Status signalling in the Coal tit (*Parus ater*): the role of previous knowledge of individuals

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Abstract. In social species, the existence of signals associated with the social status of individuals might help to reduce the intensity and the number of the agonistic interactions produced between group members. This paper analyses the importance of plumage badges on the determination of dominance relationships between Coal tits (*Parus ater*). First, I determined dominance relationships within three groups of 6 juvenil males of similar body size that had lived together for two weeks in outdoor aviaries. Dominance hierarchies among individuals were not associated to bib size. Second, experimentally, I manipulated the bib size of some of the birds. The result of encounters between manipulated and control individuals without prior knowledge of each other, showed that individuals with larger bib sizes were more often dominant than unmanipulated ones. Therefore, badge size had no impact on the outcome of conflicts among companions within groups of stable composition, but the impact was significant when knowledge was lacking.
Key words: Status signalling, bib size, Coal tit, Parus ater.

Resumen: *Señalización de estatus en el Carbonero garrapinos* (Parus ater): *el efecto del conocimiento previo entre los individuos del grupo*. En especies que viven en grupos sociales, la existencia de señales relacionadas con la señalización del estatus social de los individuos puede ayudar a disminuir la intensidad de las interacciones producidas. El presente trabajo analiza la importancia de las manchas en el plumaje del Carbonero garrapinos en la determinación de relaciones de dominancia entre individuos. En primer lugar se determinaron las relaciones de dominancia en tres grupos de seis individuos que habían convivido durante dos semanas en aviarios (todos machos juveniles de similar tamaño). Las relaciones de dominancia entre esos individuos, familiarizados los unos con los otros, no estuvieron relacionadas con el tamaño de las manchas analizadas, sino con la longitud del ala (i.e. tamaño). En segundo lugar, experimentalmente se alteró el tamaño de las manchas de plumaje en individuos experimentales. El resultado de las confrontaciones en parejas, entre individuos control no manipulados y manipulados desconocidos entre si, muestra que estos últimos fueron más a menudo dominantes sobre los controles. Los resultados obtenidos, apoyan la hipótesis que la señalización de estatus mediante algunas características del plumaje puede ser importante a la hora de establecer relaciones de dominancia entre individuos desconocidos entre si, pero no en la determinación de las relaciones dentro de grupos de composición más estable.

Introduction

Within non-breeding flocks of group living species individuals compete for priority of access to resources such as food or shelter. Competition through agonistic interactions is energetically costly (Hogstad, 1987). Thus, any individual which possessed attributes facilitating a reduction in the number or in the intensity of interactions would be presumably at an advantage. The status signalling hypothesis states that variations in plumage colour are used to signal differences in individual capabilities to win agonistic contests (Rohwer, 1975, 1977). Potential badges signalling status of individuals have been proposed in a number of species (Järvi & Bakken, 1984, Pöysa, 1988, Moller, 1987, Studd & Robertson, 1985, Senar & Camerino, 1998, Senar, 1999 for a review). However, often the evidence of a given badge signalling status is contradictory, raising the need to identify the situations where the signal may or may not work in a dominance framework. Prior knowledge of individuals might reduce advantages of a signalling system because other factors might override the dominance ability cues provided by plumage variation. Therefore, status signalling would be particularly beneficial if flocks are unstable with regard to membership, since it would reduce the cost of asserting status each time a new flock was joined (Lemel & Wallin, 1993).

Natural variation in character is a prerequisite for a plumage badge to function as a signal, being the second requirement the correlation of this variation with dominance. In the genus *Parus*, the bib of Willow tits (Hogstad & Kroglund, 1993) and the breast stripe of Great tit (Järvi & Bakken, 1984, Whitfield, 1987) seem to function as signals of resource-holding potential accomplishing these two requisites. The objective of this study was to assess the role as signal of the bib size in Coal tits (*Parus ater*) living in flocks during the non-breeding season. Particularly, the main point was to identify the importance of the bib size in contest outcome between individuals with and without prior knowledge of each other.

Methods

I captured 18 Coal tits from three different locations in the Eastern Pyrenees. The three sites were separated by at least 10 km, in order to minimise the probability that captured individuals in different places had previous knowledge of the others. All individuals were juvenile males according to Svensson (1992) and unpublished data on sexual size dimorphism of individuals in the study populations. Individuals captured at the same site (n=6) were kept together in separate outdoor aviaries (2x1.5x1 m) without visual contact. The individuals were colour ringed and the number of non moulted great covers, tarsus, tail and wing length were measured. Three bib size measures were taken: maximum width and height of the bib and width of the bib at half the value of the measured height. A relative index based on bib shape measures gave a good estimation of overall bib size in a sample of museum skins (n=32, r=0.86, p<0.001). Exact bib sizes of museum skins was calculated by drawing on paper real bib sizes of a sample museum skins and weighting them on a precision balance.

Coal tits were fed *ad libitum* with pine seeds, sun flower seeds and tenebrionidae larvae. Vitamins were added twice a week. After two weeks, the dominance hierarchies were determined in each flock after 3 hours of food deprivation. Dominance was estimated from entrance order to the feeder and from interaction outcomes. We assessed the importance of bib size and other morphological measures on dominance rank which was log transformed (see Lemel & Wallin, 1993) using a backward multiple linear regression analysis.

In the next part of the experiment, from each group, I chose five birds. The top ranking individual of each group was excluded because of size asymmetries in relation to the other individuals. Two of these five birds were chosen from every second position in the hierarchy in order to enlarge their bib size. With a black marker, bib size was enlarged on a strip 5 mm wide following its original contour. The other three individuals were painted on their original bib contours.

All birds were maintained in the experimental cage (50x 50 x 50 cm) for at least 24 hours prior to the experimental trials which took place a maximum of four days later. Therefore, no bias in the prior knowledge of the experimental cage existed. Since birds with enlarged bibs were tested pair-wise against control birds from the other two flocks, the contestants had no prior information of their opponents fighting ability. Some of the birds were used in different dyads but never against the same opponent. Experimental confrontation lasted 35 minutes. The experimental cage was supplied with a piece of pine seed (4 mm long) every fifth minute. We recorded the following variables from a hide nearby the cage: the number of times each individual had access to a food item, the total number of agonistic interactions won by each individual of the dyad; the number of direct interactions such as attacks, robberies of food items, supplants, won by each individual; and the number of indirect interactions such as waitings and non-forced withdraws.

Individuals with enlarged bibs were selected in order to avoid dominance and size biases. Dyads did not differ in size in more than 0.75 mm. In order to check further for any possible bias with respect to body size for either individuals with enlarged bibs or controls, we tested whether contest outcome was somehow influenced by this variable. I could not include the individuals of one group in the dominance analyses due to the escape of some of its members.

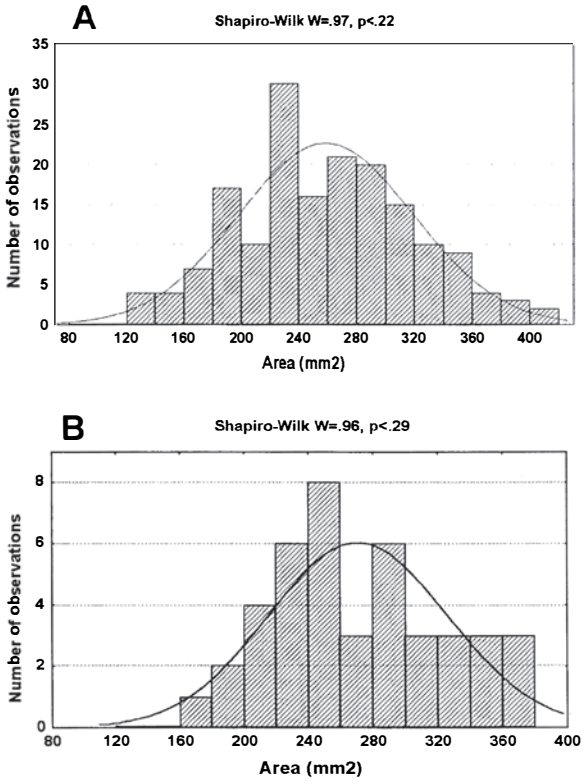

Figure 1. Range of bib size (mm^2) in a natural population of Coal tits in the Pyrenees A. Juveniles (n=172 individuals). B. Adults (n=50 individuals).

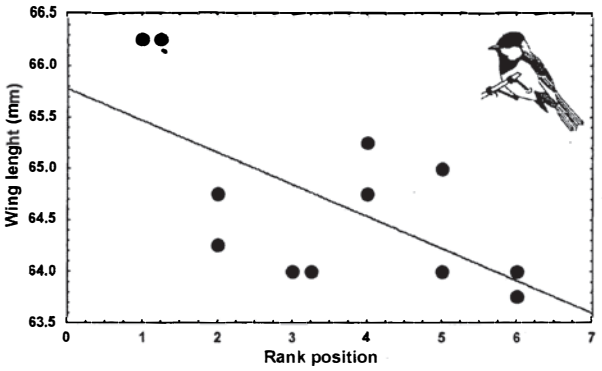

Figure 2. Linear relationship between dominance rank (corresponding 1 to the top dominant and 6 most subordinate bird) and wing length within flocks of Coal tits with stable membership. Spearman rank, n=12, r=-0.61, p<0.05.

Results

Bib size variation in natural conditions

Bib size distribution in natural conditions followed a normal distribution both in juvenile and adult birds (Figure 1). When age classes were grouped together, bib size still fitted significantly a normal distribution (Shapiro-Wilk W=0.975, n=222, N.S.). Bib size was significantly correlated to wing length in both adults and juveniles (Wing length, r=0.53, t_{219}=8.96, p<0.0001; age, r=-0.06, t_{219}=-1.06, N.S.). Furthermore, I did not detect any difference in bib size among age classes ($F_{1,219}$=1.14, N.S., Figure 1).

Dominance and prior experience about rivals

Results of a backward multiple linear regression performed on the two groups, showed that only wing length was related to the rank achieved by individuals in the dominance hierarchy (table 1, figure 2). The results were consistent among experimental groups after using them as a dummy variable in the multiple regression model (table 1). Therefore, taking into account the variation explained by the variable wing length, bib size did not seem to add any significant explanation to dominance hierarchy among individuals with previous knowledge (table 1).

Dominance and lack of experience about rivals

Each manipulated individual, with the bib enlarged, was confronted with unfamiliar unmanipulated individuals from the other two flocks. In total we performed 18 experimental trials, and 12 of them could be included into the analyses because birds interacted long enough to record dominance outcomes. Birds with enlarged bib sizes were more often dominants than unmanipulated ones. Out of 12 encounters, 10 ended with the manipulated individuals beating the bird with the smaller bib (Sign test, Z=2.02, p=0.04). Furthermore, owing to their dominant status, manipulated individuals took and consumed a larger number of food items than unmanipulated ones (Wilcoxon test, n=12, Z=3.3, p=0.0008).

Manipulated and unmanipulated individuals did not differ in the number of direct agonistic interactions they were engaged in and won by them (Wilcoxon test, n=12, Z=1.5, p=0.14, figure 3). However, manipulated birds won more indirect interactions than unmanipulated ones (Wilcoxon test, n=12, Z=2.7, p=0.007, figure 4). That is, birds with smaller bib sizes carried out more waitings and non-forced displacements than bib enlarged birds.

Table 1. Linear regression model with the number of unmoulted great covers, bib size, tarsus, tail and wing length, combined with the position in the hierarchy as the dependent variable (corresponding 1 to the top dominant and 6 most subordinate bird).

	Beta	t value	P
Wing length	-0.73	-3.41	0.006
Tail length	-0.32	-1.17	0.27
Tarsus length	-0.13	0.54	0.59
Bib size	-0.24	0.81	0.43
Number of unmoulted great covers	-0.05	-0.23	0.81
Experimental group	-0.17	-0.77	0.46

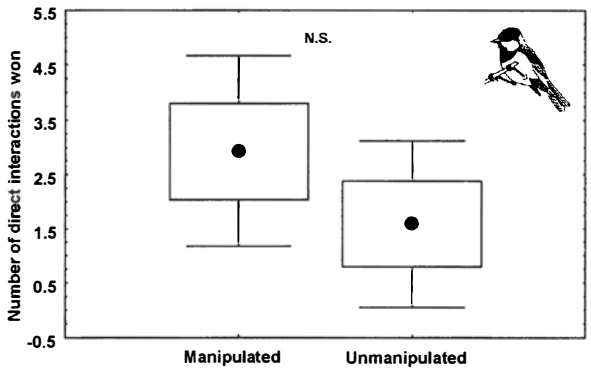

Figure 3. Number of direct interactions such as attacks, robberies of food items and supplants, won by each individual of the dyad during the experimental trials. Bars represent standard deviations and boxes standard errors.

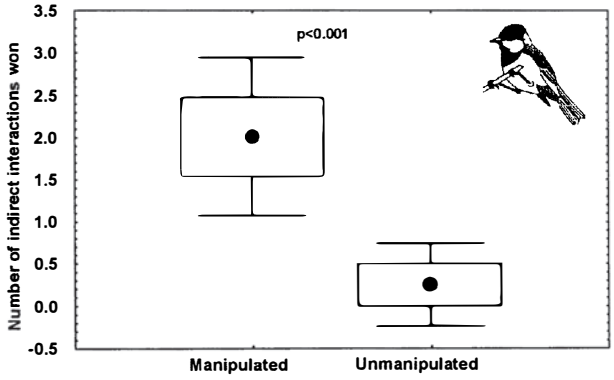

Figure 4. Number of indirect interactions such as waitings and non-forced withdraws won by each individual during the experimental trials. Bars represent standard deviations and boxes standard errors.

Discussion

Bib size did not seem to influence dominance relationships among individuals with prior knowledge of each other. Among stable groups only wing length, as the main estimator of body size, seemed to be related to dominance. On the other hand, among strangers, individuals with enlarged bibs were more likely to win encounters, mostly due to the active behaviour of unmanipulated birds which seemed avoid large badged individuals withdrawing as soon as they approached with no mediated aggression, or waiting until food was available. Un-manipulated individuals seemed to perceived the large bib sizes of rivals and reacted accordingly by reducing the intensity of the interactions in which they were subordinates. Therefore, the bib size of the Coal tit seems to function as a signal of status, and supports the status signalling hypotheses (Senar, 1999), at least in unfamiliar flocks. The fact that the badge system for status signalling in the Coal tit may fail to work within groups of stable composition may be because the relevance of variation in badge size may shift from a signalling system into a recognition system when individuals become familiar (Lemel & Wallin, 1993). In unstable flocking conditions, individuals unaware of the resource-holding potential of an opponent may use badge size to estimate dominance. In other bird species, status signalling has also been demonstrated when contestants lacked information about the fighting ability of the antagonist (Rohwer, 1985, Roskaft & Rohwer, 1987, Lemel & Wallin, 1993). My findings, with regard to the high frequency of indirect interactions lost by unmanipulated birds, lends additional support to the status signalling hypotheses.

During autumn and winter, juvenile Coal tits live in social groups of large size. These large groups appear to be of rather unstable composition (Brotons, 1997). Therefore, a status signalling system might be of importance in the Coal tit at least in two particular points of their life when stranger individuals have higher probabilities to meet. First, during juvenile dispersal, when juveniles disperse from parental territories and individuals from different areas mix, and consequently lack experience about each other's resource-holding potential (Lemel & Wallin, 1993). And second, during winter time, in encounters between transient winter flocks (Brotons, 1997, Senar, 1999).

Given that in the Coal tit status signalling system seems to work when prior experience about the rival is lacking, its importance in front of other asymmetries determining social dominance should be analysed (Arcese & Smith, 1985, Koivula et al., 1993). More concretely, the interactions between prior residence and status signalling, on unknown individuals appears of special interest in this context (Sandell & Smith, 1991). Status signalling has been shown to be an important mechanism in relation with dominance. The new questions posed by the studies so far conducted, merit without any doubt further insights in the topic.

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