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Site-related dominance in the Great Tit Parus major major

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The interrelations at the site of a feeder, the winter home range and dominance rank were studied in male Great Tits during four successive winters. In juvenile males, both those leaving the population at the end of the winter as well as those recruited to the next breeding population, dominance rank was not influenced by the site of the feeder.
In contrast, the social position of adult males was in some years clearly affected by the site of the feeder. During the territorial period (March–April) the site of the feeder as a determinant of dominance, in settled males, was not always clear.

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1. Introduction

Social hierarchical systems have been described in a number of animal populations (for a review see Schein 1975). Usually a dominance hierarchy is assessed by means of the observations of intraspecific competition for food at an artificial food supply (feeder). In most of these experiments the feeder is put up within the home range or territory of one or more birds.

Nevertheless the influence of the site on the observed social rank is still poorly understood. According to some authors dominance position is affected by the site of the food source (Allee 1942, Castoro and Guhl 1958 in laboratory experiments and Colquhoun 1942, Brian 1949 and Brown 1963 in field experiments), whereas others found no evidence for this either in the aviary (Dunham 1966) or in the field (Harzler 1970, Weise 1971, Glase 1973, Smith 1976).

This paper presents evidence for a differential influence of the feeder-site on the established dominance position during winter in a natural population of Great Tits.

2. Materials and methods

The site of an artificial feeder as a determinant of dominance, can be studied in several ways: one can look for a possible relationship between the observed dominance rank and the distance from the feeder to the winter home range or territory as did Colquhoun (1942) and Brian (1949). Another possibility is to use several feeders simultaneously to examine a possible influence of the site on the observed social rank in birds visiting different feeders (Brown 1963). In this study both methods were used although in separate years. Results of the second method will be published in another paper.

All field work was carried out in a mature beech wood (*Fagus silvatica*) of 27 ha with an understory of *Rhododendron praecox* at Zwijnaarde near Ghent (Belgium). The area was supplied with an excess of nestboxes (191) since 1964.

From November up to March in four successive years (1977-1981), the behaviour of Great Tits visiting a feeder supplied with sunflower seeds, was observed from a hide. The feeder consisted of a wooden platform as described by Blurton-Jones (1968). To minimise the influence on the winter population, sunflower seeds

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were provided during the observation hours only (30 h a month in periods of 3 h). The seeds were dispersed from a tube to allow just one bird to eat at a time, other visitors being forced either to wait or to chase away the foraging bird.

The winter domicile of wintering Great Tits was determined by inspection of all nestboxes for roosting tits twice a month. In addition, data on activities and ranges of the birds in winter were collected by walking a standard transect in the study area at regular intervals. For each individual all data were plotted on a map to draw an outline of the "winter home range" of the birds. The average distance from the feeder to the observation points of each winter home range were divided into different distance classes. For adults 0–100 m, 100–200 m, 200–300 m and > 300 m; for juveniles 0–200 m, 200–400 m and 400–600 m.

In winter, individual dominance rank was expressed as the observed proportion active and passive interactions that resulted in a victory. Each interaction represented a displacement in which the subdominant bird was driven away from the feeder by the dominant one or waited in a submissive posture. The displacement most often involved threat display and posturing while actual chases and attacks were rare. Only the individuals recorded in five or more interactions were used (cf. Fretwell 1969, Garnett 1976, Kikkawa 1980).

All males were subdivided into either: (1) Adults: resident males that bred in the study area during the previous breeding season. (2) Juveniles: Most of these males immigrate in the study area at the beginning of the winter. Many of them disappear at the end of the winter by emigration (= disappearing juveniles). Others (= remaining juveniles) however become resident within the study area, taking over the territory of disappeared adults. Adults or remaining juveniles are called "overlapping" if in the next spring they are breeding within their winter home range: "non-overlapping" birds are those breeding outside this range.

3. Results

3.1. Adults

For each winter the established hierarchy in adult Great Tit males is linear and unambiguous with few reversals. The position of the individuals does not change during the winter (Tab. 1). The percentage "overlapping" adult and juvenile males (Tab. 2) shows that a significantly larger proportion of adult males (75.8%) are

Tab. 1. Monthly dominance relationships of adult males over all winters. Kendall-coeff. of concordance ($W = 0.681$, $\chi^2 = 51.74$, df = 19, $p < 0.001$).

Ind.	Nov	Dec	Jan	Feb	Rj
1.	42.9	44.4	61.5	48.2	13.5
2.	35.7	70.5	75.5	59.1	29
3.	74.6	89.1	89.9	86.0	60
4.	63.6	66.7	65.6	76.2	31.5
5.	100.0	100.0	100.0	100.0	79
6.	77.1	69.3	61.5	47.6	29.5
7.	100.0	100.0	98.7	98.1	77
8.	57.9	54.3	52.6	85.7	25.5
9.	54.5	90.9	87.8	79.2	47.5
10.	88.2	81.1	67.4	45.5	38
11.	61.1	73.8	79.0	85.7	45
12.	63.5	76.5	70.6	57.1	38
13.	59.2	46.7	50.0	50.0	15.5
14.	97.6	71.4	70.0	73.0	45
15.	61.1	75.0	78.6	44.4	32.5
16.	89.3	87.9	92.3	87.2	64
17.	71.4	62.5	44.7	80.0	29
18.	92.7	90.9	87.7	95.0	66.5
19.	66.7	66.7	50.0	20.0	19.0
20.	90.5	93.3	69.2	78.6	54

Tab. 2. The number of overlapping resp. non-overlapping adult and juvenile males in each winter.

	Overlapping		Non-overlapping		Total		
	Adults	Juven.	Adults	Juven.	Adults	Juven.	G-test
1977–1978	6	6	2	38	8 (75%)	44 (14%)	11.94
1978–1979	6	6	1	26	7 (85%)	32 (19%)	6.36
1979–1980	6	5	2	16	8 (75%)	21 (23%)	7.72
1980–1981	7	8	3	22	10 (70%)	30 (27%)	24.00

Tab. 3. Average dominance relationships of adult resident males in different distance classes for each winter (Kruskal-Wallis analysis of variance).

	0–100 m			100–200 m			200 m–300 m			>300 m					
	x	se	n	x	se	n	x	se	n	x	se	n	df	χ^2	p
1977–1978 ...	78.53	8.68	4	26.24	12.81	6	30.73	30.72	2				2	5.75	ns
1978–1979 ...	83.49	9.10	4	59.96	5.91	4	70.20	7.27	3	67.19	9.66	4	3	4.03	ns
1979–1980 ...	87.59	0.67	3	43.63	18.63	2	42.42	8.48	6				2	6.08	$p<0.05$
1980–1981 ...	73.5	6.97	8	25.00	25.00	2	38.80	19.41	3				2	5.18	ns

Tab. 4. Monthly dominance relationships of juvenile males over all winters. Kendall coeff. of concordance ($W = 0.705$, $\chi^2 = 118.42$, $df = 42$, $p < 0.001$).

Ind.	Nov	Dec	Jan	Feb	Rj
1.	61.3	60.7	78.5	119	
2.	42.9	42.0	50.0	60.0	73.5
3.	10.0	26.1	25.0	16.7	13
4.	72.7	74.7	84.4	68.1	137
5.	14.2	22.9	21.7	32.0	12
6.	60.0	67.6	76.9	66.7	115.5
7.	96.8	89.5	92.7	78.6	159
8.	33.3	25.0	33.3	20.0	30.5
9.	71.4	80.0	84.9	82.4	146.5
10.	20.0	40.7	25.0	16.7	24.5
11.	34.8	25.0	56.1	63.2	70.5
12.	91.3	93.2	98.5	97.8	165
13.	30.8	48.6	28.6	57	
14.	52.8	49.1	53.1	70.6	94
15.	20.0	32.6	29.2	47.4	38.5
16.	78.0	73.9	50.0	58.3	116.5
17.	50.0	24.3	26.1	50.0	44.5
18.	58.3	73.2	66.7	61.5	112
19.	56.7	51.2	47.1	55.6	83
20.	20.0	34.7	26.5	44.4	36.5
21.	21.1	53.3	88.9	33.3	79
22.	14.3	28.9	35.0	50.0	40
23.	20.0	34.9	44.0	33.3	38.5
24.	99.0	99.4	98.6	99.4	171
25.	87.5	79.2	84.1	73.6	144
26.	70.0	80.0	40.0	51.9	103.5
27.	27.8	27.8	81.0	57.1	74
28.	40.0	42.9	71.4	75.9	93.5
29.	61.5	42.9	61.1	42.9	80.5
30.	72.7	42.1	80.0	37.9	89
31.	73.3	65.4	91.7	47.6	121
31.	16.7	47.1	50.0	54.6	63.5
33.	52.0	46.0	48.5	71.1	85
34.	55.6	45.0	57.9	48.0	79
35.	62.5	58.6	53.9	77.8	112.5
36.	72.9	70.4	35.3	40.0	92
37.	50.0	66.7	50.0	37.5	78
38.	92.5	94.3	100.0	87.2	166
39.	66.7	62.1	52.2	52.9	102
40.	60.0	60.0	9.1	33.3	60.5
41.	0.0	51.8	77.4	86.7	95
42.	33.3	58.8	14.3	20.0	45
43.	62.5	50.0	83.3	83.3	123.5

"overlapping". This implies the existence of a site-related dominance in these adult resident males during winter. Because a number of adult males constitute the winter population over successive years, it is not possible to combine the results over all winters. Although there exists, each winter, a tendency for higher dominance relationships at smaller distances (Tab. 3) a significant influence of the distance on dominance is only found during the winter 1979–1980.

Tab. 5. Frequency distribution (expected frequencies between brackets) of juvenile males divided in different dominance- and distance classes ($G = 2.022$, $df = 2$, $p > 0.1$).

	0–200 m	200–400 m	400–600 m	Total
Dominant (67–100%)	11 (9.46)	5 (5.69)	4 (4.86)	20
Intermediate (34–66%)	20 (19.39)	11 (11.64)	10 (9.97)	41
Subdominant (0–33%)	4 (6.15)	5 (3.69)	4 (3.16)	13
Total	35	21	18	74

Tab. 6. Average dominance relationships of juvenile males in three distance classes for each winter (Kruskal-Wallis analysis of variance).

	0–200 m			200–400 m			400–600 m					
	x	se	n	x	se	n	x	se	n	df	χ^2	p
1977–1979	58.06	6.68	12	44.12	7.19	5	55.75	9.24	7	2	0.87	ns
1978–1979	52.95	8.90	6	53.17	8.58	4	50.72	5.36	5	2	0.16	ns
1979–1980	67.81	9.92	5	46.59	8.54	7	42.22	20.26	4	2	2.01	ns
1980–1981	51.04	4.89	12	53.33	13.82	5	55.78	6.72	2	2	0.27	ns
χ^2		0.27			0.81			0.16				
df		3			3			3				
p		ns			ns			ns				

Tab. 7. The number of overlapping resp. non-overlapping adult and remaining juvenile males over all winters ($G = 0.14$, $df = 1$, $p > 0.1$).

	Overlapping	Non-overlapping	Total
Adults	25	8	33
Remaining juveniles	23	6	29
Total	48	14	62

3.2. Juvenile males

As in adult males the monthly dominance relationships of juvenile males did not change during the winter (Tab. 4). The frequency distribution of juvenile dominance rank, subdivided into three dominance classes, at different distances from their winter home range, did not deviate from a random expectation (Tab. 5). Population density and aggression can differ greatly from one year to another (DeLaet unpubl.); therefore I distinguished between years. To make comparisons between distance classes and between years, the non-parametric Kruskal Wallis analysis of variance was used (Tab. 6). This showed no significant differences either between distances or between winters.

3.3. Remaining juveniles

Site-fidelity in this group of juveniles was as high (77.4%) as in adult males (Tab. 7). Therefore it could be assumed that juvenile males, that were recruited to the next breeding population, showed a certain degree of site-related dominance in winter.

The average dominance relationships of these juvenile males grouped according to the three distance classes, over all winters, showed no differences (Tab. 8).

3.4. Disappearing juvenile males

Juvenile males leaving the area at the end of the winter showed a rather low degree of site-fidelity (Tab. 2). The dominance relationships of these males, over all winters, were not influenced by the distance to their winter home range (Tab. 8).

Tab. 8. Average dominance relationship of juveniles males over all winters according to three distance classes (Kruskal-Wallis analysis of variance).

	0–200 m			200–400 m			400–600 m					
	$\bar{x}$	se	n	$\bar{x}$	se	n	$\bar{x}$	se	n	df	χ^2	p
Remaining juveniles	65.04	5.94	12	52.12	12.33	4	41.93	16.40	5	2	4.08	ns
Disappeared juveniles	51.54	4.07	23	48.09	5.16	17	54.97	7.27	13	2	0.75	ns

Tab. 9. Average dominance relationships of resident males in two distance classes during the extreme territorial period (Mann-Whitney U-test).

	0–100 m			100–200 m			U	p
	x̄	se	n	x̄	se	n		
1978	65.29	9.29	7	29.92	14.00	4	4	<0.05
1979	79.08	15.44	4	72.41	9.38	5	7.5	ns
1980	67.91	7.33	6	42.93	8.20	5	5	<0.05
1981	71.36	8.32	6	49.51	12.21	5	8	ns

3.5. Spring

In March and April Great Tit males show an extremely high degree of territorial behaviour. As in adult males it is not possible to combine the results over all winters, because a number of males are resident over several years.

The number of males that visited the feeder in this period is obviously smaller than during winter, because of the high degree of territoriality. Therefore there could only be distinguished between two distance classes (0–100 m and 100–200 m). Although there exists a tendency for higher dominance relationships at smaller distances, significant results are only found in 1978 and 1980 (Tab. 9).

4. Discussion

Based on studies of different animal species Wilson (1975) distinguished between three types of hierarchical systems:

1. An absolute hierarchy in which the individuals only move up or down the ranks through further interactions with their rivals.
2. In a relative hierarchy even subdominant individuals can dominate high ranked ones close to their own sleeping place. This relative hierarchy with a spatial bias is intermediate between the absolute hierarchy and territoriality.
3. Territoriality.

According to Brown (1963) territoriality and site-related dominance (= the relative hierarchy of Wilson) are two aspects of the same phenomenon.

Our observations indicate a certain degree of site-related dominance in adult males during winter and an absolute hierarchical system in juvenile males. On average adult males are most dominant at feeders close to their winter home range, which overlaps significantly with their territory of next breeding season. Only for the winter 1978–1979 no site-related dominance was found. That winter was a very severe winter counting 18 d with a maximum daily temperature below zero. For the other winters, there were remarkably less real winterdays: 3 in 1977–1978, 6 in 1979–1980 and 4 in 1980–1981. This means that in adult males the degree of territoriality (site-related dominance) during winter is, probably by way of changes in food availability, determined by climatic circumstances.

Juvenile males can be divided into remaining and disappearing males. During the winter the activities of juvenile males leaving the study area before spring are less confined to a well defined area then are those of adult and remaining juveniles (Brusselaers, unpubl.). Also their site-fidelity is less pronounced, nor do they show any site-related dominance.

The high site-fidelity in remaining juveniles confirms the supposition of several authors (Creutz 1962, Dhont 1966) concerning the settlement of these juveniles before winter and suggests a certain degree of site-related dominance as in adults, although this could not be proved by our data. This means that in juvenile males, both remaining and disappearing ones, there exists during winter a very low degree of territoriality.

The high site-fidelity of remaining juvenile males, generally the most dominant juvenile males, is very important, and it remains unanswered if their high social rank is caused by a high degree of site-fidelity or vice versa. Most of these remaining juveniles arrive in their habitat at the end of October when social behaviour dominates territorial behaviour in the population. They almost immediately obtain a stable position in the winter hierarchy. This points to a site-fidelity caused by a high social rank.

From March onwards, when territorial behaviour increases very fast, a site-related dominance can be clearly shown in some years.

Brian (1949) started her investigations just in January 1949 and continued into the breeding season. She observed eight regular visitors at her feeder, 3 of which were adult resident males and 3 were juvenile males taking up a territory next breeding season. One juvenile male ringed in February 1949 and regularly seen, presented no data concerning a territory.

Her results on site-related dominance can be explained by an important increasing territoriality during this period. This fits with our results concerning adult and remaining juvenile males during the spring. Brian did not mention juvenile winter residents disappearing at the end of the winter. The absence of a significant influence of the distance in the spring of some years is possibly due to the occurrence of a severe period with snow and frost at the end of the winter. This happened in 1979 and 1981 when we noted in the last 10 d of February still 8 days with a minimum daily temperature below zero and resp. 3 and 1 days in the first half of March. In 1978 and 1980 there were yet 0 and 1 winterday at the end of February and 2 winterdays in the first half of March. Therefore, pronounced territorial behaviour during this period can be suppressed by severe circumstances. Our results suggest that especially in juvenile males, which build up most of the winter population, other factors are as important or even of more importance than site in the determination of social rank during winter.

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