Feeding consequences of the dominance status in Great Tit *Parus major* groups

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The feeding consequences of the dominance status in Great Tits feeding on sunflower seeds at artificial feeders were studied. Behavioural and morphometric correlates of feeding success and dominance status were examined. Analyses with colour-ringed Great Tits revealed marked individual differences in feeding success. Individuals with a high feeding success had a high dominance status, wide breast stripe plumage, and short seed-handling and waiting time. Breast stripe width best explained the variation in individual feeding success. Watching and avoidance, as indicated by long handling and waiting times, decreased the feeding success of subordinate Great Tits. An analysis confined to birds less than one year old indicated that males succeeded better than females. A high dominance status was associated with a wide breast stripe, and breast stripe plumage presumably signalled an individual's dominance status in the groups. This status signalling system, however, did not operate when only first-year males were considered.

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Introduction

Feeding groups during the nonreproductive season often exhibit clear dominance hierarchy among the group members, as demonstrated both in the field (Saitou 1978, Balph et al. 1979, Kikkawa 1980, Drent 1983, Ekman & Askenmo 1984, Järvi & Bakken 1984, Schneider 1984, De Laet 1985a, Hogstad 1987a) and with captive birds (Baker et al. 1981, Drent 1983, Järvi & Bakken 1984, Hegner 1985, Watt 1986a, b). Even though dominance relations have been considered as important organizing structures of many feeding groups, few studies have quantified their feeding consequences, particularly at the individual level (but see Baker et al. 1981, Schneider 1984, Enoksson 1988). The present paper does this with a winter group of free-living Great Tits *Parus major*.

The advantages of group searching for concealed food in Great Tits have been studied in laboratory conditions by Krebs et al. (1972). They also briefly considered differences in access to food between dominant and subordinate birds but did not quantify the feeding success of individual birds (see also Baker 1978, Krebs 1980). Järvi & Bakken (1984), in turn, examined the importance of some phenotypic characteristics, in particular the variation of the breast stripe plumage in signalling an individual's social status in Great Tit groups (see also Järvi et al. 1987). Finally, De Laet (1985a) considered some general foraging consequences of the dominance status in Great Tits, particularly in relation to predation risk. However, she did not consider factors affecting social status.

In this paper I examine the feeding efficiency of individually-marked birds, and some morphometric and behavioural characteristics that might affect their social status and feeding success in groups.

Methods

The data were gathered in a garden (c. 20 × 15 m with seven apple-trees, one maple and seventeen currant bushes) situated at the gable of a house in SE Finland (61°35′ N, 29°42′ E). Observations were made from inside the house.

Since 8 December 1984, Great Tits were colour-ringed. The wing length (to 0.5 mm) and the width of the breast stripe (to 1.0 mm) were measured with a sliding caliper. Three measurements of the breast stripe were taken (see Fig. 1): (1) maximum width; (2) width at the hollow of the wishbone (furcula); (3) minimum width. In their study on the function of the breast stripe in Great Tits, Järvi & Bakken (1984) measured the width of the breast stripe at the base of the sternum, namely, corresponding to measurement (2) above. I found, however, that this single mea-

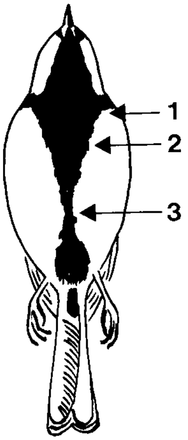

Fig. 1. Points at which the width of the breast stripe in the Great Tits was measured: 1) maximum; 2) wishbone; 3) minimum.

surement did not always sufficiently indicate the appearance of the whole black plumage on the front of Great Tits, so I also included minimum and maximum width. Morphometric measurements were taken mainly between the end of December and the beginning of March in each winter, from 1984 to 1987.

I made observations on ten colour-ringed Great Tits between 4 and 9 March 1985, on five individuals between 7 and 9 March 1986 and on eight individuals between 4 and 8 March 1987; one male was included in both the 1986 and 1987 data, but it was used only once in each analysis based on pooled data. The marked birds included one adult and 11 juvenile males and three adult and seven juvenile females. Birds took sunflower seeds from a hole (c. 6.5 x 2.0 cm) in an artificial feeder. Wire netting was set in front of the hole so that birds arriving at the feeder stopped first at the net and then picked up a seed from the hole. During separate 5 min periods I recorded the number of sunflower seeds obtained by each colour-ringed Great Tit (eight individuals in 1985, five in 1986 and eight in 1987) and unmarked individuals. Some individuals also obtained seeds from the snow just below the feeder (c. 1 m); these were also included when calculating feeding success (=no. of seeds obtained/5 min). Great Tits in the garden were counted after each 5 min period. Whenever a colour-ringed individual was observed to take part in a conflict with another bird its success (win or loss) was noted. As the dominance relation between any two Great Tits is usually stable (e.g. Saitou 1979, Drent 1983, De Laet 1984), and one Great Tit may contest with many lower-ranking individuals, while another may contest with many higher-ranking individuals, a pure proportion of wins in all encounters may give biased dominance estimates. To minimize this bias the total number of wins and losses for each individual was weighted with the number of contestants that particular Great Tit won and lost, respectively. An individual's dominance status was then expressed as the proportion of wins in all, weighted, encounters. Handling time was measured to 0.1 s with a stopwatch for eight individuals in 1987, and waiting time for ten individuals in 1985 and eight individuals in 1987. I defined seed-handling time as the time an individual spent on a branch husking a sunflower seed and eating the kernel (see also Pöysä 1985), and waiting time as the time an individual spent on the branch after the handling process and before fetching a new seed (corresponds to the "inspection time" by Lendrem 1983). Range of sample size per individual was 5–58 5 min periods for feeding success, 5–54 encounters for dominance status, 8–36 measurements for handling time and 5–29 measurements for waiting time. As similar results emerged with yearly material, the analyses presented below are based on the pooled data, if not otherwise mentioned.

Observations were made between 08.30 and 16.00 hours. Air temperature at the beginning of the study period of each day ranged from –5 to –9°C in 1985, from +2 to –2°C in 1986 and from –5 to –20°C in 1987. One exceptionally cold morning period was excluded from the data of March 1987 because low temperatures clearly affected the foraging of Great Tits, namely, there were long pauses during and after handling seeds. Weather conditions were otherwise similar and the ground was covered by snow each year.

Results

Feeding success varied considerably among individual Great Tits, between 0.6 and 4.0 seeds per 5 min. This measurement is not controlled for group size, which varied between 5.7 and 16.0 per individual, but there was no correlation between group size and the mean individual feeding success ($r = -0.09$, ns, $n = 20$). Consequently, the effects of group size on differences in individual feeding success should be minimal. There was no indication that individuals differing in feeding success would visit the feeding place, namely, the garden, at different time of the day. Similarly, no consistent association existed between feeding success and the overall frequency with which

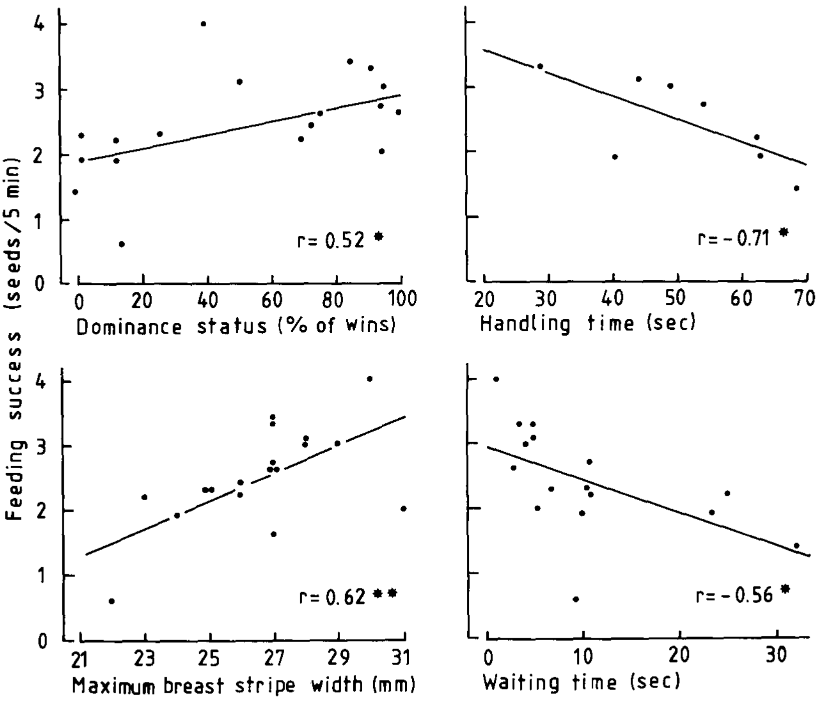

Fig. 2. Individual feeding success in relation to dominance status, maximum breast stripe width, and handling and waiting time among individually marked Great Tits; note that all characteristics were not measured for all individuals. * = $P < 0.05$, ** = $P < 0.01$.

each individual visited the feeding place ($r = 0.65$, ns, $n = 7$, in 1985; $r = 0.60$, ns, $n = 5$, in 1986; $r = -0.08$, ns, $n = 8$, in 1987). Not unexpectedly, then, individuals with a high feeding success did not only have a higher intake rate while foraging, but they also consumed more seeds in absolute terms during the study periods in each year ($r = 0.93$, $P < 0.01$, in 1985; $r = 0.83$, $P < 0.10$, in 1986; $r = 0.83$, $P < 0.05$, in 1987).

Grouping all birds, individual feeding success correlated positively with dominance status and the width of the breast stripe, and negatively with handling time and waiting time (Fig. 2). It also correlated significantly with the other two measures of breast stripe width (wishbone: $r = 0.49$, $P < 0.05$, $n = 18$; minimum: $r = 0.54$, $P < 0.05$, $n = 18$) but not with wing length ($r = 0.38$, ns, $n = 18$). Among independent variables, handling time and waiting time were positively correlated, and both tended to be shorter in individuals with a high dominance status (Table 1). In addition, dominance status was higher, and handling and waiting time shorter, in individuals with wider breast stripes and longer wings, even though all of these associations were not significant (see Table 1).

As feeding success correlated with so many independent variables, which in turn were intercorrelated, I used stepwise multiple regression analysis to find the best predictor(s) for feeding success. Data for handling time were insufficient to be used in the analysis. From the remaining independent variables, maximum breast stripe width (45%, $F = 8.8$, $P < 0.05$, $n = 13$) best explained the variation in feeding success, while the other variables together (dominance status, waiting time and wing length) only explained a

Table 1. Pearson correlation coefficients between different characteristics among individually marked Great Tits. n = number of individuals used in analyses; note that all characteristics were not measured for all individuals. ° = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	Dominance status	Handling time	Waiting time	Wing length
Handling time	–0.45 n=8			
Waiting time	–0.48 ° n=16	0.86 ** n=8		
Wing length	0.71 ** n=16	–0.69 n=5	–0.46 ° n=15	
Maximum breast stripe width	0.52 * n=16	–0.94 * n=5	–0.66 ** n=15	0.72 *** n=22

Table 2. Characteristics of individually marked first-year male and female Great Tits. Data for handling time are insufficient for comparison. Mann-Whitney U-tests used.

	Males			Females				
	Mean	SD	n	Mean	SD	n	U	P
Feeding success (no. of seeds per 5 min)	2.7	0.7	10	1.9	0.7	6	9	<0.05
Dominance status (% of wins)	78.0	21.3	9	20.4	25.5	6	2	<0.01
Waiting time (sec)	4.7	3.0	7	13.4	7.5	7	4.5	<0.05
Wing length (mm)	78.7	1.4	11	74.7	1.8	7	1	<0.002
Breast stripe width (mm)								
maximum	27.7	1.5	11	24.3	1.4	7	0.5	<0.002
wishbone	8.5	1.9	11	4.0	0.8	7	1	<0.002
minimum	5.6	1.4	11	2.4	0.8	7	2	<0.002

further 4%. The contribution of the latter three independent variables to the total regression was not significant.

Controlling for age, among individuals less than one year old males had a higher feeding success, higher dominance status, shorter waiting time, longer wings and a wider breast stripe than females (Table 2). Sex, thus, seems to have an important effect on both feeding success and social status in Great Tits.

The data allow some comparisons with males less than one year old, namely, the effect of both sex and age is controlled. At this level of examination, feeding success did not correlate significantly with any other variable (best with waiting time, r = –0.45, ns, n = 7) and, interestingly, dominance status did not correlate significantly with breast stripe width ("best" with maximum width, r = –0.21, ns, n = 9; dominance status range 39.1–99.9% and maximum breast stripe width range 26–31 mm).

Discussion

The results revealed marked differences in feeding success between individual Great Tits. These differences were dependent on the social status of the individuals. Dominants had priority of access to food and did not need to wait long for their turn, whereas subordinates had to wait longer. De Laet (1985a) also found a positive relationship between the proportion of successful feeder visits and dominance, and a negative relationship between dominance and waiting tendency (measured in a different way). In addition, feeding success correlated negatively with seed-handling time. Since the number and duration of scanning bouts performed during seed handling essentially determine total handling time (Pöysä 1985, unpubl.), subordinates evidently sacrificed effective handling time in watching for other individuals. The need for this was real since, on occasion, dominant individuals robbed seeds from subordinates. Similarly, Waite (1987) found in White-breasted Nuthatches (*Sitta carolinensis*) that subordinate foragers have additional time expenditure because they must keep higher-ranking group members under surveillance.

Relating to the discussion by Baker (1978) and Krebs (1980, see also Krebs et al. 1972) about the feeding consequences of grouping in Great Tits, my results demonstrate that the costs of group foraging may differ between individuals (see also Pulliam & Caraco 1984). At least in feeding conditions like those here, subordinates should lose more than dominants in terms of efficient feeding time and, thus, in terms of feeding rate. Furthermore, dominant Great Tits may reduce their own risk of predation at the expense of subordinates. De Laet (1985a) found that after a predator visited the feeding place, dominant Great Tits tended not to resume foraging until other individuals did so. A similar phenomenon was demonstrated by Hegner (1985) with Blue Tits *Parus caeruleus*. Dominants may also gain more time-budgeting advantages than subordinates in terms of the trade-off between feeding and being vigilant for predators, as demonstrated by Ekman (1987) in Willow Tit *Parus montanus* flocks. On the other hand, dominant Great Tits fight each other more frequently than subordinates (Järvi & Bakken 1984), and may thus have to pay more in terms of high metabolic rates (cf. Røskaft et al. 1986). Social dominance entails extra energetic costs also in Willow Tits (Hogstad 1987b).

From the independent variables considered, breast stripe width best explained the variation in feeding success. Individuals with a wide breast stripe also had a high dominance status. Järvi & Bakken (1984) similarly observed a positive association between social rank and the width of the breast stripe. Males have wider breast stripes than females and, at least among males, adults have wider breast stripes than juveniles (Pöysä unpubl.). Furthermore, in Great Tits, males dominate same-aged and younger females (Saitou 1979, Drent 1983, De Laet 1985b, this study), and adults usually dominate juveniles of the same sex (Saitou 1979). Even among juvenile Great Tits, individuals of early broods may dominate those of late broods (Garnett 1981, Drent 1983). An individual's dominance status thus seems to be both sex- and age-determined, the width of the breast stripe being a potential signal of social status in feeding groups, as also concluded by Järvi & Bakken (1984, see also Rohwer 1975, 1977).

Breast stripe width was not associated with dominance status when only Great Tit males less than one year old were considered. This result suggests that status signalling, via breast stripe plumage, may not be important among Great Tits of both the same age and sex. Similarly, very little evidence of status signalling within age classes was found by Fugle et al. (1984) with White-crowned Sparrows *Zonotrichia leucophrys gambelii* and by Watt (1986a, b) with Harris' Sparrows *Zonotrichia querula*.

Järvi & Bakken (1984) suggest that status signalling in Great Tits could be seen as a set of genetically determined strategies of a mixed ESS (evolutionary stable strategy, see Maynard Smith 1982 and Parker 1984). In other words, in any Great Tit population, an individual's social status and signalling with breast stripe plumage would be genetically determined, and each individual would exhibit its dominant/subordinate strategy accordingly. Furthermore, in a mixed ESS the different actions should have equal payoffs, and the payoffs should be determined by frequency-dependent selection (for a more comprehensive treatment of the topic, see Rohwer & Ewald 1981, Maynard Smith 1982).

However, because age may importantly determine an individual's dominance status (see above), and Great Tits are resident and have a high breeding area fidelity after their first year (e.g., Harvey et al. 1979), it is very possible that the dominance status of a given individual, in a particular population, increases during its lifetime. Remember, too, how there was no association between dominance status and the width of the breast stripe when only first-year males were considered. Furthermore, De Laet (1983) mentions that winter dominance improves survival, and Lambrechts & Dhondt (1986) show that dominant males survive longer and produce more surviving offspring. Accordingly, dominants and subordinates seem to have unequal payoffs, which is in agreement with the conditional strategy hypothesis (see Maynard Smith 1982), but in disagreement with the mixed ESS hypothesis (see also Whitfield 1987). These observations suggest that a subordinate role in Great Tit groups should perhaps not be seen as a genetically-determined lifetime strategy. At the moment, a conditional strategy in which subordinates make the best of a bad situation seems equally possible. This aspect is worth further research in Great Tits. For comparison, Ekman & Askenmo (1984), Ekman (1987) and Hogstad (1987a) suggest that, in Willow Tits, first-year birds may exhibit a hopeful dominant strategy in feeding groups (cf. West Eberhard 1975), expecting to improve their social status later in life.

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Selostus: **Dominanssiaseman vaikutus talitiaisen ruokailutehokkuuteen**

Työssä on tutkittu dominanssiaseman vaikutusta talitiaisyksilöiden ruokailutehokkuuteen. Värirengastettujen yksilöiden ruokailutehokkuutta seurattiin puutarhaan perustetulla ruokintapaikalla Parikkalassa kolmena talvena 1985–87. Rengastuksen yhteydessä määritettiin lintujen ikä ja sukupuoli sekä mitattiin siiven pituus ja rintavyön leveys (kuva 1). Lisäksi eri yksilöiltä mitattiin seuraavat ominaisuudet: ruokailutehokkuus (automaatilta haettuja auringonkukan siemeniä/5 min), sosiaalinen asema (voitettujen kahakoiden osuus), siemenen käsittelyaika ja odotusaika.

Ruokailutehokkuus vaihteli suuresti yksilöiden kesken, 0.6–4.0 siementä/5 min. Yksilöillä, joiden ruokailutehokkuus oli suuri, oli myös korkea sosiaalinen asema ja leveä rintavyö, ja ne käsittelivät siemenen nopeasti ja joutuivat odottamaan vähän ruokintapaikalle pääsyä (kuva 2). Nämä ominaisuudet olivat myös keskenään korreloituneita ja sidoksissa yksilön suureen kokoon (siiven pituus, taulukko 1). Askeltavassa regressioanalyysissa rintavyön leveys selitti parhaiten (45%) yksilöiden välisiä eroja ruokailutehokkuudessa. Korkeammassa sosiaalisessa asemassa olevien yksilöiden välttäminen, mitä pitkä käsittely- ja odotusaika ilmensivät, heikensi alisteisten yksilöiden ruokailutehokkuutta. Nuoria talitiaisia koskeva vertailu osoitti, että koiraat menestyivät naaraita paremmin (taulukko 2). Sosiaalinen asema ja ruokailutehokkuus olivat siten sidoksissa sukupuoleen.

Talitiaisen rintavyö toiminee sosiaalisen aseman epäsuorana ilmentäjänä. Tämä mekanismi ei kuitenkaan toiminut samaa sukupuolta ja ikäryhmää (nuoret koiraat) edustavien yksilöiden kesken, joiden rintavyön leveys vaihteli vähemmän. Kirjoituksessa pohditaan tätä sosiaalisen aseman ilmentämismekanismia evolutiivisena strategiana talitiaispopulaatioissa.

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15.9.1988 Kuukausikokous

Esa Lammi: "Kuinka paljon uiveloita Suomessa pesii? Tuloksia Eläinmuseon vesilintututkimuksista"
Jyrki Muona: "Trooppisen Australian linnusto" (diaesitys)

15.10.1988

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Johan Ulfvens: "Silkkiuikun ja mustakurkku-uikun ekologiasta Etelä-Pohjanmaan saaristossa"

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Lasse J. Laine: "Vuoden 1988 lintuharvinaisuudet Suomessa" (diaesitys)

Kuukausikokoukset ja syyskokous järjestetään Helsingin yliopiston eläintieteen laitoksen suuressa luentosalissa, P. Rautatiekatu 13, alkaen klo 18.30.

Yleisö tervetullut!