Etología, 4:69-75 (1994)

The use of correspondence analysis to generate cardinal dominance ranks

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ABSTRACT. *The use of correspondence analysis to generate cardinal dominance ranks.*- Several methods have been developed for obtaining cardinal dominance indices. These measures are mostly based on the number of times that an individual wins agonistic encounters. However, since it may be sometimes difficult to decide who has won an encounter and to choose the most appropriate behaviours, and since summarising a relationship in terms only of who wins encounters also has the disadvantage of a loss of potentially valuable information that could define the relationships more precisely, we propose here the use of a multivariate eigenvector method (Correspondence Analysis, CA) based on the matrix relating the different individuals of the group to the different agonistic behaviours used. This approach is conceptually similar to the use of PCA to work out an overall size measure from biometrical linear measurements. The method is illustrated using data from a group of captive Siskins (*Carduelis spinus*).

KEY WORDS. Dominance measurement, Dominance rank, Correspondence analysis

Introduction

The measurement of dominance status is of central importance in modern behavioural ecology. Commonly assessment of dominance relationships involves constructing a dyadic interaction matrix in which individuals are ordered in accordance with the number of individuals in the group that they defeat in agonistic encounters, so that the ordinal dominance ranks so obtained correspond to the number of individuals in the group that they dominate (e.g. Lehner, 1979). However, the use of ordinal ranks presents several drawbacks, since it is difficult to assess the magnitude or the significance of the difference in degree of dominance between two individuals, and it is often inappropriate to use parametric statistical techniques to relate dominance rank to other measures of interest (see Boyd & Silk, 1983 for a review). Several authors have therefore devised different methods for obtaining cardinal dominance indices rather than the traditional ordinal ones (Boyd & Silk, 1983; McMahan & Morris, 1984). However, these cardinal measures of dominance are mostly based on the number of times that an individual wins agonistic encounters against other group companions (e.g. Boyd & Silk, 1983; McMahan & Morris, 1984; Arcese & Ludwing, 1986). Since the success rate of an individual in an encounter can depend in part on the tactics it uses (e.g. Popp, 1987a,b; Senar et al., 1989, 1992), variation in its choice of behaviour can lead to different dominance scores (Rushen, 1983; Benton et al., 1980, Keys & Rothstein, 1991). In addition, it may be difficult to decide who has won an encounter, so that assessments may become subjective. Summarising a relationship in terms only of who wins encounters also has the disadvantage of a loss of potentially valuable information that could define relationships more precisely (e.g. the distinction between losing an encounter by showing submission or flight: see Senar et al., 1990).

The aim of this paper is to suggest the use of a technique for measuring dominance ranks that takes account of the variety of agonistic behaviours displayed by individuals. We think that true dominance is a composite measure of 'access to resources', 'probability of success in encounters', or 'fighting ability'. Since these are normally correlated, but *a priori* the strength of the correlations is unknown, and since we want to obtain a weighted composite new single variable, the standard method should be the use of an eigenvector analysis. Our proposed approach is conceptually similar to the use of PCA to work out an overall size measure (e.g. Rising & Somers, 1989). All these measures are calculated from the different agonistic behaviours used by the individuals of the group. In order to avoid subjective assessments of which behaviours to use to compute each measure, and in order not to lose any information in the data, we suggest that the analysis should include as many of the agonistic behaviours recorded in the raw data as possible. These behaviours, of course, will include different actions for which the outcomes are either 1. *not evident* from the action (e.g. attack may or may not result in a 'win'), 2. *defined* by the action (e.g. flights are by definition only used by the loser of the encounter), or 3. a *result* of an action (e.g. submission can only occur in response to something else). However, this is not a problem since it just allows for more 'measures' of dominance to be included into the analysis.

Material and Methods

Of the different eigenvector methods available (see James & McCulloch, 1990) we propose Correspondence Analysis (CA; Hill, 1973, 1974; Cuadras, 1981; Foucart, 1982; Greenacre, 1984; Heijden et al., 1990) for the following reasons: 1) it is a very appropriate method when using data consisting of frequencies (Cuadras, 1981; Foucart, 1982; James & McCulloch, 1990); 2) it allows the simultaneous plotting of both the populations (in this case the individual animals) and the variables (i.e. the agonistic behaviours they use), which makes interpretation of the axes much easier (Heijden et al., 1990; James & McCulloch, 1990; Miles, 1990); 3) it retains a relatively high amount of the original variation in the data (Miles, 1990) and 4) it is very robust to changes in the number of variables (i.e. columns) (Miles, 1990).

We illustrate the use of Correspondence Analysis in generating dominance ranks using data obtained from a group of 17 captive siskins (AA, AN, AB, AG, AV: adult males; BN, BV, BA, BG, BB, NV, NA, NE, NN, NB: juvenile males; and B and T: juvenile females). Birds were colour ringed for individual identification, and housed in an outdoor cage (100x100x60 cm) (see Senar et al. 1990 for details of the feeding schedule). A total of 3389 contests over resources (food, water or perches) were recorded in 23.5 observation hours between 6 and 22 March 1991. In any interaction we recorded the behaviour used by the Actor (the initiating bird) and the reply by the Reactor. The behaviours used by Siskins were categorised as follows: Attack, in which the actor pecks directly at the head, body or wings of the other bird; Supplant, in which one bird flies at another, who abandons its perch, the attacker perching in its place; Display, in which the bird faces the opponent with a threatening posture; and Tolerance, in which a bird possessing a resource allows another one to be within a radius of 10 cm (individual distance for the Siskin (Marler, 1956)). The major responses by the reactor were Flying and Hopping withdrawls, Attacks and Supplants, Displays and Submissions. If the reactor showed no clear response, continuing with its previous behaviour, it was defined as No response (see Senar et al., 1990 for further descriptions). Data were entered for both the actor and the reactor. This should not cause problems due to lack of independence, since although data from an encounter are entered twice, this allows us to describe individuals more thoroughly (i.e. by allowing us to record that some displays provoked submission and some provoked flight withdrawal). Therefore, although the results are generally similar when using only 'actor' behaviours, we prefer to include replies by the reactor. Analyses were carried out using the program developed by Foucart (1982). CA is now also available on standard statistical packages, such as SPSSPC+ or NTSYS.

Results and Discussion

The matrix analysed by CA had as cells the number of times that the different behaviour patterns were used (either given or received) by each of the 17 individuals of the captive siskin group. The independence model generated by CA was highly significant (χ^2= 4354.01, d.f.=270, p<0.001), and so we used CA to study the departure from independence and to detect significant trends in the data. Although CA analyses behaviours and individuals simultaneously, so that both forms of data can be plotted on the same axes, for reasons of clarity we have plotted them separately: the behaviours are shown in figure 1A, while the individual birds are shown in figure 1B. The first axis explained 74% of the variability in this contingency table (cf. Cuadras, 1981). Certain behaviour patterns were negatively correlated with the axis (cf. Foucart, 1982), and so helped to define it: actors that made attacks, supplants, displays and were tolerant, and, in return, received submissions, flight and hopping withdrawls (fig. 1A). All of these behaviours are clearly typical of the more dominant member of the dyad (Senar, 1990; Senar et al., 1990). In contrast, receiving tolerance, displays and supplants, and giving in response flight and hopping withdrawls and submission (all typical of subordinates (Senar, 1990; Senar et al., 1990)), had significant positive scores. This axis had therefore detected a "dominance" trend, and variability in the use of the different behaviour patterns by siskins can thus be explained to a great extent (74%) by the relative dominance status of the actor. This is quite obvious: different behaviours are known to be associated with either dominants or subordinates (e.g. Popp, 1987a; Senar, 1990; Senar et al., 1989, 1990), and we also used in the analysis some behaviours which incorporate indirectly the outcome of the interaction (e.g. supplant, submission). However, the important point is that the weightings that individuals obtain on this axis can therefore be used as 'dominance scores', so that we have a quantitative (cardinal) measure of how dominant an individual is compared to other group companions.

Table I presents the individuals in order of their dominance score obtained from this CA first axis. For comparison with the more traditional approach we have also presented the matrix of dominance relationships based purely on the number of times each bird won interactions with each other member of the group (see Lehner, 1979). An individual was considered to have won an encounter if its opponent gave a submissive posture or withdrew, and was considered to be dominant over another if it won significantly more than 50% of the encounters between them, as indicated by a log likelihood ratio test (G test) (Sokal & Rohlf, 1981) (minimum sample size of 10 interactions per dyad). Detailed inspection of table 1 shows that all the significant dominance dial relationships appear in the superior

(A)

TOLERANCE*
SUPPLANT* **NO-RESPONSE***
ATTACK* DISPLAY* **FLIGHT*** **HOPPING*** **SUBMISSION***

– 0 +

SUBMISSION* **ATTACK** **TOLERANCE***
FLIGHT* **HOPPING*** **NO-RESPONSE** **DISPLAY*** **SUPPLANT***

(B)

BV BB BA
AB AG AV AN NE NV AA NB BN NA BG NN T B

– 0 +

FIGURE 1. Plot of the first axis generated by Correspondence Analysis. A: Plot of the different agonistic behaviours used by siskins (given behaviours above the line, received behaviours below it). *: behaviours correlated significantly ($p < 0.05$) with the axis. B: Plot of the different individual siskins used in the experiment. The first axis is a measure of dominance (see text), and so the more dominant a bird is, the more negative a score it will have in relation to this axis.

[Representación gráfica del primer eje generado con el Análisis Factorial en correspondencias. A: Representación de las distintas conductas agonísticas utilizadas por los lúganos (conductas dadas sobre la línea, las recibidas bajo ella). *:Conductas significativamente correlacionadas con el eje ($p<0.05$). B: Representación de los distintos individuos utilizados en el experimetno. El primer eje es una medida de domiancia (ver texto), y por tanto cuanto mas dominante sea un individuo, mas negativo será su valor respecto a ese eje.]

half of the matrix, indicating that there was a perfect agreement between the CA ordination and that obtained from pair-wise interactions (see Lehner, 1979). This suggests that although CA dominance scores were calculated by summarising all the interactions of each individual bird with all the other members of the group, with some potential pseudoreplication problems, the method produced a good transformation of pair relationships into individual rank values (see Shawcross, 1982). Moreover, the CA technique allows the calculation of dominance scores for individuals that were involved in too few interactions with other birds for a reliable assessment of each dyadic dominance relationship (see individual NB in Table I for an extreme example). The method, of course, can have some drawbacks. Some difficulties can appear when we have disproportionately large samples from a few pairs of individuals which can overwhelm the analysis. However, this is generally not a problem since CA uses relative fiequencies, so that provided that there are not many empty cells, each individual will be weighted according to the total number of behaviours displayed. A more serious problem can appear when we have some individuals which attack subordinates but avoid interactions with dominants, so that they are erroneously weighed as dominant individuals. This problem, however, is common to

Table I. Pair-wise dominance matrix. Birds are ordered according to their score on the CA dominance axis(the more negative the score, the more dominant the birds is) (fig. 1). Left column: CA dominance score x 1000. (*): significant dyadic dominance relationship in which the bird in the left column dominated the other bird ($p<0.05$). (-): non-significant relationships. (blank) relationships not tested because of small sample size ($n<10$ interactions), but note that they are included into the CA (e.g. NB did not showed more than 10 interactions within any diad, but the sum of all his interactions with all the other birds produced a large enough sample size to be processed by CA) (see text).

[Matriz de dominancia. Cada individuo está ordenado según su índice de dominancia obtenido a partir del Análisis Factorial en Correspondencias (cuanto mas negativo es el valor de dominancia, mas dominante es el individuo) (fig. 1). Columna de la izquierda: índice de dominancia x 1000. (*): relaciones de dominancia significativas a las que el individuo de la izquierda domina ($p<0.05$). (-): relaciones de dominancia no significativas. (espacio en blanco): relaciones no analizadas debido al bajo tamaño muestral ($n<10$ interacciones), a pesar de ello, estas relaciones estan incluidas en el Análisis en Correspondencias (ej. el individuo NB no mostró mas de 10 interacciones con ninguno de los individuos del grupo, pero la suma de todas sus interacciones con todos los otros pájaros produjo un tamaño muestral suficientemente grande como para ser procesado con el Análisis en Correspondencias (ver texto).]

Dominance Scores		Individuals																
		AB	AG	AV	AN	NE	BV	NV	AA	BB	NB	BA	BN	NA	BG	NN	T	B
-776	AB	=	*	-	*	*	*	*	*	*		*	*	*	*	*	*	*
-595	AG		=		-		*	-	*	*		*	*	-	*	*	*	*
-555	AV			=			*	*		-		-		*	*		*	
-546	AN				=	-	*	*	-	*		*	*	*	*	*	*	*
-286	NE					=		-	-	-			-	-	*	*	*	*
-248	BV						=	-		-		*	-	-	*	*	*	*
-229	NV							=	-	-		-	*	*	*	*	*	*
-185	AA								=	*		-	*	*	-	*	*	*
-172	BB									=		-			-		*	*
-114	NB										=							
- 87	BA											=	*		*	*	*	*
- 72	BN												=	-	-	*	*	*
96	NA													=	*	*	*	*
156	BG														=	-	*	*
673	NN															=	*	
811	T																=	*
938	B																	=

other methods of dominance rank estimation, and so cannot be considered as an exclusive drawback of the CA approach.

We therefore suggest that using Correspondence Analysis to obtain the scores of individuals along a dominance axis according to their relative use of different agonistic behaviours has great advantages over conventional means. The method does not require a prior definition of what constitutes 'success' in an encounter, allows the use of more precise information than merely who wins encounters, and allows the inclusion of other important behaviours like tolerance or no response.

Acknowledgements

We are grateful to P.G.M. van der Heijden and P. Arcese for their comments. This is a contribution to the DGICYT research project PB92-0044-C02-02.

Resumen

Utilización del Análisis Factorial en Correspondencias para generar rangos de dominancia cardinales.

Existen en la actualidad varios métodos que permiten obtener índices de dominancia cardinal. La mayoría de esos índices se basan en el número de veces en que un individuo gana sus enfrentamientos agonísticos. Sin embargo, algunas veces es difícil decidir quien ha ganado el encuentro y cuales son los comportamientos más adecuados para ser incluidos en el análisis. Además, resumir una relación entre un par de individuos simplemente en términos de quién gana los enfrentamientos tiene también la desventaja de una pérdida de información potencialmente valuosa para definir con mayor precisión el tipo de relación. Por todo ello, se propone en el presente trabajo la utilización de un método multivariante (Análisis Factorial de Correspondencias) que extraiga los vectores propios de la matriz que relaciona a los distintos individuos del grupo con las distintas conductas agonísticas utilizadas. Este procedimiento es conceptualmente similar a la utilización del Análisis de Componentes Principales para obtener una medida de tamaño de un individuo a partir de toda una serie de medidas biométricas lineales. El método se ilustra utilizando las interacciones de un grupo cautivo de Lúganos (*Carduelis spinus*).

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Recibido: junio, 1994