ELSEVIER

Measuring social structure: A comparison of eight dominance indices

Karen L. Bayly [a], Christopher S. Evans [b,*], Alan Taylor [b]

[a] *Animal Behaviour Laboratory, Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia*
[b] *Animal Behaviour Laboratory, Department of Psychology, Macquarie University, Sydney, NSW 2109, Australia*

Abstract

Measurement of social status is an important component of many behavioural studies. A variety of techniques have been developed and adopted, but while there have been some analyses of index properties using simulated data, the rationale for selecting a method remains poorly documented. As a first step in exploring the implications of index choice, we compared the characteristics of eight popular indices by applying each to the same data set from interactions between male fowl *Gallus gallus*, the system in which social hierarchies were first described. Data from eight social groups, observed over four successive breeding seasons, were analysed to determine whether different indices produced consistent dominance scores. These scores were then used in tests of the relation between social status and crowing to explore whether index choice affected the results obtained. We also examined the pattern of dominance index use over the last decade to infer whether this has likely been influenced by tradition, or by taxa of study animal. Overall agreement among methods was good when groups of birds had perfectly linear hierarchies, but results diverged when social structure was more complex, with either intransitive triads or reversals. While all regression analyses revealed a positive relationship between dominance and vocal behaviour, there were substantial differences in the amount of variance accounted for, even though the original data were identical in every case. Index selection can hence perturb estimates of the importance of dominance, relative to other factors. We also found that several methods have been adopted only by particular research teams, while the use of others has been taxonomically constrained, patterns implying that indices have not always been chosen solely upon their merits. Taken together, our results read as a cautionary tale. We suggest that selection of a dominance index requires careful consideration both of algorithm properties and of the factors affecting social status in the system of interest.

1. Introduction

Since the landmark paper on peck order by Schjelderup-Ebbe (1935), dominance has been the subject of much theoretical debate, both as a concept (reviewed in Drews, 1993) and as a measurable individual attribute (e.g., Bekoff, 1977; Appleby, 1983; Boyd and Silk, 1983; Zumpe and Michael, 1986; de Vries, 1998; Tufto et al., 1998; Jameson et al., 1999; de Vries and Appleby, 2000). A variety of methods for analysing social structure have been proposed and compared (e.g., Appleby, 1983; Boyd and Silk, 1983; de Vries, 1998; de Vries and Appleby, 2000). It is now well understood that failure to meet underlying assumptions may limit the accuracy of a dominance estimate, particularly under conditions of non-linearity (e.g., de Vries, 1998; Jameson et al., 1999; de Vries and Appleby, 2000).

Despite the sophistication of theoretical models, it remains difficult to identify the best approach for measuring dominance in a group of social animals in which some type of hierarchy may or may not exist. Mathematically rigorous methods can prove cumbersome to apply, or inappropriate for straightforward tasks such as assessment of dominance in small groups, or over short time periods (e.g., Zumpe and Michael, 1986).

There may be considerable variation in social structure among groups that contain dominance hierarchies. These can be simple or complex, linear, near-linear or circular, and may contain reversals or intransitivities (Martin and Bateson, 1993). Hierarchies formed during group assembly tend to be linear or near-linear, while those formed as a consequence of dyadic interaction in the absence of other competitors tend to be non-linear and complex (Chase et al., 2002). In highly social animals, dominance may initially be determined by the outcome of a contest, but then subsequently maintained or modified through daily interactions such as displacements from feeding or resting areas, agonistic displays, or submissive behaviour (Crook

* Corresponding author. Tel.: +61 2 9850 9230; fax: +61 2 9850 9231.
E-mail address: chris@galliform.psy.mq.edu.au (C.S. Evans).

and Butterfield, 1970; Kalinoski, 1975; Zumpe and Michael, 1986).

Differences in the way in which hierarchies are formed can affect estimates of social status. For example, Masure and Allee (1934) found that dominance relationships among pigeons developed after many agonistic interactions, while in fowl they were dependent upon the outcome of initial combat. In systems where multiple interactions per dyad are uncommon, it may only be possible to assign dominance on the basis of a single contest (e.g., Clutton-Brock et al., 1979). The choice of technique for measurement of social structure should ideally take such variation into account. Animals that live together in long-term social groups, in which dominant and subordinate animals interact on a daily basis, are likely to require a different method than that used for animals that test their dominance status less frequently.

In group-living animals, alpha status tends to be readily discernible and stable because many alpha males exhibit despotism, while the status of subordinates is often more difficult to define (Barlow and Ballin, 1976; Oliveira and Almada, 1996a). Non-linear relationships pose serious problems for statistical analysis involving between-group comparisons (Crook and Butterfield, 1970), so many researchers have chosen a method that will produce an essentially linear rank order. If there is incomplete but significant linearity in a dominance hierarchy, there may be more than one optimal solution, and deciding between these can be a somewhat arbitrary process (de Vries, 1998).

Some researchers have elected to chose two to three indices and correlate the results obtained. They then select either the simplest (e.g., Baker and Fox, 1978) or the most complex (e.g., Mateos and Carranza, 1996), of the methods that agree well, although there is some evidence that simple indices can be just as useful as more complex ones, especially for small groups in which all individuals interact (Barlow and Ballin, 1976). Other researchers have created a unique index by calculating average dominance status from the results of several dominance indices (Göransson et al., 1990). The critical assumption in this general approach is that indices that produce highly correlated dominance estimates will also yield similar results when social status is tested for its relationship to other aspects of behaviour.

In this paper, we take a first step in exploring the measurement of dominance from a practical standpoint. We review the properties of popular techniques, measure variation in the results obtained when these are each applied to the same real data set, and document patterns of index usage as a function of study organism and research group.

A review of the literature over the last 70 years yielded eight relatively simple indices. Seven of these have been quite popular, while the last, although little used in research on Animal Behaviour, has recently been recommended (Gammell et al., 2003). We used data from interactions observed among fowl, *Gallus gallus*, the system in which the concept of dominance was first developed (Schjelderup-Ebbe, 1935) to assess consistency in descriptions of social structure. First, we examined how well the indices correlated with one another. The dominance scores generated by each index were then compared with data on individual rates of crowing, using regression analyses. These reveal whether choice of method affects the proportion of variance accounted for, in an analysis of the relation between 'rank' and social behaviour.

In addition, we tabulated index use by research group and study organism from a total of 274 papers on social behaviour. The resulting summary reveals the possible influence of social and traditional factors on selection of a technique.

2. Materials and methods

2.1. Subjects

We used 24 golden Sebright (*Gallus gallus domesticus*) bantam roosters and 27 hens. Domestic fowl are derived from the red junglefowl, *G. g. gallus* (Fumihito et al., 1994, 1996), and are still similar both genetically (Stevens, 1991; Siegel et al., 1992) and behaviourally to this subspecies (Collias and Joos, 1953; Collias, 1987; Andersson et al., 2001; Schütz and Jensen, 2001).

Observations were conducted on a series of eight social groups, each of which was housed sequentially in one of two large aviaries. These were each approximately 200 m² and contained a coop for the birds to roost in at night, grass with patches of bare ground for dustbathing, food, water and three nest boxes. Cover in the form of trees and shrubs was spread relatively evenly around the inside perimeter of each aviary. One group (pilot study) consisted of nine birds (three males and six females). The other seven groups consisted of six birds (three males and three females), a size and sex ratio consistent with that recorded for free-ranging red junglefowl (Collias and Collias, 1967). Birds were all adult, with ages ranging from 1 to 4 years for males, and 1–3 years for females. They were habituated to the presence of humans in the aviaries for data collection, feeding and maintenance. While awaiting rotation through aviaries, birds were housed in an indoor colony (see Evans and Evans, 1999 for details). Each individual was colour-banded on one leg and number-banded on the other. Males were only colour-banded using dark blue, white or light green bands to avoid possible variation in attractiveness associated with female colour biases (Burley et al., 1982; Brodsky, 1988; Rintamäki et al., 2002).

We conducted our observations between 1998 and 2001. Groups were formed in the austral spring and summer (September–March), to coincide with the main breeding period. Sebrights have not been selected for rapid growth or year-round egg production (Evans and Marler, 1995), and follow similar reproductive patterns to wild fowl in that they are photosensitive and respond to increasing day length with hormonal changes and increased egg production.

During initial encounters, all birds were monitored carefully, paying particular attention to males. Overt aggression usually lasted less than 1 min, and ended when one bird signalled subordinate status by turning away. No agonistic encounter lasted more than 3 min and there were no sparring matches involving injury. We intervened in longer encounters if either male exhibited signs of stress (e.g., panting) or if the dominant persistently chased the subordinate.

2.2. Behavioural observations

One of us (KLB) observed each group of birds for 1 h every day, beginning approximately 2 h after dawn and 2 h prior to sunset. The observer either sat or stood in the middle of the aviary. Morning and evening observations for each group were alternated daily, and observation sessions were at least 12 h apart. Data were collected using continuous observation (Altmann, 1974), with each male serving as the focal animal for one 20 min period per hour-long session, in a random sequence. As some of these birds are part of our breeding flock, observations for each group ended either when two of the three hens went broody or when the aviaries were required for breeding birds. Seven breeding groups were observed for a total of 20–25 h long sessions each (6.67–8.34 h per male). A further non-breeding group was observed for a total of 12 h long sessions (4.00 h per male).

We collected data on individual variation in production of several vocalizations as part of a larger analysis of the relationship between behaviour and mate choice. Here, we focus on crowing – a call associated with territoriality and dominance (Collias and Joos, 1953; Collias and Collias, 1967; McBride et al., 1969). For each male, we recorded the number of crows per focal session.

Dominance was scored by recording the outcomes of agonistic encounters and displacements between males. Agonistic behaviour included chasing, aggressive pecking, the lateral waltz display, frontal threatening, grabbing and sparring (Kruijt, 1964). Sparring is a complex sequence which consists of engaging another male with hackles raised, followed by head shaking, leaping, kicking, aggressive pecking and grabbing feathers. This usually occurred only briefly, within the first 10 min of introduction to an unfamiliar male. Displacements occurred when the approach of one male caused another to move away. All males in a group interacted with each other, and winners were successful in 40–100% of their dyadic encounters.

2.3. Comparison of dominance indices

We reviewed the literature on male dominance for the period 1934–2002, which included 274 peer-reviewed papers. This search yielded seven dominances indices, all of which aim to derive a simple numerical value that reflects an individual's social status. While this search was not absolutely exhaustive, it likely produced a representative sample for our purpose, which was to compare popular methods for measuring social structure. We added an eighth index (David's Score), even though it was not represented in the initial search, because this method has been recommended in a recent paper (Gammell et al., 2003). We estimated the dominance rank of males in each group using each of the techniques and compared the results obtained.

We next briefly summarise the way in which these indices calculate dominance rank, to identify both differences and similarities in approach.

2.3.1. Clutton-Brock et al.

This index of fighting success was originally designed for use with red deer stags, *Cervus elaphus*. It weights an individual's rank according to the ranks of his opponents and is based upon the number of males a male defeats, or is defeated by, adjusted by the number of males those males defeat, or are defeated by (Clutton-Brock et al., 1979). In this system, fights are relatively infrequent and costly, and the status of the individuals beaten is an important determinant of dominance status (Clutton-Brock and Albon, 1979; Clutton-Brock et al., 1979). Previous reviews have identified the Clutton-Brock et al. index as a useful measure of dominance (de Vries, 1998; de Vries and Appleby, 2000), and it has been widely adopted. We used this technique as a benchmark.

2.3.2. David's Score

Like the Clutton-Brock et al. index, David's Score calculates dominance ranks for individuals based on the outcomes of agonistic encounters with other group members, while taking the relative strength of their opponents into account (David, 1988). However, David's Score uses the proportion of wins by each individual, within each dyad. As Gammell et al. (2003) have recently emphasized, a clear advantage of this approach is that it does not produce an illogical rank order when there are repeated interactions between pairs of group members, because minor deviations in the outcomes of such interactions do not affect individual ranks disproportionately.

2.3.3. Zumpe and Michael

This index is based upon the direction of both aggressive and submissive behaviour between all possible paired combinations of animals in a group and is largely independent of the absolute number of agonistic interactions (Zumpe and Michael, 1986). It was designed for use with primate groups in which overt agonistic behaviour is uncommon. Specifically, fights are too infrequent to form the basis for constructing matrices, no reversals occur during fighting, and rank order is maintained by threats or submissive gestures. The authors suggest that this index is most suitable for stable groups of animals, and for studies with short sampling periods. It is produced by: (1) calculating the percent of aggressive behaviours given by one animal to another; (2) calculating the percent of submissive behaviours received by one animal from another; (3) for each pair of individuals, combining the percent aggression given and percent submission received and averaging these and finally (4) averaging for each animal the scores obtained in step 3.

2.3.4. Peck Order

Hailman (1994) '*Peck Order* v.1.03' is a freely distributed program that ranks individuals (1, 2, 3, etc.), calculates linearity using Landau's *h*, and identifies reversals and intransitivities. *Peck Order* summarises the interactions of an entire social group in a dominance matrix, and, by ordering the rows and columns according to the wins and losses of each individual, ranks them from most to least dominant.

The final four indices share a common approach. They are all based upon the number of wins and losses in dyadic interactions and attempt to control for variation in the frequency of encounters by each individual, or within the group. We have examined

all four to ascertain whether the subtle differences among them affect the final result.

2.3.5. Baker and Fox

Baker and Fox's index (1978) was originally designed to assess dominance in winter flocks of dark-eyed juncos, *Junco hyemalis*. In this species, dominant individuals win most, but not all, of their encounters. Baker and Fox compared two methods: one which minimised the number of dominance reversals and a second based on calculating the proportion of wins. Results were highly correlated, so Baker and Fox chose the simpler calculation of proportion of wins; this removed the problem of deciding among qualitative hierarchies when reversals occurred. We considered Baker and Fox's preferred method.

2.3.6. Crook and Butterfield

Crook and Butterfield (1970) 'Dominance Index' was designed for use with the Quelea or Black-faced Dioch, *Quelea quelea quelea*. These birds maintain a loose social structure, which is relatively stable over short periods of time in captivity. The Crook and Butterfield index adjusts for frequency of encounters by calculating the average probability of a win by a particular individual against a group member (Crook and Butterfield, 1970). This method structures the data so as to obtain a linear rank order that is suitable for statistical comparisons of dominance status between groups.

2.3.7. Index of combined attacks

The index of combined attacks (*CAtt*) was originally developed by Barlow and Ballin (1976) to measure dominance in the Midas cichlid, *Cichlasoma citrinellum*, a species in which individuals differ in both colour morph and size. It simply summarises successful attacks as a proportion of interactions and yields a score calculated from (*victories*)/(*defeats* + *victories*).

2.3.8. Frequency Success Index

The Frequency Success Index (*FSI*) was designed to assess both inter- and intra-specific dominance hierarchies in house sparrows, *Passer domesticus*, and house finches, *Carpodacus mexicanus*. It controls for the aggressiveness of individuals and the overall level of agonistic behaviour of the group in which they interact (Kalinoski, 1975). *FSI* is based upon two assumptions: (i) that highly dominant individuals maintain their status through extensive interaction with subordinates and (ii) that aggressiveness is mediated by physiological factors (e.g., testosterone level), while dominance is a product of individual physical attributes (e.g., size and ornamentation), and behavioural traits (e.g., assertiveness and willingness to keep fighting). *FSI* therefore combines measures of aggression (frequency of encounters) with dominance (proportion of wins).

2.4. Patterns of choice among dominance indices

To estimate the recent popularity of each method for measuring dominance, we searched the ISI Web of Science Citation Index for peer-reviewed journals published between 1990 and 2001 which cited the paper in which each index was first described. We did not include David's Score in this analysis because, as previously noted by Gammell et al. (2003), this index has not been adopted by researchers studying Animal Behaviour. All of the papers identified by this initial search were then checked to establish the species studied, whether the animals were in the field or captive, whether methods were observational or experimental, whether animals were free to associate or artificially paired, and whether all potential dyads in the group interacted. Our goal in collecting these data was to identify patterns of index choice within research communities.

2.5. Comparison of dominance indices

We measured agreement among indices for each group of males using Kendall's tau-b correlation (Siegel and Castellan, 1988). *Peck Order* assigns a score of 1 to the highest ranking male, 2 to the beta male and so on, but all other methods produce scores that increase with rank; we thus inverted the *Peck Order* scale for comparability. We report the median correlation coefficient between each pair of indices, together with the maximum and minimum values. As we wished to look only at overall agreement among the dominance indices, rather than inter-group variability in dominance, we used this method in preference to an overall correlation on the whole data set. Finally, for each group we tallied the number of times all indices agreed and disagreed.

We also assessed the linearity of dominance hierarchies by calculating Landau's Index of Linearity (*h*) (Bekoff, 1977). Although perfectly linear hierarchies can be obtained by chance in groups of fewer than five individuals (Appleby, 1983; but see also Chase et al., 2002), we believe that such an approach is justified in this case because (i) most groups had stable structure (Martin and Bateson, 1993) and (ii) linear dominance hierarchies are known to occur in *G. gallus* (e.g., Schjelderup-Ebbe, 1935; Guhl et al., 1945; Chase, 1982b), particularly in small groups (Chase, 1982a; Cloutier et al., 1996).

2.6. Dominance and vocal behaviour: is there an effect of index choice?

Pair-wise comparisons of dominance indices relied upon converting raw scores, which in some cases were interval measures, to integer ranks. While different methods can produce highly correlated results when assigning males to categories (alpha, beta or gamma status), this consistency potentially obscures systematic differences in estimates of the precise position of each male within a hierarchy, as indicated by original dominance scores. For example, in one representative group, the three males received scores of 0.74, 0.26, 0.00 (Baker and Fox), 0.74, −0.07, −0.67 (*FSI*) and 1.00, 0.44, 0.00 (*CAtt*). We wished to assess how this variation in scaling would affect an analysis of the relationship between social status and one aspect of vocal behaviour.

It is important to note that we here treat dominance as an environmental variable, rather than an inherent property of males. Our analyses hence ask to what extent males of equivalent social status behave similarly, not *why* they achieved a particular dominance score.

We used a standardised measure of crowing rate to account for differences among groups and across successive breeding seasons. For each male, we calculated the rate of crowing per hour, and then expressed this as a proportion of his group's total rate. All variables required transformation to reduce kurtosis and skew (Press et al., 1993). We used a $\log_{10}$ transform as this proved most effective. Transformed data had approximately normal distribution and homogenous variance.

Normalising the data eliminated the obscuring effects of overall differences between the groups (e.g., different levels of vocal activity), but it also contributed to a lack of independence between observations. One standard solution to this problem is to use groups as the unit of analysis, but this would clearly have been inappropriate because we wished to compare the behaviour of individuals. Fortunately, there is an alternative that takes into account the non-independence of observations drawn from the same social group. Huber (1967) and White (1980, 1982) independently developed a method for calculating estimates of the standard errors of regression parameters which are robust to violations of the assumption that predictor values and errors are independently and similarly distributed. This "robust" regression method has been extended by Rogers (1993) to cover the non-independence of observations and implemented in STATA statistics software (StataCorp, 2001). We used this algorithm for all analyses.

The standard errors and *p*-values produced by robust regression tend to be larger than those derived from a conventional ordinary least squares (OLS) approach. While the r^2 values are based on individual subjects, and are the same as those generated by OLS regression, calculation of standard errors, degrees of freedom, and hence *p*-values, is based on the number of independent clusters of subjects. However, for this analysis, we were not concerned with the significance of the correlation between each dominance index and rate of crowing. Rather, we wished to compare the strength of the relationship generated by each index, with rate of crowing held constant. We therefore focus upon r^2 values.

3. Results

3.1. Comparison of dominance indices

The rankings produced by most of the indices were consistent (Table 1), although there was still sufficient variation to discern patterns of agreement between methods. Baker and Fox, Crook and Butterfield, Zumpe and Michael, *David's Score* and *Peck Order* ranked males identically. Rankings produced by Clutton-Brock et al. were closer to those produced by *CAtt* and *FSI*, than

Table 1
Correlations between pairs of indices (*N* = 24)

Indices compares	Kendall's tau b		
	Lowest	Median	Highest
Clutton-Brock et al., Baker and Fox	0.333	0.908	1.000
Clutton-Brock et al., Crook and Butterfield	0.333	0.908	1.000
Clutton-Brock et al., *CAtt*	0.816	1.000	1.000
Clutton-Brock et al., *FSI*	0.816	1.000	1.000
Clutton-Brock et al., Zumpe and Michael	0.333	0.908	1.000
Clutton-Brock et al., *David's Score*	0.333	0.908	1.000
Clutton-Brock et al., *Peck Order*	0.333	0.908	1.000
Baker and Fox, Crook and Butterfield	1.000	1.000	1.000
Baker and Fox, *CAtt*	0.333	1.000	1.000
Baker and Fox, *FSI*	0.333	1.000	1.000
Baker and Fox, Zumpe and Michael	1.000	1.000	1.000
Baker and Fox, *David's Score*	1.000	1.000	1.000
Baker and Fox, *Peck Order*	1.000	1.000	1.000
Crook and Butterfield, *CAtt*	0.333	1.000	1.000
Crook and Butterfield, *FSI*	0.333	1.000	1.000
Crook and Butterfield, Zumpe and Michael	1.000	1.000	1.000
Crook and Butterfield, *David's Score*	1.000	1.000	1.000
Crook and Butterfield, *Peck Order*	1.000	1.000	1.000
CAtt, *FSI*	0.333	1.000	1.000
CAtt, Zumpe and Michael	0.333	1.000	1.000
CAtt, *David's Score*	0.333	1.000	1.000
CAtt, *Peck Order*	0.333	1.000	1.000
FSI, Zumpe and Michael	0.333	1.000	1.000
FSI, *David's Score*	0.333	1.000	1.000
FSI, *Peck Order*	0.333	1.000	1.000
Zumpe and Michael, *David's Score*	1.000	1.000	1.000
Zumpe and Michael, *Peck Order*	1.000	1.000	1.000
David's Score, *Peck Order*	1.000	1.000	1.000

rankings by Baker and Fox, Crook and Butterfield, Zumpe and Michael, *David's Score* and *Peck Order*. *CAtt* and *FSI* ranked males similarly, but not identically, to Baker and Fox, Crook and Butterfield, Zumpe and Michael, *David's Score* and *Peck Order*.

The group-by-group analysis (Table 2) reveals that the results of pair-wise index comparisons were sensitive to social structure. Agreement was perfect for groups that were strictly linear (Landau's Index of Linearity *h* = 1.0) and contained no reversals (Table 2). Similarly, all indices but one (Clutton-Brock et al.) were highly correlated for group 8, which also had a large Landau's *h* value. In contrast, there were pronounced differences in the ranking of males within groups that had either an intransitive triad (group 1), or reversals (groups 3, 6 and 8). When linearity was weak, all dominance indices agreed upon assignment of the alpha male, but they either classified beta and gamma males differently (groups 1, 3 and 6), or assigned two equal alphas (group 8).

Table 2
Agreement among the eight indices for each group of males, illustrating the effects of dominance linearity

Group	1	2	3	4	5	6	7	8
Number of times indices agreed	13	28	15	28	28	15	28	21
Number of times indices disagreed	15	–	13	–	–	13	–	7
Landau's *h*	0.11	1.0	0.78	1.0	1.0	0.74	1.0	0.99

Groups 2, 4, 5, 7 and 8 were strongly linear (Landau's Index *h* > 0.9). Groups 3, 6 and 8 had reversals; group 1 was intransitive.
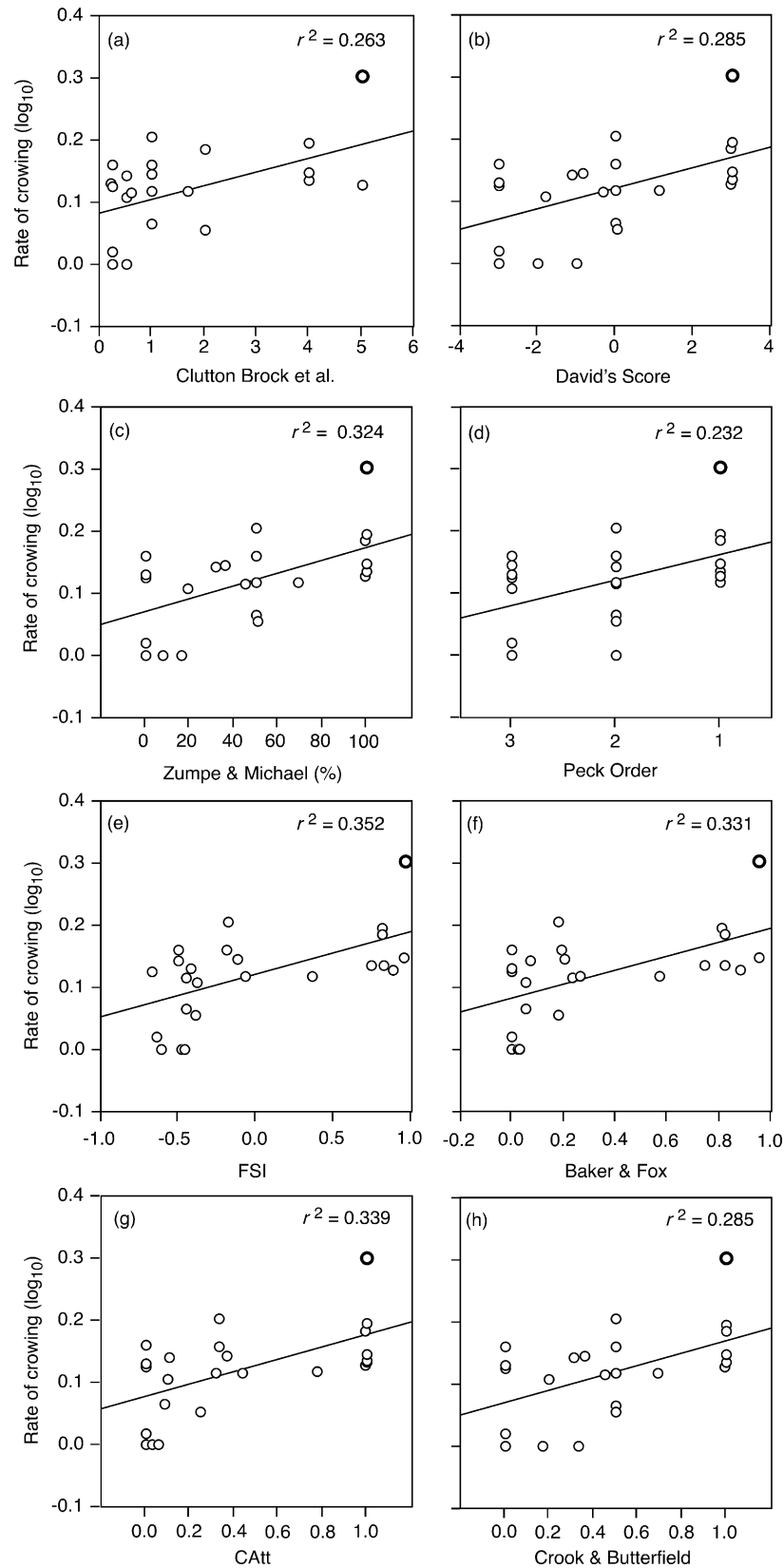
Fig. 1. Relation between dominance status and rate of crowing produced by each of the eight methods considered. Note variation caused by index characteristics. (a) Clutton-Brock et al. (range of index 0.00–5.00). (b) Zumpe and Michael (range of index 0–100%). (c) Hailman's *Peck Order* (rank range 1–3; scale reversed to facilitate comparison). (d) Kalinoski's *FSI* (range of index −1.00 to 1.00). (e) Baker and Fox (range of index 0.00–1.00). (f) *CAtt* (range of index 0.00–1.00). (g) Crook and Butterfield (range of index 0.00–1.00). One outlier male (bold) is correctly identified by all eight methods.

A closer inspection of these results reveals that Clutton-Brock et al. disagreed with Baker and Fox, Crook and Butterfield, Zumpe and Michael, *David's Score* and *Peck Order* for the intransitive triad (group 1), and for all groups with reversals (groups 3, 6 and 8). Clutton-Brock et al. also disagreed with *CAtt* and *FSI*, but only for the groups with reversals, mainly because it tended to assign equal ranks to males when there was weak linearity (Table 2: groups 3, 6 and 8). *CAtt* disagreed with Baker and Fox, Crook and Butterfield, Zumpe and Michael, *David's Score* and *Peck Order* with regard to beta and gamma males in the intransitive triad (group 1), and with *FSI* for the beta and gamma males in groups 3 and 6 (which had reversals and weak linearity).

All indices captured differences between males within a group, but only a few (Clutton-Brock et al., Baker and Fox and *FSI*) were also sensitive to differences between alpha males (i.e., assigned a score other than the maximum possible in both 'no reversals' and 'reversals' transitive groups). One outlier male was successfully identified by all eight methods (Fig. 1).

3.2. Effects of index choice on an analysis

Despite the high correlations among the indices, robust regression analyses of dominance and rate of crowing yielded varying results (Fig. 1). All regression coefficients were positive, but the proportion of variance explained (r^2) ranged from 0.353 (*FSI*) to 0.232 (*Peck Order*). Since the behavioural data were identical in each case, these differences, which amount to approximately 12% of the total variance, must reflect index characteristics. We attribute this effect to differences in the way in which the various methods distributed individual males along the dominance dimension (Fig. 1).

3.3. Influences of tradition and study organism on index choice

There was a pronounced tendency to adopt a method previously used by other researchers studying the same or similar species (Appendix A). For example, Zumpe and Michael's index was used only by primatologists, while fish researchers generally preferred *CAtt*. Similarly, Baker and Fox, Crook and Butterfield and *FSI* were used only in studies of birds. Clutton-Brock et al. was the most popular index; it was adopted by many research groups and used with a diverse array of species. In some cases (e.g., Baker and Fox and *FSI*), these apparent taxonomic influences may also (or instead) reflect traditions within particular laboratories or institutions.

Dominance was assessed primarily by observation of spontaneous, rather than staged, interactions, although some of these occurred during the course of experiments (e.g., Grahn et al., 1993a; Weerts and Miczek, 1996; Mateos and Carranza, 1997a; Blumstein et al., 1999). In all studies except Zumpe and Michael (1990), animals were free to associate. Only five of the papers reviewed provided data on whether all animals interacted (Zumpe and Michael, 1990; Freeman et al., 1992; Gore, 1993, 1994; Troisi and Carosi, 1998).

4. Discussion

Simple correlation of ranks suggested that all indices were in reasonable agreement (Table 1), but a closer examination revealed that they responded quite differently to variation in social structure. While strongly linear hierarchies generated similar results with all eight methods, the indices disagreed markedly when summarising data from groups that had weak linearity, intransitive triads or reversals (Table 2). Such groups were often characterised by a tendency for increased interaction between the alpha and one subordinate, or a lack of interaction between subordinates.

These differences in the measurement of social structure had a noticeable effect on the relation between dominance and rate of crowing, which was used as an example problem. All indices generated a positive slope, but they produced a range of r^2 values (Fig. 1). This can only have been due to differences in the placement of individual males along the dominance axis. For comparison, index choice accounted for approximately one-third to one-half of the variance explained by the dominance-crowing relation (Fig. 1).

Note that such pronounced variation exists despite the almost uniformly high correlation among dominance indices (Table 1). When we tested these methods with data on production of other vocalizations (Bayly, unpublished data), we also found that r^2 values varied inconsistently as a function of both call type and index. These results call into question the wisdom of relying exclusively upon correlation to evaluate indices. Most correlative methods convert scores to ranks prior to analysis, thus eliminating differences in scaling of dominance scores (i.e., in the intervals between males) and increasing the probability of agreement.

Whether or not index properties should be a concern cannot be answered in the abstract, but rather will be determined by both the social structure of the group studied and the theoretical question of interest. If all groups are strongly linear and the assignment of dominance rank is not of central importance, then any of the methods considered will probably be sufficiently robust for use in analyses. However, if hierarchical structure tends to be non-linear, or varies substantially across groups, then index choice has the potential to affect considerably the results obtained. This will be particularly true in any analysis that requires an estimate of effect size (Cohen, 1988), or of the relative importance of social status against other factors. In such cases, we suggest that conclusions could be influenced by choice of method.

Tradition or the culture of research groups does seem to play a role in the choice of methods. While the Clutton-Brock et al. index is ubiquitous, several other indices are restricted to particular teams or taxa (Appendix A). This might not present problems, providing that the index is used with the system for which it was originally designed. However, any deviations from the original concept (e.g., extension of an index to other contexts or to species with very different social structures) could have unanticipated effects. We next consider some of the factors that cause indices to diverge and the problem of choosing the best approach for our particular data set.

4.1. Measurement of dominance: a case study

In group 8, which was characterised by strong linearity and one reversal (Table 2), male Y-68 established himself as alpha in an initial encounter with male Y-65, but subsequently was challenged and defeated by him. The following day, Y-68 overturned this defeat. He then maintained his dominance status throughout the study period, which included 109 further interactions. Hence, in total, Y-65 won one interaction with Y-68, whereas Y-68 won 110 interactions with Y-65. Six of the seven indices assigned Y-68 as alpha, but Clutton-Brock et al. index ranked Y-68 and Y-65 as equal. Recall that this method was designed for a system in which males interact only infrequently (see Section 2), whereas males in the present study did so daily. Nevertheless, the matched-alpha rank produced by Clutton-Brock et al. seems counter-intuitive. Recent work by Gammell et al. (2003) uses an artificial data set to illustrate this problem.

4.2. Index properties

The previous example illustrates the likely effect of social system on assignment of individual status. When dominance is maintained by daily interaction, and when the outcomes of these interactions are occasionally reversed, the number of exchanges won by a male is likely to produce a better measure of dominance. We suggest that this consideration provides a better basis for index choice than assessment of algorithm properties in isolation. For example, Mateos and Carranza (1996) calculated both Kalinoski's *FSI* and the Clutton-Brock et al. index, as well as ratio of wins and losses, to measure the dominance status of captive male ring-necked pheasants, *Phasianus colchicus*. They found these results to be highly correlated and chose Clutton-Brock et al. on the basis that it was a "more complex index" that took into account the success of an opponent. However, at least with our data set, complexity fails to predict accuracy in assigning dominance.

FSI assumes that a highly dominant individual maintains its status through extensive interaction with subordinates (Kalinoski, 1975) and may hence be a more appropriate choice for social groups in which this occurs. Baker and Fox, Crook and Butterfield, *CAtt*, *David's Score* and Zumpe and Michael also incorporate frequency of encounters in the calculation of dominance status. Nevertheless, these indices may have other, less desirable, characteristics. For example, Oliveira and Almada (1996b) noted that *CAtt* generated tied scores in their work with Mozambique tilapia, *Oreochromis mossambicus*. We did not experience this problem in the present study, suggesting that it arises through an interaction with particular data sets, rather than being a fundamental characteristic of the index.

It is likely that our data set did not do justice to the Zumpe and Michael method, as the authors state that their index is most useful for groups of animals in which (1) agonistic frequencies are low, (2) there are insufficient data for constructing fight interaction matrices and (3) there are no reversals during overt fighting (Zumpe and Michael, 1986). In the present study, agonistic frequencies were high, interactions invariably ended with displacement or other submissive behaviour, and reversals during fighting occurred in three of eight groups.

Peck Order assigns status using integer ranks (e.g., 1, 2, 3, . . .), rather than a continuous interval scale. This is a useful approach when measurement of dominance is the endpoint, but it may not be an ideal choice if social status is to be used as a variable in statistical analyses; *Peck Order* effectively discards information about the structure of social groups by ignoring variation in the distribution of males along the dominance scale. This potentially increases the risk of type II error.

Finally, we note that the results obtained with a particular index may be influenced by group size. Transitive linear hierarchies are more common in small groups (Tarvin and Woolfenden, 1997; Chase et al., 2002), like those we studied, which were of a size consistent with that recorded for both wild red jungle fowl (Collias and Collias, 1967) and free-ranging feral fowl (McBride et al., 1969). Other work on captive fowl suggest that large groups are more likely to be intransitive and non-linear (Wood-Gush, 1955), and that lack of social inertia increases the likelihood of social instability (Guhl, 1968).

4.3. Choosing a method: a worked example

We recognize that index choice will necessarily be shaped by the nature of the data available, which will in turn be influenced by the social structure of the groups observed. It would hence be presumptuous (and almost certainly incorrect) to assert that there is a 'best' method in any absolute sense. Indeed, the very diversity of the techniques considered in this paper illustrates a perceived need to tailor solutions to the system of interest. Such proliferation would not likely have occurred if an appropriate standard were readily available.

Nevertheless, some general principles emerge. Selecting an index on the basis of tradition within a theoretical paradigm, or for a particular order of animals, may not be the best strategy, particularly if the study species or question differs substantially from that for which the method was originally designed. Likewise, we suggest that computational complexity is a less useful guide than consideration of those characteristics of social structure that are responsible for the establishment and maintenance of dominance status. High correlations between indices do not ensure that each will give the same results in subsequent statistical analyses (Fig. 1), but they are a useful starting point because such comparisons group methods according to how well they deal with reversals and intransitivities.

In the present study, the ability of beta males to enforce their dominance over gamma males was highly variable, with gammas having more interactions with strong betas than with weaker ones. This indicated that a dominance index that preserved the relative strength of relationships would be a better choice than a ranking system, so we eliminated *Peck Order*. We aimed ultimately to test the relation between dominance, reproductive success, and several other behavioural variables across groups, so we required that the index reflect differences among alpha males. For example, some alpha males allowed subordinates to have contact with hens, but not court or mate, whereas others actively excluded other males from any contact with hens, which

increased the rate of interactions within the group. This consideration restricted the choice of method to Clutton-Brock et al., Baker and Fox and *FSI* (see Section 3). Of these three indices, Clutton-Brock et al. and *FSI* agreed well with each other, so we considered these two.

The birds lived in stable social groups and shared resources such as food and shelter. All males interacted on a daily basis, but some groups contained males that were more aggressive than those in others. The index chosen hence needed to account for this individual variation, as well as the frequency of encounters. Based on these requirements, we selected *FSI*.

Our experience illustrates only one possible strategy for choosing a method to measure social status, but it does reveal the importance of identifying and considering carefully the factors affecting dominance in a study species. Together with correlation, which provides useful data on patterns of agreement, this approach will ensure the best match between index properties and behaviour.

Acknowledgements

Appendix A

Dominance indices 1990–2001

Index	Citation	Study taxa	Setting
Baker and Fox	Göransson et al. (1990) [a]	Birds: *Phasianus colchicus*	Captive
	Grahn et al. (1993a) [a]	Birds: *Phasianus colchicus*	Captive
	Grahn et al. (1993b) [a]	Birds: *Phasianus colchicus*	Captive
Clutton-Brock et al.	Berdoy et al. (1995)	Rodents: *Rattus norvegicus*	Captive
	Choudhury and Black (1993)	Birds: *Branta leucopsis*	Captive
	Choudhury and Black (1994)	Birds: *Branta leucopsis*	Captive
	Festa-Bianchet et al. (1990)	Ungulates: *Dama dama*	Field
	Freeman et al. (1992)	Ungulates: *Cervus elaphus*	Field
	Mateos and Carranza (1997a)	Birds: *Phasianus colchicus*	Captive
	Mateos and Carranza (1997b)	Birds: *Phasianus colchicus*	Captive
	Mateos and Carranza (1999)	Birds: *Phasianus colchicus*	Captive
	Mattiangeli et al. (1998)	Ungulates: *Dama dama*	Field
	McElligott et al. (1999)	Ungulates: *Dama dama*	Field
	McElligott et al. (2001)	Ungulates: *Dama dama*	Field
	Moore et al. (1995)	Ungulates: *Dama dama*	Field
	Pélabon and Joly (2000)	Ungulates: *Dama dama*	Captive
	Pizzari and Birkhead (2001)	Birds: *Gallus gallus*	Captive
	San Jose and Braza (1997)	Ungulates: *Dama dama*	Field
	Sauter and Morris (1995)	Ungulates: *Cervus elaphus*	Captive
	Tinker et al. (1995)	Seals: *Halichoerus grypus*	Field
	van den Bos and De Cock Buning (1994)	Cats: *Felis lybica, F. catus*	Captive
	Watts (1994)	Primates: *Gorilla gorilla beringei*	Field
	Wolff (1998)	Ungulates: *Bison bison*	Field
Crook and Butterfield	Göransson et al. (1990)	Birds: *Phasianus colchicus*	Captive
	Grahn et al. (1993a)	Birds: *Phasianus colchicus*	Captive
	Grahn et al. (1993b)	Birds: *Phasianus colchicus*	Captive
CAtt (Barlow, Oliveira)	Gomez-Laplaza and Morgan (1993)	Fish: *Pterophyllum scalare*	Captive
	Oliveira and Almada (1996a)	Fish: *Oreochromis mossambicus*	Captive
	Oliveira et al. (1996)	Fish: *Oreochromis mossambicus*	Captive
	Oliveira and Almada (1998)	Fish: *Oreochromis mossambicus*	Captive
FSI (Kalinoski)	Göransson et al. (1990)	Birds: *Phasianus colchicus*	Captive
	Grahn et al. (1993a)	Birds: *Phasianus colchicus*	Captive
	Grahn et al. (1993b)	Birds: *Phasianus colchicus*	Captive
Peck Order (Hailman)	Troisi and Carosi (1998)	Primates: *Macaca fuscata*	Captive
	Blumstein et al., 1999	Macropods: *Macropus eugenii*	Captive
Zumpe and Michael	Butovskaya et al. (1996)	Primates: *Macaca fascicularis*	Captive
	Butovskaya and Kozintsev (1996)	Primates: *Macaca arctoides*	Captive
	Fornasieri et al. (1993)	Primates: *Lemur macaco*	Captive
	Gore (1993)	Primates: *Macaca mulatta* and *Papio hamadryas*	Captive
	Gore (1994)	Primates: *Macaca mulatta* and *Papio hamadryas*	Captive

Appendix A *(Continued)*

Index	Citation	Study taxa	Setting
	Michael and Zumpe (1990)	Primates: *Macaca mulatta*	Captive
	Rasmussen and Farrington (1994)	Primates: *Macaca arctoides*	Captive
	Weerts et al. (1993a)	Primates: *Saimiri sciureus*	Captive
	Weerts et al. (1993b)	Primates: *Saimiri sciureus*	Captive
	Weerts and Miczek (1996)	Primates: *Saimiri sciureus*	Captive
	Zumpe and Michael (1990)	Primates: *Macaca fascicularis*	Captive

[a]Used three indices and averaged the result.

References

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour 49, 227–267.

Andersson, M., Nordin, E., Jensen, P., 2001. Domestication effects on foraging strategies in fowl. App. Anim. Behav. Sci. 72, 51–62.

Appleby, M.C., 1983. The probability of linearity in hierarchies. Anim. Behav. 31, 600–608.

Baker, M.C., Fox, S.F., 1978. Dominance, survival, and enzyme polymorphism in dark-eyed juncos, *Junco hyemalis*. Evolution 32, 697–711.

Barlow, G.W., Ballin, P.J., 1976. Predicting and assessing dominance from size and coloration in the polychromatic midas cichlid. Anim. Behav. 24, 793–813.

Bekoff, M., 1977. Quantitative studies of three areas of classical ethology: social dominance, behavioural taxonomy, and behavioural variability. In: Hazlett, B.A. (Ed.), Quantitative Methods in the Study of Animal Behaviour. Academic Press Inc., New York, pp. 1–46.

Berdoy, M., Webster, J.P., MacDonald, D.W., 1995. Parasite-altered behaviour: is the effect of *Toxoplasma gondii* on Rattus norvegicus specific? Parasitology 111, 403–409.

Blumstein, D.T., Evans, C.S., Daniel, J.C., 1999. An experimental study of behavioural group size effects in tammar wallabies, *Macropus eugenii*. Anim. Behav. 558, 351–360.

Boyd, R., Silk, J.B., 1983. A method for assigning cardinal dominance ranks. Anim. Behav. 31, 45–58.

Brodsky, L.M., 1988. Ornament size influences mating success in male rock ptarmigan. Anim. Behav. 36, 662–667.

Burley, N.T., Krantzberg, G., Radman, P., 1982. Influence of color banding on the conspecific preferences of zebra finches *Peophila guttata*. Anim. Behav. 30, 444–455.

Butovskaya, M., Kozintsev, A., Welker, C., 1996. Conflict and reconciliation in two groups of crab-eating monkeys differing in social status by birth. Primates 37, 261–270.

Butovskaya, M.L., Kozintsev, A.G., 1996. Gender-related factors affecting primate social behavior: grooming, rank, age, and kinship in heterosexual and all-male groups of stumptail macaques. Am. J. Phys. Anthrop. 101, 39–54.

Chase, I.D., 1982a. Behavioural sequences during dominance hierarchy formation in chickens. Science 216, 439–440.

Chase, I.D., 1982b. Dynamics of hierarchy formation: the sequential development of dominance relationships. Behaviour 80, 218–238.

Chase, I.D., Tovey, C., Spangler-Martin, D., Manfredonia, M., 2002. Individual differences versus social dynamics in the formation of animal dominance hierarchies. Proc. Natl. Acad. Sci. U.S.A. 99, 5744–5749.

Choudhury, S., Black, J.M., 1993. Mate-selection behaviour and sampling strategies in geese. Anim. Behav. 46, 747–757.

Choudhury, S., Black, J.M., 1994. Barnacle geese preferentially pair with familiar associates from early life. Anim. Behav. 48, 81–88.

Cloutier, S., Beaugrand, J.P., Laguë, P.C., 1996. The role of individual differences and patterns of resolution in the formation of dominance orders in domestic hen triads. Behav. Process. 38, 227–239.

Clutton-Brock, T., Albon, S.D., 1979. The roaring of red deer *Cervus elaphus* and the evolution of honest advertisement. Behaviour 69, 145–169.

Clutton-Brock, T.H., Albon, S.D., Gibson, R.M., Guinness, F.E., 1979. The logical stag: adaptive aspects of fighting in red deer. Anim. Behav. 27, 211–225.

Cohen, J., 1988. Statistical Power Analysis for the Behavioral Sciences. Lawrence Erlbaum Association, Hillsdale, NJ.

Collias, N.E., 1987. The vocal repertoire of the red junglefowl: a spectrographic classification and the code of communication. Condor 89, 510–524.

Collias, N.E., Collias, E.C., 1967. A field study of the red jungle fowl in north-central India. Condor 69, 360–386.

Collias, N.E., Joos, M., 1953. The spectrographic analysis of sound signals of the domestic fowl. Behaviour 5, 175–188.

Crook, J.H., Butterfield, P.A., 1970. Gender role in the social system of Quelea. In: Crook, J.H. (Ed.), Social Behaviour in Birds and Mammals: Essays on the Social Ethology of Animals and Man. Academic Press, London, pp. 211–248.

David, H.A., 1988. The Method of Paired Comparisons. Charles Griffin, London.

de Vries, H., 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Anim. Behav. 55, 827–843.

de Vries, H., Appleby, M.C., 2000. Finding an appropriate order for a hierarchy: a comparison of the I&SI and the BBS methods. Anim. Behav. 59, 239–245.

Drews, C., 1993. The concept and definition of dominance in animal behaviour. Behaviour 125, 283–313.

Evans, C.S., Evans, L., 1999. Chicken food calls are functionally referential. Anim. Behav. 58, 307–319.

Evans, C.S., Marler, P., 1995. Language and animal communication: Parallels and contrasts. In: Roitblat, H., Arcady-Meyer, J. (Eds.), Comparative Approaches to Cognitive Science. MIT Press, Boston, pp. 341–382.

Festa-Bianchet, M., Apollonio, M., Mari, F., Rasola, G., 1990. Aggression among lekking male fallow deer (*Dama dama*) - territory effects and relationship with copulatory success. Ethology 85, 236–246.

Fornasieri, I., Caubere, M., Roeder, J.J., 1993. Social dominance and priority of access to drinking in *Lemur macaco*. Aggress. Behav. 19, 455–464.

Freeman, L.C., Freeman, S.C., Romney, A.K., 1992. The implications of social structure for dominance hierarchies in red deer *Cervus elaphus* L. Anim. Behav. 44, 239–245.

Fumihito, A., Miyake, T., Sumi, S.-I., Takada, M., Ohno, S., Kondo, N., 1994. One subspecies of the red junglefowl (*Gallus gallus gallus*) suffices as the matriarchic ancestor of all domestic breeds. Proc. Natl. Acad. Sci. U.S.A. 91, 12505–12509.

Fumihito, A., Miyake, T., Takada, M., Shingu, R., Endo, T., Gojobori, T., Kondo, N., Ohno, S., 1996. Monophyletic origin and unique dispersal patterns of domestic fowls. Proc. Natl. Acad. Sci. U.S.A. 93, 6792–6795.

Gammell, M.P., de Vries, H., Jennings, D.J., Carlin, C.M., Hayden, T.J., 2003. David's score: A more appropriate dominance ranking method than Clutton-Brock et al.'s index. Anim. Behav. 66, 601–605.

Gomez-Laplaza, L.M., Morgan, E., 1993. Social isolation, aggression, and dominance in attacks in juvenile angelfish, *Pterophyllum scalare*. Aggress. Behav. 19, 213–222.

Göransson, G., von Schantz, T., Froberg, I., Helge, A., Wittzell, H., 1990. Male characteristics, viability and harem size in the pheasant *Phasianus colchicus*. Anim. Behav. 40, 89–104.

Gore, M.A., 1993. Effects of food distribution on foraging competition in rhesus monkeys, *Macaca mulatta*, and hamadryas baboons, *Papio hamadryas*. Anim. Behav. 45, 773–786.

Gore, M.A., 1994. Dyadic and triadic aggression and assertiveness in adult female rhesus monkeys, *Macaca mulatta*, and hamadryas baboons, *Papio hamadryas*. Anim. Behav. 48, 385–392.

Grahn, M., Göransson, G., von Schantz, T., 1993a. Territory acquisition and mating success in pheasants, *Phasianus colchicus*: an experiment. Anim. Behav. 46, 721–730.

Grahn, M., Göransson, G., von Schantz, T., 1993b. Spacing behaviour of male pheasants, *Phasianus colchicus*, in relation to dominance and mate acquisition. Anim. Behav. 45, 93–103.

Guhl, A.M., 1968. Social inertia and social stability in chickens. Anim. Behav. 16, 219–232.

Guhl, A.M., Collias, N.E., Allee, W.C., 1945. Mating behaviour and the social hierarchy in small flocks of white leghorns. Physiol. Zool. 18, 365–390.

Hailman, J.P., 1994. Peck Order 1.03. Department of Zoology, University of Wisconsin, Madison, Wisconsin.

Huber, P.J., 1967. Proceedings of the Fifth Berkeley Symposium on Mathematic Statistics and Probability, Berkeley, CA.

Jameson, K.A., Appleby, M.C., Freeman, L.C., 1999. Finding an appropriate order for a hierarchy based on probabilistic dominance. Anim. Behav. 57, 991–998.

Kalinoski, R., 1975. Intra- and interspecific aggression in house finches and house sparrows. Condor 77, 375–384.

Kruijt, J.P., 1964. Ontogeny of Social Behaviour in Burmese red Junglefowl. E.J. Brill, Leiden.

Martin, P., Bateson, P., 1993. Measuring Behaviour: An Introductory Guide. Cambridge University Press, Cambridge.

Masure, R.H., Allee, W.C., 1934. The social order in flocks of the common chicken and pigeon. Auk 51, 306–327.

Mateos, C., Carranza, J., 1996. On the intersexual selection for spurs in the ring-necked pheasant. Behav. Ecol. 7, 362–369.

Mateos, C., Carranza, J., 1997a. The role of bright plumage in male–male interactions in the ring-necked pheasant. Anim. Behav. 54, 1205–1214.

Mateos, C., Carranza, J., 1997b. Signals in intra-sexual competition between ring-necked pheasant males. Anim. Behav. 53, 471–485.

Mateos, C., Carranza, J., 1999. Effects of male dominance and courtship display on female choice in the ring-necked pheasant. Behav. Ecol. Sociobiol. 45, 235–244.

Mattiangeli, V., Mattiello, S., Verga, M., 1998. Factors affecting the duration of fights in fallow deer (*Dama dama*) during the rut. Ethol. Ecol. Evol. 10, 87–93.

McBride, G., Parer, I.P., Foenander, F., 1969. The social organization and behaviour of the feral domestic chicken. Anim. Behav. Monogr. 2, 127–181.

McElligott, A.G., Gammell, M.P., Harty, H.C., Paini, D.R., Murphy, D.T., Walsh, J.T., Hayden, T.J., 2001. Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? Behav. Ecol. Sociobiol. 49, 266–272.

McElligott, A.G., O'Neill, K.P., Hayden, T.J., 1999. Cumulative long-term investment in vocalization and mating success of fallow bucks, *Dama dama*. Anim. Behav. 57, 1159–1167.

Michael, R.P., Zumpe, D., 1990. Sexual preferences during artificial menstrual cycles in social groups of Rhesus monkeys *Macaca mulatta*. Primates 31, 225–242.

Moore, N.P., Kelly, P.F., Cahill, J.P., Hayden, T.J., 1995. Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population. Behav. Ecol. Sociobiol. 36, 91–100.

NHMRC, 1997. Australian Code of Practice for the Care and Use of Animals for Scientific Purposes. Commonwealth of Australia, Canberra.

Oliveira, R.F., Almada, V.C., 1996a. Dominance hierarchies and social structure in captive groups of the Mozambique tilapia *Oreochromis mossambicus* (Teleostei Cichlidae). Ethol. Ecol. Evol. 8, 39–55.

Oliveira, R.F., Almada, V.C., 1996b. On the (in)stability of dominance hierarchies in the cichlid fish *Oreochromis mossambicus*. Aggress. Behav. 22, 37–45.

Oliveira, R.F., Almada, V.C., 1998. Maternal aggression during the mouth-brooding cycle in the cichlid fish, *Oreochromis mossambicus*. Aggress. Behav. 24, 187–196.

Oliveira, R.F., Almada, V.C., Canario, A.V.M., 1996. Social modulation of sex steroid concentrations in the urine of male cichlid fish *Oreochromis mossambicus*. Horm. Behav. 30, 2–12.

Pélabon, C., Joly, P., 2000. What, if anything, does visual asymmetry in fallow deer antlers reveal? Anim. Behav. 59, 193–199.

Pizzari, T., Birkhead, T.R., 2001. For whom does the hen cackle? The function of postoviposition cackling. Anim. Behav. 61, 601–607.

Press, W.H., Teukolsky, S.A., Vetterling, W.T., Flannery, B.P. (Eds.), 1993. Numerical Recipes in C: The Art of Scientific Computing. Cambridge University Press, Cambridge.

Rasmussen, D.R., Farrington, M., 1994. Relationships between position in the central-peripheral structure, age, and the dominance index in the Tanaxpillo colony of stumptail macaques (*Macaca arctoides*). Primates 35, 393–408.

Rintamäki, P.T., Hastad, O., Odeen, A., Alatalo, R.V., Hoglund, J., Lundberg, A., 2002. Sexual selection, colour perception and coloured leg rings in grouse (Tetraonidae). Avian Sci. 2, 145–152.

Rogers, W.H., 1993. sg17: Regression standard errors in clustered samples. Stata Tech. Bull. 3, 88–94.

San Jose, C., Braza, F., 1997. Ecological and behavioural variables affecting the fallow deer mating system in Donana. Ethol. Ecol. Evol. 9, 133–148.

Sauter, C.M., Morris, R.S., 1995. Dominance hierarchies in cattle and red deer (*Cervus elaphus*): their possible relationship to the transmission of bovine tuberculosis. N.Z. Vet. J. 43, 301–305.

Schjelderup-Ebbe, T., 1935. Social behaviour of birds. In: Murchison, C. (Ed.), A Handbook of Social Psychology. Russell and Russell, New York, pp. 947–972.

Schütz, K.E., Jensen, P., 2001. Effects of resource allocation on behavioural strategies: a comparison of red junglefowl (*Gallus gallus*) and two domesticated breeds of poultry. Ethology 107, 753–765.

Siegel, P.B., Haberfeld, T.K., Mukherjee, T.K., Stallard, L.C., Marks, H.L., Anthony, N.B., Dunnington, E.A., 1992. Jungle fowl–domestic fowl relationships: a use of DNA fingerprinting, World's Poult. Sci. J. 48, 147–155.

Siegel, S., Castellan Jr., N.J., 1988. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill Book Company, New York.

StataCorp, 2001. Stata Statistical Software: Release 7.0. Stata Corporation, College Station, TX.

Stevens, L., 1991. Genetics and Evolution of the Domestic Fowl. Cambridge University Press, Cambridge.

Tarvin, K.A., Woolfenden, G.E., 1997. Patterns of dominance and aggressive behavior in blue jays at a feeder. Condor 99, 434–444.

Tinker, M.T., Kovacs, K.M., Hammill, M.O., 1995. The reproductive behavior and energetics of male gray seals (*Halichoerus grypus*) breeding on a land-fast ice substrate. Behav. Ecol. Sociobiol. 36, 159–170.

Troisi, A., Carosi, M., 1998. Female orgasm rate increases with male dominance in Japanese macaques. Anim. Behav. 56, 1261–1266.

Tufto, J., Solberg, E.J., Ringsby, T.-H., 1998. Statistical models of transitive and intransitive dominance structures. Anim. Behav. 55, 1489–1498.

van den Bos, R., De Cock Buning, T., 1994. Social behavior of domestic cats (*Felis lybica, F. catus* L.): A study of dominance in a group of female laboratory cats. Ethology 98, 14–37.

Watts, D.P., 1994. Agonistic relationships between female mountain gorillas (*Gorilla gorilla beringei*). Behav. Ecol. Sociobiol. 34, 347–358.

Weerts, E.M., Miczek, K.A., 1996. Primate vocalizations during social separation and aggression: effects of alcohol and benzodiazepines. Psychopharmacol 127, 255–264.

Weerts, E.M., Tornatzky, W., Miczek, K.A., 1993a. "Anxiolytic" and "anxiogenic" benzodiazepines and beta-carbolines: effects on aggressive and social behavior in rats and squirrel monkeys. Psychopharmacol 110, 451–459.

Weerts, E.M., Tornatzky, W., Miczek, K.A., 1993b. Prevention of the pro-aggressive effects of alcohol in rats and squirrel monkeys by benzodiazepine receptor antagonists. Psychopharmacol 111, 144–152.

White, H., 1980. A heteroskedasticity-consistent covariance matrix estimator and a direct test for heteroskedasticity. Econometrica 48, 817–830.

White, H., 1982. Maximum likelihood estimation of misspecified models. Econometrica 50, 1–25.

Wolff, J.O., 1998. Breeding strategies, mate choice, and reproductive success in American bison. Oikos 83, 529–544.

Wood-Gush, D.G.M., 1955. The behaviour of the domestic chicken: a review of the literature. Br. J. Anim. Behav. 3, 81–110.

Zumpe, D., Michael, R.P., 1986. Dominance index: a simple measure of relative dominance status in primates. Am. J. Primatol. 10, 291–300.

Zumpe, D., Michael, R.P., 1990. Effects of the presence of a second male on pair tests of captive Cyomolgus monkeys (*Macaca fascicularis*): role of dominance. Am. J. Primatol. 22, 145–158.