



The function of threat display in wintering great tits

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It is generally accepted that threat displays have signal function and serve to repel opponents, but why they should have such an effect is a matter of debate. Using videotaped interactions from 2 years and nine flocks each year, we analysed the pattern of occurrence of agonistic displays and attacks in captive flocks of wintering great tits, *Parus major*. One currently influential perspective is to view threat interactions as sequences of distinct moves and countermoves, in which stronger threats can reliably indicate aggressive motivation because they carry a cost of eliciting counterattacks from certain opponents. We found little evidence for this kind of mechanism operating in great tits. Another possibility is that social dominance is important in ensuring reliable communication, for instance because an individual needs both to display and to attack to maintain its rank. It would be hard to test the importance of this kind of mechanism directly, but our observations were consistent with such an idea. Dominants won the majority of bouts of interaction and had higher rates of display and attack than subordinates, but a subordinate could temporarily overcome a dominant through intense aggression. We also found that the level of displaying in one bout provided information about the rate of aggression in following bouts. As a general interpretation of great tit aggressive behaviour, we suggest that particular displays form part of a graded signal of motivational state, so that a greater rate of displaying or a greater proportion of intense displays, together with a greater rate of attacking, correspond to a greater aggressive motivation.

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In many group-living birds, such as wintering passerines, agonistic behaviour is common and may range from more or less ritualized display to direct fighting. Aggressive display is usually defined as distinct agonistic behaviours not involving physical contact (e.g. Huntingford & Turner 1987; Bradbury & Vehrencamp 1998). Although aggressive display has been studied extensively for many decades, several issues remain unresolved, including the function of displays and the costs involved when an individual engages in a conflict. There is general agreement that displays in some contexts may indicate the fighting ability of an opponent (Parker 1974), as in cichlids, *Nannacara anomala* (Enquist & Jakobsson 1986), or in red deer, *Cervus elaphus* (Clutton-Brock & Albon 1979). Equally accepted is the general idea that displays have a signal function and serve to elicit a response (Lorenz 1935; Tinbergen 1952), for instance by causing an opponent to withdraw. If displays reliably indicate fighting ability, it makes sense that a weaker opponent might be repelled. However, this cannot be the only function of threat display. For instance, wintering great tits, *Parus major*, live in relatively stable flocks where

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members meet repeatedly, allowing individual recognition and the memorizing of fighting ability. This means that individuals should know each other's fighting ability, so that the main function of threat display is unlikely to be assessment of relative fighting ability.

The important question of why there is variability in displays has also received attention. Tinbergen (1959) held the view that different displays are adapted for specific purposes, and are used in different contexts, such as close-range versus long-distance threats. Later authors suggested that more aggressive and more effective displays might elicit counterattacks, so that only highly motivated individuals would use them (Maynard Smith 1979; Andersson 1980; Hinde 1981; Caryl 1982; Enquist et al. 1985). This kind of relation, where more effective displays are costlier to perform because of the risk of retaliatory attacks, would thus allow participants to communicate their levels of motivation reliably (Enquist et al. 1985; Bradbury & Vehrencamp 1998; Hurd & Enquist 2001). The idea has had a strong influence on current thinking about threat signalling, so that the risk of counterattack is now believed to be an important factor promoting the evolutionary stability of aggressive communication (Bradbury & Vehrencamp 1998, pp. 655–658, 702–708; Hurd & Enquist 2001). Our first aim in this

study was to examine the relevance of this idea to threat signalling in wintering great tits.

Some studies on group-living birds indicate that high-level displaying can provoke counterattacks (Popp 1987a, b), but in one study this pattern was not found (Wilson 1994). In general, however, there are difficulties in using observational data to examine possible cause-effect relations between the behaviours of interacting individuals. If there is variation between sampling periods (e.g. between days) in the overall level of aggression, and samples are subsequently pooled, there is a risk of spurious correlation between behaviours of the interacting individuals. Such variation may for instance be caused by fluctuating weather conditions, which are perceived by all individuals, affecting the value of gaining access to a feeder. Thus, when an individual is aggressively motivated and likely to use high-level threats, its opponents are also likely to be in a state of increased aggressive motivation, for reasons other than the individual's behaviour. In our analysis of great tit interactions, we avoided simple pooling of data and instead analysed the relative timing of behaviours within a dyadic interaction.

An alternative and frequently proposed idea concerning the evolutionary stability of aggressive displays is that repeated interactions between acquainted individuals ensure reliable communication (e.g. van Rhijn 1980; van Rhijn & Vodegel 1980; Hauser & Nelson 1991; Silk et al. 2000). For instance, for birds living in relatively stable social groups structured in a hierarchy, the repeated interactions in a social dominance system could ensure a reliable relation between displaying and attacking. Thus, a bird that frequently performs intense displays but never attacks might not be able to maintain a high rank. It would be difficult to make observations bearing directly on this hypothesis, but one can at least check its general feasibility. Examples of prerequisites for the hypothesis are that both displaying and attacking should be needed to maintain a dominant position and that an individual's rates of display and attack should be positively correlated when one compares different dominance categories or different points in time. A second aim in our study was to look for these kinds of relations in flocks of great tits.

The question of which type of information displays can transmit is closely related to the issue of evolutionary stability. A number of authors have focused on displays as predictors of future actions of the signaller, such as attacking or fleeing (e.g. Stokes 1962a; Blurton Jones 1968; Andersson 1976). This predictive relation may be seen in two ways. First, aggressive displays could operate like intention movements, indicating that attack is imminent (Tinbergen 1952). Second, threat displays could reflect the motivational state of the sender without indicating specific immediate actions, thus leading to a more indirect relation with future aggression (Hinde 1981; Popp 1987a). This relation might be fairly weak, so that little information is transmitted (Caryl 1979; Maynard Smith 1979; Andersson 1980), corresponding to the idea of 'typical intensity' (Morris 1957). There is also a view that displays do not convey information but instead manipulate opponents to withdraw, possibly

against their own interest (Dawkins & Krebs 1978). Our third aim in this study was to investigate the predictive role of displaying in great tit aggressive interactions.

METHODS

We used data from two separate studies on agonistic displays and attacks in captive flocks of great tits. After an initial phase of hierarchy establishment, we videotaped interactions at feeders. Since the birds were well acquainted at this time, the outcome of interactions was probably determined by dominance positions and fluctuating motivational states such as hunger, rather than by ongoing assessment of fighting ability.

Study Animals and Trial Set-up

We carried out the studies at Tovetorp Zoological Research Station in south-central Sweden between 10 December 1998 and 12 March 1999 (referred to as '1999') and between 2 February and 8 March 2000, respectively. During this time, the outdoor temperature varied from +7 to -18°C. We used nine flocks of three to five great tits in 1999 and nine flocks of three birds in 2000. All the birds were male and the majority were in their first winter (age was scored according to Svensson 1994). The birds were caught in the vicinity of the research station and released in the same area after 11–14 days. They were caught in a small wire-net cage, which was baited with sunflower seeds and equipped with a remote-controlled trap door. After capture, they were colour banded and grouped into flocks; each flock spent its entire period of captivity in an outdoor aviary, where the trials were performed. In the trials, grapple fights were rare and no injury resulting from aggressive behaviour was observed. All birds survived the trials and maintained their weight during captivity. The study was approved by the Linköping ethical board.

We used different kinds of outdoor aviaries in the 2 years. In 1999 the aviaries were 3.5 × 7 m and 3 m high, roofed and placed ca. 7 m apart. Each contained two remote-controlled seed feeders, a remote-controlled suet-cake feeder and some branches and bushes for shelter. In 2000 we used three nonroofed aviaries measuring 2.5 m (width at inner end) × 5.5 m × 4.5 m (width at outer end) and 2.2 m high. These were equipped with feeders and shelter as in the previous year, with the addition of an extra suet-cake feeder. The birds had ad libitum access to water and were fed commercial sunflower seeds and suet cakes, as well as home-made 'trial' suet-cakes, consisting of a mixture of chopped mealworms, ground sunflower seeds and suet moulded into cakes. The feeders allowed easy access to only one bird at a time, but had a 20-cm-long array of perches attached, along which intruders could approach the feeding bird. Observations were made with two video cameras (Panasonic NV-DX100 digital video) that were set up in fixed positions outside the aviaries, facing the trial feeders.

For the first 3–5 days, the birds received ad libitum food, including occasional access to trial food, during

which time they could establish dominance ranks. After this initial period, we recorded dominance interactions by preventing access to food and then allowing access to one trial feeder. We did this twice, with 1 day of ad libitum food in between. After 1 more day the trials started, with 1 day of ad libitum food between trials. On the morning of the trial days of the 1999 study, all feeders were closed for between 0.5 and 3 h, depending on weather conditions and temperature, after which the trial feeder was opened. The ensuing interactions were videotaped for 15 min, after which we stopped the trial, and opened all feeders. The 1999 data were originally collected to investigate the influence of predation risk on threat display (Lange & Leimar 2001), so that half of the trials were preceded by a brief predator presentation (a stuffed owl). Data from these types of trials are pooled here. The predator presentation caused the birds to take cover and to give warning calls. When the trial feeder was opened, the birds commenced feeding and interacting on the feeder in a similar way as without a predator presentation, although the level of vigilance was elevated after the predator presentation (Lange & Leimar 2001).

On trial days in 2000, the flocks were allowed access to one or both of the two cake feeders during three 45-min periods in randomized sequence from first light until noon. The feeding periods alternated with periods of 30–60 min without food. Videotaping took place in the first 5 min after the opening of a single feeder. A trial consisted of a period of food deprivation followed by a single-feeder period, giving two trials per day. After mid-day the feeders were all opened and ad libitum food allowed until dusk.

Aggressive Behaviour

Our classification of threat displays and other aggressive behaviours (Table 1) largely follows Blurton Jones (1968). In traditional descriptions a display usually consists of several distinctive elements, some of which may occur in more than one display. Instead we used such distinctive elements as units, and we refer to these units as ‘displays’. For the analyses, we formed three groups of such displays and assigned them the levels low, medium and high (Table 1). Because of the variable structure of aggressive interactions, the details of this scheme, including the number of levels used, are inevitably somewhat subjective. Our aim for the scheme was that low-level displays should be shown in most phases of a conflict, and medium and high levels only in situations of greater aggressive motivation, corresponding to the staircase model in Fig. 1. In our classification, low-level display contained only crest flattened, which was shown almost throughout a conflict, even when no other aggressive behaviours were performed. The next step of our staircase was the medium level, which contained the main body postures that are part of threat signalling. For the high level, we included displays such as wings out and open bill, which can be added to the body postures. We also grouped full attacks, lunges and displacing attacks into a single category referred to as attacks (Table 1).

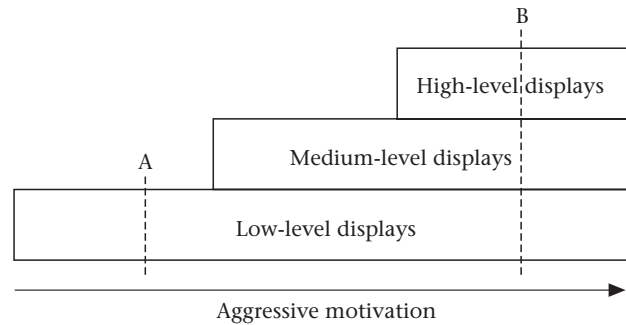


Figure 1. A hypothetical staircase model of the tendency to perform different displays as a function of aggressive motivation. The staircase represents the addition of more display elements with increasing aggression. For a low level of motivation (A) only a limited set of displays is used; for a higher level of motivation (B) the repertoire includes a number of additional displays. Attacks can be launched at different points along the staircase, but the probability of attack increases with aggressive motivation.

A conflict between two individuals could extend over a considerable part of a trial, and could consist of multiple aggressive encounters on the feeder, interspersed with feeding and scanning. We refer to such an encounter as a bout of aggressive interaction; it had to contain at least some medium-level displays, which means that a bout had to start with at least a medium-level display by one bird. A bout ended when a bird either escaped from the feeder or stopped displaying completely. Thus, a bout could consist of only two behaviours (e.g. bird A: ‘Lunge’; bird B: ‘Retreat’), or any number of exchanged threat signals and attacks.

Data Recording and Analysis

The videotaped behaviours were transcribed on to Microsoft Excel worksheets as sequences of behaviours. A row of such a worksheet referred to the behaviour of a single bird at a given instant and contained entries for time, colour band identity and behaviour performed. Birds present at the feeder were recorded in this way in an alternating fashion, with new rows of the worksheet being added when behaviour changed or individuals arrived or left. On average, there were 1.75 rows/s during interactions (1.7 in 1999 and 1.8 in 2000). A Visual Basic program was used to extract data from the worksheet. We also divided the worksheet sequences of behaviours into dyadic bouts. For our definition of a bout of aggressive interaction, as mentioned above, we required that it should start with at least a medium-level threat, even if behaviours thereafter dropped to low again. Thus, a bout was considered to start with the first such (medium-level or higher) aggressive behaviour since the ending of the previous bout. A bout was considered to end when either the initiator or recipient of the initial aggression escaped (left) or stopped displaying completely. The bird remaining at the feeder was considered the winner of the bout. Thus, ‘winning’ could be achieved either by chasing off the opponent with displays or attacks, or simply by holding one’s ground at the feeder, perhaps showing only

Table 1. Classification of some agonistic behaviours in the great tit

Display	Description	Level
Crest flattened, CF	Crest feathers flattened against skull	Low
Erect, ER	Body held erect, straight up, with head at 90° to body	Medium
Crouch, CH	Crouching down with head forward, usually facing opponent	Medium
Head down, HD	Head held down, at 90° to body, which is held horizontally	Medium
Horizontal body, HB	Body held horizontally along the substrate with head forward	Medium
Open bill, OB	Bill held stiffly open	High
Wings out, WO	Wings extended from body to lesser or greater degree, points drooping slightly	High
Tail fan, TF	Tail fanned out	High
Chest display, CD	Head held upwards, showing chest stripe	High
Turn head, TH	Head slowly turning from side to side or kept still, stretched out to one side	High
Full attack, FA	Attack carried through to chasing, aerial combat or grapple fight	Attack
Lunge, LUN	Attack cut short before contact is made	Attack
Displacing attack, DA	Landing on top of (usually) and thus removing a bird from its position	Attack

Several of the displays can be performed in a more or less accentuated manner. For two of the displays (OB and WO) this kind of variation was grouped into classes (OB1, OB2 and WO1, WO2) corresponding to the amplitude of the display. The displays can also be combined (e.g. HB with OB and WO, etc.). We also observed the crest raised (CR) behaviour, which is mainly submissive and is not included in the table. The crest feathers are raised stiffly from the skull.

low-level display, until the opponent withdrew or left. Between bouts, birds often used the low-level crest-flattened display, for instance when perching near the feeder.

Dominance Ranks

Because dominance status is likely to influence aggressive behaviour and, in particular, because one of the hypotheses we tested in this study directly concerns aggressive behaviour in relation to dominance status, we needed to assign relative ranks for each pair of birds that was observed to interact in the trials. Our basic design for the study was to use several flocks, which means that there was a large number of potential pairwise relations (a total of 109 pairs; there were three pairs in a flock of three, six in a flock of four and 10 in a flock of five). Because of the large number of pairs and the tendency of some pairs to interact rather little, it was not feasible to collect enough information on wins and losses within each pair to establish a statistically significant higher number of wins by one of them (given that there could be wins in both directions, this would probably require the observation of well over 1000 bouts). Dominance relations in the great tit are not characterized by strict unidirectional aggression and can also change over a few days (e.g. Verbeek et al. 1999).

Instead, we collected much less data and used this to assign approximate ranks. For the purpose of our study, in which we looked for differences in aggressive behaviour between dominants and subordinates, it was sufficient for the assignment of rank to be substantially better than random. To check this, we tested statistically whether birds that we classified as dominant in a pair overall won more than half of the interactions with the subordinate.

The number of pairs interacting in the trials was 81, somewhat below the potential figure mentioned above. To assign relative dominance within pairs we used a matrix of dyadic wins and losses, obtained separately

from the trial data. As mentioned, dominance interactions were observed on two successive occasions, with 1 day in between, with an average of 4.1 interactions/pair (varying from 0 to 29). An individual that won the majority (more than 50%) of the interactions with another was considered to be dominant in that particular pair. In many pairs, the dominance relation seemed clear, in the sense that the dominant won all bouts, but there were also pairs with several wins in each direction, as well as pairs with few or no interactions (of the 81 pairs, 13 showed a statistically significant difference between the number of wins by the dominant and the subordinate). When needed, we used additional information such as submissive behaviour and avoidance of confrontation to classify dominance.

Statistical Analysis

For several of the questions we investigated, the most natural unit of observation is the sequence of interaction between a given pair of birds during a trial, and we refer to this unit as a dyad or a dyadic interaction. For questions where instead a single bout of interaction was the natural unit, we averaged over the bouts of a dyad to extract a data point. Mean values are reported \pm SEs. All statistical tests are two tailed.

Since a given bird can take part in several dyads, it is not clear that dyads can be regarded as independent units. To deal with this issue, we used the flock as a unit ($N=18$ flocks), either by averaging over the dyads in a flock, or by computing a correlation between two variables separately for each flock. When reporting a comparison with the Wilcoxon signed-ranks test we indicate the number of nonzero differences (N_{diff}) out of the total, because only those differences are actually used in the test. Although flocks will be independent, they are somewhat artificial as units of observation of threat display, and we used this perspective only to perform statistical tests of the main positive findings in our data.

Table 2. Co-occurrence of behaviour patterns in bouts

Display level	Focal display level		
	Medium	High	Attacks
Low	96% (83%)	98% (83%)	80% (83%)
Medium		92% (70%)	73% (70%)
High			70% (21%)

The percentage of bouts in which an individual's low-, medium- or high-level displays co-occurred with focal medium- or high-level displays or with attacks, by the same individual. The percentages are based on the total number of bouts in which the focal behaviour was shown and are averaged over dominance categories and years. The percentage values in parentheses represent the occurrence of the behaviour (low-, medium- or high-level display) among all bouts, again averaged over dominance categories and years.

RESULTS

General Observations

In the trials, a single bird approached the feeder and was soon joined or supplanted by one or more birds. During bouts, one bird was usually sitting at the feeder and the other(s) at varying distances along the attached array of perches. Displays, supplants and lunges were all performed on the feeder, but a full attack almost always caused both individuals to leave the feeder temporarily, after which at least one would return. We observed 574 bouts (320 in 1999 and 254 in 2000) that included both threat displays and occasional attacks. Mean bout duration (s) was 3.17 ± 0.24 in 1999 and 3.55 ± 0.29 in 2000. When a bout ended, the winner had a chance to feed until another (or the previous) opponent appeared, thus making the bouts something of an interruption in the main activity of feeding. We also observed birds queuing by sitting and waiting near the feeder, but we did not record this behaviour. Since the trials took place outdoors, several factors such as variable temperature, drifting snow or rain, the presence of raptors near the aviaries and warning calls from other birds outside might have influenced the individual bird's motivation to compete at the feeder.

Joint occurrence of behavioural components

We first tested the relevance of the staircase model (Fig. 1) by investigating whether a bird using a given focal level display would also use lower-level displays shortly before or after ('focal' refers to a set of behaviours with which certain other behaviours co-occur). Most bouts with the focal display level also contained lower-level displays and this was not just because of the general prevalence of the lower-level displays (Table 2). This is consistent with our suggestion that the display units of the three levels are added to one another as aggression increases. Considering the detailed pattern of display within a bout, lower-level displays were as common or more common immediately before or after a focal display than elsewhere in the bout (Fig. 2), showing that

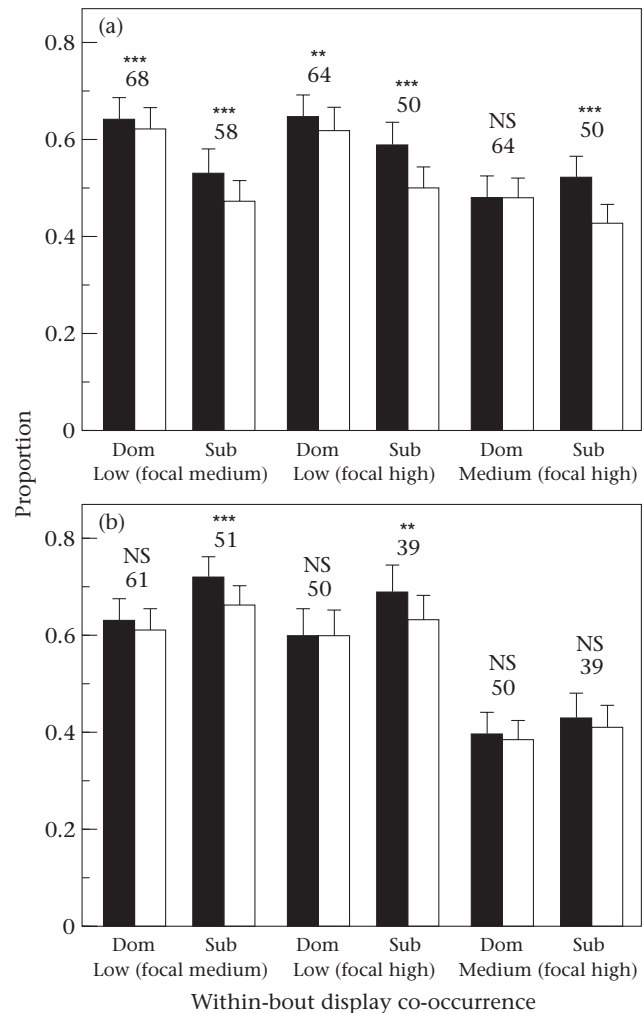


Figure 2. Levels of display within bouts in (a) 1999 and (b) 2000. ■: Proportion of snapshot observations from bouts in which an individual's low- or medium-level displays occurred immediately before or after focal medium- or high-level displays, by the same individual. □: Background proportion of the low- or medium-level displays in the bout. The proportions were computed using only bouts containing the focal displays. Dyad mean proportions for dominant (Dom) and subordinate (Sub) individuals were used as data points. Numbers refer to the number of dyads used (i.e. those showing the focal displays) and error bars indicate SEs. For testing, Wilcoxon pairwise comparisons were made between dyad means within dominance classes: ** $P < 0.01$; *** $P < 0.001$.

different levels of display did not suppress each other. The temporal pattern of display behaviour thus seems consistent with the model.

One could also consider adding the 'attacks' category as a further step of the staircase in Fig. 1. Although such a picture would roughly explain the pattern of co-occurrence between attacks and displays, the fit to data would not be as close as for the different levels of display (Table 2). An appreciable proportion of the bouts with attacks did not contain high-level displays by the attacking individual, which implies that attacks also occurred in bouts containing low- and medium-level displays but lacking high-level displays.

High-level Display and Counterattack

Some dyadic interactions consisted of two or more bouts (1999: 63 dyads, 74%; 2000: 51 dyads, 71%). For these dyads we divided the interaction into an early and a late part. When there was an even number of bouts, the first half was referred to as early and for an odd number we made a split by simply excluding the middle bout from consideration. This splitting into early and late bouts made it possible to investigate to what extent an individual's aggressive behaviour could be seen as a response to the opponent's behaviour, in particular whether attacks were elicited by an opponent's displays. Since the rate of displaying varied between bouts, attacks should have been more frequent in bouts where the opponent's rate of displaying was higher. If one looks at the difference in an individual's rate of attacking (attack behaviours/s of bout time) between late and early bouts (in a dyadic interaction with several bouts), one would consequently expect it to have been positively related to the late–early difference in the opponent's rate of displaying. However, we failed to find any such effect (Fig. 3), which suggests that attacks were not primarily elicited by variation in an opponent's display behaviour. In a similar way, we also investigated whether an individual's displays had tended to be elicited by the opponent's displays, again without finding any significant correlation.

As a further test, we analysed the detailed within-bout temporal pattern to see whether attacks were an immediate response to an opponent's displays. Just before a dominant's attack, the frequency of subordinate high-level displaying was similar to the overall frequency during the bout, but we did find a tendency for more high-level displaying by the dominant immediately before a subordinate's attack (significant only in 2000; Fig. 4). A flock-level analysis supported the results in Fig. 4: before a subordinate's attack the frequencies of high-level displays by the dominant and by the subordinate were higher than the corresponding overall frequencies in the bout (Wilcoxon signed-ranks test: $T=0$, $N_{\text{diff}}=6$, $P=0.03$ in both cases), whereas there were no significant differences for dominant attacks. Thus, subordinate displays seem not to elicit dominant attacks, but dominant displays may elicit subordinate attacks. Since subordinate attacks were rare and high-level displays by dominants were common, the effect would be weak. However, the observation that subordinate displaying was elevated before a subordinate attack complicates the issue and it is not clear that the attacks were really elicited by dominant displays.

A positive correlation between the levels of aggressive motivation of the opponents in a bout or a dyadic interaction, which is already present before the interaction, could produce spurious correlations between the behaviours of the opponents. The two analyses above avoid this problem by looking only at the temporal pattern of displays and attacks within a single bout or between the bouts within a single dyadic interaction. To demonstrate that such spurious correlations can be a problem, let us look at the covariation between the rates

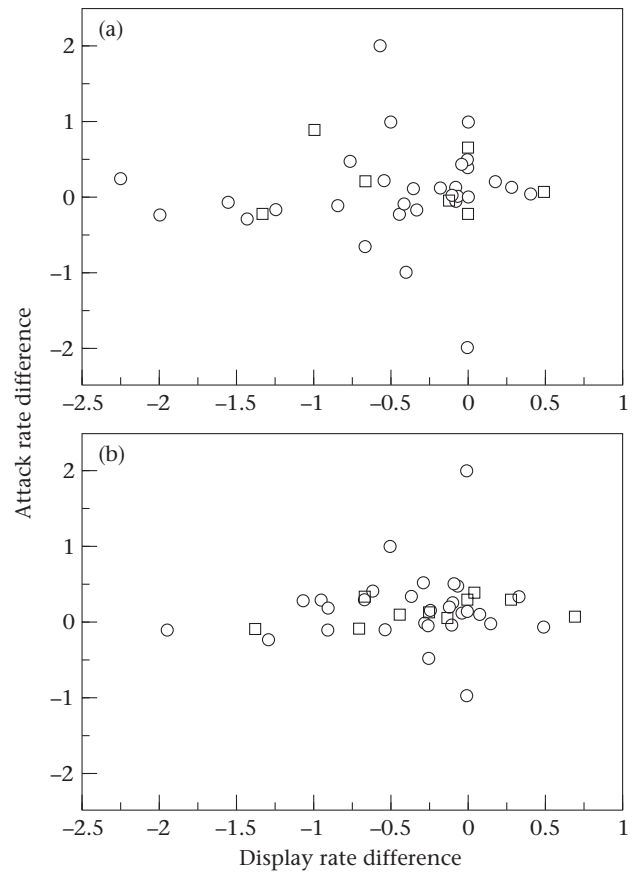


Figure 3. The difference in attack rate between late and early bouts plotted against the opponent's difference between late and early display rate in (a) 1999 and (b) 2000. \circ : Attacks by the dominant; \square : subordinate attacks. Early and late rates of behaviour refer to the first and second half of a dyadic interaction. Only dyads with more than two bouts and a nonzero attack rate were included. For the display rate only high-level displays were considered. Pearson correlations: (a) dominant attack: $r_{32}=0.04$, $P=0.82$; subordinate attack: $r_6=-0.11$, $P=0.80$; in (b) dominant attack: $r_{30}=0.09$, $P=0.63$; subordinate attack: $r_{10}=0.30$, $P=0.35$.

of subordinate high-level displays and dominant attacks among all 574 bouts in our data. The correlation between these variables was statistically significant ($r_s=0.23$, $N=574$, $P<0.001$), although our analyses in Figs 3 and 4 suggest that there was no cause–effect relation. A possible reason for the correlation is that the average level of aggression varied from trial to trial. We found statistically significant variation between trials in both display and attack rates, both for dominants and subordinates (Kruskal–Wallis tests: dominants: display: $H_{50}=126.0$, $P<0.001$; attack: $H_{50}=89.3$, $P<0.001$; subordinates: display: $H_{50}=84.5$, $P=0.002$; attack: $H_{50}=83.2$, $P=0.002$). An alternative method of investigating whether one behaviour tends to elicit another could be to construct contingency tables for pairs of behaviours that follow each other, pooling over all observations. This kind of method has often been used, but it also suffers from the problem of a risk of spurious correlation.

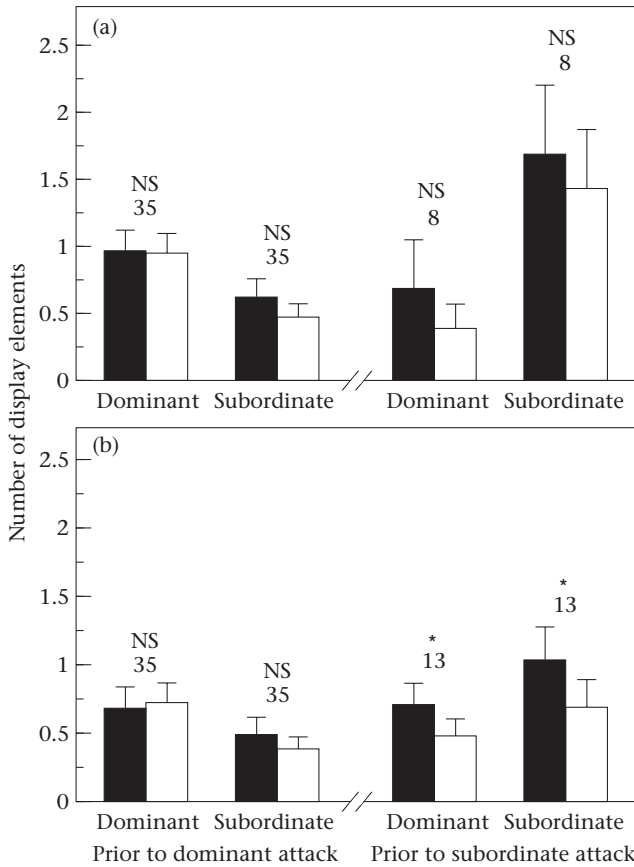


Figure 4. The number of high-level display elements per snapshot observation performed immediately prior to an attack (■) compared to the background level during the bout (□) in (a) 1999 and (b) 2000. Numbers refer to the number of dyads containing attacks by the dominant and by the subordinate, respectively, and error bars indicate SEs. All tests are Wilcoxon pairwise comparisons: * $P < 0.05$.

Displays, Attacks and Dominance

Most, but not all, bouts were won by the dominant bird in a dyad (1999: 87%; 2000: 88%). For each of the 18 flocks, dominants won a higher proportion of bouts than subordinates (Wilcoxon signed-ranks test: $Z = 3.72$, $N = 18$, $P < 0.001$), which corroborates our classification of dominance. However, the outcome of a bout was not determined through immediate recognition of a dominant's privilege. Instead, dominants displayed or attacked more in the bouts that they won, whereas this was not the case in the bouts they lost (Fig. 5). Thus, although the dominance relation had a strong influence on the outcome of a bout, this effect seemed to be mediated at least partly through aggressive behaviour. This ought to mean that the dominance relation was being continually tested. A winning subordinate seemed to display or attack at about the same rate as a winning dominant (Fig. 5), whereas a losing dominant might display or attack more than a losing subordinate. We performed a flock-level analysis of the data presented in Fig. 5 by averaging over the bouts of a flock, which confirmed the results. Wilcoxon pairwise

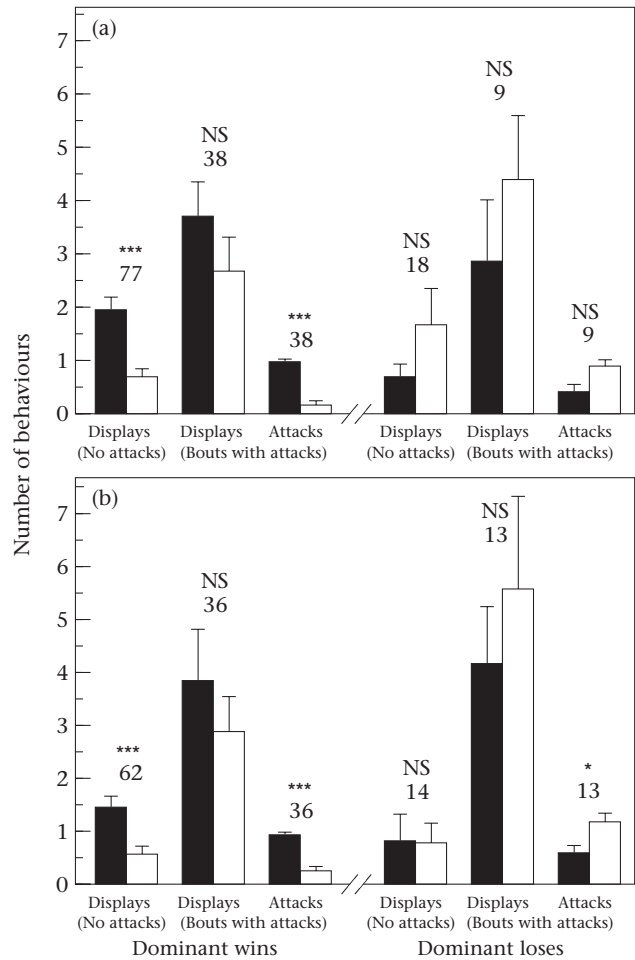


Figure 5. Displays and attacks by winners and losers in (a) 1999 and (b) 2000. Data from bouts with no attacks and bouts with attacks by either bird are shown separately. ■: Dominant behaviour; □: subordinate behaviour. For testing, dyad means for dominant and subordinate individuals were used as data points. Numbers refer to the number of dyads used and error bars indicate SEs. Wilcoxon pairwise comparisons were made between dominance classes, using dyad means: * $P < 0.05$; *** $P < 0.001$.

comparisons between dominance classes showed that there were more dominant displays and attacks in bouts won by the dominant (displays: $Z = 3.62$, $N_{\text{diff}} = 17$, $P < 0.001$; attacks: $Z = 3.52$, $N_{\text{diff}} = 16$, $P < 0.001$) and a non-significant tendency towards more subordinate attacks in bouts won by the subordinate ($T = 5.5$, $N_{\text{diff}} = 8$, $P = 0.08$). It thus seems likely that both displaying and attacking are important in maintaining dominance.

For the overall averages, regardless of winning or losing, we also found a positive relation between the rates of high-level display and attack when comparing dominance categories. With flocks as data points, the dominant display rate was higher than the subordinate display rate (0.79 ± 0.12 versus 0.33 ± 0.06 ; Wilcoxon signed-ranks test: 3.59 , $N_{\text{diff}} = 18$, $P < 0.001$) and the dominant attack rate was higher than the subordinate attack rate (0.069 ± 0.012 versus 0.013 ± 0.004 ; $T = 0$, $N_{\text{diff}} = 15$, $P < 0.001$), so that dominant behaviour was characterized by both more displaying and more attacking.

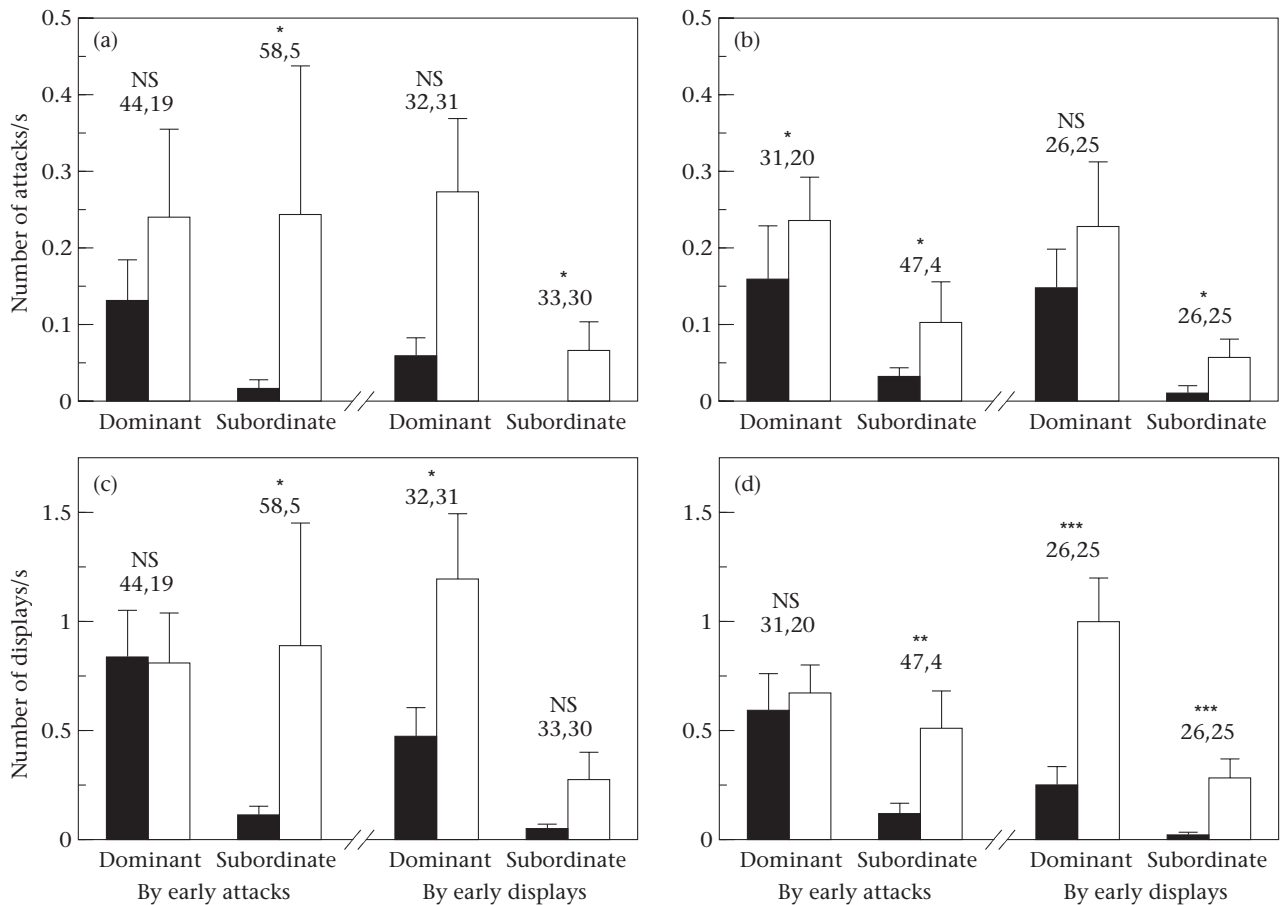


Figure 6. Attack and high-level display rates in the second half of dyadic interactions lasting two or more bouts, as a function of the rate of behaviour in the first half of the interaction (a, c) 1999; (b, d) 2000. ■: Individuals with low early rates; □: individuals with high early rates. The categories low and high indicate whether the early rate of behaviour, either attack or display, was below or above the median. Numbers are the number of dyads in each category and error bars indicate SEs. Dyads with low and high early rates were compared with exact Mann–Whitney U tests: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Information Contained in Displays

We first looked at the variation between the dyads in a flock by computing the rank correlations between display and attack rates, separately for each flock and dominance category (dominants: $r_s = 0.54 \pm 0.07$; subordinates: $r_s = 0.60 \pm 0.07$), and testing whether they tended to be positive (Wilcoxon one-sample test: dominants: $Z = 3.68$, $N_{\text{diff}} = 18$, $P < 0.001$; subordinates: $T = 1$, $N_{\text{diff}} = 15$, $P < 0.001$). These strong positive relations imply that a bird with a high display rate normally also had a high attack rate, but they do not show that current display rates predict future attack rates.

To investigate the question of prediction, we used the division of dyadic interactions into early and late parts. With the early rate of behaviour categorized as below or above the median, the observed late rate was overall higher in dyads with high early values (Fig. 6). This means that an individual's rate of displaying early in an interaction gave information about its rate of attacking later on, but similar information was also available in the early rate of attacking (Fig. 6a, b). Late and early display rates were related in a similar way. To perform a flock-

level analysis of the predictive value of displaying, we computed the rank correlations between early display rates and late attack rates, separately for each flock and dominance category (dominants: $r_s = 0.40 \pm 0.10$; subordinates: $r_s = 0.54 \pm 0.08$), and tested whether they tended to be positive (Wilcoxon one-sample test: dominants: $Z = 2.86$, $N = 17$, $P = 0.005$; subordinates: $T = 1$, $N_{\text{diff}} = 14$, $P = 0.001$).

The observed covariation of aggressive behaviour in early and late parts of a dyadic interaction (Fig. 6) could have come about in various ways. It might mainly reflect a discrete variation, where an absence of intense aggression in early parts is often followed by an absence in later parts, but there could also have been a more graded variation in the behaviour performed. To examine the issue, we created measures of display intensity by assigning points to the different display elements, reflecting their assigned level in Table 1 (low = 0.2, medium = 0.5 and high = 1–1.5 depending on amplitude). Considering only individuals with both early and late display intensities greater than zero, we found a positive correlation between early and late intensities (Fig. 7), indicating the presence of a graded variation in display behaviour. By

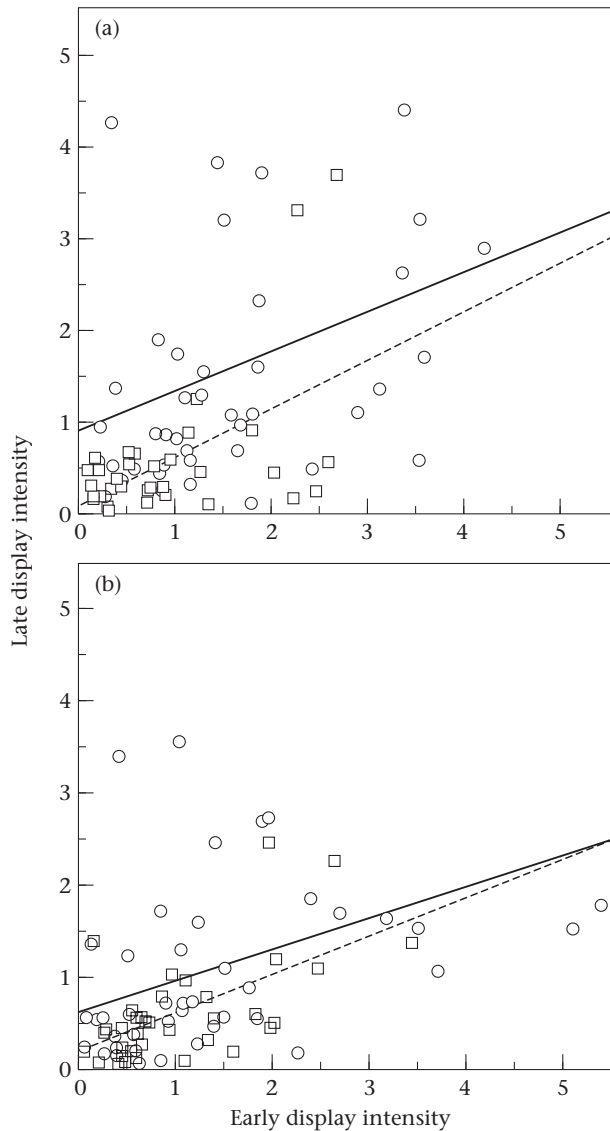


Figure 7. Covariation in fine-scale display intensity between early and late bouts of dyads lasting two or more bouts in (a) 1999 and (b) 2000. Data from an individual (○: dominants; □: subordinates) were included only when both early and late display intensities were greater than zero. Measures of display intensities were computed by assigning ‘threat value’ points to the different display elements, reflecting their assigned level in Table 1. —: Dominants; ---: subordinates. Pearson correlations: (a) dominants: $r_{41}=0.29$, $P=0.06$; subordinates: $r_{32}=0.54$, $P=0.001$; in (b) dominants: $r_{41}=0.52$, $P<0.001$; subordinates: $r_{34}=0.60$, $P<0.001$.

computing the early–late correlations separately for each flock, and testing whether they tended to be positive, we confirmed the result in Fig. 7 (Wilcoxon one-sample test: dominants: $Z=2.24$, $N_{\text{diff}}=18$, $P=0.03$; subordinates: $Z=3.52$, $N_{\text{diff}}=16$, $P<0.001$).

We also analysed the detailed within-bout temporal pattern, to see whether high-level displaying might advertise imminent attack. However, looking at all bouts where high-level display was used, we found no significant increase in the probability of attack immediately after a high-level display for either dominants or subordinates.

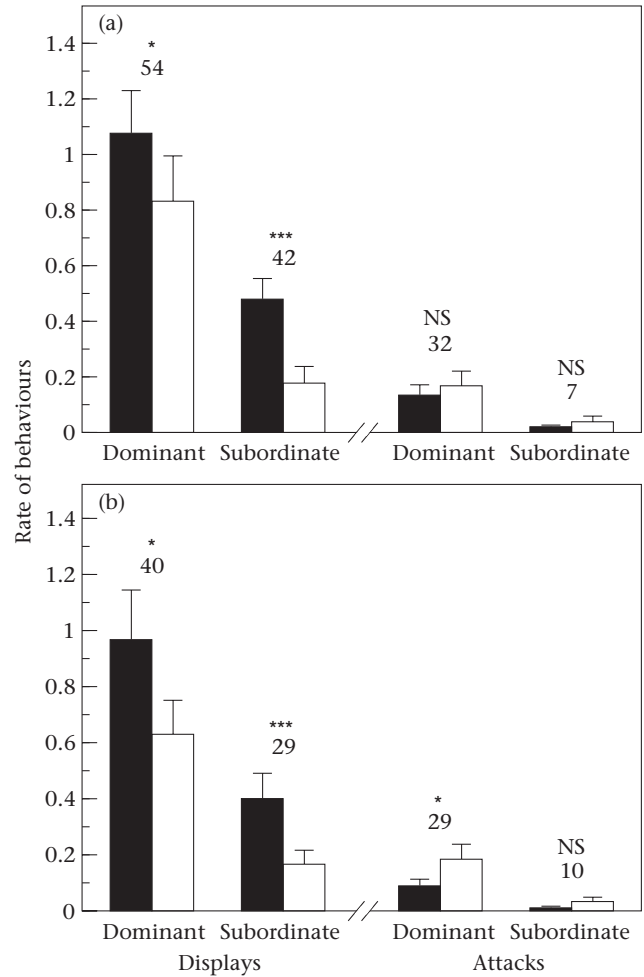


Figure 8. Changes in rates of display and attack between early (■) and late bouts (□) of dyads lasting more than two bouts in (a) 1999 and (b) 2000. Only high-level displays were included in the calculation of the rate of display behaviour. Values ($\bar{X}\pm\text{SE}$) are based on 63 dyads for 1999 and 51 dyads for 2000. Numbers refer to the number of dyads with a nonzero difference between early and late rates of the relevant behaviour. The Wilcoxon matched-pairs test was used to compare early and late rates: * $P<0.05$; *** $P<0.001$.

The division into late and early bouts also made it possible to look for trends in the use of displays and attacks over the course of a dyadic interaction. We found evidence of a gradual escalation, in the sense that there was a tendency towards more attacks in the later bouts and more displays in the early bouts (for attacks, significant only for dominants in 2000; Fig. 8). However, this describes the average tendencies in early and late bouts and the majority of bouts were resolved using displays only. Flock-level comparisons showed a significant decrease in subordinate displaying (Wilcoxon signed-ranks test: $Z=3.52$, $N_{\text{diff}}=16$, $P<0.001$) and significant increases in dominant and subordinate attacking (dominant: $T=25$, $N_{\text{diff}}=15$, $P=0.05$; subordinate: $T=4$, $N_{\text{diff}}=9$, $P=0.03$).

One behaviour pattern showed a particularly strong relation with losing a bout. The crest-raised display (CR) occurs in agonistic situations but has been regarded as

submissive rather than aggressive (e.g. Stokes 1962b) and our data support this interpretation. Looking at both years and averaging over dominance classes, we found only two cases of bout winners showing CR in a total of 87 bouts containing the display. Thus, CR is a reliable signal of submission. The converse pattern CF, which defines our low-level display category (Table 1), appeared in most bouts and thus seemed to be associated with agonistic activity in general.

DISCUSSION

From our analyses of the temporal pattern of an individual's display behaviour and the opponent's attacks (Figs 3 and 4), it seems that the attacks were not directly elicited by intense displaying. This means that the risk of an immediate counterattack is unlikely to be important in shaping display behaviour in the great tit. Nevertheless, an individual's aggressive behaviour is likely to be important in evoking aggression in opponents, but this influence seems to be more general and indirect than a simple sequence of moves and countermoves.

Two studies on wild flocks of wintering passerines, on purple finches, *Carpodacus purpureus* (Popp 1987a), and on American goldfinches, *Carduelis tristis* (Popp 1987b), suggest that high-level displaying can provoke counterattack. These studies, however, are not conclusive, because they involved pooling of data over interactions, with a risk of spurious correlation between the behaviours of opponents. More work would be needed to resolve the issue for these species. There is also a study on captive flocks of wintering silvereyes, *Zosterops lateralis* (Wilson 1994), for which the most effective displays were the least likely to provoke counterattack. Thus, although there are still too few studies for a definite conclusion, it is at least not clear that the risk of counterattack is of general importance for the evolutionary stability of threat signalling, and its role might have been overestimated.

An alternative idea, which might apply to group-living birds, is that repeated interactions between individuals that know and recognize each other could promote reliable aggressive signalling (van Rhijn 1980; van Rhijn & Vodegel 1980; Hauser & Nelson 1991). The way this might work is that other group members learn to interpret an individual's display behaviour, for instance being less intimidated by the displays of an individual that never attacks. These kinds of effects could be channelled through a social dominance system, in which both displaying and attacking are needed to maintain a high rank. It would be difficult to verify experimentally how different hypothetical strategies, such as frequent and intense displaying without attacking, would affect an individual's dominance rank; the best one can do is to make observations on the normal operation of the dominance system.

In the present study, we found that dominants had a considerable advantage in gaining access to the feeder. They achieved this advantage by displaying and attacking more than subordinates (Fig. 5), which suggests that to maintain its rank, a bird needed to keep up a sufficiently

high intensity of aggression. On the other hand, a subordinate bird would also need to be fairly aggressive at times, to secure access to the feeder, at least when its motivation was particularly strong, which is corroborated by our observations (Fig. 5). A combination of dominants acting to maintain their ranks and subordinates needing to overcome dominants could be important in ensuring evolutionary stability of aggressive displays. Although wintering great tits do not live in completely stable groups, dominance hierarchies readily form over a few days (Verbeek et al. 1999), which may be enough to make rank an important social characteristic.

There are also other ways in which the reliability of aggressive communication could be ensured. Vulnerability to predators is a potential cost that could vary with the intensity or form of displaying, since displaying individuals tend to direct a larger part of their attention towards each other, lessening their vigilance (cf. Jakobsson et al. 1995). In a previous study, we found that manipulation of the perceived risk of predation influenced aggressive behaviour in flocks of great tits (Lange & Leimar 2001). The top-ranked bird in a flock used high-level displays at about the same rate regardless of predation risk, but the other flock members reduced their rate of displaying under high risk. This observation is consistent with the idea that predation risk could dissuade less motivated individuals from intense displaying, and it might thus promote the evolutionary stability of aggressive communication.

From our investigation, it is clear that threat displays in wintering great tits convey information, in the sense of allowing prediction of future aggressive behaviour (Figs 6 and 7). The relation between displays and attacks, however, is not an immediate one, but seems rather to be that both behaviours are at least partly caused by the same aggressive motivation. In this way, displaying says little about the exact timing of an attack, but more about the overall risk of attack in the current bout or in the bouts that may follow. The tendency towards escalation from display to attack (Fig. 8) is also consistent with a predictive role for the display behaviour. These points are in good agreement with previous analyses of threat displaying in birds, where the lack of an immediate relation between display and attack was noted as an interesting illustration of the withholding of information about intentions (Caryl 1979; Maynard Smith 1979), whereas the evident general relation between different forms of aggressive behaviour was seen as showing that some type of communication of intentions must be prevalent (Maynard Smith 1979; Hinde 1981; Popp 1987a; Senar 1990).

Our interpretation of great tit display behaviour, in particular the staircase model of the relation between aggressive motivation and behaviour (Fig. 1), has been important in our analysis of the behavioural data, but differs somewhat from previous approaches. Agonistic communication in wintering parids has been dealt with in a number of studies (e.g. Stokes 1962a; Blurton Jones 1968; Wilson 1992; Lemel & Wallin 1993; Scott & Deag 1998; Lange & Leimar 2001). There has been a tendency to treat different threat displays as distinct units with

separate 'meanings', in the sense of having different predictive values, and to view an interaction as a sequence of discrete moves and countermoves. However, because of the variable and complex structure of interactions, we feel that such a perspective may not fit so comfortably with reality. Dyadic bouts of interaction are usually brief, but may contain both attacks and a range of different displays, and several bouts may follow over a period of a few minutes. The considerable number of elements of behaviour used and the innumerable ways in which these are combined into sequences make it hard to imagine how the details of this variability could entail communication of important distinctions. Instead, we suggest that particular displays may be added on to each other, forming part of a more or less graded signal of motivational state, so that a greater rate of displaying and/or a greater proportion of high-level displays, combined with a greater rate of attacking, correspond to a greater aggressive motivation. The staircase model (Fig. 1) is intended as a rough simplification of such a graded signal.

Although an interpretation of displaying as a graded signal of aggressive motivation could help in providing an understanding of the present function of the behaviour, it cannot by itself explain the existing repertoire of different displays. For example, a single behaviour that is varied in amplitude or frequency could also serve to indicate the level of aggressive motivation. It is therefore unlikely that display elements would have been incorporated into the repertoire and modified over evolutionary time because of their effectiveness in communicating aggressive motivation. A more plausible explanation might be along the lines suggested by Andersson (1980), that a display is initially efficient because it signals imminent attack, or simply because it manages to subdue an opponent, but it is then transformed to become a partly redundant alternative to previously existing displays. Something like our staircase model (Fig. 1) could perhaps emerge as the end result of such an evolutionary process. This is, of course, somewhat different from the traditional theory of ritualization (Cullen 1966), in which the need for efficient and precise communication of motivational state was supposed to shape the behaviour over evolutionary time.

In this connection, the contrast between the complexity and disorderliness of great tit aggressive displays and the simple regularity of the crest-raised/crest-flattened polarity is illustrative. As long as a bird reduces the risk of being attacked by raising its crest (such attacks sometimes occur), there would seem to be a considerable element of common interest between sender and receiver, which is probably the reason for the simplicity of the signal. Although there is also a common interest in reducing costs incurred when competing for food, the conflict of interest ought to be greater in that situation, leading to more complex and wasteful communication. The possibility of such effects of conflicts of interest on the form of signalling behaviour has been suggested a number of times (Dawkins 1993).

In conclusion, because several selective forces may have acted to shape display behaviour in great tits, many of the

suggestions put forward to explain this kind of behaviour could be relevant. The traditional idea that displaying communicates internal states (Lorenz 1935; Tinbergen 1952; Cullen 1966) has some validity, but does not in itself clarify when or to what extent communication should be expected. The possibility of 'bluffing' intentions or of manipulating opponents could limit communication and produce redundancy (Caryl 1979; Maynard Smith 1979; Andersson 1980), whereas various consequences associated with aggression could ensure a reliable relation between motivation and display behaviour. In our opinion, there is likely to be considerable redundancy in great tit aggressive displaying, but also some dependence on states such as hunger or perceived risk of predation. Among the factors promoting a relation between displaying and attacking, the need to engage in at least some physical aggression to maintain a dominance position may be particularly important. A bird that displayed extensively but refrained from attacking would be likely to drop in the hierarchy, and in that social position displaying might not be an effective tool. On the other hand, given that a bird ought both to attack and to display, it would be advantageous to concentrate these activities to times when the need for limited resources is particularly great. In this way, displaying and attacking would tend to occur together and to be in rough proportion to each other.

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References

- Andersson, M. 1976. Social behaviour and communication in the great skua. *Behaviour*, **58**, 40–77.
- Andersson, M. 1980. Why are there so many threat displays? *Journal of Theoretical Biology*, **86**, 773–781.
- Blurton Jones, N. G. 1968. Observations and experiments on causation of threat displays of the great tit (*Parus major*). *Animal Behaviour Monographs*, **1**, 75–158.
- Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.
- Caryl, P. G. 1979. Communication by agonistic displays: what can games theory contribute to ethology? *Behaviour*, **68**, 136–169.
- Caryl, P. G. 1982. Telling the truth about intentions. *Journal of Theoretical Biology*, **97**, 679–689.
- Clutton-Brock, T. H. & Albon, S. D. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour*, **69**, 145–170.
- Cullen, J. M. 1966. Reduction of ambiguity through ritualization. *Philosophical Transactions of the Royal Society of London, Series B*, **251**, 363–374.

- Dawkins, M. S.** 1993. Are there general principles of signal design? *Philosophical Transactions of the Royal Society of London, Series B*, **340**, 251–255.
- Dawkins, R. & Krebs, J. R.** 1978. Animal signals: information or manipulation? In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 282–309. Oxford: Blackwell Scientific.
- Enquist, M. & Jakobsson, S.** 1986. Decision making and assessment in the fighting behaviour of *Nannacara anomala* (Cichlidae, Pisces). *Ethology*, **72**, 143–153.
- Enquist, M., Plane, E. & Röed, J.** 1985. Aggressive communication in fulmars (*Fulmarus glacialis*) competing for food. *Animal Behaviour*, **33**, 1007–1020.
- Hauser, M. D. & Nelson, D. A.** 1991. 'Intentional' signaling in animal communication. *Trends in Ecology and Evolution*, **6**, 186–189.
- Hinde, R. A.** 1981. Animal signals: ethological and games-theory approaches are not incompatible. *Animal Behaviour*, **29**, 535–542.
- Huntingford, F. A. & Turner, A.** 1987. *Animal Conflict*. London: Chapman & Hall.
- Hurd, P. L. & Enquist, M.** 2001. Threat display in birds. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **79**, 931–942.
- Jakobsson, S., Brick, O. & Kullberg, C.** 1995. Escalated fighting behaviour incurs increased predation risk. *Animal Behaviour*, **49**, 235–239.
- Lange, H. & Leimar, O.** 2001. The influence of predation risk on threat display in great tits. *Behavioral Ecology*, **12**, 375–380.
- Lemel, J. & Wallin, K.** 1993. Status signalling, motivational condition and dominance; an experimental study in the great tit, *Parus major* L. *Animal Behaviour*, **45**, 549–558.
- Lorenz, K.** 1935. Der Kumpan in der Umwelt des Vogels. *Journal für Ornithologie*, **83**, 137–213, 289–413.
- Maynard Smith, J.** 1979. Game theory and the evolution of behaviour. *Proceedings of the Royal Society of London, Series B*, **205**, 475–488.
- Morris, D.** 1957. 'Typical intensity' and its relation to the problem of ritualisation. *Behaviour*, **11**, 1–12.
- Parker, G. A.** 1974. Assessment and the evolution of fighting behaviour. *Journal of Theoretical Biology*, **47**, 223–243.
- Popp, J. W.** 1987a. Agonistic communication among wintering purple finches. *Wilson Bulletin*, **99**, 97–100.
- Popp, J. W.** 1987b. Risk and effectiveness in the use of agonistic displays by American goldfinches. *Behaviour*, **102**, 141–156.
- van Rhijn, J. G.** 1980. Communication by agonistic displays: a discussion. *Behaviour*, **74**, 284–293.
- van Rhijn, J. G. & Vodegel, R.** 1980. Being honest about one's intentions: an evolutionary stable strategy for animal conflicts. *Journal of Theoretical Biology*, **85**, 623–641.
- Scott, G. W. & Deag, J. M.** 1998. Blue tit (*Parus caeruleus*) agonistic displays: a reappraisal. *Behaviour*, **135**, 665–691.
- Senar, J. C.** 1990. Agonistic communication in social species: what is communicated? *Behaviour*, **112**, 3–4.
- Silk, J., Kaldor, E. & Boyd, R.** 2000. Cheap talk when interests conflict. *Animal Behaviour*, **59**, 423–432.
- Stokes, A. W.** 1962a. Agonistic behaviour among blue tits at a winter feeding station. *Behaviour*, **19**, 118–138.
- Stokes, A. W.** 1962b. The comparative ethology of great, blue, marsh, and coal tits at a winter feeding station. *Behaviour*, **19**, 208–218.
- Svensson, L.** 1994. *Identification Guide to European Passerines*. Stockholm: Lars Svensson.
- Tinbergen, N.** 1952. 'Derived' activities; their causation, biological significance, origin, and emancipation during evolution. *Quarterly Review of Biology*, **27**, 1–32.
- Tinbergen, N.** 1959. Comparative studies of the behaviour of gulls (Laridae): a progress report. *Behaviour*, **15**, 1–70.
- Verbeek, M. E. M., De Goede, P., Drent, P. J. & Wiepkema, P. R.** 1999. Individual behavioural characteristics and dominance in aviary groups of great tits. *Behaviour*, **136**, 23–48.
- Wilson, J. D.** 1992. Correlates of agonistic display by great tits *Parus major*. *Behaviour*, **121**, 168–214.
- Wilson, J. M.** 1994. Variation in initiator strategy in fighting by silveryeyes. *Animal Behaviour*, **47**, 153–162.