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THE PERFORMANCE OF DOMINANCE INDICES FOR CONSTRUCTING DOMINANCE HIERARCHIES IN MISCHOCYTTARUS AND POLISTES WASPS (HYMENOPTERA, VESPIDAE)

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Abstract

A common problem during the construction of dominance hierarchies is the occurrence of tied ranks that make it difficult to find correlations between the dominance hierarchy and other biological variables. Among the factors that affect the ability of indices to give unique ranks are the noninteracting pairs of individuals and reversals. Based on these two factors, researchers have compared the performance of dominance indices, among them, the Clutton-Brock index (CBI), an index that measures wins and losses with quality values between pairs of individuals and does not consider the number of wins and losses; the David's score (DS), that corrects for this drawback in one way by considering the proportion of the wins and losses of each individual; and the frequency-based dominance index (FDI), which also consists of a modification of the CBI by considering the frequencies of direct and indirect wins and losses. Since there is no universal index for all interaction networks, comparing different indices could be a helpful step before selecting one for use. Additionally, studies on *Polistes* and *Mischocyttarus* have used different, non-standardized and subjective ways to access dominance hierarchies. In this study, we first described the proportion of non-interacting pairs and reversals in colonies of the social wasps *Mischocyttarus cassununga*, *Mischocyttarus cerberus*, *Polistes simillimus* and *Polistes versicolor*. Then, the efficiencies of 3 dominance indices, CBI, DS and FDI in given unique ranks (absence of tied ranks) were compared.

Key Words: Dominance behavior; Dominance rank; *Mischocyttarus cassununga*; *Mischocyttarus cerberus*; *Polistes simillimus*; *Polistes versicolor*

Resumo

Um problema comum durante a construção de hierarquias de dominância é a ocorrência de ranks empatados, que dificulta o encontro de correlações entre a hierarquia de dominância e outras variáveis biológicas. Entre os fatores que afetam a habilidade dos índices em gerar ranks únicos estão os pares de indivíduos que não interagem e as reversões. Baseado nesses dois fatores, pesquisadores têm comparado a performance de índices de dominância, entre eles, o índice de Clutton-Brock (CBI), que mede vitórias e derrotas com valores de qualidade entre pares de indivíduos e não considera o número de vitórias e derrotas; David`score (DS), que corrige o índice anterior por considerar as proporções de vitorias e derrotas de cada indivíduo, e o índice de dominância baseado na freqüência (FDI), que também consiste em uma modificação do CBI por considerar as freqüências diretas e indiretas de vitórias e derrotas. Uma vez que não existe um índice universal para todas as redes de interações, comparar diferentes índices é um passo útil para considerar seu uso. Em adição, estudos com *Polistes* e *Mischocyttarus* têm utilizado métodos diferentes, não padronizados e subjetivos para acessar a hierarquia de dominância. Nesse estudo, nós primeiro descrevemos as proporções de pares de indivíduos que não interagem e a proporção de reversões em colônias das vespas sociais *Mischocyttarus cassununga*, *Mischocyttarus cerberus*, *Polistes simillimus* and *Polistes versicolor*. Em seguida, a eficiência dos 3 índices de dominância, CBI, DS e FDI em gerar ranks únicos (ausência de ranks empatados) foi comparada.

Translation provided by authors.

In primitively eusocial societies like those of Polistinae wasps, work regulated by aggression is widespread (Pardi 1948; West-Eberhard 1969; Jeanne 1972; Reeve 1991; O'Donnell 1998; Gadagkar 2001; Lamba et al. 2008). In such cases, a dominance hierarchy is established according to the aggressiveness of each individual, determining the division of labor in the colonies. One can detect the relationship between aggression and division of labor by correlating the hierarchical

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position of individuals and the frequency in which they perform specific tasks (De Souza et al. 2008). A common problem during the construction of dominance hierarchies is the occurrence of tied ranks that prevent the total ordering of individuals, and consequently, prevent the correlation of dominance hierarchy with other biological variables. Thus, a good method for constructing such hierarchies should generate as few tied ranks as possible. Several dominance indices have been proposed (Bayly et al. 2006), among them, the Clutton-Brock Index (CBI), an index that measures wins and losses with quality values between pairs of individuals, and does not consider the number of wins and losses (Clutton-Brock et al. 1979). Another index, David's Score (DS), corrects for this drawback in one way by considering the proportion of the wins and losses of each individual (David 1987). Finally, the frequency-based dominance index (FDI), which also consists of a modification of the CBI, by considering the frequencies of direct and indirect wins and losses (Premnath et al. 1990).

To our knowledge, the sole study concerned in electing an appropriate index to construct dominance hierarchies in social wasps was conducted recently by Bang et al. (2010). They found that non-interacting pairs of individuals and reversals affect the performance of dominance indices. So, it is important to consider these 2 parameters when choosing the best index. They elected the FDI for *Ropalidia marginata* and *Ropalidia cyatiformis*. These paper wasps have a very particular social organization system, because, differently from other primitively eusocial wasps, queens are never at the top of the hierarchy, and aggression is not related to reproduction, but is used by workers to regulate foraging activity (Premnath et al. 1995, 1996; Gadagkar 2001; Lamba et al. 2008). On other hand, the widespread *Polistes* and the more restricted *Mischocyttarus* genera have social organization systems in which the queens are the most aggressive individuals, occupying the top positions in the hierarchy. In *Polistes* aggression is used to regulate reproduction, while in *Mischocyttarus* aggression is additionally used to regulate foraging behavior and resource sharing (Pardi 1948; West-Eberhard 1969; Jeanne 1972; Reeve 1991; O'Donnell 1998).

Given the diversity of social organization systems in wasps, additional studies with other species of wasps are desirable. In fact, Bang et al. (2010) highlight that there is no universal index for all interaction networks. In this way, comparing different indices for a given species could be a helpful step before its use. Additionally, studies on *Polistes* and *Mischocyttarus* have used different, non-standardized and subjective ways to access dominance hierarchy (Noda et al. 2001; Prezoto et al. 2004; Oliveira et al. 2006; De Souza et al. 2010). In this study, we first described the proportion of noninteracting pairs and reversals in colonies of the social wasps *Mischocyttarus cassununga*, *Mischocyttarus cerberus*, *Polistes simillimus* and *Polistes versicolor*. Then, the efficiencies of the 3 dominance indices, CBI, DS and FDI in given unique ranks (absence of tied ranks) were compared to determine the best dominance index for each of these societies.

Materials and Methods

Tables listing frequencies of dominance behavior for all possible pairs of individuals were obtained by video recordings in 31 colonies of 4 neotropical social wasp species in Brazil. In the municipality of Rio Claro, São Paulo State, we observed 7 *M. cerberus* colonies containing 8 ± 4 (3-15) individuals for a total of 113 h between Sep 1998 and May 1999. In the municipality of Juiz de Fora, Minas Gerais State, we observed 13 *P. versicolor* colonies containing 13 ± 6 (5 - 23) individuals for 107 h from Nov 2009 to Oct 2010, 5 *P. simillimus* colonies with 10 ± 7 (3-22) individuals for 25 h during Mar to Sep 2006, and 6 colonies of *M. cassununga* with 4 ± 1 (3-8) individuals for 60 h from Nov 2008 to Nov 2009. Before recordings, each female received a paint dot on the thorax, allowing her to be identified. The dominance behavior was defined as aggressive contact of a target wasp with another, for example, when an individual rushed or with her mandible bit part of the body of another wasp (Noda et al. 2001; Grazinoli et al. 2010).

By just comparing unique ranks given by the 3 indices for each one of the 4 species we were not able to select the best index (Mann-Whitney test: U = 12.00-37.50; P = 0.28-1.00). Thus, we decided to compare the performance of indices according to the number of non-interacting pairs and the number of reversals observed for each species. This procedure is the same as that used by Bang et al. 2010.

For each studied colony, the proportion of non-interacting pairs of individuals and the proportion of reversals were registered and the 3 dominance indices, CBI as described in Clutton-Brock et al. (1979), DS as described in David (1987) and FDI as described in Premnath et al. (1990), were computed. Both indices are described in detail in Bang et al., 2010. Since the proportion of non-interacting pairs of individuals and the proportion of reversals were statistically indistinguishable between the 4 species (Mann-Whitney test: U = 14.00-45.50; P = 0.23-0.89) we decided to analyze these data considering all colonies together.

Using each one of the 3 indices, dominance hierarchies were constructed by arranging all individuals in decreasing order of their value of the index and assigning them in ranks from 1 to n, where n is the number of individuals. When 2 or more individuals obtained the same rank, they

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were ranked as follows. If 2 individuals were tied at the first position, they were both given rank 1.5 and the next individual was given rank 3. Similarly, if 3 individuals were tied at the 7th position, they were each given rank 8 and the next individual was given rank 10.

Data were compared by using Man-Whitney or Spearmann's correlation test, because the data did not fit the assumptions of parametrical tests. In all tests were a 5% significance level was adopted. We used BioEstat version 5.0.

Results

The analysis of tables of dominance and subordination interactions in *M. cassununga*, *M. cerberus*, *P. simillimus* and *P. versicolor* showed that these societies have a proportion of non-interacting pairs around 75 ± 17 (25-96)%, and a proportion of reversals around 6 ± 10 (0-34)% (Fig. 1). The proportion of non-interacting pairs affected the performance of the 3 indices (Fig. 1). Thus, in the range of 20-40%, DS gave a higher proportion of unique ranks. However, statistical comparison was not possible because there were only 2 colonies in this range. In the range of 40-60% (n = 3 colonies) and 80-100% (n = 14 colonies), there were no statistical differences in the number of unique ranks generated by each index (Mann-Whitney U = 3.5-91, $P > 0.05$). The only range where statistical differences were observed was 60-80% (n = 12 colonies), where FDI gave a greater proportion of unique ranks than either DS (U = 41.50, $P < 0.05$) or CBI (U = 34.50, $P < 0.05$). DS and CBI did not differ in this range (U = 63.50, $P > 0.05$).

The proportion of reversals also affected the performance of the indices (Fig. 1). Between 0-20% of reversals, FDI generated a greater number of ranks than DS (U = 249.00, $P < 0.05$) and CBI (U = 217.00, $P < 0.05$). DS and CBI did not differ in this range (U = 338.00, $P > 0.05$). In the range of 20-40% of reversals, there was no significant differences (U = 8.12, p > 0.05).

There was no correlation between group size and the performance of the indices in giving unique ranks (Spearmann correlation test: r = 0.11-0.35, P = 0.31-0.57).The ranks given by each index in each colony were always positively correlated (Table 1). In general, this correlation was significant. Exceptions were observed for colonies with less than 5 individuals (4 *M. cassununga*, 2 *M. Cerberus*, 3 *P. simillimus* and 2 *P. versicolor* colonies). Although this correlation was not always significant, the ordering of each individual in the hierarchy was never changed.

Discussion

Colonies of the neotropical social wasps *M. cassununga*, *M. cerberus*, *P. simillimus* and *P. versicolor* are characterized by a high proportion of non-interacting pairs and a lower proportion of reversals. The first can be explained, in part, by the presence of recently emerged individuals who rarely engage in aggressive interactions in their first days of life. In addition, some individuals leave to forage and remain outside the nest for a variable period of time (De Souza et al. 2008), which changes the probability of occurrence of such interactions. Finally, Noda et al. (2001) identified the presence of neutral individuals, the future queens, who do not engage in aggressive interactions.

The ability of dominance indices to give unique ranks may vary depending on the proportion of non-interacting pairs and reversals. Under these conditions, how can an appropriate index be selected to construct dominance hierarchies in neotropical social wasps? For the 4 studied social wasps species, the average proportion of non-interacting pairs was around 75% (Fig. 1). This value is contained in the range of 60-80%. Upon comparing the performance of the 3 indices in this range, it was observed that the FDI generates more unique ranks than either the DS or the CBI (Fig. 1). Bang et al. (2010) applied the same indices to *R. cyatiformis* and *R. marginata* and found that when the proportion of non-interacting pairs was 75% or more, the FDI gave more unique ranks than either the DS or the CBI. Their finding is corroborated by the results of this study. In addition, in the 4 studied species the proportion of reversals was around 6% (range of 0-20%), and in this range the FDI was also more efficient than either the DS or the CBI in giving unique ranks.

The fact that the ranks given by the indices are correlated with each other and that the positions

Table 1. Mean values and range of Spearmann correlation coefficient (r) between the three dominance indices, FDI, CBI and DS for four eusocial wasp species.

	FDI-DS	FDI-CBI	DS-CBI
M. cassununga	0.93 (0.87-1)	0.96 (0.87-1)	0.95 (0.86-1)
M. cerberus	0.92 (0.85-1)	0.92 (0.86-1)	1 (0.99-1)
P. similimus	0.94 (0.77-1)	1 (1-1)	0.94 (0.77-1)
P. versicolor	0.97 (0.91-1)	0.97 (0.91-1)	0.98 (0.93-1)

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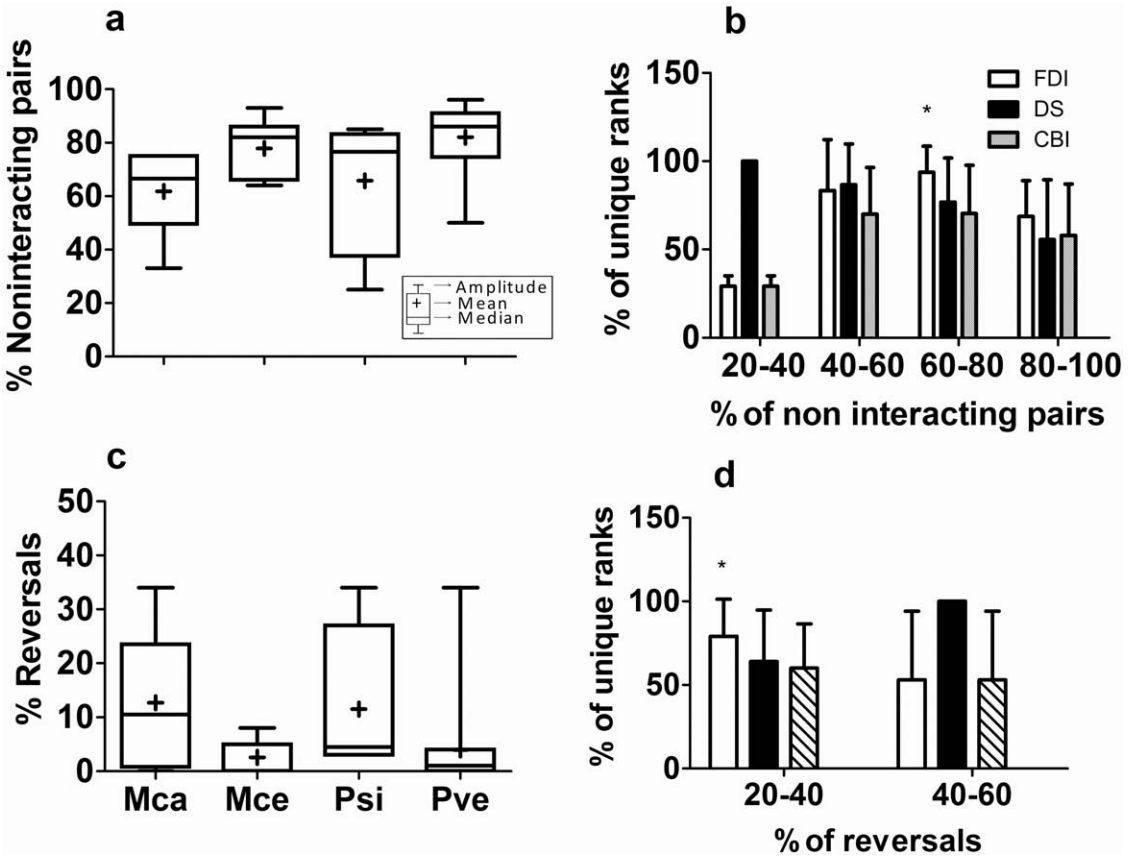


Fig. 1. To the left, the proportion of non-interacting pairs (a) and reversals (c) in colonies of *M. cassununga* (Mca), *M. cerberus* (Mce), *P. simillimus* (Psi) e *P. versicolor* (Pve). To the right, the proportion of unique ranks given by three dominance indices (FDI, DS and CBI), according to the proportion of noninteracting pairs (b) and reversals (d). * indicates statistically significant difference between thee indices (Mann-Whitney test, $P < 0.05$).

of individuals in the hierarchies was the same for the 3 indices was comforting and validates our comparison. The lack of correlation between group size and the performance of indices suggest that non-interacting pairs and reversals seem to be adequate parameters to choose an appropriate index. Thus, in societies with a high proportion of non-interacting pairs and a low proportion of reversals, such as *Mischocyttarus*, *Polistes*, and *Ropalidia*, the best index to construct dominance hierarchies is the FDI.

In some previous studies involving *M. cassununga* (Prezoto et al. 2004), *M. cerberus* (Noda et al. 2001), *P. versicolor* (Oliveira et al. 2006), *P. simillimus* (Grazinoli et al. 2010) and *Polistes ferreri* (De souza et al. 2010), the authors constructed dominance hierarchies in a more subjective way, because they did not use an index. However we strongly defend the use of an objective and standardized method, and the FDI seems to be a largely applicable index to construct dominance hierarchies in primitively eusocial wasps.

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