

Dominance and anti-predator behaviour of Great Tits *Parus major*: a field study

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During the winter of 1981-82 the hierarchical system of free-living Great Tits *Parus major* that visited a feeder supplied with sunflower seeds was studied in relation to the appearance of a predator. Without a predator, dominant birds were more successful in feeding and had to wait less before feeding. A significant negative correlation was found between dominance and the sequence of initial arrival.

After a Sparrowhawk *Accipiter nisus* had flown over the feeder, a correlation was found between the birds' dominance and the sequence of their return to the feeder. This field study supports the results of an analogous investigation on anti-predator behaviour and dominance in captive Blue Tits *P. caeruleus*.

Few field and laboratory studies on Passerines have shown that birds change their foraging behaviour after being exposed to a predator. Caraco *et al.* (1980) showed that, following an overflight by a hawk, wild Juncos *Junco phaeonotus* devoted a greater proportion of their time budgets to scanning at the expense of searching for food. Cowie *et al.* (1981) reported that Great Tits *Parus major* increased their prey handling time following presentation of a stuffed Sparrowhawk *Accipiter nisus*. This increase was largely attributable to increased scanning while handling prey.

Lendrem (1983) investigated the temporal organization of vigilance behaviour in free living Blue Tits *P. caeruleus* in response to manipulation of predation risk. In a recent study, Hegner (1985) related the sequence of return to feeding (following the presentation of a hawk) to the dominance status of each member of four flocks of captive Blue Tits. He found that after a model hawk was flown over birds at a feeder, dominant individuals were likely to wait for subordinate members of their flock to resume feeding before doing so themselves; he suggested that subordinate birds take more risks while foraging. From his study it was not clear whether dominant birds waited longer because of their social status *per se*, or because of different hunger levels which in turn were influenced by social status. An attempt had been made to control hunger levels, but there was a tendency for dominants to spend more time at the feeder prior to the appearance of the hawk.

The agonistic behaviour of wild Great Tits visiting a feeder was studied in Belgium from 1977. During the winter of 1981-82, a Sparrowhawk regularly swooped down over foraging tits. In this study the behaviour of free living Great Tits visiting a feeder is described in relation to the presence of a predator and discussed in relation to Hegner's findings.

MATERIAL AND METHODS

Field studies were conducted at Zwijnaarde near Ghent, Belgium, in a 27 ha mature beech wood *Fagus sylvatica* with an understory of *Rhododendron praecox*. Since 1964 a surplus of nestboxes (7 per ha), suitable for Great Tits, has been available. During the winter, Great Tits were regularly mist-netted and the nestboxes checked for roosting tits. All birds trapped were individually colour-

marked. In our study area no clear flocks could be distinguished so that all birds were assumed to belong to the same social unit.

From November 1981 to February 1982 the behaviour of Great Tits visiting a feeder, which followed the design of those used by Blurton-Jones (1968), was observed from a hide approximately 8 m away from the feeder. To minimize the effects of the feeder's presence, sunflower seeds were provided only during observation periods, a total of ten 3 h sessions per month. Generally there was little immigration and emigration of Great Tits in the woodland during these months.

The identity and observed activity of every bird were recorded. A visit was 'successful' if the tit left the feeder unhampered and with a sunflower seed. If an individual was forced to leave without food, or had to wait for more dominant birds to leave first (= 'waiting contact'), the visit was called 'unsuccessful'. Interactions with other birds were recorded as 'neutral' when both birds fed without any aggression and 'aggressive' when one or both birds displayed. In this case the winner and the loser could be distinguished clearly. Birds arranged in a hierarchy can be assigned a dominance rank. Individual dominance rank was expressed as the proportion of the observed active and passive interactions that resulted in a victory (De Laet 1984). This value was closely correlated with the proportion of aggressive encounters and with an assigned 'dominance score'. A dominance score was the number of individuals dominating a bird subtracted from the number of individuals it dominated, and was calculated from all encounters with that particular individual (De Laet 1985). During the course of our investigations, there were 14 occasions on which a Sparrowhawk flew over the Great Tits at the feeder, although on no occasion were the Tits actually attacked. Only those birds that visited the feeder ten minutes prior to the appearance of the hawk were included in the analysis, since certain individuals might visit the feeder shortly after the appearance of the hawk and be unaware of its recent appearance. For each individual analysed, its dominance relationship was related to its position in the sequence of return to the feeder.

Observation normally began before sunrise, so that it was possible to determine the relationship between status and the sequence of arrival at the feeder without any disturbance from a predator.

RESULTS

Most birds visited the feeder within an hour of sunrise, and visits continued over the course of the 3 h observation period. Table 1 shows for each 'hawk-day' the correlation between the dominance position of the tits and the sequence of their initial arrival at the feeder. Although none of the 14 correlation coefficients was statistically significant at the 5% level, 13 had a negative sign which suggests that dominant birds tended to arrive earlier (Two-way Binomial test, $P = 0.002$). When data from all days were combined, this result is confirmed by the positive correlation between the average dominance relationship and the sequence of initial arrival (Fig. 1).

The proportion of successful visits in relation to dominance (Fig. 2) gives for both males and females a significant increase with dominance. An inverse relationship was found between dominance and the percentage 'waiting contacts' (Fig. 3). Additionally it was found that during the extreme cold period of 1978-79 dominant males lost less weight than subdominants (Fig. 4). Following the appearance of a Sparrowhawk, birds at the feeder either moved directly to cover or froze in place briefly before doing so. Other birds in the vicinity gave clear alarm calls for a few seconds and all stayed motionless for up to a minute. Birds then began to move from branch to branch in the shrubs making contact calls without feeding, for some time thereafter. The duration of time spent motionless in the shrubs and the time between

TABLE 1

The Spearman-Rank correlation coefficient (r_s) between the dominance relationship of free living Great Tits, the sequence of initial arrival and the sequence of return to feeding following the appearance of a Sparrowhawk

Date	Time of hawk arrival (h)	Initial arrival		Return	
		r_s	n	r_s	n
17 11 81	1050	-0.202	30	0.257	14
22 11 81	1045	-0.025	17	0.655	17
23 11 81	1100	-0.30	14	0.317	9
28 11 81	0840	-0.117	9	0.114	15
5 12 81	0955	-0.028	12	-0.600	5
15 12 81	0940	-0.183	9	0.607	9
31 12 81	0840	0.533	9	0.086	6
2 1 82	0910	-0.139	9	-0.051	14
4 1 82	1020	-0.236	11	0.358	10
14 1 82	0925	-0.231	14	0.721	10
20 1 82	0905	-0.029	15	0.829	6
4 2 82	1105	-0.343	15	-0.190	8
16 2 82	0910	-0.321	7	0.779	10
18 2 82	0950	-0.080	15	0.310	14
Total		Binomial $P = 0.01$		Binomial $P = 0.03$	

Notes: ¹ $P < 0.05$
² $P < 0.01$

the departure of the Sparrowhawk and the return of the Great Tits to the feeder depended on the behaviour of the hawk. Both were longer when the hawk flew very low over the feeder. Most birds returned to the feeder 5–15 minutes after the hawk had appeared (mean = 9.2 min, s.d. = 6.5 min) and 13% of the birds returned within 5 minutes.

Table 1 shows for each 'hawk-day' the hour of the hawk's appearance and the correlation between the dominance position and the sequence of return to the feeder. In five out of the 14 cases a significant positive correlation was found between the dominance position of the birds that visited the feeder within 10 minutes prior to the appearance of the hawk and their sequence of return to the feeder following the departure of the hawk. In 11 of 14 cases the correlation was positive, which suggests

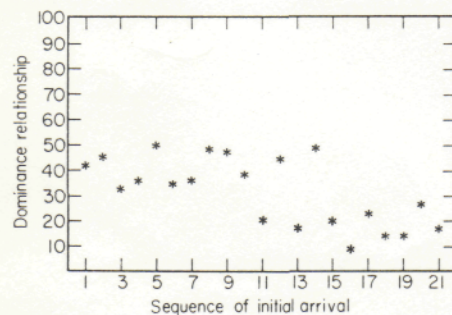


FIGURE 1. Relationship between the average dominance relationships and the sequence of initial arrival of Great Tits at the feeder $r_s = -0.630$, $n = 21$, $P < 0.01$.

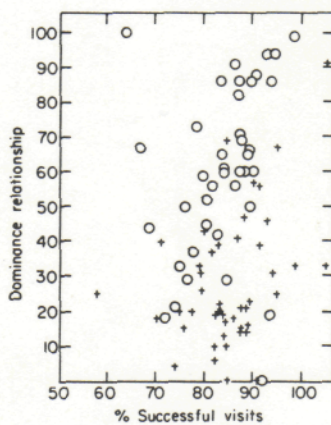


FIGURE 2. Dominance and the percentage successful visits of male Great Tits (circles) and females (crosses): r_s males: 0.373, $n = 40$, $P < 0.05$; r_s females: 0.279, $n = 46$, $P < 0.05$.

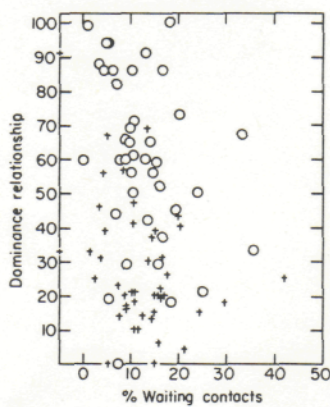


FIGURE 3. Dominance and the percentage waiting contacts of male Great Tits (circles) and females (crosses): r_s males: -0.337, $n = 40$, $P < 0.05$; r_s females: -0.302, $n = 46$, $P < 0.05$.

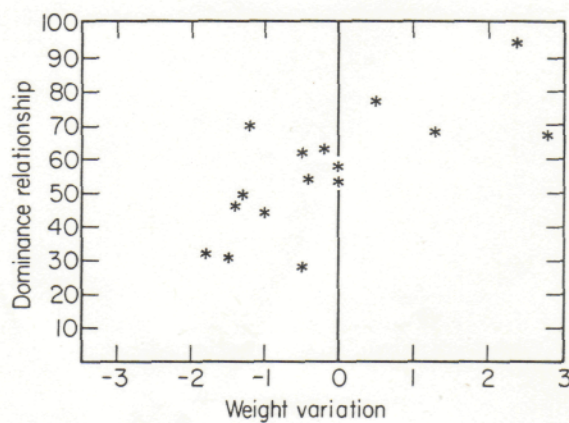


FIGURE 4. Dominance and weight variation of Great Tits during the severe winter 1978-79: $r_s = 0.712$, $n = 16$, $P < 0.01$.

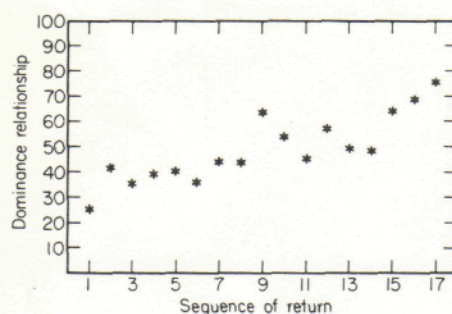


FIGURE 5. Relationship between the average dominance relationships and the sequence of return to feeding by Great Tits $r_s = 0.659$, $n = 17$, $P < 0.05$.

an earlier return of subdominants after the appearance of a Sparrowhawk (Two-tailed Binomial test, $P = 0.058$). For the combined data this result can be confirmed by the significant correlation between the average dominance rank and the sequence of return to feeding (Fig. 5).

DISCUSSION

Two major conclusions can be derived from these results. First, dominant birds tend to arrive earlier in the morning than subordinates and second, following the appearance of a hawk, dominant individuals tend to return later than subordinates. The trade-off between obtaining food and avoiding predators has been studied by several authors who compared the proportion of time individuals spend searching for food *versus* scanning for predators. Most results focus on the advantage of flocking behaviour (the 'many-eyes' hypothesis) that allows individuals to spend less time scanning and more time feeding (Pulliam 1973, Powell 1974, Siegfried & Underhill 1975, Lazarus 1979, Caraco 1979a,b, Bertram 1980). Others examined the effect of predation risk on vigilance tactics (McVean & Haddlesley 1980, Caraco *et al.* 1980, Cowie *et al.* 1981). Another aspect concerns what happens following the appearance of a predator. Lendrem (1983) manipulated predation risk in Blue Tits and found increased scanning rates when predation risk increased. Scan durations, however, remained constant.

When birds apparently perceived an increased risk of predation, foraging birds usually move to cover, while other birds nearby give clear alarm calls for a few seconds. They freeze in place for a time that is dependent upon the height the hawk flew over the feeder. At this point each individual has to decide how long to wait before resuming foraging and again exposing itself to the predator. It may reduce its own risk of predation by waiting until others resume foraging. In this way the individual may be more certain that the predator has departed (Hegner 1985). In periods of food shortage, hunger increases as the period of waiting becomes longer. In our field population of Great Tits, the proportion of successful visits by dominant individuals is higher than for subordinates, while subordinates have to wait more frequently. During an extremely cold spell, subordinates lost more weight than dominants and the local winter survival of adult and juvenile birds is related to their dominance status (De Laet, unpubl.). These results suggest that dominants receive priority and thus obtain the bulk of the food. Therefore they are likely to be in better physical condition than subordinates and hunger levels are probably related to social status. During periods of danger dominants can therefore afford to wait longer

before resuming foraging. According to Gaston (1978) subdominants have to 'pay' for joining a winter group and this decreases the 'pay-off' risk that dominants will attack them. Subordinates could serve as food-finders or as 'sitting ducks' for predators. To Ekman & Astenmo (1984) a payment as a sitting duck seems more likely since predators take a heavier toll among subordinate first year tits in winter (Ekman *et al.* 1981). Following the actual appearance of a hawk in the field, there was a positive correlation between dominance and sequence of return to the feeder. These results support the laboratory results of Hegner after a model hawk was flown over captive flocks of Blue Tits at a feeder.

In undisturbed conditions dominant birds arrived earlier than subdominants. This was possibly caused by the energy loss during a long winter night after which the hunger state of all individuals increased. Because of the better food intake and early access to food of dominant individuals they will, in undisturbed conditions, force subdominants to wait not necessarily by active aggressive behaviour (*cf.* greater 'pay-off' of subdominants). Finally we can conclude that both the laboratory experiments and the field observations suggest that dominants may utilize subordinates as a means of ascertaining whether or not a predator is in the vicinity. Our study produced some evidence that this may be mediated indirectly through hunger levels, which in turn were due to social status.

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