Status signalling and the ability to recognize dominants: an experiment with siskins (*Carduelis spinus*)

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Because dominants usually exploit others and take a disproportionate share of the available resources, we should expect foragers to be choosy as to which individuals they join. Here we show that siskins (*Carduelis spinus*) discriminate between dominant and subordinate individuals on the first encounter without requiring cues such as overt aggression, and prefer to join subordinate individuals. Experimental enlargement or removal of the siskin black bib, which has been shown previously to be a reliable predictor of dominance, strongly suggests that dominance discrimination is based on the use of badges of status.

Keywords: status signalling; recognizing dominance; badges of status; plumage manipulation; dominance; *Carduelis spinus*

1. INTRODUCTION

It is generally stated that in winter flocking birds, the intake rate of group foragers is higher than that of solitary individuals (e.g. Pulliam & Caraco 1984). This is partly a consequence of the higher efficiency of groups at finding food patches and the sharing of food. However, this higher intake rate is normally only the case for an average individual: it is well established that some members of the group (e.g. dominants) exploit others or take a disproportionate share of the resources, so that only some individuals increase their intake rates (Pulliam & Caraco 1984; Barnard 1984). Therefore, we should expect individuals to tend to avoid feeding alongside dominant conspecifics (e.g. Ekman 1989). Indeed, several studies have shown how habitats or groups containing the most aggressive 'despots' tend to be avoided (Fretwell 1969; Harper 1982; Metcalfe 1986).

However, it is important to know whether animals can recognize the relative dominance ability of other individuals without requiring cues such as overt aggression, and whether they prefer to join groups of 'subordinate' individuals. Preference tests have been carried out between the situations of feeding alone or socially (e.g. Ekman & Hake 1988; Caraco *et al.* 1989), but not with individuals having to choose between two conspecifics differing in dominance ability. Correlative studies (e.g. Carrascal & Moreno 1992) suggest a preference, but we do not know whether animals recognize the difference between dominants and subordinates. Aviary experiments in which birds can choose among different interconnected cages suggest that subordinates avoid dominants (Caraco *et al.* 1989), but as dominants can behave aggressively towards subordinates, it is unclear whether or not subordinates really recognize dominants, or if they are only responding to aggression. In addition, the researcher needs to be able to discriminate *a priori* (i.e. without

recording interactions) the dominance relationship between the tested individuals before any experiment of this kind, but this is normally difficult to achieve.

Several bird species have been shown to have colour patches that have been related to dominance status (i.e. 'badges of status') (Roper 1986; Whitfield 1987; Butcher & Rohwer 1989; Savalli 1995). Manipulation of badges of status provide therefore one of the best opportunities to test for the ability to recognize dominance (Geist 1966; Watt 1986). Several experiments, in which the presumed signal of dominance was enlarged, have been carried out in different bird species (Rohwer & Rohwer 1978; Parsons & Baptista 1980; Fugle *et al.* 1984; Fugle & Rothstein 1987; Järvi *et al.* 1987; Møller 1987b; Lemel & Wallin 1993; Grasso *et al.* 1996). However, most of these experiments were designed to test whether the manipulated bird was able to rise in a dominance hierarchy, and although these experiments implicitly assume a change in the behaviour of unmanipulated birds as a result of opponent's badge enlargement, a true test of dominance recognition should test whether birds show any preference (or avoidance) between two individuals differing in apparent dominance (i.e. the tested bird is not the manipulated one, but the individual reacting to the manipulation). The few studies that have used models were carried out in the breeding period on territorial species or simultaneously using only one model (Järvi & Bakken 1984; Studd & Robertson 1985; Møller 1987a; Jones 1990; Procter-Gray 1991), so that they were not really testing for a choice of flock companion. In addition, we should also record whether birds avoid probable dominants (e.g. manipulated birds) on the first encounter(s) (Geist 1966; Watt 1986). Finally, and for a robust test of the hypothesis, experiments should include not only an enlargement of the badge of status, but also a reduction of it. This has rarely been carried out (e.g. Rohwer (1977), but with a very small sample size of $n=2$; Grasso *et al.* (1996) with a sample size

of $n=7$). In this study we have therefore used a novel approach, testing whether individuals can recognize dominant competitors by recording active choice between feeding close to a cage containing a dominant bird or close to another cage containing a subordinate. The species used for these experiments was the siskin (*Carduelis spinus*), as dominance can be predicted very accurately *a priori* by the size of the black bib (Senar *et al.* 1993).

2. MATERIAL AND METHODS

Siskins used in experiments were captured in the winter of 1995–96. Only transient male siskins were used for the experiments (Senar *et al.* 1992). The use of a mist net associated with live decoy birds allowed us to ascertain which birds were transients in the area, as transients are highly attracted by live decoys (and therefore were trapped in the net), whereas residents usually ignore them (Senar & Metcalfe 1988). All the birds trapped with the use of decoys were unringed (i.e. newly arrived into the area), which additionally supported our assumption about their transient status. The high mobility of these individuals (Senar *et al.* 1992), and the fact that the birds were trapped over a period of three months and at two localities more than 100 km apart, makes it very improbable that the different individuals could be familiar to each other. In a few instances in which several birds were simultaneously trapped we designed experiments to ensure that all the tested birds were unfamiliar to each other. Bib size was measured by tilting the bird's head back in line with the body, and measuring length and breadth. Badge area was *a posteriori* computed following Senar *et al.* (1993). In that paper we used transparent graph paper to measure the 'true' area of 12 museum skins, and regressed it to the product of length by breadth. However, an error was detected in that procedure, as it did not allow for badges of 0 mm². We therefore recomputed the regression relating badge area (A) to the product of length (L) by breadth (B), but this time forcing the line to the origin. This gave another regression line, and badge area was calculated as $A=0.594LB$ ($r=0.97$). Except during experiments, the birds were held visually but not vocally isolated, in individual cages. We used a total of 45 male siskins as test subjects (median bib size 24 mm², 95% confidence interval (CI) 18–28 mm²). As stimulus birds we used 11 small-badged males (bib size < 5 mm², median 0 mm², 95% CI 0 mm²), five large-badged males (bib size > 35 mm², median 40 mm², 95% CI 35–46 mm²), and 25 female siskins. Because 10 of the 11 'small-badged' birds had a black bib size of 0 mm², when we refer to small-badged birds we are mostly speaking of birds lacking a black bib.

Experimental design consisted of releasing a bird into a test cage 2 m × 1 m. The test cage contained two small cages (20 cm × 10 cm), each one at one extreme of the large test cage (figure 1). The small cages contained individual siskins with small, large, removed or enlarged black bibs, or a female, according to the experiment. A small equal quantity of food was provided at a side of each cage. Food consisted of canary commercial mixture plus some pine seeds. Birds were trained to feed close to the cages for several days before the experiment. Each released bird was food deprived for 2 h and was then introduced into a small cage located at one side of the test cage, in a position equidistant from the other two small cages. The door of the side cage was automatically opened by the operator, allowing the bird to enter the test cage. Test birds were therefore presented with a choice between two food patches that differed

Figure 1. Design of the cage as used for the different experiments.

only in the identity (and relative dominance) of the adjacent stimulus flock companion. An experiment consisted of 20–40 trials, each trial within an experiment run with a different experimental male who had to choose between two stimulus males. To ensure independence between trials, we selected two of the different available stimulus males, which fitted the badge size necessary for the experiment, in such a way that we did not repeat combinations of males and all males were used in an approximately equal number of trials. Thus, each released (experimental) male siskin in the experiment was presented with a unique combination of stimulus males. To eliminate position effects we rotated stimulus birds among the two positions in such a way that each badge size class spent an approximately equal number of trials in each position. Trials lasted 3 min. We measured the percentage of time spent by test males feeding in association with the two potential choice birds. This time was normalized relative to the total time that they spent feeding close to the stimulus birds (generally less than the 3 min), and was used as a measure of preference (or avoidance). We analysed the data with a Wilcoxon signed-rank test (Neave & Worthington 1992). Our null hypothesis was that 50% of the time spent associating with either bird should be with one of the two stimulus birds, and a significant deviation from 50% indicated a significant preference. In most cases the test bird remained with the first chosen stimulus individual. Birds were observed through one-way glass (figure 1). We counted only trials in which at least one small cage was visited and the released bird was recorded feeding. This caused differences in sample sizes among the different experiments. Availability of appropriate stimulus males also caused some differences in sample sizes, especially in relation to experiments four and six (see below). We conducted six related experiments.

Experiment 1. The two small cages contained no bird.

Experiment 2. Both cages contained a bird with a small badge. Experiments 1 and 2 were used as controls.

Experiment 3. The released bird had to choose between a female (i.e. clearly subordinate individual (Senar 1985)) and an empty small cage. This was done to test that with abundant food, birds prefer to feed socially (see Ekman & Hake 1988).

Experiment 4. The released bird had to choose to feed alongside a bird with a small or a large badge. The aim of this experiment was to test whether birds with large black bib sizes were avoided.

Figure 2. Results from the six experiments in which the different test birds (all males) were presented with a choice between two food patches that differed only in the identity (and relative dominance) of the adjacent stimulus flock companion (see figure 1). In the first experiment neither stimulus cage contained a bird, whereas in the second experiment both contained a bird with a smaller badge than the test bird (i.e. subordinates). In the third experiment the released bird had to choose between a female (i.e. clearly subordinate individual) and an empty small cage. In the fourth experiment the stimulus birds were two male siskins differing in bib size, so that one was clearly dominant and the other clearly subordinate. In the fifth experiment we used two birds with small badges, but one of the individuals had its black bib experimentally enlarged. In the last experiment we used a bird with a small badge and a bird with a large badge, but both badges had been experimentally removed. Results are expressed as the percentage of time that the test bird stayed close to one or another stimulus bird from a total of 3 min. The outcome of Wilcoxon signed-rank tests and number of trials are also provided.

Experiment 5. We used two birds with small badges, but one of the individuals had its black bib enlarged to a size of 40 mm^2 , which was still in the range for the species (median 23 mm^2 , range $0\text{--}66 \text{ mm}^2$, $n=1053$ males (Senar *et al.* 1993)), and was

also the median size for the unmanipulated, large-badged individuals. We used a permanent black marker Edding 3000. The black could be removed after each experiment using alcohol. The other bird was painted with water (i.e. it was manipulated

in a similar way). The aim of this experiment was to test whether bib colour alone was sufficient to elicit an avoidance response.

Experiment 6. We used a bird with a small badge and a bird with a large badge (the same individuals as in experiment 4). This time, however, the black bib was removed by painting it yellow–green (the natural colour of the breast). About 10–20% of birds in natural populations have no badge (Senar *et al.* 1993), so that birds with the bib removed were still in the range for the species. We used Arabic gum mixed with an iron yellow pigment. The bird with the small badge was also painted yellow. The yellow was later removed with water. Birds did not show any aberrant behaviour because of painting. The aim of this experiment was to test that previous avoidance of large-badged birds in experiment 4 was only because of their larger black bib size.

It should be noted that experiments were not carried out sequentially (from 1 to 6), but at random (the order used being 1, 3, 4, 2, 6 and 5).

To facilitate comparison, the same test birds were used for the different experiments. Test birds had therefore similar size badges in all six experiments (Kruskal–Wallis one-way ANOVA, using individuals visiting at least one small cage, $H=2.81$, $p=0.73$, $k=6$ groups, $N=158$).

3. RESULTS

Experiment 1. Released birds had to choose between feeding close to either the left or right empty small cage. No preference was detected because test birds stayed a similar percentage of time at both cages (Wilcoxon signed-rank test, $T=153$, n.s., $N=25$ trials) (figure 2).

Experiment 2. Both small cages contained a male siskin with a small black bib (i.e. subordinate). No preference was detected (Wilcoxon signed-rank test, $T=102$, n.s., $N=20$ trials) (figure 2).

Experiment 3. Released siskins had to choose between a female (i.e. clearly subordinate bird) and an empty small cage. A significant preference to feed socially was detected (Wilcoxon signed-rank test, $T=64$, $p<0.01$, $N=24$ trials) (figure 2).

Experiment 4. Released birds had to choose between feeding close to a bird with a naturally small badge (i.e. subordinate) or close to a naturally large-badged bird (i.e. dominant). Stimulus birds differed therefore in badge size as well as in behaviour. Siskins significantly preferred to feed close to the small-badged bird (Wilcoxon signed-rank test, $T=35.5$, $p<0.01$, $N=25$ trials) (figure 2).

Experiment 5. Released siskins had to choose between a small-badged bird and a bird with a naturally small bib manipulated to look large. Stimulus birds differed therefore in badge size but not in behaviour. A preference to feed close to the small-badged bird was detected (Wilcoxon signed-rank test, $T=261$, $p<0.05$, $N=40$ trials) (figure 2).

Experiment 6. Released birds had to choose between a small-badged bird and a bird with its black bib removed. Stimulus birds therefore differed in behaviour, but not in badge size. Stimulus birds were the same pairs used in experiment 4. This time, no preference was detected (Wilcoxon signed-rank test, $T=131$, n.s., $N=24$ trials) (figure 2).

It could be argued that the lack of preference in experiment 6 could be due to familiarization with stimulus

birds and the test apparatus. However, as pointed out in §2, experiment 6 was in fact the fifth in order, meanwhile experiment 5 was really the sixth one and was conducted later. Because birds still continued displaying a preference in experiment 5, which was the last experiment to be carried out, this rules out the possibility of habituation in intervening experiments where no preference was obtained.

Although, in each experiment, each experimental test bird was presented with a unique combination of stimulus males, stimulus birds were used several times within each experiment (see §2). To test that avoidances or preferences by experimental birds were not due to the effect of some individual stimulus birds, we carried out three logistic regressions using as categorical independent variables the small-badged individuals, the large-badged individuals and the kind of experiment (only experiments 4–6 were used as these were the only ones in which a choice between small- and large-badged birds was presented). The dependent variable was set to 0 when within each pair the small-badged individual was chosen (i.e. the test bird stayed a higher percentage of time with the small-badged bird), or 1 when the large-badged bird was chosen (this could be either a natural, enlarged or reduced large bib). Results showed that the identity of the individual used had no significant effect on avoidance/choosiness (small-badged individuals, $\chi^2=14.17$, d.f.=10, $p=0.17$ (experiments 4–6); large-badged individuals, $\chi^2=3.4$, d.f.=4, $p=0.50$ (experiments 4 and 6)), but the kind of experiment had a significant effect (i.e. painting or deleting the bib had an effect on choice of where to stay) ($\chi^2=6.05$, d.f.=2, $p<0.05$ (experiments 4–6)). When carrying out a stepwise logistic regression simultaneously using the three independent variables, only the variable ‘kind of experiment’ was retained in the model (goodness-of-fit test, $\chi^2=89.00$, d.f.=86, $p=0.39$). Summarizing, the analysis suggests that results obtained were due to treatment effects rather than to effects of some particular stimulus birds.

An additional logistic regression on the choice of small-versus large-badged birds (experiments 4 and 5) in relation to the bib size of the test bird produced a non-significant result ($\chi^2=0.08$, d.f.=1, $p=0.77$), indicating that the preference for small-badged birds was shown by any bird, irrespective of its own bib size.

4. DISCUSSION

The status-signalling hypothesis, which relates variation in plumage colour to dominance, was proposed by Rohwer (1975) to account for the great deal of winter plumage variability among individuals of many bird species. A fundamental assumption of the hypothesis is that coloration is a reliable predictor of rank (i.e. plumage and dominance are highly correlated), and that strangers recognize the signal prior to physical interactions (Geist 1966; Watt 1986). In a previous study we have already shown that the black bib of the siskin is correlated to dominance (Senar *et al.* 1993). Here we demonstrate that this plumage patch alone can work as a true signal of social status: siskins avoid individuals with large bibs, either natural or enlarged, but do not if the black bib has been removed. Therefore, these data show that siskins

pay attention to plumage, and that colour plumage may be sufficient to signal dominance.

According to the status-signalling hypothesis, superior fighters benefit from distinctive colour markings ('badges of status') because they reduce the number of aggressive contests in which they are involved in order to maintain dominance status or priority access to resources, and subordinates benefit by avoiding interactions with superior individuals (Rohwer & Rohwer 1978; Whitfield 1987). There is, however, another most important consequence of badges of status, not so commonly stated in the status-signalling literature: by the use of badges of status birds should be able to recognize the relative dominance ability of other individuals without requiring overt aggression, and therefore could avoid staying alongside highly dominant individuals (Ekman 1989). Our choice experiments clearly demonstrate that this is the case: siskins perceive the fighting ability of possible flock companions as soon as they meet, without any mediated aggression, and although they prefer to feed socially, they are selective and show a clear preference for feeding with subordinate flock companions. This ability to recognize easily dominant individuals from badge size is demonstrated here for, we believe, the first time.

Status signalling may not only allow a reduction of needless and potentially injurious fighting over social position (Rohwer & Rohwer 1978), but it may allow a more efficient redistribution of dominants and subordinates at foraging patches and habitats, without requiring repeated monitoring of the dominance status of competitors (see also Metcalfe & Thomson 1995). An important potential evolutionary consequence of our finding is that if large-badged birds are avoided, siskins with a large bib might have less ability to attract other individuals to join them. This might be quite a serious cost in a flock bird like siskins, and perhaps very much so in first year birds, as they are less experienced in foraging and escaping predators (e.g. Maccarone 1987; Sullivan 1989; Desrochers 1992). Hence, this may select for small bib size among first year birds in particular. The fact that small badges are more common in the yearling siskin class supports this view (Senar *et al.* 1993). The potential cost of social isolation could be especially important in situations in which food is clumped in small patches, as in small spots of wild grasses or at certain tree species with highly clumped cones (e.g. see Benkman 1997). There are, however, many other natural situations in which aggression rate is low, so that subordinates do not need to avoid dominant flock companions; for instance when birds are feeding at open cones scattered in trees (Benkman 1997). Therefore, although a potential cost of social isolation by dominants is recognized (Ekman 1987; Caraco *et al.* 1989), and this could, according to our data, partly operate through status signalling, it is still unclear how often this cost will really occur.

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