

## ECOLOGICAL ASPECTS OF DOMINANCE HIERARCHIES IN BLACK-CAPPED CHICKADEES

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SINCE Schjelderup-Ebbe (1922) first described intraspecific dominance relationships in flocks of domestic hens (*Gallus gallus*), a great many studies have been made of dominant-subordinate behavior in a wide variety of avian species (e.g. Masure and Allee 1934, Tordoff 1954, Guhl 1968).

Two major categories of dominance hierarchies within bird flocks have been recognized. The more rigid system is a linear relationship such as Schjelderup-Ebbe observed with chickens; here the top bird never gets defeated, the second bird can be dominated only by the top bird, and so on. This has been called "peck-right" and has been demonstrated both in field studies (Collias and Taber 1951; Sabine 1949, 1959) and in groups of captive birds (Tordoff 1954, Marler 1955). The other major type of hierarchy is often called "peck-dominance"; here the top bird is the one that wins the greatest proportion of encounters, but the outcome of any one battle is not predictable. This more fluid system has been described many times (Masure and Allee 1934, Shoemaker 1939, Goforth and Baskett 1971), but most such studies, including all cited here, were done with captive birds.

Allee (1942) showed that for captives of several species the outcome varied with the site of encounter. Watson (1970), also working with captive birds, got similar results, but neither Dilger (1960) nor Dunham (1966) found site-related dominance in their caged birds. Field demonstrations of site-related dominance within bird flocks are rare. Colquhoun (1942) found that dominance among the top five birds at a single feeder in a stable winter flock of Blue Tits (*Parus caeruleus*) was inversely correlated with distance to the places where they roosted and later bred. Brian's (1949) demonstration of site-related dominance in Great Tits (*P. major*) was done during the breeding season, and thus can be explained by simple territoriality; but Brown (1963) clearly demonstrated site-related dominance within nonbreeding winter flocks of Steller's Jays (*Cyanocitta stelleri*).

In North American species of Paridae, linear peck-right dominance hierarchies within flocks have been demonstrated for Black-capped Chickadees (*Parus atricapillus*) (Odum 1942, Hartzler 1970, Glase 1973), and also in flocks of Carolina Chickadees (*P. carolinensis*) (Dixon 1963) and Mountain Chickadees (*P. gambeli*) (Dixon 1965, Minock 1971).

With the exception of Glase's work, these studies were done primarily at feeders, even though some bird species apparently show differences in hierarchies at and away from feeders (Dunham 1966, Crook and Butterfield 1970). Furthermore, although Dixon (1965) showed site-related dominance among male Mountain Chickadees from neighboring flocks, very few studies have searched for site-related dominance within flocks of chickadees.

As well as looking at the kind of hierarchy shown by a species, perhaps an even more interesting question is: why a hierarchy at all? A conventional explanation for the prevalence of dominance hierarchies within bird flocks is that, by establishing rank among members of a stable unit, the incidence of fights is lessened, and thus the danger of being injured is lowered for every member of the group (Lockie 1956). However, higher ranking birds probably have to withstand more challenges and thus run a greater risk of injury than do lower ranking birds of the same flock. Some measurable ecological benefit must be associated with rank that compensates for this extra risk. Rank may well act as a secondary sexual character, such that the highest ranking males are chosen preferentially by females; this is so in many lek species (Kruijt and Hogan 1967, Ballard and Robel 1974). Also, in times of extreme food shortage, higher ranking individuals may survive while lower ones starve. Krebs et al. (1972) found that captive hand-reared Great Tits readily formed dominance hierarchies, and that the dominant birds visited more food sources per minute than did the subordinate birds. Moreover, when they transferred a dominant male to a new group, it fell to the bottom of the hierarchy and its searching rate fell correspondingly.

Another benefit may be associated with high rank: the most dominant birds may be able to obtain the highest quality breeding territories. Although this idea is certainly not new (Coulson 1968, Watson and Moss 1970), little has been done to investigate it with passerines. As territory quality may well have a great effect on the survival of offspring, such a benefit would yield a real selective advantage.

The present study on Black-capped Chickadees was designed to look at the kind of dominance hierarchy found within winter flocks both at and away from feeders, to search for any site-related dominance within flocks, and to investigate the possibility that high rank enables a chickadee to obtain better quality breeding territories.

#### STUDY AREA AND METHODS

The study area was approximately 300 acres of the Wellesley, Massachusetts college campus containing second growth mixed woods interspersed with several buildings and parking lots. The mixed woods were roughly 25% coniferous and 75%

deciduous; the most common coniferous species were eastern hemlock (*Tsuga canadensis*) and eastern white pine (*Pinus strobus*); the most common deciduous trees were oaks, especially *Quercus borealis*, *Q. alba* and *Q. vetulina*, and maples, especially *Acer rubrum*. These tree species were not all evenly distributed; certain species such as the hemlocks occurred only in a few large clumps.

The study lasted from autumn 1970 to spring 1973. Chickadees were caught with mist nets each fall, and a few were trapped at or near the nest sites during the breeding season. Each bird received a unique color combination formed by a numbered aluminum Fish and Wildlife Service band and from one to three colored plastic bands. Nestlings from accessible nests were banded when they were approximately 9 days old. Starting in the fall of 1971 every adult was weighed before release.

Two types of feeders were used during the nonbreeding season, small plastic feeders that only one bird could use at a time, and chunks of suet covered by hardware cloth that had enough room for several birds, although two birds rarely visited them simultaneously for more than a split second. Observations on winter flocks were made at least once weekly, interactions being recorded both at and away from the feeders. In the first year I maintained widely spaced feeders within each flock territory in an effort to check for site-related dominance, and made most of the observations at these feeders. In the next 2 years the feeders were used primarily for trapping birds in the fall, and most observations were made away from the feeders.

I used three types of interactions to determine hierarchies: chasing of one bird by another, supplanting of a stationary bird by a newcomer, and the withdrawal of one bird at the approach of another. This last type I used only with caution, usually in situations at feeders where a bird left without having eaten. In the summer of 1972 I used three measures to estimate territorial quality: territory size, volume and type of cover, and nestling feeding rates. Territorial boundaries I determined primarily by plotting sites of aggressive encounters between members of neighboring pairs. Volume and type of cover I determined from an aerial photograph of the campus together with sample transects of wooded areas. Feeding rates were gauged throughout the nesting period from hourly observations of food brought to the nestlings. Most of the rates were obtained from 0630 to 0930 and 1930 to 1900, recording the size and kind (where possible) of food at every visit.

## RESULTS

*The flocks.*—In all three winters the chickadee flocks in the study area were stable, discrete units apparently formed sometime around August. The most common size was 6 birds, the average, 6.6. As far as could be determined, the sex ratio was essentially even in every flock. Some unmarked birds moved through the study area in August and September each year; several chickadees banded then stayed for a few days and then disappeared. This was particularly evident in 1971. These movements did not continue into October in any year of the study.

Only one bird in one of the 3 years regularly shifted from flock to flock after October. This bird was banded and could be found with one of three adjacent flocks, or, more frequently, foraging alone within one

TABLE 1  
A SAMPLE HIERARCHY: AGGRESSIVE INTERACTIONS 1972-73 IN FLOCK 1<sup>1</sup>

	R/G	Blk/G	A/R O/O	A/R G/G	Ble/G	A/R Y/O	A/Y O	Sex
Loser:								
R/G	X							Male
Blk/G	10 (5)	X						Male
A/R O/O	13 (3)	10 (4)	X					Male
A/R G/G	5 (3)	7 (3)	10 (5)	X	1 (0)			Male
Ble/G	6 (1)	1 (0)	6 (2)	1 (1)	X			Female
A/R Y/O	3 (1)	1 (1)	12 (5)	2 (1)	4 (2)	X		Female
A/Y O	1 (0)	9 (5)	2 (1)	—	7 (4)	2 (2)	X	Female

<sup>1</sup>X indicates no interactions possible; 10 (5) indicates that of a total of 10 interactions observed, 5 occurred away from feeders. Total interactions: 113.

of their flock territories. It disappeared the next spring, and its sex was not determined. It was never recorded dominating another bird.

*The hierarchies.*—In every winter of the study, the birds formed linear peck-right dominance hierarchies that were identical at and away from the feeders (Table 1), and I found no consistent indication of dominance being site-related. In the first winter I did not know where the birds had nested, and thus simply maintained widely spaced feeders within the flock territories; nevertheless no instances of dominance reversal were correlated with location. In the following 2 years I was able to find all the nests. Table 2 contains seven records of an alpha male dominating the beta male of the flock within 10 feet of the latter's last previous nest site. These records provide strong evidence that dominance within a Black-capped Chickadee winter flock is not site-related.

In general, males were dominant over females. Males also averaged heavier than females (males 12.1 g, females 11.3 g), though weights overlapped considerably. Usually I weighed each bird only once and did not try to measure possible weight changes over a winter. Neverthe-

TABLE 2  
RECORDS OF AN ALPHA MALE DOMINATING THE FLOCK'S BETA MALE WITHIN 10 FEET OF THE LATTER'S PREVIOUS NEST SITE

Date	Winner	Loser
3 November 1971	R/A R/Y	R/G
28 November 1971	O/R	Y/Ble
3 December 1971	O/R	Y/Ble
17 January 1972	O/R	Y/Ble
8 March 1972	O/R	Y/Ble
9 November 1972	A/R R/G	Blk/Y
18 February 1973	A/R R/G	Blk/Y

less the few data I obtained do not indicate that rank within either sex group was related to weight.

An interesting shift in dominance occurred in 1972–73. The shift involved two old females, and was correlated with the disappearance of the mate of one of them. Blk/R, originally the higher ranking female, was mated to the top-ranking male of the flock. When he disappeared at the end of October 1972, G/Blk's mate became the alpha male. From then on, every record of interactions between these females show G/Blk the winner. However female rank is not always correlated with her mate's rank; for example, in another flock (of 7 birds) the same winter, the beta male's mate was the lowest bird in the hierarchy, even though the pair had been formed the previous August.

*Territory quality.*—Fig. 1 shows the territorial boundaries in the study area in 1972. These represent the outermost limits of the territories. Table 3 shows the territory sizes and estimated volume of cover, as well as the approximate ratio of coniferous:deciduous trees for each territory.

To obtain nestling feeding rates, I collected specimens of the most common food items and determined their dry weights. Using these values, mg dry weight/h for each brood could be calculated, as shown in Table 4. The broods were not all the same size, but varied from one to seven nestlings. Therefore I also calculated the feeding rates as mg/young/h (Fig. 2).

#### DISCUSSION

*The hierarchies.*—Linear, peck-right dominance hierarchies existed within every winter flock of Black-capped Chickadees studied over a 3-year period. The flocks themselves were stable, discrete units that remained intact throughout the winter; hence the hierarchies, once established, functioned over a period of 7–8 months. The dominance shown in these flocks was not restricted to artificial situations like feeders, nor was it site-related. Dixon (1965) pointed out that site-related dominance would be unlikely to occur within such stable units.

The sex of an individual apparently can have a strong effect on its position within the hierarchy; the majority of males were dominant over the majority of females in every flock studied. Others have also found this to be the case in *Parus* (Kluyver 1957, Glase 1973). Indeed the consistent dominance of one sex over another is often found in flocking birds. In some species the females are dominant, even in nonbreeding flocks, as Thompson (1960) found in the House Finch (*Carpodacus mexicanus*).

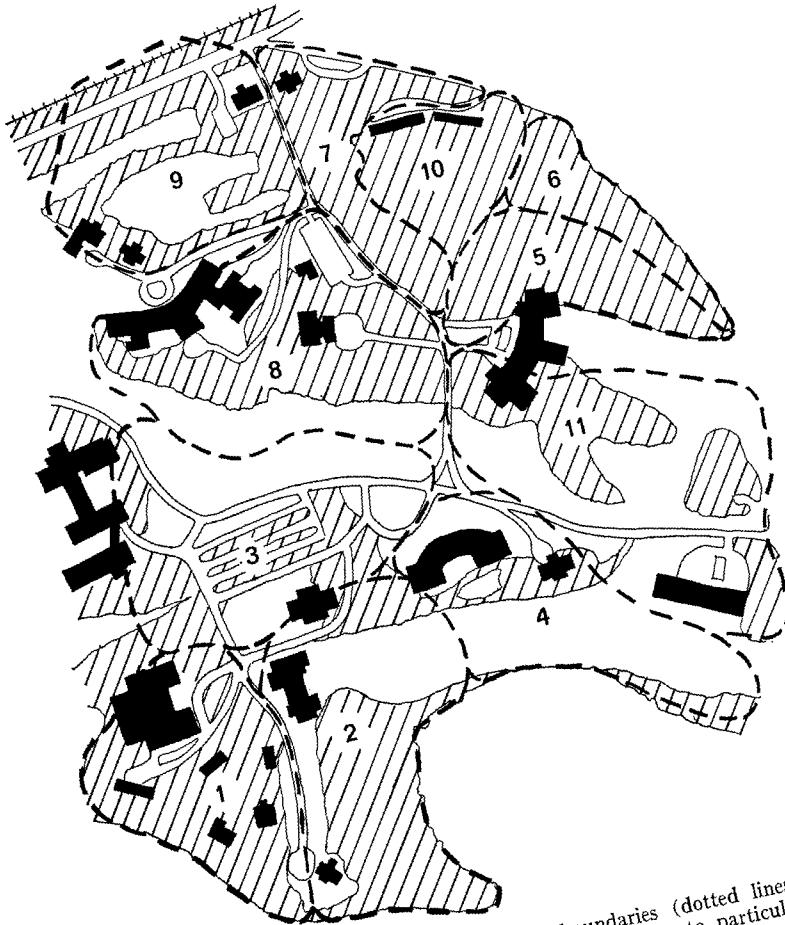


Fig. 1. Breeding territories in 1972, showing boundaries (dotted lines) and approximate amount of canopy (shaded areas). Numbers refer to particular pairs.

Weight did not appear to play much role in determining rank in chickadees. Though the males as a group weighed more than females and were dominant over them, rank within one sex group was not correlated with weight. Thompson (1960) obtained similar results in House Finches and Glase (1973) in Black-capped Chickadees. Though weights were not taken repeatedly throughout the winter, it would be very interesting to do this regularly to see whether subordinate birds lose proportionately more weight over a winter than do dominant birds. Every flock in the last 2 years of the study (i.e. after the first breeding season's data) had as its top-ranking bird a male that had nested within

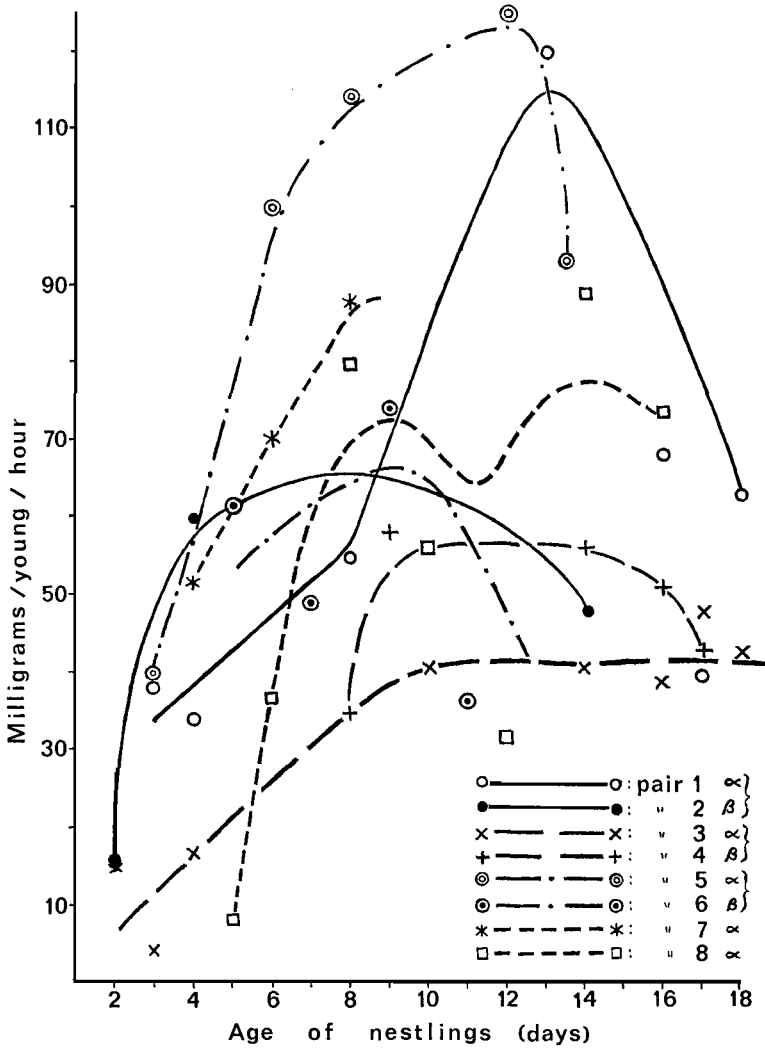


Fig. 2. Nestling feeding rates (mg/young/h).

the flock territory the previous summer. I have no records of any male banded as a newcomer at the beginning of a winter being dominant over even the lowest-ranking male that had been in the area the previous winter. It is difficult to say whether this is an effect of age or of experience. In this resident species it seems extremely unlikely that any male having once obtained a breeding territory would leave and attempt to join a new flock in the winter. However suitable nesting habitat is

TABLE 3  
TERRITORY SIZES, WITH TYPE AND VOLUME OF CANOPY

Pair no. <sup>1</sup>	Male dominance	Total acres	Type of cover (Decid.:Conif.)	% cover	Total cover (acres)
1	1	10.4	2:3	80	8.32
2	2	12.5	3:1	65	8.12
3	1	12.0	8:1	33	3.96
4	2	12.0	1:1	37	4.44
5	1	6.5	3:2	100	6.50
6	2	3.8	3:2	100	3.80
7	1	7.0	1:1	98	6.86
8	1	17.9	1:1	45	8.05
9	1	12.9	1:1	85	10.96
10	1	6.5	3:2	100	6.50
11	1	16.0	1:1	45	7.20

<sup>1</sup>In the previous winter, pairs 1 and 2 were in one flock, pairs 3 and 4 in another, and pairs 5 and 6 in a third. Pairs 7 to 11 were each in separate flocks.

constantly being destroyed as cities expand, and it would be very interesting to see how an older "newcomer" would fare in rank within a new flock.

This effect of age and/or experience does not necessarily apply to females; in some cases females banded in the same area in previous years

TABLE 4  
NESTLING FEEDING RATES (MG/H)

Age of nestlings	Pair number							
	1	2	3	4	5 <sup>1</sup>	6	7	8
2	—	80	110	—	—	—	—	—
3	190	—	25	—	40	—	—	—
4	168	300	120	—	—	—	—	—
5	—	—	—	—	—	245	260	8
6	—	—	—	—	100	—	—	37
7	—	—	—	—	—	195	360	—
8	275	—	—	210	114	—	—	—
9	—	—	—	350	—	298	442	80
10	—	—	285	—	—	—	—	56
11	—	—	—	—	—	145	—	—
12	—	—	—	—	125	F	—	32
13	600	—	—	—	93	—	—	—
14	—	240	285	342	—	—	—	89
15	—	—	—	—	F	—	F	—
16	342	—	270	312	—	—	—	74
17	200	F	335	358F	—	—	—	—
18	313F	—	300F	—	—	—	—	F
Brood size:	5	5	7	6	1	4	5	1

<sup>1</sup>Second brood. All the rest: first broods. F indicates fledging.



ranked lower than newcomer females. Several studies of captive birds (e.g. Tordoff 1954, Thompson 1960) indicate that age played little role in determining rank of even the males, but the field studies of Collias and Taber (1951) suggest that age may well affect social rank of Ring-necked Pheasants (*Phasianus colchicus*).

Finally, a factor that may play a part in determining the rank of females is the rank of her mate. With very few exceptions, the rank of females whose mates were known was correlated with the rank of their mates (see also the reversal of dominance between two females mentioned above.)

*Territory quality.*—For five of the eight winter flocks in the study area in the winter of 1971–72, only one pair per flock survived the flock breakup to hold a breeding territory within the flock range in the summer of 1972. Of these, the three males that were banded before the 1972 breeding season were all alpha males in their flocks. The other two, from flocks not previously studied, were banded at the nests, and were the alpha males in their respective flocks the following winter. Clearly the territorial advantage of dominance in these five flocks was great.

In three other flocks, both the alpha and beta males obtained breeding territories within the flock range in 1972: pairs 1 and 2, 3 and 4, and 5 and 6 (Fig. 1). The measures of territory quality used can thus be evaluated generally among all the pairs studied, and also with regard to the three possible comparisons of alpha and beta males.

In general the smallest territories had the highest percentage cover, and the breeding density was greatest in the wooded parts of the study area. Sturnam (1968) found that breeding density of Black-capped Chickadees in Washington was most accurately predicted by the canopy volume; similarly Krebs (1971) and Balen (1973) found greater breeding densities of Great Tits in habitats with greater canopy volume, but none of these studies included the relative dominance of the territory holders. In the one instance in the present study where both dominant and subordinate males had territories with identical percentages of canopy (pairs 5 and 6), the alpha male's territory was almost twice that of the beta male (Table 3).

There was no apparent correlation between type of cover (deciduous: coniferous ratio) and territory quality in the present study. Sturnam (1968) also found that for *P. atricapillus* total canopy volume, rather than the presence or proportion of any type of tree, was the most important factor in predicting breeding density.

Feeding rates also appear to be an important indication of territory quality. Kluyver (1961) studied food consumption of nestling Black-

capped Chickadees in pine woods and mixed forest in Massachusetts, but measured only number of feedings; as Royama (1966) pointed out, differing size of food items should be included before comparisons can be made. Although Kluyver found no significant difference in nestling weights between broods in the two habitats, the nestlings in his pine woods box appear to have been lighter just prior to fledging than were those in the mixed woods (Kluyver 1961). Unfortunately he gave no data either for dominance or for the relative size of the territories involved.

One of the most striking comparisons of feeding rates in the present study is between pair 5 and pair 8 (Fig. 2). Although this was the second brood of pair 5 and the first of pair 8, the second brood was early, coinciding with many other first broods. Both of these broods consisted of one infertile egg and one hatched young; both were raised in July. But although the territory of pair 8 (17.9 acres) was almost three times that of pair 5 (6.5 acres), the feeding rate of the woodland pair (5) was far greater than that in the larger, more open territory. Yet the more open territory actually had more total acreage of canopy than the woodland territory. The greater searching and flying times in the larger territory probably contributed to its lower feeding rate.

Royama (1966) found in Great Tits that larger broods need less food per nestling because they have smaller heat loss. Looking at the three alpha-beta comparisons in the present data, pair 1 (alpha) had a smaller territory, but a higher percentage and total acreage canopy than pair 2, and also a higher feeding rate. As both had five nestlings, each of the differences may reflect territory quality. Similarly in pairs 5 and 6 the alpha pair 5 had a larger territory with more acres of canopy, and a far greater feeding rate than pair 6. Although pair 5 had only one nestling and pair 6 had four, the difference in feeding rates is possibly greater than can be explained by differential heat loss of the two broods alone (Fig. 2). The final comparison is between pair 3 (alpha) and pair 4. Pair 3's brood of seven is comparable with pair 4's brood of six, but here the beta male 4 had a greater percentage and absolute acreage canopy than did alpha male 3; moreover, the beta pair's feeding rate was considerably higher than that of the alpha pair. Yet I twice recorded male 3 (A/R R/G) dominating male 4 (Blk/Y) within 10 feet of male 4's nest site the following winter (Table 2). I suspect this can be explained by site tenacity of the alpha male. A yearling male's best chance of obtaining a breeding territory is to take over a territory whose previous owner died during the winter; hence he seldom has the opportunity to choose the quality of his first territory. Subsequently he can expand and modify its boundaries; indeed, that is what

I would predict A/R R/G would do in later years; he would be less likely to desert altogether and try to obtain an entirely new territory. Krebs (1971) found very similar behavior in removal experiments with Great Tits: having demonstrated that hedgerow territories were inferior to woodland territories, he showed that yearling hedgerow males were more likely to move into woodland vacancies than were hedgerow adults, even hopping over hedgerow adult territories to obtain adjacent woodland sites.

Dhondt and Hublé (1968) and Dhondt (1971) showed that older Great Tits had better quality territories than younger birds, quality being determined by more and bigger trees and also by the presence of nest boxes. Similarly Krebs (1971) found that the less wooded territories had a higher proportion of first-year Great Tits than did woodland territories, and Ralph and Pearson (1971) found first-year White-crowned Sparrows (*Zonotrichia leucophrys*) had significantly smaller territories than did older birds. Although none of these studies investigated the relative dominance of the birds involved, it seems likely that the older birds were, at least on the average, more dominant.

Much more work needs to be done on this topic. Especially the aspect of site tenacity lends itself to further study. Nevertheless the Black-capped Chickadee apparently possesses a social system in which older more experienced birds tend to be dominant, and this dominance is apparently often reflected in the quality of breeding territory these birds are able to obtain, the most dominant birds thus gaining the best reproductive opportunities.

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#### SUMMARY

Dominance hierarchies in winter flocks of Black-capped Chickadees were linear peck-right relationships in all three winters of the study. They were not site-related, and remained the same whether at or away from feeders. Possible factors affecting the rank of an individual within such hierarchies are discussed. The data for the most part support the theory that higher ranking chickadees can obtain better quality breeding territories.

#### LITERATURE CITED

- ALLEE, W. C. 1942. Social dominance and subordination among vertebrates. Biol. Symp. 8: 139-162.

- BALEN, J. H. VAN 1973. A comparative study of the breeding ecology of the Great Tit *Parus major* in different habitats. *Ardea* 61: 1-93.
- BALLARD, W. B., AND R. J. ROBELL. 1974. Reproductive importance of dominant male Greater Prairie Chickens. *Auk* 91: 75-85.
- BRIAN, A. D. 1949. Dominance in the Great Tit *Parus major*. *Scottish Naturalist* 61: 144-155.
- BROWN, J. L. 1963. Aggressiveness, dominance and social organization in the Steller Jay. *Condor* 65: 460-484.
- COLLIAS, N. E., AND R. E. TABER. 1951. A field study of some grouping and dominance relations in Ring-necked Pheasants. *Condor* 53: 265-275.
- COLQUHOUN, M. K. 1942. Notes on the social behaviour of Blue Tits. *Brit. Birds* 35: 234-240.
- COULSON, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. *Nature* 217: 478-479.
- CROOK, J. H., AND P. A. BUTTERFIELD. 1970. Gender role in the social system of *Quelea*. Pp. 211-248 in *Social behaviour in birds and mammals* (J. H. Crook, Ed.). London, Academic Press.
- DHONDT, A. A. 1971. Some factors influencing territory in the Great Tit (*Parus major* L.). *Giervalk* 61: 125-135.
- DHONDT, A. A., AND J. HUBLÉ. 1968. Age and territory in the Great Tit (*Parus m. major* L.). *Angew. Ornithol.* 3: 20-24.
- DILGER, W. C. 1960. Agonistic and social behavior of captive redpolls. *Wilson Bull.* 72: 114-132.
- DIXON, K. L. 1963. Some aspects of the social organization of the Carolina Chickadee. *Proc. 13th Intern. Ornithol. Congr.* 1: 240-258.
- DIXON, K. L. 1965. Dominance-subordination relationships in the Mountain Chickadee (*Parus gambeli*). *Condor* 67: 291-299.
- DUNHAM, D. W. 1966. Agonistic behavior in captive Rose-breasted Grosbeaks, *Pheucticus ludovicianus* (L.). *Behaviour* 27: 160-173.
- GLASE, J. C. 1973. Ecology of social organization in the Black-capped Chickadee. *Living Bird* 12: 235-267.
- GOFORTH, W. R., AND T. S. BASKETT. 1971. Social organization of penned Mourning Doves. *Auk* 88: 528-542.
- GUHL, A. M. 1968. Social inertia and social stability in chickens. *Anim. Behav.* 16: 219-232.
- HARTZLER, J. E. 1970. Winter dominance relationship in Black-capped Chickadees. *Wilson Bull.* 82: 427-434.
- KLUYVER, H. N. 1957. Roosting habits, sexual dominance and survival in the Great Tit. *Cold Spring Harbor Symp. Quant. Biol.* 22: 281-285.
- KLUYVER, H. N. 1961. Food consumption in relation to habitat in breeding chickadees. *Auk* 78: 532-550.
- KREBS, J. R. 1971. Territory and breeding density in the Great Tit *Parus major* L. *Ecology* 52: 2-22.
- KREBS, J. R., M. H. MACROBERTS, AND J. M. CULLEN. 1972. Flocking and feeding in the Great Tit *Parus major*—an experimental study. *Ibis* 114: 507-530.
- KRUIJT, J. P., AND J. A. HOGAN. 1967. Social behavior on the lek in Black Grouse, *Lyrurus tetrix tetrix* (L.). *Ardea* 55: 203-240.
- LOCKIE, J. 1956. Winter fighting in feeding flocks of rooks, jackdaws and carrion crows. *Bird Study* 3: 180-190.

- MARLER, P. 1955. Studies of fighting in chaffinches. 1. Behaviour in relation to the social hierarchy. *Brit. J. Anim. Behav.* 3: 111-117.
- MASURE, R. H., AND W. C. ALLEE. 1934. The social order in flocks of the common chicken and the pigeon. *Auk* 51: 306-327.
- MINOCK, M. E. 1971. Social relationships among Mountain Chickadees. *Condor* 73: 118-120.
- ODUM, E. P. 1942. Annual cycle of the Black-capped Chickadee, 3. *Auk* 59: 499-531.
- RALPH, C. J., AND C. A. PEARSON. 1971. Correlation of age, size of territory, plumage, and breeding success in White-crowned Sparrows. *Condor* 73: 77-80.
- ROYAMA, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits, *Parus major*. *Ibis* 108: 313-347.
- SABINE, W. S. 1949. Dominance in winter flocks of juncos and tree sparrows. *Physiol. Zool.* 22: 64-85.
- SABINE, W. S. 1959. The winter society of the Oregon Junco: intolerance, dominance, and the pecking order. *Condor* 61: 110-135.
- SCHJELDERUP-EBBE, T. 1922. Beiträge zur Sozialpsychologie des Haushuhns. *Z. Psychol.* 88: 226-252.
- SHOEMAKER, H. H. 1939. Social hierarchy in flocks of the canary. *Auk* 56: 381-406.
- STURNAM, W. A. 1968. Description and analysis of breeding habitats of the chickadees, *Parus atricapillus* and *P. rufescens*. *Ecology* 49: 418-431.
- THOMPSON, W. L. 1960. Agonistic behavior in the House Finch. 2. Factors in aggressiveness and sociality. *Condor* 62: 378-402.
- TORDOFF, H. B. 1954. Social organization and behavior in a flock of captive non-breeding Red Crossbills. *Condor* 56: 346-358.
- WATSON, A., AND R. MOSS. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. Pp. 167-220 in *Animal populations in relation to their food resources* (A. Watson, Ed.). London, Blackwell.
- WATSON, J. R. 1970. Dominance-subordination in caged groups of House Sparrows. *Wilson Bull.* 82: 268-278.

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