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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

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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.

Keywords: Social status; Methods; Behaviour in groups

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).

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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). Nonlinear 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 m^2 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.