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

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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

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CBI, DS and FDI because we wished to (1) examine the claim by Gammell et al. (2003) that DS is superior to CBI and (2) evaluate FDI as routinely used by us, in relation to CBI and DS.

METHODS

For comparing the three indices of dominance, namely, CBI, DS and FDI, we used both natural and artificially generated data sets.

Natural Data Sets

Our natural data sets come from observation of colonies of the primitively eusocial wasps *R. marginata* and *R. cyathiformis*. Six colonies of each species (colony sizes ranged from 12 to 34 adult wasps for *R. marginata* and 13 to 25 adult wasps for *R. cyathiformis*) were observed first in their natural queenright conditions and then in the queenless condition (created by experimentally removing the queen), thus yielding 24 data sets. We considered data on queenright and queenless colonies separately because the structure of dominance hierarchies can differ under these two conditions (Sumana & Gadagkar 2001). The species, the colonies and the observation methods are all described in Sumana & Gadagkar (2001) for *R. marginata* and in Kardile & Gadagkar (2003) for *R. cyathiformis*. In these wasp species, nine types of dominance behaviours can be recognized: aggressive bites, attack, chase, crash, hold in mouth, nibble, peck, sit over and being offered liquid. We summed the frequencies/h of each to yield the frequency/h of dominance behaviour. Similarly, we summed the frequencies/h of the nine corresponding subordinate behaviours to yield the frequency/h of subordinate behaviour (for a description of the dominance and subordinate behaviours, see Gadagkar 2001).

Artificial Data Sets

Natural colonies of *R. marginata* and *R. cyathiformis* have a small percentage of pairs showing reversals in wins and losses (mean $\pm$ SD $=$ 0.06 $\pm$ 0.14%) and a large percentage of pairs that do not interact with each other (89 $\pm$ 4%). To generate more variation in percentage of reversals and of noninteracting pairs, we created artificial data sets in which 5%, 10%, 25%, 50%, 75% or 95% of the pairs showed reversals or did not interact at all. Each artificial data set consisted of a 20 $\times$ 20 matrix whose cells could all potentially be filled except the 20 diagonal cells. Three kinds of data sets were generated.

For data sets to be used as controls, 190 random integers between 1 and 10 were generated using the MS-Excel random number generator function. These 190 numbers were input in the diagonal bottom half of the matrix, so that the cells in that part of the interaction matrix were occupied and cells above the diagonal were unoccupied. Thus, in the control data sets, all the individuals interacted with each other without any reversals. Six such data sets were generated.

For data sets with noninteracting pairs, control data sets were first generated as above and then depending on the percentages of noninteracting pairs, that is, 5%, 10%, 25%, 50%, 75% and 95% noninteracting pairs, the contents of 9, 19, 48, 95, 142 and 180 cells, out of the 190 filled cells, respectively, were replaced with zeros. The positions of cells with zeros were chosen randomly by drawing random numbers between 1 and 190. Six data sets for each percentage of noninteracting pairs were thus generated.

For data sets with reversals, control data sets were first generated in the same manner and then depending on the desired percentage of reversals, that is, 5%, 10%, 25%, 50%, 75% and 95% pairs, 9, 19, 48, 95, 142 and 180 cells, out of 190 cells, were chosen randomly. Randomly chosen values between 1 and 10 were input in the corresponding diagonally opposite cells. Six data sets for each percentage of reversals were thus generated.

Calculation and Comparison of Dominance Indices

For each natural and artificial data set, the three indices of dominance viz, 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 as follows.

CBI

CBI for each member of a group was calculated with the formula:

$$\mathrm{CBI} = (B + b + 1)/(L + l + 1)$$

where B = number of individuals whom the subject dominates, b = number of individuals whom those dominated by the subject in turn dominate, L = number of individuals who dominate the subject, l = number of individuals who dominate those dominating the subject. For an illustrated example, see Table 1.

DS

DS for each member of a group was calculated with the formula:

$$\mathrm{DS} = w + w_2 - l - l_2$$

where w = sum of proportion of wins by the subject, w_2 = sum of weighted proportion of wins of the individuals against whom the subject has won, l = sum of proportion of losses by the subject, l_2 = sum of weighted proportion of losses of the individuals against whom the subject has lost. To calculate w_2 and l_2, weight is given by multiplying an opponent's proportion of wins or losses by its respective w or l value. For an illustrated example, see Table 2.

FDI

FDI for each member of a group was calculated with the formula:

$$\mathrm{FDI} = \frac{\sum_{i=1}^{n} Bi + \sum_{i=1}^{n} \sum_{j=1}^{m} b_{ij} + 1}{\sum_{i=1}^{p} Li + \sum_{i=1}^{p} \sum_{j=1}^{q} l_{ij} + 1}$$

where $\sum B_i$ = the rate at which the subject shows dominance behaviour towards colony members and n is the number of individuals over which the subject shows dominance, $\sum b_{ij}$ = the sum of the rates at which all individuals dominated by the subject in turn show dominance behaviour towards colony members and m for each summation is the number of individuals over which the

Table 1
Computation of the Clutton-Brock index, CBI, for each member of a hypothetical interaction matrix involving animals α, β, γ and δ

		Win					
		α	β	γ	δ	*L*	*l*
Loss	α	—	1	0	2	2	4
	β	1	—	4	0	2	5
	γ	2	2	—	3	3	6
	δ	3	0	1	—	2	5
	B	3	2	2	2		
	b	6	5	4	5		
	CBI	1.43	1	0.7	1		

The numbers in the 4 $\times$ 4 matrix are the numbers of wins/losses between the animals mentioned in the column and row headings. B = number of individuals whom the subject dominates, b = number of individuals whom those dominated by the subject in turn dominate, L = number of individuals who dominate the subject, l = number of individuals who dominate those dominating the subject.

Table 2
Computation of David's score, DS, for each member of a hypothetical interaction matrix involving animals α, β, γ and δ

		Win					
		α	β	γ	δ	l	l_2
Loss	α	—	1 (0.50)	0 (0.00)	2 (0.40)	0.90	0.93
	β	1 (0.50)	—	4 (0.67)	0 (0.00)	1.17	1.84
	γ	2 (1.00)	2 (0.33)	—	3 (0.75)	2.08	1.92
	δ	3 (0.60)	0 (0.00)	1 (0.25)	—	0.85	1.06
	w	2.10	0.83	0.92	1.15		
	w_2	2.03	1.35	0.84	1.53		
	DS	2.30	−0.83	−2.24	0.77		

The numbers in the 4 × 4 matrix are the numbers of wins/losses between the animals mentioned in the column and row headings. The numbers in parentheses denote proportions of wins or losses of the appropriate pairs. w = sum of proportion of wins by the subject, w_2 = sum of weighted proportion of wins of the individuals against whom the subject has won, l = sum of proportion of losses by the subject, l_2 = sum of weighted proportion of losses of the individuals against whom the subject has lost. To calculate w_2 and l_2, weight is given by multiplying an opponent's proportion of wins or losses by its respective w or l value.

individual in question shows dominance, $\sum L_i$ = the rate at which the subject shows subordinate behaviour towards colony members and p is the number of individuals to which the subject shows subordinate behaviour, $\sum l_{ij}$ = the sum of the rates at which those individuals towards whom the subject shows subordinate behaviour in turn show subordinate behaviour towards other colony members and q is the number of individuals to whom the individual in question shows subordinate behaviour. For an illustrated example, see Table 3.

Using each of the indices, we constructed dominance hierarchies by arranging all individuals in decreasing order of their value of the index and assigning them ranks from one to n, where n is the number of individuals. When two or more individuals obtained the same rank, they were tied as follows. If two individuals were tied at the first position, they were both given rank 1.5 and the next individual was given rank 3. Similarly, if three individuals were tied at the 20th position, they were each given rank 21 and the next individual was given rank 23. The ranks obtained by different individuals with the different dominance indices were compared using Kendall's rank correlation with Statistica 7 (StatSoft, Tulsa, OK, U.S.A.). In addition, the numbers of unique ranks (absence of tied ranks) obtained by each index were calculated and compared using the Wilcoxon signed-ranks test, in Statistica 7.

Table 3
Computation of the frequency-based index of dominance, FDI, for each member of a hypothetical interaction matrix involving animals α, β, γ and δ

		Win					
		α	β	γ	δ	$\sum L_i$	$\sum l_{ij}$
Loss	α	—	1	0	2	3	9
	β	1	—	4	0	5	10
	γ	2	2	—	3	7	12
	δ	3	0	1	—	4	10
	$\sum B_i$	6	3	5	5		
	$\sum b_{ij}$	13	11	8	11		
	FDI	1.54	0.94	0.70	1.13		

The numbers in the 4 × 4 matrix are the numbers of wins/losses between the animals mentioned in the column and row headings. $\sum B_i$ = the rate at which the subject shows dominance behaviour towards colony members and n is the number of individuals over which the subject shows dominance, $\sum b_{ij}$ = the sum of the rates at which all individuals dominated by the subject in turn show dominance behaviour towards colony members and m for each summation is the number of individuals over which the individual in question shows dominance, $\sum L_i$ = the rate at which the subject shows subordinate behaviour towards colony members and p is the number of individuals to which the subject shows subordinate behaviour, $\sum l_{ij}$ = the sum of the rates at which those individuals towards whom the subject shows subordinate behaviour in turn show subordinate behaviour towards other colony members and q is the number of individuals to whom the individual in question shows subordinate behaviour.

RESULTS

Similarity in Dominance Ranks

Natural data sets

Ropalidia marginata queenright and queenless colonies showed significant positive correlation (Kendall's rank correlation: $P < 0.05$) between the dominance ranks attributed by the three indices, when the colonies were analysed separately as well as when data from all colonies were pooled (Table 4).

The same trend was observed in *R. cyathiformis* queenright and queenless colonies, where significant positive correlation was seen (Kendall's rank correlation: $P < 0.05$) between the dominance ranks attributed by the three indices, when the colonies were analysed separately as well as when pooled (Table 4).

In both species, queenright colonies showed higher tau values than queenless colonies and in both queenright and queenless colonies, the ranks given by CBI and DS were better intercorrelated than were the ranks given by FDI.

Artificial data sets

In control data sets, all the indices showed 100% agreement in assigning ranks (Kendall's rank correlation: $\tau = 1$, $P < 0.001$).

Significant positive correlation was seen between the ranks attributed by the three indices for all proportions of noninteracting pairs (Fig. 1). The agreement between FDI and CBI and between FDI and DS decreased with increasing numbers of individuals that did not interact, whereas it did not have any effect on the agreement between ranks given by CBI and DS.

For pairs showing reversals, a significant positive correlation was seen between the ranks attributed by the three indices for different levels of reversals, except for 95% pairs showing reversals, where FDI and CBI were significantly positively correlated but their respective correlations with DS broke down (Fig. 1). Thus, the agreement between FDI and DS and between CBI and DS decreased with increasing numbers of individuals that showed reversals, whereas it did not seem to have any effect on the agreement between FDI and CBI.

Number of Unique Ranks

Natural data sets

In all natural data sets for both species, FDI gave significantly more unique ranks than both CBI and DS; the latter two indices were indistinguishable in this regard, except in queenright *R. marginata* colonies where CBI gave more unique ranks than DS (Mann–Whitney U test: $P < 0.05$; Fig. 2).

Table 4
Values of Kendall's rank correlation coefficient (τ) between the three dominance indices, FDI, CBI and DS, in natural data sets

Type of colony	Comparison		
	FDI–CBI	FDI–DS	CBI–DS
R. marginata queenright	0.78–0.94 (0.88)	0.80–0.96 (0.90)	0.77–0.96 (0.94)
R. marginata queenless	0.58–0.83 (0.63)	0.58–0.84 (0.72)	0.82–1.00 (0.89)
R. cyathiformis queenright	0.82–0.99 (0.87)	0.81–1.00 (0.89)	0.95–0.99 (0.97)
R. cyathiformis queenless	0.71–0.87 (0.77)	0.55–0.87 (0.73)	0.53–1.00 (0.91)

For each category, the range of τ values is given along with the median in parentheses. All comparisons are significant and positive ($P < 0.05$).

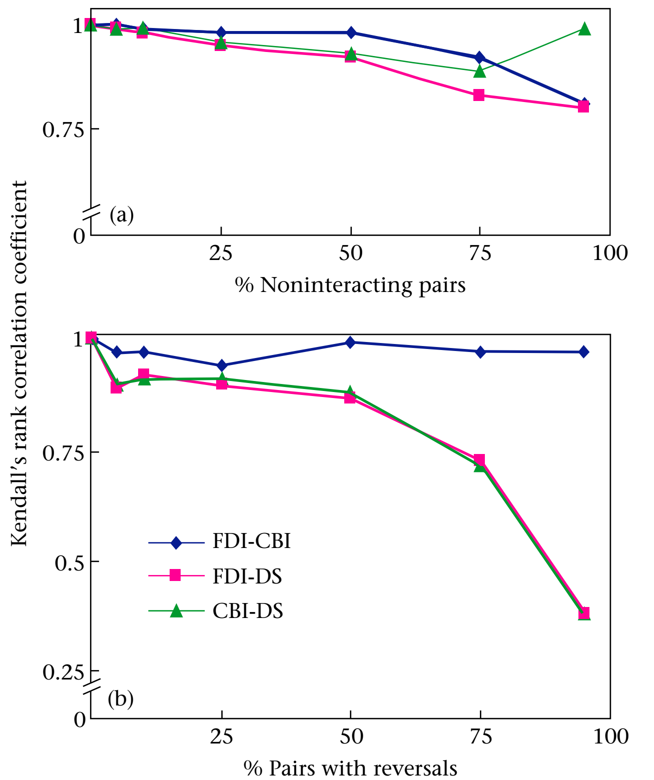

Figure 1. Values of Kendall's rank correlation coefficient (τ) between the three dominance indices, FDI, CBI and DS, pooled over artificial data sets with varying percentages of (a) noninteracting pairs and (b) pairs showing reversals.

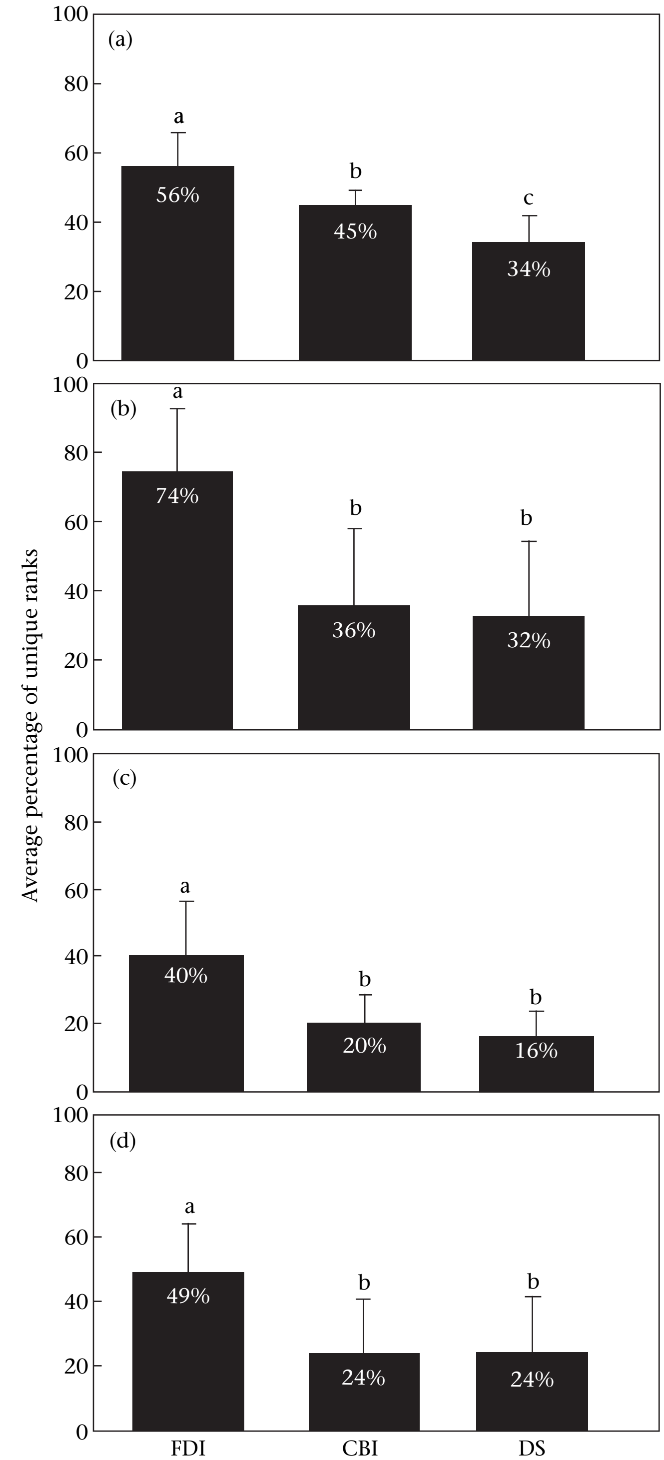

Figure 2. The average percentage of unique ranks attributed by the three dominance indices, FDI, CBI and DS, in (a) queenright and (b) queenless colonies of *R. marginata* and in (c) queenright and (d) queenless colonies of *R. cyathiformis*. Bars with different letters (a, b) are significantly different from each other ($P < 0.05$; Mann–Whitney *U* test: $U = 1.00–16.5$).

Artificial data sets

For artificial data sets with noninteracting pairs, FDI once again emerged as the best index that gave the maximum number of unique ranks. All the ranks given by FDI were untied between 0 and 75% noninteracting pairs. Beyond that, at 95% noninteracting pairs, it dropped to about 50% unique ranks on average. CBI was the second best index in terms of unique ranks with almost 100% unique ranks between 0 and 50% noninteracting pairs beyond which it fell to 15% unique ranks at 95% noninteracting pairs. DS gave the fewest unique ranks, as all the ranks given were unique only between 0 and 10% noninteracting pairs. Beyond that it fell to about 12% unique ranks on average, for 95% noninteracting pairs (Fig. 3).

For artificial data sets with reversals, all three indices showed considerable agreement between 0 and 75% pairs showing reversals, wherein every index attributed nearly 100% unique ranks. Beyond that, at 95% pairs showing reversals, DS gave 98% unique ranks on average, followed by FDI with 50% unique ranks on average, followed by CBI with 23% unique ranks on average (Fig. 3).

Effect of Number of Interactions on Analysis

It is possible that differences in number of unique ranks given by the three indices arose because of inadequate sampling effort. In such a case, an index would not be able to distinguish between two individuals with similar dominance profiles for lack of adequate number of interactions. To avoid any such possibility, we simulated artificial data sets in the same way as stated in the Methods, except that the interaction frequency was now set between 1 and 100 instead of between 1 and 10. The prediction was that if the interaction frequency of 1–10 was not enough for an index to give unique ranks, with an increased interaction frequency of 1–100, the number of unique ranks attributed by the index would go up. On the other hand, if the interaction frequency of 1–10 was optimal, with increased interaction frequency, the number of unique ranks would remain the same. Note that in this section, the comparison is not between the indices, but between the two types of data sets with different interaction frequencies for every index.

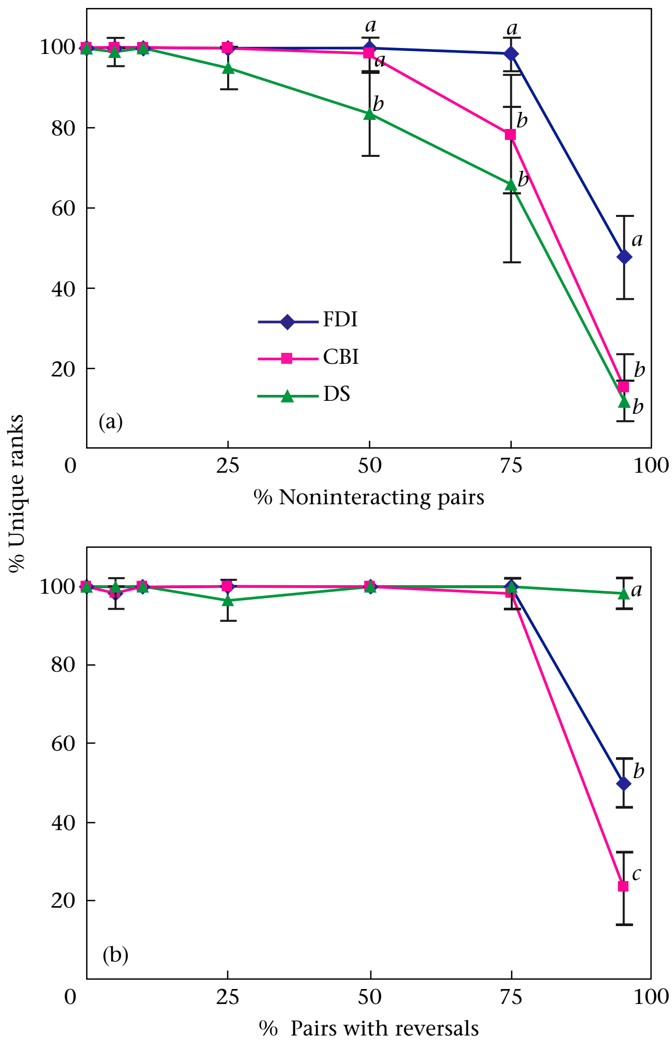

Figure 3. The average percentage of unique ranks attributed by the three dominance indices, FDI, CBI and DS, in artificial data sets with varying percentages of (a) noninteracting pairs and (b) pairs showing reversals. Different letters (a, b) indicate that the comparisons are significantly different ($P < 0.05$; Mann–Whitney U test).

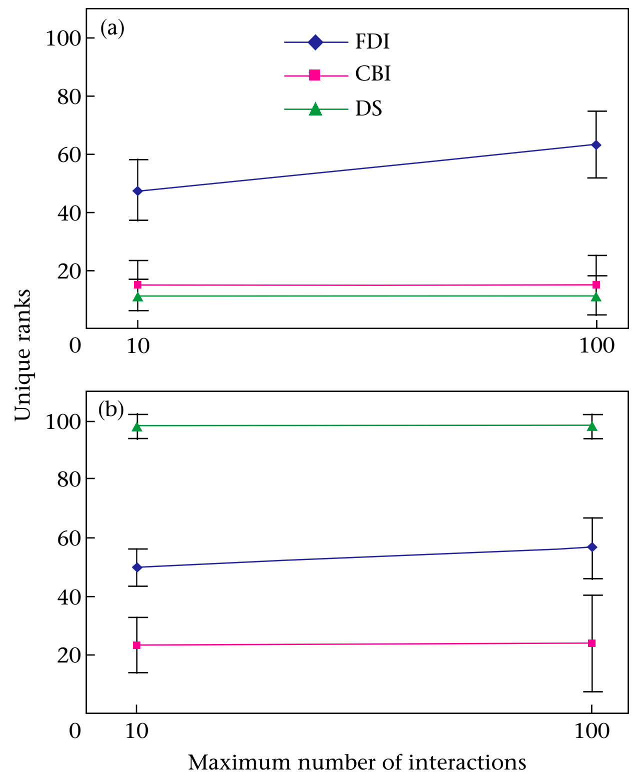

Figure 4. Effect of number of interactions on the number of unique ranks given by the three dominance indices, FDI, CBI and DS, in data sets with (a) 95% noninteracting pairs and (b) 95% pairs with reversals.

This part of the analysis was carried out for only two categories of data sets: data sets with 95% noninteracting pairs and 95% pairs showing reversals, as only for these two categories was the percentage of unique ranks less than 100% for all the indices (Fig. 3).

Although there was no significant change in the number of unique ranks attributed by each of the three indices for 95% no interactions and 95% reversals, there were some interesting trends. With CBI and DS, the numbers of unique ranks were unchanged (Wilcoxon signed-ranks test: $P > 0.75$). With FDI, however, the number of unique ranks increased, although only with marginal significance (Wilcoxon signed-ranks test: $P = 0.06$ for 95% noninteracting pairs and $P = 0.1$ for 95% pairs showing reversals; Fig. 4). This result showed that given more sampling effort, FDI would give an even higher number of unique ranks, whereas the number of unique ranks given by CBI and DS would remain unchanged.

DISCUSSION

It is comforting to see that the dominance ranks attributed by all three indices are positively and significantly correlated with each other. Indeed, in control artificial data sets, the correlations were always perfect (1.00). In natural data sets, the correlation values, although significant, were somewhat lower in magnitude (mean ± SD = 0.84 ± 0.12). Two obvious differences between natural and artificial data sets are that the former have several noninteracting pairs, and occasional reversals in who wins and who loses in a pair of interacting individuals. Artificial data sets with varying proportions of noninteracting pairs and reversals had lower correlations mimicking the natural data sets and thus confirmed that the reduction could be attributed to these differences between natural and control artificial data sets. Nevertheless, the ranks attributed by each of the indices were always positively and significantly correlated, even when the data sets had noninteracting pairs and reversals.

From the above analysis all three indices seem to yield very similar results. How then does one choose between the three indices for empirical studies? In constructing dominance hierarchies one sometimes encounters the problem of tied ranks, which make it difficult to correlate dominance ranks with other biological variables. An index that gives the largest number of unique ranks is therefore preferable to one that gives many tied ranks. We therefore compared the numbers of unique (untied) ranks attributed by the three indices. In control artificial data sets, all the indices gave 100% unique ranks, indicating that in interaction networks where all individuals interact and the dyadic dominance direction is always one way (with no reversals), the indices are indistinguishable even by this criterion. The situation with natural data sets and artificial data sets with varying proportions of noninteracting pairs and reversals, however, is very different, permitting us to choose between the three indices.

Thus for species such as *R. marginata* and *R. cyathiformis* where most of the pairs do not interact, and among those that do there are very few reversals, FDI can be recommended as the best choice. Artificial data sets confirm that this superiority of FDI over the other two indices persists even when 95% of the pairs do not interact and even when there are as many as 75% reversals. Similarly, the inferiority of CBI and DS in giving more tied ranks is not attributable to inadequate sampling because FDI gives fewer tied ranks at both low (10 interactions) and high (100 interactions) sampling effort. However FDI gives fewer unique ranks than DS at very high rates of reversals (>75% reversals). Moreover, in the special case when the individuals in a pair show reversals between each other and show dominance behaviour towards the same set of individuals and subordinate behaviour towards the same set of individuals, FDI attributes the same index value to both of the individuals regardless of the win–loss asymmetry between them. This is independent of the rate of reversals. FDI should therefore be avoided in such situations.

DS is best suited for societies with reversals in direction of dominance, especially when more than 75% of the interacting pairs show reversals. FDI and CBI cannot withstand very high rates of reversals, and when 100% of pairs show reversals, both the indices give zero unique ranks. Unlike FDI and DS, CBI does not consider either frequency or proportion of agonistic interactions and hence ignores information regarding the magnitude of agonistic interactions. Nevertheless, CBI, which was originally formulated for red deer, *Cervus elaphus*, a species in which multiple interactions are uncommon (Clutton-Brock et al. 1979), remains suitable for such animal societies. Moreover, when only qualitative data on the interaction between two individuals are available and no information on the rate of interactions is available, CBI may be the best option available. After the completion of this study it was brought to our attention that de Vries et al. (2006) have proposed an index adapted from DS that appears to combine the advantages of both FDI and DS when there are many reversals and/or many noninteracting pairs. This index is similar to DS but based on the dyadic dominance index corrected for chance (called *Dij*) rather than on the simple proportion of wins *Pij*. See de Vries et al. (2006) for details.

We are not advocating any single dominance index as the universal solution for all interaction networks in all species because DS is useful for species in which there are many pairs showing reversals, FDI is useful for species in which there many noninteracting pairs and CBI is useful in the absence of information on rates of interaction. Thus we believe that different indices would be suitable for different species and it would therefore be useful to examine such features of the species under study such as numbers of noninteracting pairs and numbers of reversals before choosing an appropriate index to construct dominance hierarchies.

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