

Cheek plumage uniformity as a social status signal in great tits

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Some plumage patterns in birds, such as irregularities of feathers, are potential amplifiers because they can reveal damage by conspecifics and therefore social status. We experimentally manipulated the pattern of the white cheeks of male great tits (*Parus major*) in order to simulate the effects of peckings by others and thus investigate possible changes in dominance during agonistic encounters at artificial feeders exposed to different risks of predation during winter. As predicted, manipulated birds were displaced by controls from safe feeders, and performed a lower number of aggressions and with lower success, although they did not receive more aggressions as expected from the fact that efficient agonistic displays can avoid the occurrence of overt aggressions. Thus, our manipulation changed the social status of birds by converting individuals with manipulated cheeks into subordinates. We propose that cheek colour uniformity acts as an amplifier of the outcomes of aggressions in great tits.

Introduction

Amplifiers are signals that improve the perception of other signals or cues that are correlated with the signaler's specific quality as assessed by the receiver. Thus, high quality individuals will benefit from expressing an amplifier related to such a quality, while low quality individuals will unavoidably improve the perception by others of their inferiority (Hasson 1989, 1990, 1991, 1997). Thus, amplifiers need not be costly, and their reliability is based on their design rather than on their costs (Hasson 1997). The only cost associated with amplifiers is a lower mating success for low quality individuals (Hasson 1989, 1990, 1991, 1997). This could be an effect cre-

ated by the survival costs generated by social interactions (West-Eberhard 1983).

The immaculateness of avian plumage has been proposed as an indicator of individual quality, with the possibility that it could reveal damage on feathers produced as a consequence of fighting in agonistic encounters (Ferns & Lang 2003, Ferns & Hinsley 2004, Bortolotti *et al.* 2006). If low ranking birds are frequently pecked by others birds, these signs of feather wear may be used to assess the quality of rivals and, ultimately, of potential mates. Thus, plumage immaculateness could act as an amplifier of aggressive outcomes, enhancing differences between individuals with respect to their competitive interactions (Titman & Lowther 1975,

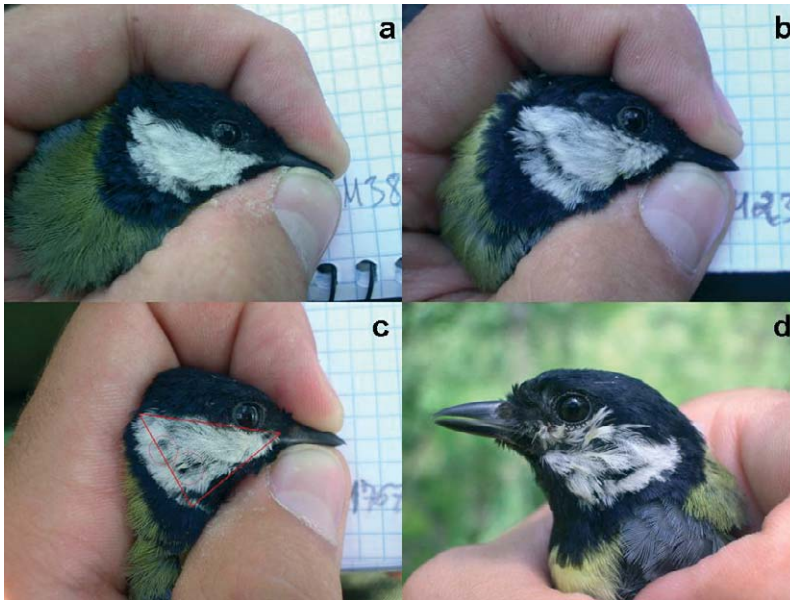


Fig. 1. Variability in color uniformity in the cheek plumage patch of great tits. — **a** and **b**: Examples of unmanipulated males with high and low levels of pattern uniformity, respectively. — **c**: Result of the experimental manipulation carried out on the cheek of a male great tit. The circles denote the areas affected by the manipulation. The lines indicate the linear measurements taken to measure the size of the cheek patch. — **d**: Extreme case of injury on a male great tit cheek caused by attacks by conspecifics. This male had been manipulated during the winter (as in **c**), and the photograph corresponds to a recapture during the breeding season four months later. The rest of plumage patches of head and body were intact.

Ferns & Lang 2003, Ferns & Hinsley 2004), as demonstrated in the case of the white plumage patch of great tits (*Parus major*) (Galván & Sanz 2008).

The great tit is a passerine bird with a well defined social hierarchy between ages and sexes, with males dominating same-aged and younger females and adults dominating juveniles of the same sex (e.g. Carrascal *et al.* 1998 and references therein). These hierarchical relationships are especially important in winter, when the birds become gregarious and agonistic interactions are more frequent (Carrascal *et al.* 1998). During agonistic interactions, great tits perform the “head-up” display, in which both cheeks are consecutively shown to the opponent by moving the head from side to side while the bill is directed upwards (Hinde 1952, Blurton Jones 1968). The cheeks of these birds are white, clearly contrasting with the surrounding black feathers of the rest of the head (Fig. 1). When a great tit pecks on another bird during an aggressive encounter, it frequently directs the attacks

to the cheek area of the opponent (Fig. 1, pers. obs.), thus creating small black patches because of the loss or damage of white feathers.

Galván and Sanz (2008) demonstrated that the cheek patch acts as an amplifier in male great tits, as the mating success of high-quality birds increases with their cheek size but the opposite is observed in low-quality birds. However, the exact mechanism causing those differences in mating success is still unknown. The aim of this study is to investigate whether the immaculateness of the colour of the cheek patch area of male great tits is used to assess the social status of rivals during aggressive encounters in wintering groups by experimentally manipulating this character. The social status of birds usually depends on the level of aggression displayed by individuals and the expression of characters signalling such aggressiveness, aggressive dominant birds receiving a lower number of attacks by other individuals during agonistic interactions, which in turn allows them to have better territories and a higher mating success (Wingfield

et al. 1987). Since the cue the cheek feather pattern supposedly amplifies is the level of aggressions suffered by birds (Galván & Sanz 2008), we predict that great tits should perceive lower social status levels from those great tits whose cheek colour uniformity had been experimentally reduced than from controls. Control birds should displace manipulated birds from high quality food sources, artificial feeders exposed to low predation risk in this case, if subordinates recognized dominants by the character treated here (Ekman & Askenmo 1984, Senar & Camerino 1998, Ferns & Hinsley 2004). For the same reason, the success of aggressions should be higher in controls. As aggressions use to occur among dominant individuals (Senar 2006 and references therein), the number of aggressions performed and received should be higher in control than in manipulated birds.

Material and methods

The study was carried out in January–March 2006 in a deciduous forest of the Pyrenean oak (*Quercus pyrenaica*) in Miraflores de la Sierra, central Spain (40°49'N, 03°46'W). Artificial feeders baited with husked peanuts were installed in different points of the area with a separation of at least 100 m. Feeders were metallic cylinders (20 × 5 cm) made of a 4.8-mm mesh net. Four feeders were placed at each point, though we removed three of them during the observation periods (*see below*). The feeders were placed at the study area two months before the beginning of the study in order to let birds identify them as a food source.

In order to create different levels of predation risk, two feeding points were 15–20 m from cover, while the other three were inside forest plots. The most common bird predator in the study area is the Eurasian sparrowhawk (*Accipiter nisus*), and although predation events were not observed, these raptors were frequently seen during the conduction of the study. Thus, birds feeding at feeders far from cover were exposed to a higher risk of predation than those feeding at the more protected feeders, as was shown to occur in a forest near to that of the present study (Carrascal & Alonso 2006). Furthermore, during

11 observation periods (*see below*) we recorded the time during which the feeders were occupied by great spotted woodpeckers (*Dendrocopos major*), as this species does not tolerate the presence of other birds on the feeders, and found that the exposed feeders were more intensively used by woodpeckers than the safe ones (*t*-test on arcsine-squared-root transformed proportion of time used by woodpeckers in relation to total observation time on feeders: $t_9 = 3.00$, $p = 0.015$). Thus, great tits might perceive exposed feeders as low quality food sources.

Cheek colour manipulation

A total of 44 male great tits were captured at the feeders with funnel-traps (Senar *et al.* 1997) and classified as of one or more years according to plumage characteristics (Jenni & Winkler 1994). In total, the dataset comprised 36 adults, 7 yearlings and one individual of an unknown age. We focused on males because of the lower affinity of female great tits for artificial feeders (Senar *et al.* 1999). The birds were individualized with a code of colour (blue, red and white) rings. A digital calliper was used to measure the tarsus length and the size of the black ventral stripe by measuring the minimum width to the nearest 0.01 mm. We chose this measure for the stripe size because it is well correlated with the total area of the stripe and can be taken with a lower measuring error (Senar 2004). The birds were weighed on a portable electronic balance to the nearest 0.1 g. We also measured the size of the cheek patch as described in Galván and Sanz (2008). Ventral stripe width and cheek size could not be measured in all cases because some birds escaped before all measures were taken. In particular, ventral stripe width could be measured in only 35 birds and cheek size in 43 birds. We also recorded whether great tits in hand screeched or not as an approach to collect their stress-related behaviour.

The birds were randomly assigned to either a manipulated group or to a control group. The manipulated group was formed by birds in which we cut the tips of seven–eight white feathers of the cheek with scissors, thus creating small black irregularities in this plumage patch (Fig. 1C).

Although we don't know the natural variation of this character because it is composed of subtle changes in the separation of white feathers and thus is difficult to quantify, we are confident that the irregularity in cheek colour we created with our manipulation is inside the natural range of the species because it only involved the generation of small gaps and thus constitutes a subtle modification (*see* Fig. 1). Great tits with small gaps in their cheeks are commonly observed in many populations of the species (*pers. obs.*). On the other hand, we cut the tip of a few black feathers from the back of the head in other birds that served as controls. Manipulated and control birds did not differ in neither cheek patch size (ANCOVA with treatment as a fixed factor and tarsus length as a covariate to control for body size: $F_{1,40} = 0.05$, $p = 0.817$), breast stripe (one-way ANOVA: $F_{1,33} = 0.83$, $p = 0.367$), age (logistic regression: $\chi^2_1 = 2.99$, $p = 0.083$) nor body condition measured as body mass divided by the cube of tarsus length (one-way ANOVA: $F_{1,40} = 0.40$, $p = 0.529$).

In addition, we tested a possible effect of the colour of the rings in the treatments. Because sample size was low, ring colour could not be introduced in the different models (*see* below), but we tested whether the presence of red rings was biased towards one of the two treatments (*i.e.* manipulated or control), as this colour seems to generate sensorial biases associated with dominance in birds and other vertebrates (His & Barton 2005, Healey *et al.* 2007, Pryke 2007). The probability of bearing red rings did not differ between control and manipulated great tits (logistic regression: $\chi^2_1 = 1.45$, $p = 0.228$).

Behavioural observations

After the capture of birds, we made observations with a telescope from the inside of a hide 10 m from the feeders. Although we initially set a time of 120 min for the observations, adverse climate conditions created by snowfalls prevented us from finishing some of the observation periods. In total, our data were obtained from 17 observation periods with a duration that ranged from 75 to 120 min that comprised a total observation time of 1717 min. All behavioural observations

were made by a single observer (IG).

Continuous observations of ringed birds on the feeders were carried out, excluding those waiting nearby. The time that ringed birds spent on the feeder (measured with a chronometer) during all their stays and the number of aggressions carried out or received by the birds were recorded, distinguishing between escalated fights and agonistic displays. The reason for making this distinction is that the great tits exhibit their cheeks during the agonistic displays (*see* Introduction), so that this type of aggression may be more effective than direct escalated aggressions in permitting actors or receivers to know the social status of the rivals. The small size of feeders (*see* above) made that not many birds could use them at the same time, which allowed us to identify all ringed birds on feeders, including those involved in escalated fights. We also recorded the outcome of the aggressions, considering that an actor was successful when it clearly displaced the receiver from a site at the feeder to another site or away from the feeder, and unsuccessful when the receiver could not be displaced. For a given marked individual, we recorded any interactions with any other bird, marked or not.

As some birds were recaptured during the course of the experiment, we recorded the stress-related behaviour during these recaptures (no other measurements were collected during recaptures, the birds being immediately liberated) in order to test whether the cheek manipulation affected the behaviour of birds. The stress-related behaviour during the first captures (*i.e.* before manipulation) was significantly related to that during second captures (*i.e.* after manipulation) in 21 great tits (logistic regression: $\chi^2_1 = 14.68$, $p < 0.001$), meaning that our experimental manipulation did not greatly affect the behaviour of birds.

Statistical analyses

As we rarely observed interactions between two marked birds, the analyses on aggressions were done separately from the perspective of the actor (number and success of aggressions performed) and of the receiver (number and success of aggressions received).

The number of aggressions performed or received by a bird depends of course on the time spent on the feeder and on the number of other birds with which the feeder is shared in that moment. However, we could not film the feeders during observations, so that the number of birds present on the feeder at the moment at which each aggression occurred could not be determined. Because of that, in order to calculate the number of aggressions performed or received per unit of time spent on the feeder we only considered the duration of the stays on the feeder during which the aggressions were observed. That is, rather than considering the total time during which a bird was observed on the feeder, we only used the duration of the stays during which the aggressions had occurred, excluding the duration of stays during which no aggressions took place. This way we considered only the stays that were made under conditions that were appropriate for the occurrence of aggressions, and excluded the stays during which no aggressions occurred because the context did not allow it (for example because the bird was alone on the feeder). Therefore, we divided the total number of aggressions observed for each bird by the duration of those stays.

In order to investigate the factors affecting the total time that great tits spent on feeders of different quality, we performed general linear model analyses (GLM) in which the dependent variable was the total time during which a bird was observed on a feeder divided by the observation time that had been spent on that feeder. We transformed these proportions by calculating the arcsine of the squared root. The sampling unit was the individual bird. As the same bird was frequently observed in more than one feeder, we calculated the mean time spent on feeders of the same type (safe or exposed), and when the same individual was observed on both types of feeders, we chose one of them at random to use in the analyses and thus avoid pseudoreplication. Experimental treatment (manipulated or control) and feeder location (safe or exposed) were introduced as fixed factors. We controlled for the social status that birds had before capture by introducing the width of the black ventral stripe as a covariate, as this trait is positively correlated with dominance in the great tit (Senar

2006 and references therein). As ventral stripe size is correlated with body size (e.g. Järvi & Bakken 1984, Wilson 1992) we did not introduced any additional variable to control for the effects of this trait. The saturated models were thus formed by treatment, feeder location, treatment \times feeder location, stripe width, stripe width \times treatment and treatment \times feeder location \times stripe width. Starting from this model we subsequently removed non-significant terms, setting a probability of 0.1 to abandon the model and not removing a factor until all the interactions that contained it had been previously removed. However, sample size did not allow us to consider the effect of age.

The same was done to determine the factors affecting the number of aggressions observed in which the number of aggressions performed or the number of aggressions received were the dependent variables. Separate analyses were made for escalated aggressions, agonistic displays and data pooled for both types of aggressions. Age (first year or older) was introduced as a fixed factor, and thus in this case the saturated model was formed by treatment, age, treatment \times age, stripe width and stripe width \times treatment. Sample size prevented us to include a three-order interaction.

The success of aggressions was analysed with additional GLMs. We counted all the aggressions performed or received by each bird and calculated the proportion that were successful, using only data from individuals from which we observed three or more aggressions. This proportion was arcsine-squared-root transformed and introduced as dependent variable in the models. In the case of aggressions performed, we only included treatment and stripe width in the models, but the effect of age could be also considered in the case of aggressions received because sample size was higher.

In all the models, inspections of residuals were made to determine if the conditions of homoscedasticity and normality were fulfilled. Degrees of freedom differ between models because age and stripe width were not measured in all birds. When an interaction was significant, Duncan's post-hoc test was performed to explore differences between the levels of factors. When sample sizes were too small to perform GLMs,

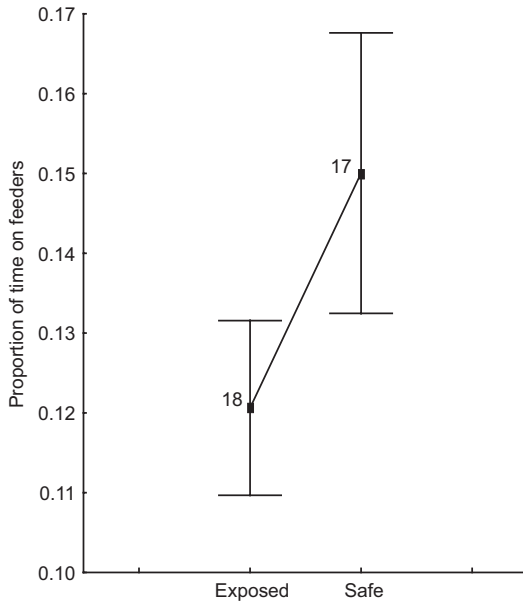


Fig. 2. Proportion of time (\pm SE) spent by male great tits in exposed and safe feeders. The values are the arcsine of the squared root of proportions. Numbers are sample sizes (individual birds).

differences between medians were analysed with Mann-Whitney's *U*-test.

Results

We recorded a total of 848 stays of great tits of known identity, during which 294 aggressions (213 escalated aggressions and 81 agonistic displays) could be observed. This permitted us to obtain information on the time spent on feeders by 35 different males, on the number of aggressions performed for 32 males and on the number of aggressions received for 30 males. The success could be determined for 23 and 27 males for performed and received aggressions, respectively.

Feeder use

The model to investigate the factors affecting the time spent on feeders by male great tits explained a considerable amount of variance in this variable (adjusted $R^2 = 0.13$, $F_{3,31} = 2.63$, p

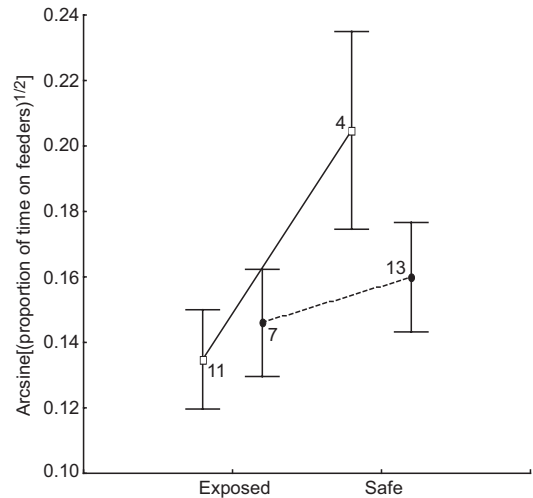
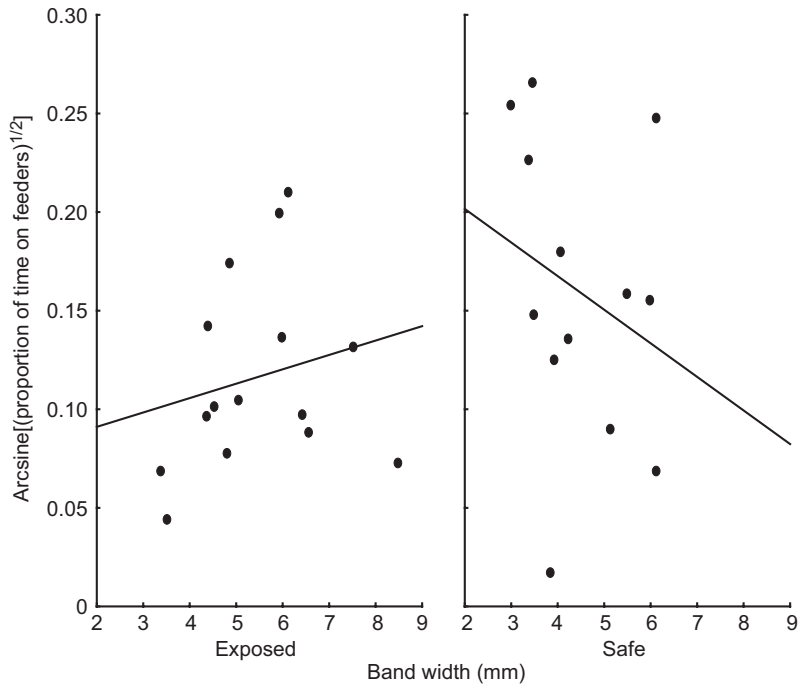


Fig. 3. Proportion of time (\pm SE) spent in exposed and safe feeders by manipulated male great tits in which the plumage pattern of the white cheeks was manipulated (circles, dashed line) and those that served as controls (squares, solid line). The values are the arcsine of the squared root of proportions. Numbers are sample sizes (individual birds).

$= 0.067$), and showed that the proportion of time spent in safe feeders was higher than in exposed feeders ($F_{1,31} = 4.49$, $p = 0.042$, Fig. 2), though experimental treatment had no significant effect ($F_{1,31} = 1.15$, $p = 0.291$). However, the interaction between feeder location and treatment was significant ($F_{1,31} = 5.08$, $p = 0.031$, Fig. 3), and a post-hoc test showed that this was due to a longer time spent on safe feeders as compared with that spent on exposed feeders by control birds ($p = 0.007$) and to a longer time spent by controls on safe feeders as compared with the time during which manipulated birds were observed on this type of feeder ($p = 0.032$). In contrast, manipulated birds spent the same amount of time feeding on exposed and on safe feeders ($p = 0.924$), and there were no differences between manipulated and control birds on exposed feeders ($p = 0.438$).

When only individuals in which stripe width was measured were considered, this variable was included as a covariate, and after non-significant terms were removed (treatment \times stripe width: $F_{1,20} = 0.05$, $p = 0.828$, and treatment \times feeder location \times stripe width: $F_{1,21} = 0.15$, $p = 0.705$),

Fig. 4. Relationship between the proportion of time spent in exposed and safe feeders and stripe width in male great tits. The values are the arcsine of the squared root of proportions. Each point represents the mean value for a individual bird. Lines are regression lines.



the significance of the model improved (adjusted $R^2 = 0.28$, $F_{5,22} = 3.14$, $p = 0.027$). This was due to a marginally significant interaction between feeder location and stripe width ($F_{1,22} = 4.06$, $p = 0.056$) that appeared because the slope of the regression line between time spent on feeders and stripe width was negative and approached significance in the case of safe feeders ($\beta = -1.04$, $p = 0.086$, Fig. 4) but was far from significance in the case of exposed feeders ($\beta = 0.31$, $p = 0.709$, Fig. 4), though stripe width *per se* did not contribute significantly to the model ($F_{1,22} = 1.25$, $p = 0.276$). The contributions of the other factors were as in the model without stripe width (treatment: $F_{1,22} = 1.78$, $p = 0.195$, feeder location: $F_{1,22} = 6.72$, $p = 0.017$, treatment \times feeder location: $F_{1,22} = 9.04$, $p = 0.006$).

Aggressions performed

The model obtained to investigate the factors affecting the total number of aggressions carried out by great tits included only the experimental treatment effect (adjusted $R^2 = 0.09$, $F_{1,30} = 4.14$, $p = 0.051$), indicating that control birds tended

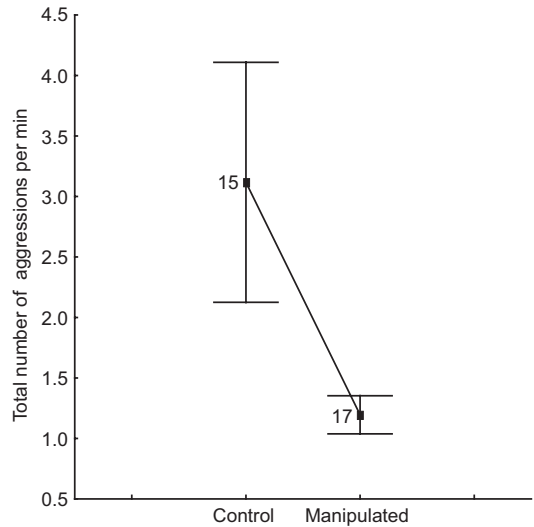


Fig. 5. Total number of aggressions (escalated interactions plus agonistic displays) carried out by manipulated great tits in which the plumage pattern of the white cheeks was manipulated and those that served as controls. Numbers are sample sizes (individual birds).

to initiate a higher number of aggressive interactions than manipulated birds (Fig. 5). The rest of factors considered were not significant and

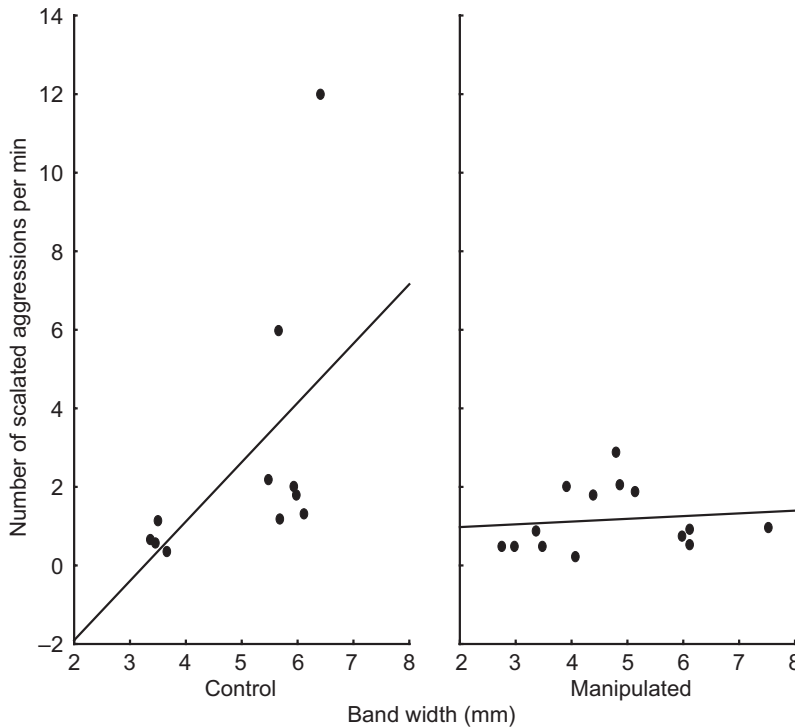


Fig. 6. Relationship between the number of escalated aggressions initiated by great tits and stripe width in manipulated birds in which the plumage pattern of the white cheeks was manipulated and those that served as controls. Each point represents the mean value for a individual bird. Lines are regression lines. The positive correlation in control birds was maintained after removing the two upper points of the figure.

were thus subsequently removed from the model (treatment \times age: $F_{1,19} = 1.16$, $p = 0.294$, age: $F_{1,20} = 1.40$, $p = 0.250$, treatment \times stripe width: $F_{1,22} = 2.22$, $p = 0.150$, stripe width: $F_{1,23} = 1.97$, $p = 0.174$).

When only escalated interactions were considered, the obtained model included the treatment effect, stripe width and the interaction of both, being excluded the effect of age ($F_{1,19} = 0.89$, $p = 0.359$) and its interaction with treatment ($F_{1,18} = 0.20$, $p = 0.663$). This model explained a significant portion of variance in the number of aggressions carried out by great tits (adjusted $R^2 = 0.25$, $F_{3,21} = 3.66$, $p = 0.029$), and showed that stripe width was positively correlated with that variable ($\beta = 0.42$, $F_{1,21} = 5.34$, $p = 0.031$) and that the interaction between treatment and stripe width was also significant ($F_{1,21} = 4.44$, $p = 0.047$), though treatment *per se* did not contribute to the model ($F_{1,21} = 2.79$, $p = 0.110$). The interaction effect was due to a positive and significant slope of the regression line between the number of escalated aggressions and stripe width in controls ($\beta = 1.66$, $p = 0.011$, Fig. 6) that was not found in manipulated birds ($\beta = 0.07$, $p = 0.871$, Fig. 6). When only

agonistic displays were considered, the sample size was too small to control for the effects of stripe width, but the test performed on treatment effect did not show significant differences only between the number of displays initiated by control and manipulated birds ($U = 13.5$, $N_1 = 5$, $N_2 = 6$, $p = 0.784$).

The success of escalated aggressions initiated by great tits was not affected by neither experimental treatment nor stripe width (adjusted $R^2 = -0.02$, $F_{2,12} = 0.84$, $p = 0.454$, treatment: $F_{1,12} = 1.40$, $p = 0.259$, stripe width: $F_{1,12} = 0.35$, $p = 0.562$), and the removal of stripe width from the model did not change the results (adjusted $R^2 = -0.03$, $F_{1,20} = 0.45$, $p = 0.508$). The same applied to the success of escalated aggressions and agonistic displays taken together (adjusted $R^2 = 0.03$, $F_{2,13} = 1.23$, $p = 0.323$, treatment: $F_{1,13} = 1.91$, $p = 0.190$, stripe width: $F_{1,13} = 0.51$, $p = 0.486$, model with treatment effect only: adjusted $R^2 = 0.03$, $F_{1,21} = 1.57$, $p = 0.224$). Although sample size was small, and this prevented us from controlling for the effects of stripe width, differences were significant in the case of agonistic displays ($Z = 2.12$, $N_1 = 3$, $N_2 = 4$, $p = 0.034$), indicating that the success of displays

performed by manipulated birds was lower than that of controls (Fig. 7).

Aggressions received

The total number of aggressions received by great tits was not explained by any of the factors considered (treatment \times age: $F_{1,16} = 0.04$, $p = 0.851$, age: $F_{1,17} = 0.02$, $p = 0.896$, treatment \times stripe width: $F_{1,19} = 0.26$, $p = 0.619$, treatment: $F_{1,20} = 0.02$, $p = 0.895$, stripe width: $F_{1,21} = 0.11$, $p = 0.740$), and the same applied to escalated aggressions only (treatment \times age: $F_{1,14} = 0.60$, $p = 0.452$, age: $F_{1,15} = 0.01$, $p = 0.923$, treatment \times stripe width: $F_{1,17} = 0.36$, $p = 0.555$, stripe width: $F_{1,18} = 0.97$, $p = 0.337$, treatment: $F_{1,26} = 0.31$, $p = 0.584$). Sample size for agonistic displays was too small and only experimental treatment and stripe width were included in the model, but there were no significant effects (stripe width: $F_{1,8} = 0.05$, $p = 0.828$, treatment: $F_{1,13} = 1.65$, $p = 0.222$).

The observed variation in the success of total aggressions received by great tits could be explained by a marginally significant model including only the experimental treatment effect (adjusted $R^2 = 0.10$, $F_{1,20} = 3.39$, $p = 0.081$), as the rest of factors did not contribute to explain the variance in that variable (stripe width: $F_{1,12} = 0.11$, $p = 0.747$, treatment \times age: $F_{1,17} = 0.11$, $p = 0.738$, age: $F_{1,18} = 0.27$, $p = 0.610$). Thus, the success of aggressions tended to be higher when directed to a manipulated bird than when directed to a control bird (Fig. 7). None of the factors was significant when only escalated aggressions were considered (treatment \times age: $F_{1,12} = 0.22$, $p = 0.648$, age: $F_{1,13} = 0.16$, $p = 0.699$, stripe width: $F_{1,15} = 1.37$, $p = 0.261$, treatment: $F_{1,20} = 1.34$, $p = 0.261$). Sample size only permitted us to search for possible differences between manipulated and control birds in the median proportion of agonistic displays directed to great tits that were won by actors, but the test was not significant ($U = 1.5$, $N_1 = 5$, $N_2 = 2$, $p = 0.175$).

Discussion

Overall, the great tits made a differential use of

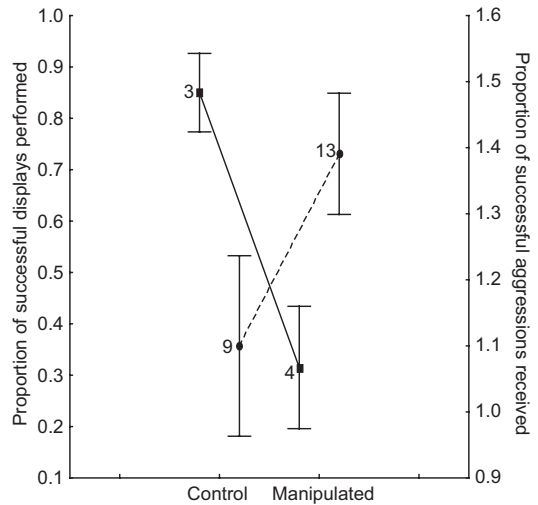


Fig. 7. Proportion of successful agonistic displays initiated (\pm SE, left axis, squares, continuous line) and of successful aggressions received (\pm SE, right axis, circles, broken lines) by manipulated great tits in which the plumage pattern of the white cheeks was manipulated and those that served as controls. Only the values of the right axis are transformed (arcsine of the squared root of proportions) because the statistical test on the data shown in the left axis was performed with untransformed values (see text). Numbers are sample sizes (individual birds).

artificial feeders according to the predation risk they encountered, the time spent on safe feeders being longer than that on exposed ones. Thus, we successfully created different regimes of predation risk, which made the safe feeders high-quality food sources that should be mainly exploited by dominants when hierarchical classes exist (Ferns & Hinsley 2004, Carrascal & Alonso 2006). In fact, control birds did not allow for more intense use of safe feeders by birds with manipulated cheeks, whereas control birds spent a significantly higher proportion of time on safe than on exposed feeders. However, manipulated birds were not relegated to exposed feeders, as they spent the same time in both types of feeders. Thus, manipulated birds were just limited to make use of safe (i.e. preferred) feeders. This is according to the fact that effective agonistic interactions do not cause the retreat of subordinate individuals, but permit dominants to utilize the resource, being irrelevant to the dominants if subordinates also use it or not (Senar 1994, Galván 2004). Therefore, the results on the usage

of feeders indicated that the manipulation of the cheek colour uniformity changed the social status of great tits.

On the other hand, aggressions used to occur among dominant individuals, which could be a mechanism for avoiding cheating individuals with dishonest badges of status (social control hypothesis, Senar 2006). Although the hypothesis is controversial, there are plenty of data supporting, at least, that most aggressions take place between dominants (Senar 2006). We could not analyse interactions between two individuals of known identity but actors and receivers separately, and thus predicted that the number of aggressive interactions observed would be higher in control than in manipulated birds. The results were in the expected direction, as control birds initiated more aggressions than manipulated birds. Interestingly, this was not found when only agonistic displays were considered, but, even with a small sample size, the success of these displays was higher in controls. Thus, the receivers of displays may have recognized manipulated birds as subordinate individuals, which thwarted the attempts of displaying birds to avoid overt aggressions (Senar & Camerino 1998). This inefficiency of manipulated birds may make them increase the number of displays performed, which could be the cause of the lack of differences in that variable between manipulated and control individuals (Greig *et al.* 1983). The performance of escalated aggressions is probably too fast once initiated to detect differences in their success between manipulated and control birds.

Differences between manipulated and controls were not found in relation to the number of aggressions received. Hence, control individuals produced more aggressions than manipulated birds, but they did not receive more aggressions, though the success tended to be higher when the aggressions were directed to manipulated birds. This was found in other contexts and species with a hierarchical social organization (e.g. Galván 2004), and could be explained by the fact that the pre-attack display (i.e. showing the cheek plumage pattern in this case) represents an efficient form of agonistic communication. Thus, the cheek colour pattern of control birds prevented them from becoming victims of greater numbers of attacks, which is probably caused by

avoidance of dominants by subordinates (Senar & Camerino 1998). However, an alternative explanation may be that manipulated birds felt less confident during interactions. Therefore, the results on the number and success of aggressions also indicated that our experiment converted manipulated birds into subordinate individuals.

Our results were consistent after controlling for the effects of the 'intrinsic' dominance of great tits (i.e. dominance before capture) through the size of the black ventral stripe. This trait is positively correlated with dominance in this species (Senar 2006 and references therein), and, in accordance, we found that male great tits with larger stripes performed more escalated aggressions overall. Interestingly, there was also a significant interaction between experimental treatment and stripe size that indicated that the positive effect of stripe width on the number of escalated aggressions performed was observed in control but not in manipulated birds. Therefore, the size of the ventral stripe no longer predicted the dominance of great tits after the plumage pattern of cheeks was manipulated, which suggests that the uniformity of the cheek colour may be a better indicator of dominance than stripe size. This may explain why some authors failed to find a relationship between stripe size and dominance (e.g. Wilson 1992).

Other authors provided previous results that are in agreement with the findings of the present study. In pied flycatchers (*Ficedula hypoleuca*), males modified their behaviour after the white forehead patch size was artificially reduced, providing a higher parental effort than non-manipulated males because they probably perceived their low competitive ability (Sanz 2001). Blanco and de la Puente (2002) found that the testes volume, a measure of aggressiveness, of black-billed magpies (*Pica pica*) tended to decrease with the level of damage in tail feathers. Ferns and Lang (2003) observed that male shelducks (*Tadorna tadorna*) with sharper chest bands had access to preferred feeding sites. Thus, the purity or uniformity, probably in addition to the immaculateness of patch borders, seems to have a compelling role in the behaviour of birds during and outside the breeding season.

In conclusion, male great tits with uniform cheek patches dominated those with small gaps

simulating the effect of peckings by other birds, which makes cheek colour uniformity a badge of status that had not been previously described. Therefore, this plumage patch seems to evolve as an amplifier (Galván & Sanz 2008) because it can reflect the outcome of intraspecific aggressions and information that great tits use to determine the social status of conspecifics.

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