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THE BODY RUFFLING DISPLAY OF THE BLACK-CAPPED CHICKADEE

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ABSTRACT.—Body ruffling displays of Black-capped Chickadees (*Parus atricapillus*) consist of extreme ruffling of the breast and back feathers and often are associated with wing extension and spread primaries. Body ruffling was observed throughout the non-breeding season but was more frequent in the fall. Birds of all ages and sexes exhibited the display, but juvenile males did so most frequently. Body ruffling was directed toward individuals of any age or sex and to familiar as well as to new birds in the area. Contrary to our prediction, the display was given less frequently, rather than more frequently, toward the eventual mate of the displayer. The seasonal frequency of the display paralleled the frequency of arrival of new birds at the feeders rather than the frequency of all aggressive behavior. The display appears to function in maintaining individual distance and gaining access to food, and it is not involved in pair formation as has been suggested for other parids. *Received 21 Aug. 1990, accepted 7 March 1991.*

A key task in examining animal interactions is assessing the functions of displays (Tinbergen 1963). Responses to the displayer can reveal function in some cases, while in others the function is not immediately obvious. A type of display reported in many parids consists of extreme ruffling of the breast and back feathers, accompanied sometimes by partial wing extension (Fig. 1). The display has been ascribed a pairbonding or courtship function in the Black-capped Chickadee (*Parus atricapillus*) (Allen 1929, Ficken et al. 1985), Great Tit (*P. major*) (Hinde 1952), Willow Tit (*P. montanus*), and Marsh Tit (*P. palustris*) (Fitter 1973). In the Carolina Chickadee (*P. carolinensis*), a body ruffling posture was observed in what were apparently agonistic interactions between two or more birds, but the posture was not studied in detail (Smith 1972). Body ruffling has also been noted in autumn in Boreal Chickadees (*P. hudsonicus*) and Mountain Chickadees (*P. gambeli*) (Ficken, pers. obs.). Thus, the display is widespread in the genus but has not been analyzed in detail in any species.

We analyzed interactions involving this display in an attempt to determine its function. Two hypotheses were tested: (1) body ruffling is involved in pair formation in juveniles (i.e., first-year birds) and/or adults, and (2) it is associated with aggressive behavior among flock members,

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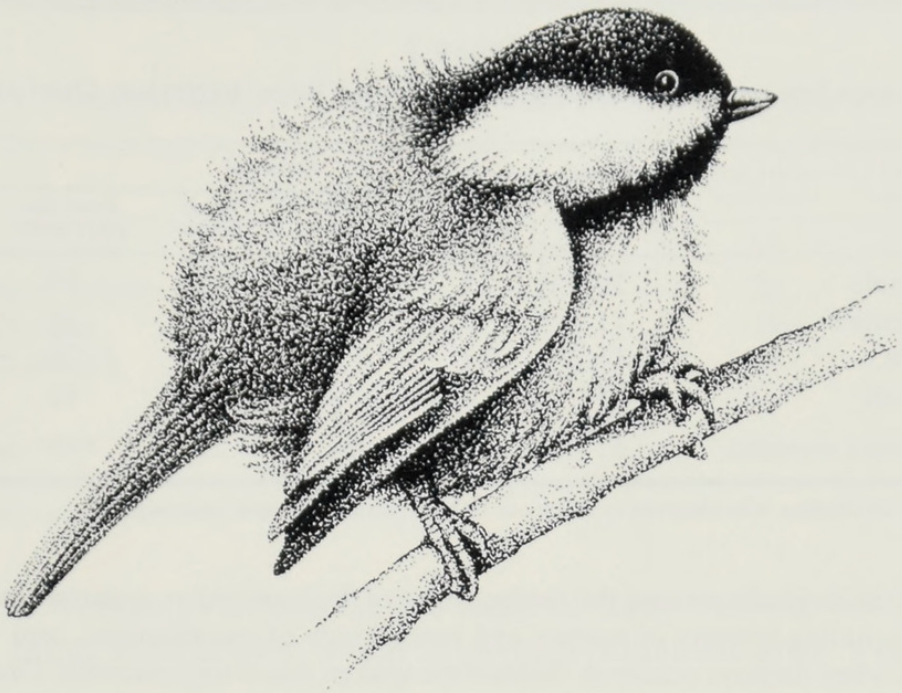


FIG. 1. Black-capped Chickadee exhibiting the body ruffling display.

especially as new birds become integrated into the flock. By studying the occurrence of the behavior for a full year, we were able to obtain data on seasonal patterns as well as on the context of usage of the display. Chickadees live in flocks of both sexes and mixed ages during the non-breeding season (Odum 1942, Glase 1973, Weise and Meyer 1979) and as monogamous pairs on territories during the breeding season (late April–July in Wisconsin).

METHODS

Since 1967, most chickadees at the Univ. of Wisconsin–Milwaukee Field Station, Ozaukee County, Wisconsin, have been color-banded for individual recognition in conjunction with studies of population ecology, vocalizations, and social behavior (e.g., Weise and Meyer 1979, Ficken et al. 1981). The birds we studied had winter flock ranges and breeding territories in a 45-ha tract of maple-beech upland forest and adjoining small patches of wetland deciduous forest. Adult chickadees were color banded by Weise in the winter and spring of 1987. Post-dispersal juveniles were captured either in special mist nets in July and early August 1987, or in the feeder traps mentioned below. Most of the observations were made at three feeders located along one edge of the forest and provisioned with waxworms (*Galleria mellonella* larvae), water and sunflower seeds (July–October), or sunflower seeds and suet (November–April). The use of three feeders enhanced observer discrimination of flocks and movements. Additional observations of territorial and courtship behavior were made in the woods at the time of territory establishment (March–April) and nesting (May–July).

The primary observer (Piaskowski) watched birds at the feeders or in the near vicinity three times weekly, mainly in the mornings. On each day, there were two sessions at each feeder at least one hour apart. In addition to description of the ruffling display, the following

TABLE 1

AGE AND SEX OF DISPLAYER AND RECIPIENT OF BODY RUFFLING DISPLAYS

	Recipient					
	Juvenile male	Juvenile female	Adult male	Adult female	Total displays given	Total bird-days
Juvenile male	30	22	15	18	85	1095
Juvenile female	11	6	4	7	28	860
Adult male	11	5	1	3	20	603
Adult female	5	0	4	1	10	653
Total displays received	57	33	24	29	143[a]	3211

[a] An additional 58 displays were observed in which one or both participants were unidentified.

were recorded: individuals visiting the feeder, times of flock arrival or departure, aggressive interactions including identity of winner and loser, kinds of vocalizations, and distances between birds when displays occurred. Notes were spoken into a tape recorder. One session, on 12 September 1987, was videotaped. Total time at the feeders for the primary observer was 220 h.

This was a blind study, i.e., the primary observer did not know the age, sex, or history of any of the birds until the study ended. New, unbanded birds were marked, aged, and sexed by Weise. Age was determined by rectrix shape (Laaksonen and Lehikoinen 1976) or skull ossification. Sex was provisionally determined by wing chord (70% of the birds) and later verified by sex-specific behavior during the breeding season (Weise 1979).

Statistical tests included the G (log likelihood ratio) test and Spearman rank correlation, r_s (Sokal and Rohlf 1981). To standardize for encounter possibilities, we used "bird-days." Each day that a particular individual was observed at a feeder was defined as one bird-day for that individual. By using dates and feeder locations, we could then estimate the number of opportunities for interaction between that bird and any other. If all displays were distributed evenly, a bird would be expected to display in proportion to the number of days it spent at the feeders. For Tables 1 and 2, the expected frequencies were calculated as follows: Table 1—expected displays = (total displays for all ages and sexes) × (number of bird-days for specific age and sex category/total bird-days for all categories). Table 2—expected displays for bird A = (bird-days for A when its mate was present/bird-days A spent with mate and non-mates) × total displays for A.

Because some individuals were observed to display more than once, our counts of displays were not truly independent. To ensure that our conclusions regarding more frequent use of the display by a particular age and sex class were not due to one or a few individuals displaying a large number of times, we prepared a standardized frequency distribution of displays for all of the 92 birds in the study. This was calculated as follows. Expected displays for each individual = total number of displays for all individuals/total bird-days for all individuals × total bird days for the individual. To obtain the frequency distribution seen in Fig. 2, we standardized for the amount of observation time on each individual as follows: (observed displays for individual − expected displays for individual)/(bird-days for individual).

RESULTS

In 64% of the 201 displays observed, wing extension with primaries spread also occurred. The display, lasting 1–2 sec, was observed on feeder

TABLE 2
BODY RUFFLING DISPLAYS DIRECTED TOWARD EVENTUAL MATE AND OTHERS[a]

	Displays to mate	Exposure to mate (bird-days)	Displays to non-mate	Exposure to non-mates (bird-days)
Juvenile male	4	368	63	3018
Juvenile female	0	260	26	2036
Adult male	0	222	19	2050
Adult female	1	104	6	933
Total	5	954	114	8037

[a] Includes only those birds whose 1988 mate is known.

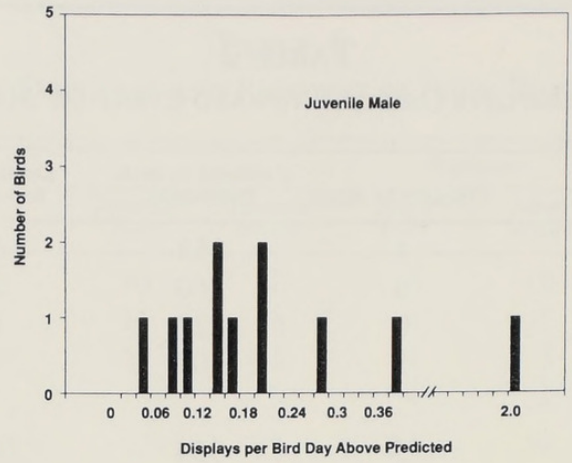
perches as well as in trees near the feeders. Body ruffling was given only in close range encounters, when inter-individual distance was 0.5 m or less.

During the time when the feeders were in use, 92 individual birds were observed. The ruffling display was seen in 15 (47%) of 32 juvenile males, nine (43%) of 21 juvenile females, nine (50%) of 18 adult males, and six (29%) of 21 adult females for a total of 39 (42% of all birds). Many birds that attended the feeders frequently were never seen to give the display, although they were involved in agonistic interactions of other types. We could not discern any behavioral or physical differences between displayers and non-displayers.

Table 1 lists the age and sex of the displayers and recipients of the encounters in which both individuals were identified by color code (N = 143). A large proportion of the displays were given by juvenile males ($G = 38.0$, df = 1, $P < 0.01$). Conversely, there were no age and sex differences among recipients of the display ($G = 2.27$, df = 3, $P > 0.05$). As some displaying individuals gave the display much more frequently than others (range 1–26, mean ± SE = 4.8 ± 0.84), we needed assurance that our statistical test was not unduly influenced by a few individuals. We prepared a standardized frequency distribution of displays for all birds; this showed that the higher display rate of juvenile males was not due to just a few individuals. As shown in Fig. 2, many juvenile males displayed at much higher frequencies than predicted by their bird-days at feeders, while relatively few of the other age-sex classes did so.

Although usually directed toward conspecifics, chickadees occasionally gave the display toward White-breasted Nuthatches (*Sitta carolinensis*) (one observation for each age and sex category of displayer; not included in Table 1).

The frequency of body ruffling displays was analyzed by month and observation hours and compared with the frequency of all aggressive


Juvenile Male
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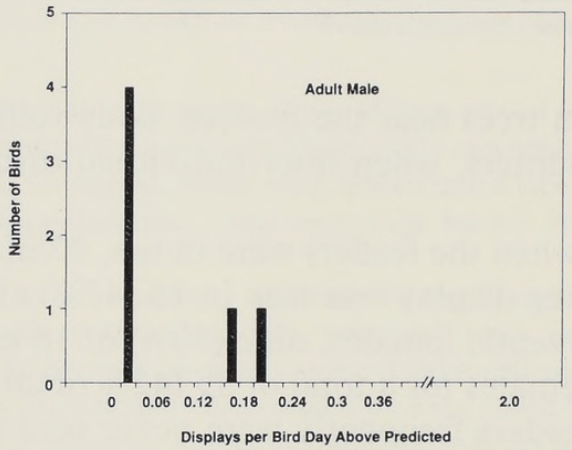
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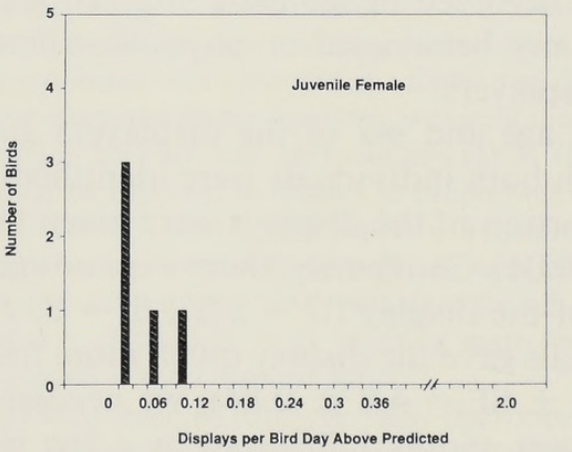
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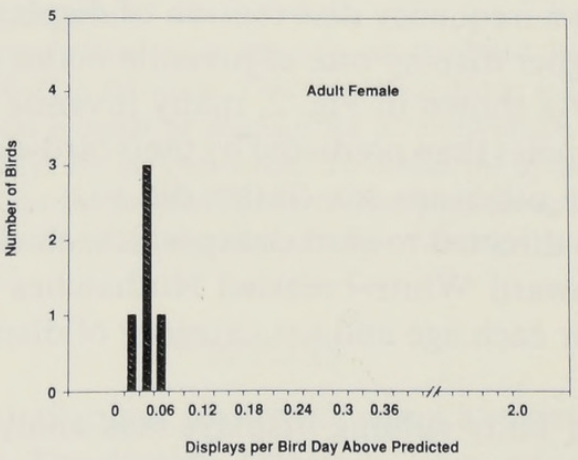
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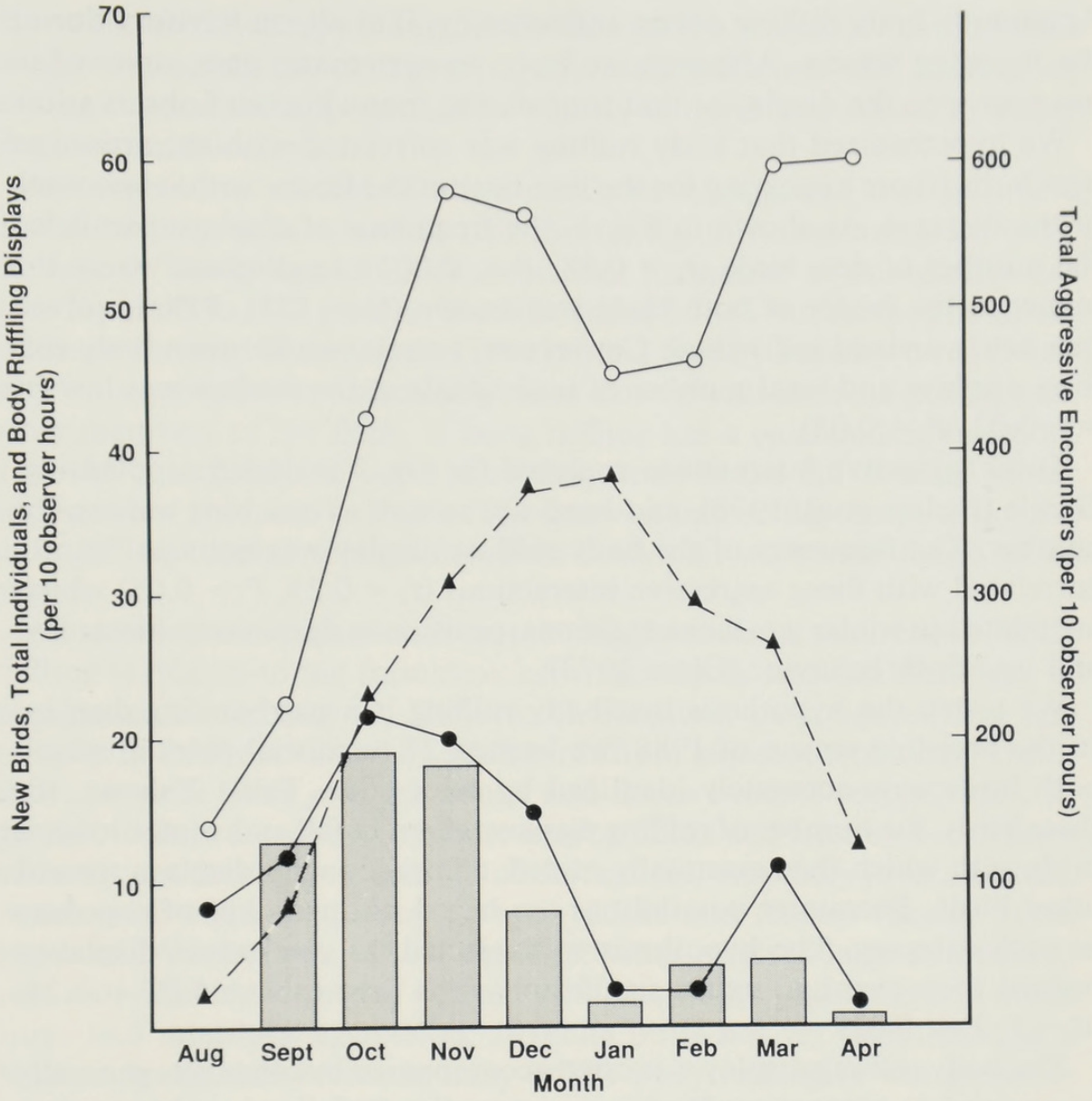

FIG. 3. Relationship of body ruffling displays to new birds, total individuals, and total aggressive encounters. Bars represent body ruffling displays per 10 observer-h. Closed circles represent new birds arriving at the feeders during the month. Open circles represent total individuals using feeders. Dashed line represents aggressive encounters per 10 observer-h.

interactions, the number of new arrivals, and the total number of individuals present at the feeders (Fig. 3). The display was not seen in July or August (in 25 h of observation) but occurred throughout the nonbreeding season, more commonly in the fall (Oct–Dec) than in all other months combined (Aug, Sept, Jan–Apr) ($G = 48.4$, df = 1, $P < 0.001$).

←

FIG. 2. Standardized frequency distributions showing occurrence of ruffling display in relation to bird-days of feeder use. The graph shows only those birds that displayed more frequently than predicted.

Apparently body ruffling occurs infrequently, if at all, on territory during the breeding season. Although we have no systematic data, none of us has ever seen the display at that time during many hours of observation.

We hypothesized that body ruffling was correlated with the arrival of new birds (those appearing for the first time at the feeder within one week of the display). As shown in Fig. 3, the frequency of displays paralleled the number of new birds ($r_s = 0.88$, $P < 0.005$). In displays where the tenure at the feeder of both birds was known (N = 175), 87% involved one newly arrived individual. Conversely, correlation between body ruffling displays and total number of individuals at the feeders was low ($r_s = -0.02$, $P > 0.05$).

Total aggressive interactions analyzed for Fig. 3 included supplanting, Gargle (Ficken et al. 1978), and head-up, as well as one bird waiting for another. The frequency of the body ruffling display was not significantly correlated with these aggressive interactions ($r_s = 0.25$, $P > 0.05$) which are related to winter weather conditions, position in dominance hierarchy, and interflock behavior (Glase 1973).

We tested the hypothesis that body ruffling is a pairbonding display. In the breeding season of 1988, we located 27 territorial pairs in which both birds were accurately identified by color code. Table 2 shows, for these birds, the number of ruffling displays given in fall and winter toward birds with which they eventually mated, compared with displays toward other birds. Encounter possibilities are based on bird-days of exposure to each category. The hypothesis was rejected, as chickadees displayed toward their eventual mates significantly less than expected ($G = 7.24$, df = 1, $P < 0.01$).

The body ruffling display was often accompanied by other acts generally recognized as aggressive. During or immediately following the display, one bird often supplanted another by lunging at it, and in some instances chasing it. In the 201 displays observed, further aggression by the displayer occurred in 47 (23%) and by the recipient in 18 cases (9%). In some cases, a bird approaching another within 0.5 m resulted in one displaying while the other moved away. The recipient of the ruffling display reciprocated with the same display in 24 (12%) of the interactions. The bird giving the ruffling display at a feeder was most likely to win the encounter and win access to the food source. Where the outcome was a distinct win or loss (N = 173), the displayer won access in 102 encounters and the recipient in 71 ($G = 5.58$, df = 1, $P < 0.05$).

DISCUSSION

The body ruffling display seems to exhibit a "typical intensity" (Morris 1957) in that variations in degree of ruffling of feathers are slight. It is

also sometimes a composite signal (Wilson 1975), with other components being wing extension or, more rarely, head lowering, tail fanning, or leaning toward the opponent. The display is rapid and suited to short-range communication.

Although some studies of other parids have suggested that this, or a similar display, is involved in pair formation, this does not seem to be the case in Black-capped Chickadees. Pair formation in this species has been reported to take place in the fall (Smith 1984), but there is no direct evidence for this. Ficken et al. (1981) found that by January birds found later to be paired were associating more closely with each other than with other members of the flock. If body ruffling has a pairbonding function, it would be expected to occur most frequently in the fall or early winter and between prospective mates. The first was indeed the case, but not the second. The display seldom involved birds that were later found to be mated.

An alternative explanation is that the highly seasonal occurence of body ruffling is related to the formation of winter flocks and establishment of dominance hierarchies (S. Haftorn, O. Hogstad, pers. comm.). In late summer, a feeder is visited by adult birds from adjacent territories. Gradually, juvenile birds join the adults and flocks become recognizable. In the fall, feeders are visited by these nearby flocks and later by flocks from more distant areas. Also, individual chickadees, especially juvenile birds, switch with some frequency between flocks and feeders (Smith 1984, Smith and VanBuskirk 1988). These activities result in large numbers of new individuals coming in contact with each other, and there is much intra- and interflock aggression. Juvenile birds not yet established in a flock or dominance hierarchy may utilize body ruffling to win access to food. As winter approaches, attendance at feeders stabilizes, dominance hierarchies are firmly established, birds switch less frequently, and the incidence of body ruffling decreases. In contrast, the frequency of other aggressive interactions continues to increase and peaks in mid-winter when competition for access to food is most intense.

Chickadees use a variety of agonistic behavior patterns, some of which frequently lead to the immediate departure of the opponent. In social species, however, some displays do not necessarily lead to the retreat of the opponent but may increase the actor's ability to have first access to resources (Senar 1990). Body ruffling seems to belong to this category of agonistic displays. The posture is used by juvenile males in the fall as flocks and dominance hierarchies are becoming established. The immediate function is to maintain individual distance or to win access to a food source. Perhaps by increasing apparent size, it helps juveniles compete more effectively for dominance status.

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