepts Inc.) and non-parametric tests (exact and Monte Carlo) were run in StatXact 4.0 (Cytel Software Corporation).

Results

Effect of the choice of socio-spatial level

We estimated linearity at the four socio-spatial levels: whole local population, breeding zone, breeding area, and harem. There was a gradual increase in magnitude of linearity with the increase of socio-spatial resolution, from whole populations ($h' = 0.151 \pm 0.075$, $n = 6$ seasonal hierarchies with 52–92 males each), to zones ($h' = 0.300 \pm 0.105$, $n = 12$ hierarchies with 19–49 males), to areas ($h' = 0.504 \pm 0.167$, $n = 24$ hierarchies with 6–24 males), to harems ($h' = 0.552 \pm 0.179$, $n = 18$ hierarchies with 6–18 males). Significance of linearity, tested with randomisation, increased with the increase of socio-spatial resolution. In whole populations all null hypotheses were rejected at the 0.05 level ($P = 0.0001$ to 0.0103); in breeding zones they were again all rejected at the 0.05 level ($P = 0.0001$ to 0.0050); in breeding areas null hypotheses were rejected at the 0.05 level in 58.3% of 24 tests ($P = 0.0001$ to 0.5213); in harems they were rejected at the 0.05 level in 61.1% of 18 tests ($P = 0.0001$ to 0.5873). It is important to emphasise that the hierarchies are independent among each socio-spatial level, but the four sets of tests are not independent of each other because the sample of males is the same in all sets. Hence, P values should be considered with caution.

Linearity was higher at SLI than at DEL (0.199 vs 0.056). By taking into account the socio-spatial structure, we found again a higher degree of linearity at SLI, but the difference between the populations varied at different levels. It was large and significant at zone ($h' = 0.355 \pm 0.072$, $n = 8$ hierarchies vs 0.188 ± 0.058, $n = 4$; exact Klotz test: $T = 3.786$, $P = 0.39$; exact Mann–Whitney test: $U' = 31.5$, $P = 0.0061$) and area level ($h' = 0.574 \pm 0.386$, $n = 15$ vs 0.386 ± 0.150, $n = 9$; exact Klotz test: $T = 9.762$, $P = 0.22$; exact Mann–Whitney test: $U' = 114$, $P = 0.0044$) but was small and non-significant at harem level ($h' = 0.596 \pm 0.118$, $n = 8$ vs 0.516 ± 0.215, $n = 10$; exact Klotz test: $T = 10.11$, $P = 0.13$; exact Mann–Whitney test: $U' = 57$, $P = 0.1395$; power of equivalent t-test: $d = 0.47$, 1–beta = 0.24).

Effect of the social interactions coverage

The mean percentage of unknown relationships in dominance hierarchies was higher at DEL than at SLI, at all socio-spatial levels, although at harem level the difference was not significant (BZs: 73.0% vs 48.9%; exact Klotz test: $T = 3.869$, $P = 0.35$; exact Mann–Whitney test: $U' = 32$, $P = 0.0040$; BAs: 64.0% vs 38.4%; exact Klotz test: $T = 8.169$, $P = 0.62$; Exact Mann–Whitney test: $U' = 115$, $P = 0.0033$; Hs: 55.9% vs 31.8%; exact Klotz test: $T = 9.757$, $P = 0.20$; exact Mann–Whiteney test: $U' = 62$, $P = 0.0514$). We estimated linearity using the improved index h' of De Vries (1995), which should correct the effect of unknown relationships. Hence, we expected linearity to be quite insensitive to variation in coverage of social relationships and completeness of dominance matrices. On the contrary, we found that unknown relationships had a significant effect on linearity at all socio-spatial levels: h' was negatively correlated to percentage of unknown relationships at zone level (Spearman's correlation coefficient: $r_s = -0.879$, $P_{exact} = 0.0003$), area level ($r_s = -0.863$, $P_{20,000} = 0.0000$), and harem level ($r_s = -0.917$, $P_{20,000} = 0.0000$). We found negative correlations also after splitting data between populations.

To understand better how unknown relationships affected the estimation of linearity, we started with zone-level hierarchies and we excluded males with unknown relationships, obtaining ten complete dominance matrices (four with 8–9 males each at DEL, six with 6–12 males at SLI). In this reduced set, linearity was almost perfect both at DEL (h ranging from 0.967 to 1, two hierarchies with $h = 1$) and SLI (h ranging from 0.964 to 1, four hierarchies with $h = 1$). In each of the four hierarchies with reversals, there was just one reversal, with strength (i.e. absolute difference between ranks of the two individuals that are involved in the reversal; De Vries et al. 1993) equal to 2–3. All randomisation tests on complete dominance matrices were significant at the 0.001 level.

Determinants of coverage: observational effort and interaction rate

Variation in the percentage of unknown relationships may be due to different observational effort, different local interaction rate, or different propensities to interact of males of different hierarchies. Although we observed all harems of our study populations, observational effort was not completely balanced, mostly because different harems have different durations (DEL: 18–75 days, $n = 33$ harems; SLI: 19–72 days, $n = 47$). The duration of harems influences the presence of males in different areas and zones, and, hence, the bias in observational effort propagates at higher socio-spatial level. We analysed the effect of observational effort at area level only, to maximise the sample of dominance hierarchies. The number of observation periods spent observing each specific breeding area was not related to h' (Spearman's correlation coefficient: $r_s = -0.212$, $n = 20$, $P_{20,000} = 0.36$), nor to the percentage of unknown relationships ($r_s = -0.091$, $P_{20,000} = 0.69$).

Interaction rate per observation period was notably higher at DEL, both as absolute rate (median = 12 vs 3 interactions per period; Mann–Whitney test: $U'_{456, 2,430} = 821,375.5$, $P < 0.0001$) and per male rate (median = 1.095 vs 0.750 interactions per male per period; Mann–Whitney test:

$U'_{456, 2,430} = 656,619.5$, $P < 0.0001$). Interaction rate was different not only between populations, but between different zones, areas, and harems of the same population, and breeding season (Kruskall–Wallis test: $P < 0.05$ in all cases, and $P < 0.0001$ in all cases for areas and harems). We expected interaction rate to have a positive correlation with linearity, because an increase in interaction rate should reduce the likelihood of unknown relationships. On the contrary, we found small, negative, non-significant correlations between interaction rate and both h' (Spearman's correlation co-efficient: $r_s = -0.094$, $P_{20,000} = 0.68$) and percentage of unknown relationships ($r_s = -0.256$, $P_{20,000} = 0.25$). Analogous results were obtained for the correlations interaction rate per male and per period of observation (h': $r_s = -0.025$, $P_{20,000} = 0.91$; percent unknown relationships: $r_s = -0.240$, $P_{20,000} = 0.30$).

Discussion

The analysis of dominance hierarchies is a hot topic in animal behaviour studies. Older studies on small social groups in different species demonstrated the presence of strong, well-resolved, linear hierarchies, whereas more recent studies, involving larger groups of individuals, often produced ambiguous results (Drews 1993). The most striking differences between these two set of studies is the coverage of social relationships, that is, the completeness of the dominance matrix. Whereas it is easy to obtain full dominance matrices in small groups of animals under controlled conditions, matrices from agonistic interactions observed in the wild are often sparse, due not only to observational zeros, as in our elephant seals case, but also to structural zeros, which present specific, and yet unresolved, methodological problems (De Vries 1995). The prevalence of sparse matrices in studies of natural populations was the driving force of a recent spurt of theoretical work on calculation of dominance rank and indices (Jameson et al. 1999). These attempts to improve methods of dominance hierarchy analysis are mostly welcome but have resulted in the overlooking of more basic methodological issues, such as the choice of the socio-spatial level at which to carry out the analysis, the set of individuals to consider, the evaluation of the effect of unknown relationships, and the determination of factors that produce sparse matrices in the first place.

The choice of individuals to be included in the hierarchy

The determination of dominance hierarchies requires a first, inescapable step, that is, the choice of the individuals to be included. This step is usually easy to accomplish in controlled situations, when a single social unit is observed, and movements of individuals are severely limited. On the contrary, in natural populations, dispersion and roaming of individuals severely complicate the choice. Even when the definition of group limits is based on quantitative methods (e.g., Clutton-Brock et al. 1982), the distinction between groups is not always clear cut, and the group membership of each specific individual is questionable. In southern elephant seals, harem-holding males are stable, but non-holders are not, and they may roam freely between different harems, looking for better mating opportunities (Baldi et al. 1996; Galimberti et al. 2000). Movements of individuals may also differ between populations. DEL males were less stationary than SLI males, because at DEL the population is less localised, and harems are distributed over a much longer coastline (Campagna et al. 1993). The result is the presence of a large number of roaming males, and this obviously affects the stability and linearity of dominance structure. This is confirmed by the difference in linearity of hierarchies between the two populations, which is evident at high socio-spatial resolution (zone), but almost disappears when only stable males are included.

The choice of socio-spatial level

Another methodological issue, related to the previous one, is the choice of the optimal socio-spatial level at which to carry out the analysis. To analyse dominance only at the population level means to consider natural populations as homogeneous, both spatially and socially. This homogeneity is quite unlikely (Heisler and Damuth 1987). In southern elephant seals, local populations present a clear hierarchical structure of socio-spatial levels, which affects both individual behavioural tactics and breeding success (Galimberti et al. 2002). The structure of the population affects the likelihood of interaction between males that occupy different socio-spatial units, and the strength of this constraint depends on the socio-spatial level. In elephant seals, the majority of males tend to be linked to a specific breeding zone, and the change of zone is not frequent because breeding zones are separated by habitat not suitable for breeding and without female groups. Although this effect is not so strong to produce structural zeros in dominance matrices, it obviously affects interaction rates. This is particularly evident at SLI, where the two main breeding zones are separated by only about 500 m of straight distance on land, but movements of males between breeding zones are scarce (Galimberti and Boitani 1999). Although some peripheral males roam around widely and frequently in search of mating opportunities, harem holders and other peripheral males are stable during the core of the breeding season. This effect may be even more pronounced in social systems where the structuring of the population is more pronounced, the distance between social units is bigger, and the capability and propensity of individuals to move is lower than in elephant seals.

The choice of the right socio-spatial resolution for analysis is not easy. When there is no a priori biological reason to choose a specific level, hypothesis testing should be repeated at all levels. In southern elephant seals, linearity was higher at the harem level, but, at the same time, significance of linearity was lower, because the increase in mag-

nitude of linearity was smaller than the decrease in size of dominance matrices to be tested, which produced a reduction of statistical power.

The effect of unknown relationships

In southern elephant seals the main correlate of linearity was the percentage of unknown relationships, and the effect of this factor was very significant even when an improved index, which takes into account unknown relationships (De Vries 1995), was used. On the other side, the analysis of complete matrices, without observational zeros, demonstrated that dominance is linear and transitive, with no circular relationships. Moreover, the difference in linearity between populations, although present in all analyses, was reduced and non-significant when only complete matrices were considered. The results of the analysis on this reduced set of hierarchies are in agreement with the information available on the agonistic behaviour in southern elephant seals (McCann 1981; Fabiani 1996), which should, in principle, produce an almost perfect linearity.

In conclusion, from a theoretical point of view our results confirm the idea that dominance is the result of a social relationship between two individuals, is a property of the dyad, not of the single individuals (Francis 1988; Drews 1993), and may be defined and understood only in reference to a local social habitat (Barrette 1993). Hence, dominance should be clearly distinguished from individual competitive success and should not be extrapolated to large sets of individuals that are never observed to interact, due to socio-ecological constraints or inadequate observational effort. The methods that have been proposed to extract "dominance" scores or indices using sparse matrices from large assemblages of males are in fact extracting generic competition success indices more than dominance ranks. These indices will have a variable degree of correlation with the local dominance hierarchies, depending on the specific social system and the effort put into behavioural observations. From an operational point of view, any functional analysis of dominance correlates carried out at the population level should be backed up by an analysis carried out at the local level, taking into account the socio-spatial structure of the population, and using as much as possible complete dominance matrices as data source. Results from the various independent local dominance hierarchies may then be easily combined, using standard meta-analytic techniques (Arnqvist and Wooster 1995).

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