Wilson Bull., 102(4), 1990, pp. 623–633

DOMINANCE RANK AND RESOURCE ACCESS IN WINTER FLOCKS OF BLACK-CAPPED CHICKADEES

MILLICENT SIGLER FICKEN, CHARLES M. WEISE, AND JAMES W. POPP[1]

ABSTRACT.—We investigated the relationship between dominance rank and access to a winter feeding station in Black-capped Chickadees (*Parus atricapillus*). Although there was considerable inter-individual variation, dominance rank was not strongly related to number of visits to the feeder or length of visit. Because dominants were more likely than subordinates to approach a bird on the feeder, dominants tended to have access to the feeder at any time, while subordinates had to wait for the feeder to be unoccupied. Dominant individuals were involved in more agonistic encounters than subordinates. Interactions occurred between high-ranking individuals more often than expected by chance, while middle-ranking birds interacted less often than expected with individuals of all ranks. Birds also interacted more than expected with members of their own flock and less often with members of other flocks.
Received 27 Sept. 1989, accepted 5 Mar. 1990.

Dominance hierarchies occur in many species, yet the costs and benefits of holding a particular rank are not always clear (Huntingford and Turner 1987). Among birds forming flocks, dominants have been shown to benefit by increased access to food resources (Baker et al. 1981, Ekman and Askenmo 1984, Poysa 1988, Hogstad 1989) or to locations safest from predators (Schneider 1984, Hegner 1985, Ekman 1987, Desrochers 1989, Hogstad 1989). Potential costs to dominants include increased rates of aggression (Rohwer and Ewald 1981) or higher metabolic rates (Røskaft et al. 1986, Hogstad 1987). In this study, we examined some of the costs and benefits of dominance among Black-capped Chickadees (*Parus atricapillus*) in winter flocks. We tested the following hypotheses: (1) Higher-ranking birds have greater access than lower-ranking birds to an artificial point source of food; and (2) Higher-ranking birds face increased costs, as measured by number of agonistic encounters (Hogstad 1989). In addition, we investigated whether individuals interacted with each other at random or if they interacted with certain individuals more than others.

METHODS

We made observations at a feeder at the University of Wisconsin–Milwaukee Field Station, Saukville, Ozaukee County, Wisconsin (a site described by Weise and Meyer 1979), from 27 November 1982 to 24 March 1983. The feeder was always available to the chickadees from 15 November 1982 until 1 May 1983.

[1] Dept. of Biological Sciences and Field Station, Univ. of Wisconsin–Milwaukee, Milwaukee, Wisconsin 53201.

The feeder was designed to facilitate observation of aggressive encounters. It had two perches 23 cm apart and projecting 5.5 cm from the front of the feeder. Between the perches was a single entrance to a chamber enclosed by wire mesh, within which the sunflower seed hopper was located. Only one bird entered the feeder at a time and usually stayed only long enough to select a seed, which was then carried away from the feeder. Agonistic encounters took place on the two perches or with one bird on a perch and the other inside the feeder. Birds could take their seed either from the hopper or from the floor of the feeder. Seeds on the floor were usually ones that had been dropped and may have been inferior in quality.

The chickadees were individually color banded as part of a long-term study of this population by CMW. We knew the sex and ages of most adult birds. We recognized first-year birds by skull ossification (August–November) or by shape of rectrices (Pyle et al. 1987). We tentatively sexed these birds by wing chord length (Weise 1979); we confirmed or more rarely corrected by sex-specific behavior the sex designations of those individuals that later entered the breeding population (Weise 1979). We attempted to note the color bands of all birds visiting the feeder during videotaping, although this was not always possible.

We videotaped all observations using a Sony video camera equipped with a Nikon lens. The observer and camera were concealed in a blind 10 m from the feeder, and we turned the camera on whenever chickadees were in the vicinity of the feeder. Between 0900 and 1200 CST, we videotaped four, 33 min tapes each week, with two tapes per day of observations, for a total of 82 tapes.

The video tapes were later rerecorded with a timer on the tape (recording to 0.01 sec). We noted the time each bird arrived at the feeder, whether or not it obtained a seed, whether that seed came from the hopper or the floor, and the departure time of the bird. If an aggressive encounter occurred, we noted the winner and loser. An aggressive encounter was said to have occurred when one bird supplanted another at the feeder or two chickadees gave an exchange of postures and/or calls with one bird eventually gaining access to the seeds. We defined the winner as: (1) the first bird to obtain a seed, or (2) in the rare cases when neither bird obtained a seed, the last bird to leave the feeder.

We analyzed 7126 visits to the feeder, during which 1200 interactions occurred. To ensure a sample size large enough for comparisons among individuals, we selected for analysis 20 individuals that visited the feeder at least 80 times (Table 1). The individuals chosen for analysis were from four different flocks, and included both males and females. We determined the dominance hierarchy by ranking individuals so as to minimize the number of losses to individuals ranked higher. Using the number of individuals dominated to determine the dominance hierarchy produced an identical hierarchy.

For each individual, we determined the number of times it visited the feeder, the number of encounters in which it was involved, the percentage of visits in which it had an agonistic encounter, and the mean duration of its visit from the time it arrived at a perch. In addition, we noted the percentage of visits in which each individual obtained a seed, and the percentage of seeds taken from the floor (as opposed to the hopper). We also determined for each individual the percentage of visits to the feeder in which that individual approached a bird already present there, and the percentage in which that individual was on the feeder and was approached by another bird. We used Spearman rank correlations to compare dominance rank and each of these measures for all individuals, and separately for males and for females. Correlations with a $P < 0.05$ were considered significant.

To investigate whether individuals interacted with certain individuals more than expected by chance, we assumed that the number of times individuals visited the feeder reflected the opportunities those individuals had to interact with each other. We calculated the expected number of interactions between any two individuals from the number of visits each individual made. The expected number represented the number of encounters expected if in-

TABLE 1

THE SEX, AGE AND FLOCK MEMBERSHIP FOR EACH BLACK-CAPPED CHICKADEE IN THE STUDY, LISTED FROM HIGHEST TO LOWEST RANKING INDIVIDUAL (TOP TO BOTTOM)

Individual	Sex	Hatch year	Flock No.
1	Male	1980	1
2	Male	1981	1
3	Male	1982	1
4	Male	1981	1
5	Male	1980	1
6	Male	1982	1
7	Male	1982	2
8	Male	1981	3
9	Male	1979	3
10	Female	1982	1
11	Male	1982	3
12	Female	1980	1
13	Male	1982	1 or 4?
14	Female	1978	2
15	Female	1982	1
16	Female	1981	3
17	Female	1982	3
18	Female	1980	1
19	Male	1982	1
20	Female	1981	4

dividuals interacted at random. Expected values were calculated for each tape and then summed for all tapes. We grouped individuals as high-ranking (birds 1–7), middle-ranking (birds 8–13), or low-ranking (birds 14–20). We compared observed and expected numbers of interactions within and between each dominance group. We also compared observed and expected numbers for interactions between individuals of the same flock versus individuals of different flocks and for encounters between males, between females, and between males and females. We made these comparisons of observed and expected values using the *G*-statistic for goodness-of-fit. To detect trends among individuals, we calculated Freeman-Tukey deviates (Sokal and Rohlf 1981). Deviates greater than two or less than negative two suggest significant differences between observed and expected values.

RESULTS

Access to food.—The number of visits made by each individual to the feeder varied greatly (extremes: 83–814). The number of visits was significantly correlated with rank (Fig. 1, all individuals, $r_s = 0.44$) but only because of the high number of visits made by birds 6 and 7. When males and females were considered separately, the correlations were not significant for either group ($r_s = 0.27$ and 0.13, respectively). The mean time the individual spent on the feeder per visit was not significantly correlated

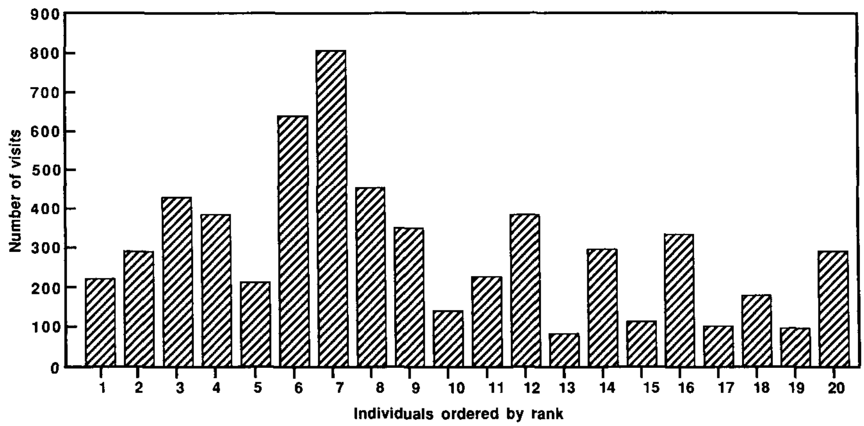

FIG. 1. Number of visits made to the feeder by each individual.

with rank (for all individuals, $r_s = -0.24$; males only, $r_s = -0.45$; females only, $r_s = -0.26$). For most individuals, the mean visit time was between 4.0 and 5.5 sec.

All individuals obtained seeds in most of their visits to the feeder (in 80% to 100% of visits). Accordingly, rank was not significantly correlated with percentage of visits in which a seed was obtained (for all individuals, $r_s = 0.27$; for males only, $r_s = 0.35$; for females only, $r_s = -0.02$). Chickadees could obtain seeds from the hopper or from the floor of the feeder. Rank was not correlated with the percentage of seeds taken from the floor

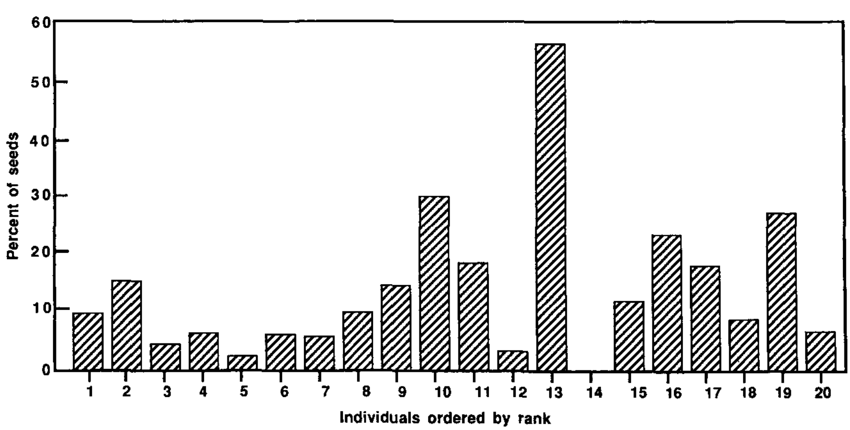

FIG. 2. Percent of seeds that each individual obtained from the floor of the feeder.

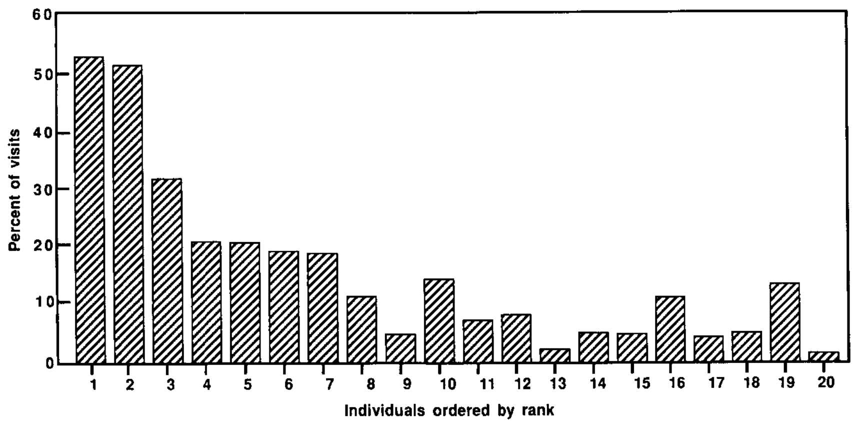

FIG. 3. Percent of visits in which each individual approached the feeder when another bird was already present on the feeder.

(Fig. 2, $r_s = -0.29$). Most of the birds that took more than 20% of their seeds from the floor were, however, in the lower half of the dominance hierarchy. The absence of a significant correlation was due to the considerable variation among these low-ranking birds. This correlation was significant when males were considered alone ($r_s = -0.57$).

One potential advantage of taking a seed from the floor rather than the hopper would be a reduced time spent at the feeder. To test this hypothesis, we used a paired t-test to compare for each individual the time spent per visit when a seed was obtained at the hopper versus when a seed was obtained from the floor. This comparison was nonsignificant ($t = 1.13$, df = 18, $P > 0.05$).

Priority to food.—The percentage of visits in which an individual approached a bird on the feeder (as opposed to visits when the feeder was unoccupied) was correlated with rank (Fig. 3, $r_s = 0.89$). Dominant birds were more likely than subordinate birds to visit when a bird was on the feeder. This correlation was significant for both males ($r_s = 0.90$) and females ($r_s = 0.67$). In contrast, there was no significant correlation between rank and the percentage of visits in which an individual was approached while on the feeder (Fig. 4, for all individuals, $r_s = -0.28$; for males, $r_s = -0.13$; for females, $r_s = 0.33$).

Encounters.—The number of encounters in which each individual was involved was significantly correlated with rank (Fig. 5, all individuals, $r_s = 0.68$). Higher ranking birds were involved in more encounters than lower ranking birds. This comparison was significant for males ($r_s = 0.64$), but not for females ($r_s = 0.55$). The percentage of visits in which there

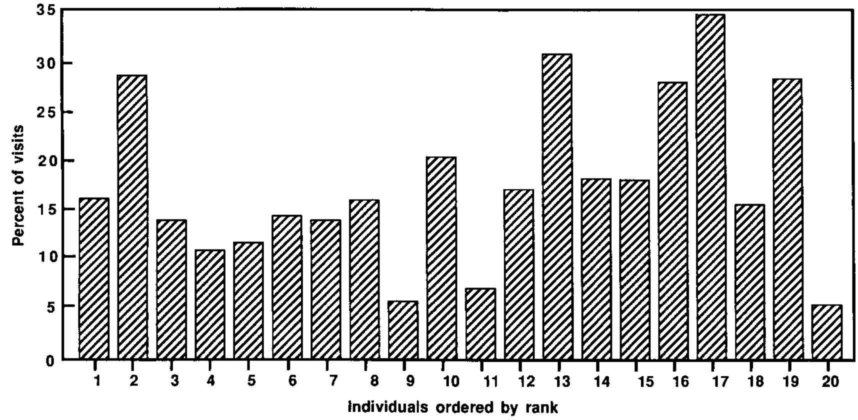

FIG. 4. Percent of visits in which each individual was approached by another bird while they were on the feeder.

were encounters was also significantly correlated with rank (Fig. 6, r_s = 0.44). This significant correlation was due to the high percentages for the two most dominant birds. Again this comparison was significant for males (r_s = 0.51), but not for females (r_s = 0.40).

Observed and expected numbers of encounters within and between dominance groups were significantly different (Table 2, G = 127.4, df = 5, $P < 0.001$). Interactions were more frequent than expected among high-ranking birds, while middle-ranking birds interacted less than expected with individuals of all ranks. Individuals also interacted with mem-

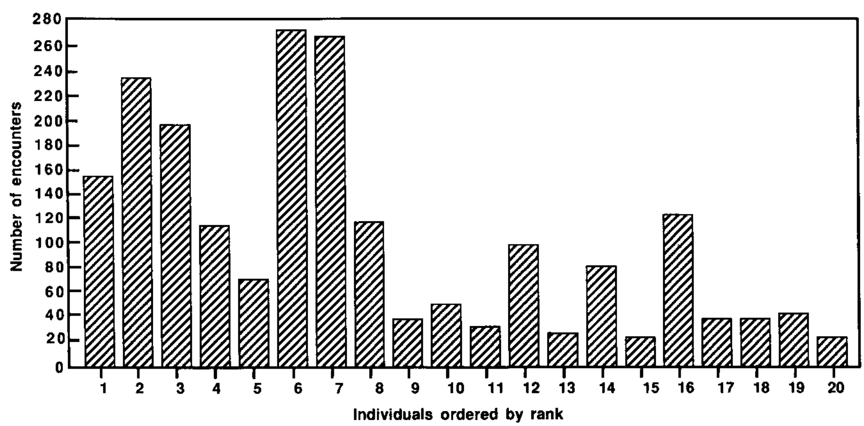

FIG. 5. Number of agonistic encounters in which each individual was involved.

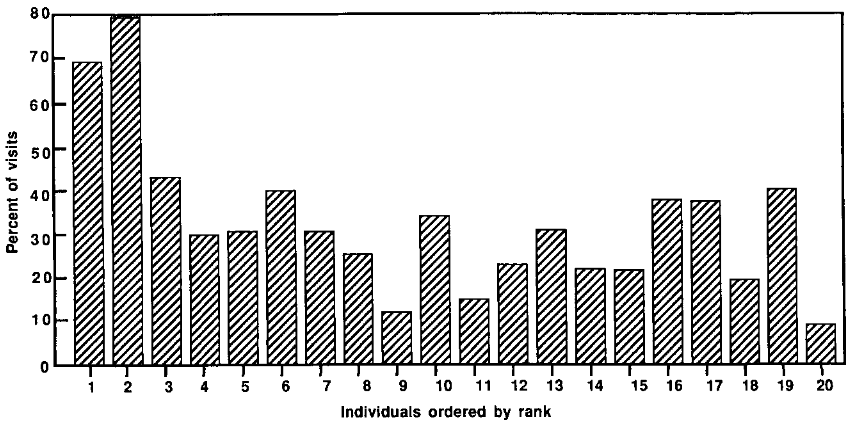

FIG. 6. Percent of visits to the feeder in which each individual was involved in an agonistic encounter.

bers of their own flock more than expected and with members of other flocks less than expected (members: obs 432, exp 262; non-members: obs 342, exp 513; G = 156.2, $P < 0.001$). Interactions among males were more frequent than expected, while females interacted less than expected with both males and other females (Male-male: obs 417, exp 378; female-female: obs 31, exp 53; female-male: obs 326, exp 347; $G = 16.1$, df = 2, $P < 0.001$).

Comparisons of rank, sex, and flock membership are not independent (i.e., most high-ranking birds are males from flock 1). To avoid this lack of independence, we compared observed and expected values on an individual basis using Freeman-Tukey deviates. Significant positive deviates (observed values greater than expected) were most commonly asso-

TABLE 2

OBSERVED AND EXPECTED NUMBER OF INTERACTIONS BETWEEN AND WITHIN EACH DOMINANCE GROUP

Dominance rank of contestants	Observed	Expected
High-high	302	179
High-middle	163	229
High-low	188	178
Middle-middle	22	53
Middle-low	81	105
Low-low	18	30

ciated with the two highest ranking birds. Particularly high deviates were found for interactions between birds 1 and 2 and for interactions birds 1 and 2 had with birds 3, 6, and 7. Significant negative deviates were mostly associated with interaction among middle-ranking birds (especially birds 9, 11, and 12). Bird 9 interacted with other birds much less than expected; 15 of 19 deviates were negative (6 were significant).

Male-female differences.—We compared mean values of males with those of females for the eight measures described above. We found significant differences for only two measures: number of encounters and percentage of times an individual approached a bird on the feeder. Males were more than twice as likely as females to be in an encounter (males: $\bar{x} = 130.1$, females: $\bar{x} = 60.4$, t for unequal variances = 2.36, $P < 0.05$). Males also approached a bird in a greater percentage of their visits to the feeder (males: $\bar{x} = 21.2\%$, females: $\bar{x} = 6.4\%$, t for unequal variances = 2.93, $P < 0.05$).

DISCUSSION

Dominance has previously been reported to affect foraging in winter flocking birds. High-ranking birds may have greater access to food resources (Ekman and Askenmo 1984, Enoksson 1988, Hogstad 1988) or face reduced risk of predation (Schneider 1984, Hegner 1985, de Laet 1985). A relationship between rank and access to feeding sites has been previously suggested for Black-capped Chickadees (Glase 1974), and Desrochers et al. (1988) have shown a positive relationship between rank and winter survival. In this study, we found considerable individual variation in access to a super abundant, highly concentrated food source, but this variation was not strongly related to rank. As the chickadees obtained a seed in most of their visits and as their visits varied little in length, the number of visits to the feeder was a good indicator of resource access. There was nearly a ten-fold difference among individuals in number of visits. The highest numbers of visits, however, were made by middle-ranking males (birds 6 and 7), while the two highest-ranking birds made fewer visits than some low-ranking birds (i.e., 14, 16, and 20). Poysa (1988) also reported large variation among individual Great Tits (*P. major*) in their visits to a feeder. In that study, however, resource access was related to dominance rank.

Despite not having greater access to the feeder, high-ranking birds were involved in more agonistic encounters than low-ranking birds. Why did dominants pay a cost (increased encounters) to maintain their high rank, without a compensatory benefit of increased resource access? The costs of being in an agonistic encounter may have been low. Actual physical fights were not observed, although encounters were often long with several exchanges of displays (Popp et al. 1990). Maintaining a high rank may also have provided benefits: (1) away from the feeder, (2) later during the breeding season, or (3) during times of severe weather when access to the feeder may be more important (Brittingham and Temple 1988).

High-ranking birds did have an advantage in being able to approach the feeder at any time, while low-ranking birds were more likely to wait until the perches were unoccupied. At natural food sources that are quickly depleted (i.e., a seed head on a plant or a leaf with insect eggs), this may give high-ranking birds a definite advantage. In addition, by having to wait near the feeder for access to it, subordinates may be in more exposed positions and face higher rates of predation (Lima 1985, Waite 1987, Poysa 1988). Subordinates also have to wait for access to feeders in social groups of Scrub Jays (*Aphelocoma coerulescens*) (Craig et al. 1982).

By using the number of visits to the feeder as a measure of the opportunity individuals had to interact with one another, it was possible to test whether or not individuals interacted with each other in a random pattern. The suggestion that high-ranking birds were involved in more encounters than lower-ranking ones is supported by the greater than expected number of encounters among high-ranking birds. In general, middle-ranking birds were involved in fewer encounters than expected; this fact is also supported by examination of individual deviates. Flock membership also affected frequency of interactions, with individuals being more likely to interact with flock members than members of other flocks. This result may indicate that it is most important for individuals to maintain dominance relationships with members of their own flocks. It is important to note that these comparisons (rank, flock membership, and sex) are not independent. An examination of individual deviates suggests that the larger than expected number of encounters among males and among flockmates may have been due to the large number of observed interactions among the three highest ranking birds (males from flock 1).

The results of this study may have been affected by the feeder being within the home range of flock 1. The six highest-ranking birds were from flock 1, although the other individuals from flock 1 were distributed throughout the dominance hierarchy. Birds from flock 1 did not appear to visit the feeder more than ones from the other flocks. A bird from flock 2 was the most frequent visitor to the feeder and some individuals from flock 3 (i.e., birds 8, 9, and 16) were frequent visitors. Members of different flocks often visited the feeder at the same time as demonstrated by the large number of aggressive encounters between different flock members.

ACKNOWLEDGMENTS

We thank L. Bunkfeldt-Popp, J. Ekman and A. Dhondt for their comments and J. Reinartz for his assistance with computer programming. Contribution No. 123 of the University of Wisconsin–Milwaukee Field Station.

LITERATURE CITED

BAKER, M. C., C. S. BELCHER, L. C. DEUTSCH, G. L. SHERMAN, AND D. B. THOMPSON. 1981. Foraging success in junco flocks and the effects of social hierarchy. Anim. Behav. 29: 137–142.

BRITTINGHAM, M. C. AND S. A. TEMPLE. 1988. Impacts of supplemental feeding on survival rates of Black-capped Chickadees. Ecology 69:581–589.

CRAIG, J. L., A. M. STEWART, AND J. L. BROWN. 1982. Subordinates must wait. Z. Tierpsychol. 60:275–280.

DE LAET, J. F. 1985. Dominance and anti-predator behaviour of the Great Tit, *Parus major*: a field study. Ibis 127:372–377.

DESROCHERS, A. 1989. Sex, dominance, and microhabitat use in wintering Black-capped Chickadees: a field experiment. Ecology 70:636–645.

———, S. J. HANNON, AND K. E. NORDIN. 1988. Winter survival and territory acquisition in a northern population of Black-capped Chickadees. Auk 105:727–736.

EKMAN, J. 1987. Exposure and time use in Willow Tit flocks: the cost of subordination. Anim. Behav. 35:445–452.

—— AND C. ASKENMO. 1984. Social rank and habitat use in Willow Tit groups. Anim. Behav. 32:508–514.

ENOKSSON, B. 1988. Age- and sex-related differences in dominance and foraging behavior of nuthatches *Sitta europaea*. Anim. Behav. 36:231–238.

GLASE, J. 1974. Ecology of social organization in the Black-capped Chickadee. Living Bird 12:235–267.

HEGNER, R. E. 1985. Dominance and anti-predator behaviour in Blue Tits (*Parus caeruleus*). Anim. Behav. 33:762–768.

HOGSTAD, O. 1987. It is expensive to be dominant. Auk 104:333–336.

———. 1988. Rank-related resource access in winter flocks of Willow Tit *Parus montanus*. Ornis Scand. 19:169–174.

———. 1989. Social organization and dominance behavior in some *Parus* species. Wilson Bull. 101:254–262.

HUNTINGFORD, F. AND A. TURNER. 1987. Animal conflict. Chapman and Hall, London, England.

LIMA, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the Black-capped Chickadee. Oecologia 66:60–67.

POPP, J. W., M. S. FICKEN, AND C. M. WEISE. 1990. How are agonistic encounters among Black-capped Chickadees resolved? Anim. Behav. 39:980–986.

POYSA, H. 1988. Feeding consequences of the dominance status in Great Tit *Parus major* groups. Ornis Fennica 65:69–75.

PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California.

ROHWER, S. AND P. W. EWALD. 1981. The cost of dominance and advantage of subordination in a badge-signalling system. Evolution 35:441–454.

RØSKAFT, E., T. JARVI, M. BAKKEN, C. BECH, AND R. E. REINERTSEN. 1986. The relationship between social status and resting metabolic rate in Great Tits (*Parus major*) and Pied Flycatchers (*Ficedula hypoleuca*). Anim. Behav. 34:838–842.

SCHNEIDER, K. J. 1984. Dominance, predation and optimal foraging in White-throated Sparrow flocks. Ecology 65:1820–1827.

SOKAL, R. R. AND F. J. ROHLF. 1981. Biometry, 2nd ed. Freeman, San Francisco, California.

WAITE, T. A. 1987. Vigilance in the White-breasted Nuthatch: effects of dominance and sociality. Auk 104:429–434.

WEISE, C. M. 1979. Sex identification in Black-capped Chickadees. Univ. of Wisconsin-Milwaukee Field Station Bull. 12:16–19.

——— AND J. R. MEYER. 1979. Juvenile dispersal and development of site-fidelity in the Black-capped Chickadee. Auk 96:40–55.

NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANT AWARDS 1990

The North American Bluebird Society is pleased to announce the presentation of the seventh annual research grant awards. The 1990 recipients are as follows:

BLUEBIRD GRANTS

DR. JANIS L. DICKINSON, Hastings Natural History Reservation, Carmel Valley, California. Topic: Use of DNA fingerprinting to determine paternity in Western Bluebird nests.

KEVIN L. BERNER, State University of New York, College of Agriculture and Technology, Cobleskill, New York. Topic: Field tests of acceptance of Eastern Bluebirds of nest boxes which deter raccoon predation.

GENERAL GRANTS

DR. MICHAEL J. DEJONG, Department of Biology, College of St. Thomas, St. Paul, Minnesota. Topic: Indirect effects of the larvicide *Bacillus thuringiensis* on Tree Swallow breeding success.

CHARLOTTE C. CORKRAN, Northwest Ecological Research Institute, Portland, Oregon. Topic: Reproductive success of Western and Mountain Bluebirds in grasshopper control areas, and potential for using bluebirds to reduce grasshopper densities.

STUDENT GRANTS

SUSAN MEEK, Biology Department, Queen's University, Kingston, Canada. Topic: Parental investment and the maintenance of monogamy in Eastern Bluebirds.

JONATHAN H. PLISSNER, Department of Biological Sciences, Clemson, University, Clemson, South Carolina. Topic: Does social dominance drive natal dispersal in Eastern Bluebirds?

The North American Bluebird Society annually provides research grants in aid for ornithological research directed towards cavity nesting species of North America with an emphasis on the genus *Sialia.* Information and application materials are available from Kevin Berner, Research Committee Chairman, College of Agriculture and Technology, State University of New York, Cobleskill, New York 12043.