Choosing an appropriate index to construct dominance hierarchies in animal societies: a comparison of three indices

Alok Bang [a], Sujata Deshpande [a], Annagiri Sumana [b,1], Raghavendra Gadagkar [a,c,*]

[a] Centre for Ecological Sciences, Indian Institute of Science
[b] Indian Institute of Science Education and Research
[c] Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research

A plethora of indices have been proposed and used to construct dominance hierarchies in a variety of vertebrate and invertebrate societies, although the rationale for choosing a particular index for a particular species is seldom explained. In this study, we analysed and compared three such indices, viz Clutton-Brock et al.'s index (CBI), originally developed for red deer, *Cervus elaphus*, David's score (DS) originally proposed by the statistician H. A. David and the frequency-based index of dominance (FDI) developed and routinely used by our group for the primitively eusocial wasps *Ropalidia marginata* and *Ropalidia cyathiformis*. Dominance ranks attributed by all three indices were strongly and positively correlated for both natural data sets from the wasp colonies and for artificial data sets generated for the purpose. However, the indices differed in their ability to yield unique (untied) ranks in the natural data sets. This appears to be caused by the presence of noninteracting individuals and reversals in the direction of dominance in some of the pairs in the natural data sets. This was confirmed by creating additional artificial data sets with noninteracting individuals and with reversals. Based on the criterion of yielding the largest proportion of unique ranks, we found that FDI is best suited for societies such as the wasps belonging to *Ropalidia*, DS is best suited for societies with reversals and CBI remains a suitable index for societies such as red deer in which multiple interactions are uncommon.
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In animal societies individuals often engage in aggressive interactions with each other. When winners and losers are easily identified, such interactions are usually referred to as dominance–subordinate interactions. Based on who wins against whom, all or most individuals can be ranked in a dominance hierarchy. Ever since the discovery of this phenomenon in the domestic chicken, *Gallus gallus*, by Schjelderup-Ebbe (1922), dominance hierarchies have been studied in a large number of vertebrate and invertebrate animal societies. The construction of dominance hierarchies is much more complicated when animals are studied in their natural habitats and are involved in repeated but unequal numbers of interactions and winners and losers may exchange positions. A large number of indices of dominance for such situations have been proposed and compared (Bayly et al. 2006). Perhaps the most important advance in constructing dominance hierarchies for natural situations was made by Clutton-Brock et al. (1979) who

created an index of dominance that considered, for each individual, both direct and indirect wins and losses (direct wins are given by the number of individuals against whom the focal animal wins and indirect wins are given by the total number of individuals against whom each individual that the focal animal wins against in turn wins). This has now come to be known as CBI and is widely used, especially for vertebrate species (Watts 1994; Berdoy et al. 1995; Tinker et al. 1995; Mateos & Carranza 1997; Pizzari & Birkhead 2001).

Nevertheless, a potential problem with CBI is that it measures wins and losses as a qualitative binary decision between any pair of individuals and does not consider the number of wins and losses. David's score (DS) corrects for this drawback in one way by considering the proportion of the interactions of each individual that result in wins or losses (David 1987). Although DS has not yet become very popular, it has recently been strongly recommended with the claim that it is superior to CBI (Gammell et al. 2003). In our studies of the primitively eusocial wasps *Ropalidia marginata* and *Ropalidia cyathiformis*, we have dealt with the same problem by modifying CBI differently, that is, by considering the frequencies of direct and indirect wins and losses (Premnath et al. 1990; Gadagkar 2001). For convenience we refer to this modified CBI as FDI (frequency-based dominance index). In this study, we compared