BREEDING BIOLOGY OF THE BOREAL CHICKADEE

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The reproductive biology of some species of North American chickadees (Paridae) is well-known (Odum 1941a, 1941b; Bent 1946; Brewer 1961); however there have been no detailed studies of the breeding behavior of the Boreal Chickadee (*Parus hudsonicus*), a species of the northern coniferous forests. This paper presents both quantitative and qualitative information about the breeding behavior of the Boreal Chickadee, from the stage of early pair formation to the dispersal of the young.

STUDY AREA AND METHODS

Field observations were made in Algonquin Provincial Park, Nipissing District, Ontario, from April through July in 1971 and 1972. The major tree species of the study area are white spruce (*Picea glauca*), black spruce (*P. mariana*), and balsam fir (*Abies balsamea*), but there is some interspersion of trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*).

Approximately 1500 hours were spent observing birds or nests. Data were recorded in a notebook or taped. Hatching dates were obtained by inspecting the nest cavity; when this was impossible, these were estimated within 1 or 2 days on the basis of the behavior of the male, which changes markedly at the hatching of the young. In all cases, either fledging was observed, or young known to have been in the nest the previous day were seen in the nearby trees a day later. Some birds were individually recognizable by plumage characteristics, but many were not; most of the latter were caught and individually marked with colored leg bands. I marked 8 adult and 13 juvenile chickadees.

RESULTS AND DISCUSSION

Flock break-up, pair formation, and territoriality.—Pair bonds in the Boreal Chickadee develop gradually as winter flocks break up. With the onset of warmer weather aggressive activity within the flock increases, with chases and supplanting attacks occurring frequently. Chases fall into 3 categories. In the most common type (A), the sex of the participants cannot be determined by their behavior. Birds of either sex fly from the vicinity of the aggressor when attacked. As the season advances a second type of chase (B) becomes evident. Some birds, presumably females nearing breeding condition, merely move 2 to 3 m when attacked by a male. This behavior is similar to that observed by Hinde (1952) in the Great Tit (*Parus major*) and by Brewer (1961) in the Carolina Chickadee (*P. carolinensis*).

Although females usually withdraw only a short distance when attacked, a third type of chase (C) was observed on 5 occasions. These chases always began near the top of a tree; from there the pair spiraled downward, flying

rapidly around the tree with the male 15 to 20 cm behind the female. On 4 occasions the male gave one or several musical calls (McLaren, in prep.) while chasing, and in all 5 instances the chase ended with the female giving solicitation calls. Although I could never see the birds at the end of any of these chases, I do not believe copulation occurred. My reasons for this interpretation are that the birds reappeared almost immediately and I never heard the calls usually given by a mounting male. Whether such chases do actually play a part in pair formation is difficult to say. Two chases, which took place within an hour of each other, involved birds apparently already paired, as they had been together on the territory for more than a week. The other 3 chases were in flock situations.

The most striking characteristic of type C chases was the constancy of the distance (about 20 cm) between the birds in flight over a distance of 3 to 4 m. By comparison, in type A chases, which often proceeded downward through one tree and were frequently accompanied by musical calls from the male, the 2 birds were occasionally as close as 15 to 20 cm; usually they were farther apart, and typical chases never ended with solicitation.

Hole inspection may play some part in pair formation in this species. On 20 April 1972, a banded male, in a flock of 4 birds, flew to the stub of a broken branch in a white birch and was followed by a female, his mate of the previous year. Thereupon the male flew away, whereas the female made 4 excavating trips, carrying wood chips out of the cavity each time. She then rejoined the remaining birds, but the male made another flight to the prospective nest hole before returning to the flock. After 10 min this flock flew across a river and was not further observed intact. Later in the day, the same male and female were found together in their territory of the previous year. Brewer (1961) suggests that hole inspection in the Carolina Chickadee, if involved in pair formation at all, is of importance only after the pair has been associated for a time. There is considerable evidence that *Parus* species mate for life (Hinde 1952), and this seems likely the case in the Boreal Chickadee. My only color-banded pair in 1971 was again mated in 1972.

Once a pair separates from the flock, a pre-nesting period elapses before nesting behavior begins; this period is of variable duration, depending upon whether the pair was formed in late April or not until early May. The paired birds forage close together, usually on the ground where melting snow has revealed material dropped from the trees, and occasionally in trees—most frequently in the upper third.

After the members of a pair have been associated for 2 to 3 weeks and have established a territory, the female begins to beg food from the male. Begging behavior is characterized by specific calls and often by wing fluttering. Wing fluttering consists of vertical movements of the wings as they are

held slightly away from the body. Begging by the female in the presence of the male continues until hatching of the eggs, a period of 4 to 5 weeks. Begging in this species may be advantageous to the female during incubation in terms of her energy expenditure. Krebs (1970) has shown that in the Blue Tit (*P. caeruleus*), a female receives 2.5 times as much food when fed by the male as when foraging for herself.

Once a pair has been formed, it may either immediately establish a territory or wander for a short time before settling in an area. The use of vocalizations to advertise ownership of a territory in this species is debatable, but pairs defend their territories by use of vocalizations, as well as by chasing and supplanting attacks. Chases vary widely from rapid aerial twisting and turning, to slower flights in which rivals remain 3 m or more apart. Physical contact was not observed in territorial conflicts. Chasing and calling continue up to 15 min, after which, as in lower intensity encounters, one or both pairs move away. After retreat by one pair, the remaining pair flies from branch to branch and vocalizes at an accelerated rate for 5 to 10 min. These birds then return to their quiet foraging activities. The latest date that a territory was seen to be defended was 4 July 1971, by a male whose young had fledged 25 June 1971. This prolonged encounter was not intense, and chases were not close or rapid.

Territories in the study area were larger than 5 ha. As territories are seemingly not advertised vocally, boundaries are undoubtedly frequently trespassed. Unless the resident male actually encounters the interloper, nothing comes of the intrusion. In 2 instances, I followed an unbanded pair for more than 15 min through the territory of another pair without their being detected and attacked. Undetected intrusions may also occur in other species that have large territories and do not regularly patrol them, such as in the Gray Jay (*Perisoreus canadensis*) (D. Strickland, pers. comm.).

Nest site selection, hole excavation, and nest construction.—Hinde (1952) indicates that it is advantageous for a species to be able to occupy suboptimal as well as optimal nest sites, so that reproduction occurs even though nest sites are not ideal. Perhaps this helps explain why Boreal Chickadees explore many holes of varying suitability that they find early in the season. At first, both sexes merely inspect holes, but within a few days the females begin to make excavation trips. Males do not at first show as much interest in excavation as females and often wander away giving *chickadee* calls. The female either follows him away or remains at the hole, also giving *chickadee* calls. Within a few days both sexes excavate with equal intensity. Unlike Black-capped Chickadees (*P. atricapillus*) (Butts 1931) and Carolina Chickadees (Tanner 1952), Boreal Chickadees apparently do not tend to nest in the same tree in succeeding years, as none of the 6 nest sites studied in 1971 were

occupied in 1972; nor were 2 other sites found in 1961 and 1969 reused (H. Scott, pers. comm.).

Softness of the heartwood rather than a preference for a specific species of tree seems to determine nest site choice. Of 22 nest sites used and/or excavated, all were in trees or stumps in which the heartwood was soft from rotting but the outer layers and bark were still hard. The length of time required for completion of the cavity apparently depends on how soft the wood has become. In some cases a bird enters a hole and immediately emerges carrying chips or pieces of rotted material (up to 3 cm long), repeating the activity 4 or 5 times in succession. When the wood is harder, a bird may spend 40 to 50 sec inside the hole hammering with its bill before carrying chips out. One pair dug a cylindrical hole 20 cm deep and 5 cm in diameter in a day, whereas another pair worked for 10 days in harder wood to complete a cavity 15 cm deep. Interestingly, even after a hole has been partially excavated as a nest, the pair may not nest there. Once, a hole was excavated for 5 days and then deserted.

In most North American chickadee species, the entrance hole is on the side of the nest stub (Odum 1941b, Brewer 1961). However, Gabrielson and Lincoln (1959) noted that the Boreal Chickadee seems to choose stumps with the hole facing upwards. I found 9 of the 22 more or less permanently selected cavities with this orientation. This differs significantly (χ^2, $P < 0.05$) from observations by Odum (1941b) of Black-capped Chickadee nests where only 1 of 18 had the entrance in this position.

In my study one bird excavated appreciably more than the other, and this was the female in all cases where the sexes were distinguishable (5 of 11 cases). The number of times different males entered their holes ranged from about 2 to 25% of the trips observed. Known females never departed the hole without carrying excavated material, whereas males made apparent "inspection trips" or merely hammered without bringing material out.

Despite the apparent abundance of holes in Algonquin Park, there is some interspecific competition for them. Red-breasted Nuthatches (*Sitta canadensis*) twice displaced excavating Boreal Chickadees, once appropriating a hole for their own use. Black-capped and Boreal chickadees, which were not found to be interspecifically territorial, did not compete for nest holes. In one case, Black-capped Chickadees nested successfully in a hole excavated, but then abandoned, by Boreal Chickadees.

Although neither all European *Parus* nor all North American titmice regularly excavate holes (Hinde 1952), all North American chickadees do (Bent 1946). When Boreal Chickadees select a site lacking a hole, the initial excavation behavior closely resembles that described by Brewer (1961) for Black-capped and Carolina chickadees in this situation. The bird hammers

some chips loose with its bill and drops them to the ground with shakes of the head. Shortly, the Boreal Chickadee begins carrying chips some distance from the nest site; these it usually inserts among the needles of a conifer with a few pushes of the bill, rather than simply dropping them as in the other 2 species. Other trees may also be used for deposition of chips such as leafless yellow birch (*Betula alleghanensis*) and northern white cedar (*Thuja occidentalis*); from these sites the chips immediately fall. I suggest that arboreal deposition of chips is stereotyped behavior in *P. hudsonicus*.

Upon completion of the cavity, Boreal Chickadees may either begin the nest immediately (4 of 6 cases) or allow several days to elapse before starting it. In 1972, perhaps owing to the lateness of the spring, one bird excavated and built a nest concurrently, entering the cavity with nesting material and a minute or 2 later departing with chips. The female alone builds the nest. As in other *Parus* species (Hinde 1952), the cavity forms the structural part of the nest, with the soft material merely serving as a mat for the eggs and young. Nesting material, consisting of plant down, animal hair, strands of fruticose lichen, and similar material, does not seem to be brought in any particular order. Egg-laying generally begins after 2 or 3 days of nest-building, but small quantities of nesting material may be brought as late as the first few days of incubation.

Both excavation and nest-building show rhythmic characteristics. Both birds excavate, or the female builds, for a period usually not exceeding 45 min; then both birds depart. While the female builds, the male remains nearby, where he calls occasionally, forages, or watches the female. Absence from the cavity rarely exceeds 1 hour except during the period after the cavity is complete and before the female has begun to build the nest. In this period the pair may visit the nest site only 2 or 3 times a day and excavate briefly. When the female returns to the nest after a protracted absence, she brings nesting material from wherever she has been in the territory; subsequent material is gathered within about 10 m of the nest.

Copulation and egg-laying.—Sixteen copulations were observed totally or in part. Copulation may be initiated by either the male (4 of 12) or the female (8 of 12). Typically, the sequence begins with solicitation calls and wing-quivering by one of the pair. (Wing-quivering is similar to wing-fluttering but the movements are more rapid and of smaller amplitude.) If the second bird is not immediately receptive, calling may continue as long as 40 sec. If the mate is ready to copulate, it responds with wing-quivering. The response of females also includes solicitation calls; these were not heard from responding males. The male mounts the female for no more than 2 sec, during which time he may give 1 of 3 different calls (14 of 16 cases) or not call. After the male dismounts, one or both birds may continue to give solicita-

tion calls and wing-quiver for several seconds before returning to normal activities.

In European *Parus* species, fighting in a pair may occur immediately before or after coition, but aggression does not seem to be an important part of the copulatory sequence itself (Hinde 1952, Stokes 1960). Among North American species, Boreal, Carolina, Black-capped, and Mountain (*P. gambeli*) chickadees use calls associated with aggression during copulation (pers. obs., Brewer 1961, Dixon et al. 1970). The Black-capped Chickadee apparently calls only prior to mounting, whereas Boreal and Mountain chickadees both give aggressive calls while mounted.

In both years I observed coition in several different pairs subsequent to their first nesting. Apparently no birds raised second broods, and only in 1971 did any pairs excavate cavities or build nests after their first nesting.

Egg-laying always began before the nest was complete. In the 2 cases in which it could be determined, an egg was laid daily before 06:00. Incubation began on the day of laying the ultimate or penultimate egg. Prior to the beginning of incubation, the eggs were covered by nesting material when the female was away from the nest ($N = 4$); once incubation had begun they were left exposed when she left.

Incubation.—The female alone incubates, and the male enters the nest only to feed her. Incubation behavior, as in many passerines, is marked by attentive periods (when the female sits on the eggs) and inattentive periods (when she forages, either alone or with the male). In 193.2 hr of observation the mean attentive and inattentive periods of 8 females were respectively: 32.9 min (range: 3 to 92) and 8.0 min (range: 1 to 41). The mates of these females fed them at the mean rate of 0.65 times per attentive hour (range 0.1 to 1.54, 120.9 hr of observation).

An attentive period may end either by the female departing alone or by the arrival of the male. When the male arrives at the nest, he perches on a nearby branch and calls softly. The female then comes to the nest entrance or she flies to a branch near the nest; in both cases she is fed by the male. When the female occasionally does not come up to the entrance when the male calls, he enters and feeds her; after that she may or may not follow h'm out of the cavity. In the first day or 2 of incubation, a male arriving at the nest when the female is absent enters and quickly leaves the hole several times. He may then leave, but usually he remains and feeds the female when she returns. The female then goes directly to the nest hole. After the first few days of incubation, the members of the pair appear to become synchronized, and the male arrives only when the female is present. One male came to the nest while the female was absent 4 times in the first 4 days of incuba-

TABLE 1

LENGTHS OF ATTENTIVE PERIODS BY INCUBATING BOREAL CHICKADEES

	Length of period and sample size					
	When called by male			When not called by male		
Pair	Mean (min)	S.D. (min)	N	Mean (min)	S.D. (min)	N
71-1	28.8	13.0	4	38.9	9.0	22
71-2	33.4	24.0	8	31.9	9.3	9
71-3	15.4	9.5	10	28.5	12.0	10
71-4	27.8	10.6	23	33.0	0	1
72-1	28.6	15.2	9	34.2	15.6	18
72-2	22.7	5.9	4	36.3	16.7	27
72-3	28.6	12.9	5	44.1	13.1	24
72-4	24.4	7.3	4	33.8	13.3	25

tion (9 hr of observation), but never again in the female's absence (19 hr of observation).

If the female leaves the nest when the male is not present, she flies across the territory giving loud *chickadee* calls. If she encounters the male, she stops calling, begs for food and is fed by the male. If the female does not encounter the male, she forages on her own. A female leaving with the male continually begs throughout the inattentive period. Whether she is with the male or not, she returns to incubate suddenly, flying swiftly and directly to the nest.

Odum (1941b) suggested that the male Black-capped Chickadee influenced the length of incubation bouts, because attentive periods of the female were shorter when she emerged in response to his calls than when she emerged spontaneously. Table 1 shows a similar and significant relationship in 7 of 8 Boreal Chickadees (Wilcoxon matched-pairs signed-ranks test, $P < 0.01$, 1-tailed). As I studied attentive periods at all times of day in each third of the incubation period, if there was variability in period length as a function of time of day or phase of the incubation period, it would be unlikely to bias the data on attentive period length.

Weather seemingly affected the length of attentive periods to a certain extent. In very cold weather attentive periods tended to be longer, but this was by no means absolute. For example, on 10 June 1972 the high temperature was 5° C. Two attentive periods of one female were shorter than her mean incubation period, and 2 were longer. However, all 5 inattentive periods the same day were shorter than average.

In my study the incubation period ranged from 11 to 16 days, with most eggs hatching at 15 days. This is slightly longer than the incubation period of other North American chickadees. The incubation period in the Black-capped Chickadee is 11 to 13 days (Forbush 1929), in the Carolina Chickadee 11 (Bent 1946) or 12 (Tanner 1952) days, and in the Mountain Chickadee 14 days (Wheelock 1904). Eggs in a clutch frequently did not all hatch on the same day, and in one case 3 days were required for complete hatching.

As far as I could determine, the female ate the egg shell. Twice there were only eggs at one inattentive period and a hatched young at the next inattentive period. In neither instance was the egg shell observed in the nest after the female left, nor was it carried out by her.

Nestling stage.—In the first few days after hatching of the young, the female continues to alternate attentive and inattentive periods; she sometimes, but not always, brings food back to the young when she returns from an inattentive period. Once the young have hatched, the behavior of the male changes markedly in that he brings food far more frequently. In addition, the female exits from the nest far more often when he calls.

As Brewer (1961) observed in the Carolina Chickadee, in Boreal Chickadees brooding attentiveness is about the same as incubation attentiveness in the first 3 days after hatching. After this, brooding declines rapidly and is discontinued by about the 11th day (the day of cessation varies individually). In some pairs, the female still enters the hole and remains 3 or 4 min at a time even on the day before fledging; other females remain for only a few seconds to feed the young from the 11th day.

A behavior pattern apparently not reported in other parids is "nest watching" by the female after cessation of brooding. The female sits on a branch 1 to 5 m from the nest, where she preens, looks around, or rests, while the male does most of the feeding of the nestlings. This behavior was especially noticeable at 3 of 9 nests, and at another nest I observed it on 4 occasions in the 5 days before fledging. In the last case, the bird spent only a few minutes at a time watching, rather than periods of 15 to 20 min spent by the other 3. Potential predators were not chased by watching females, although they were scolded.

The amount of food brought to the young increases as the nestling period progresses. Table 2 gives the rate of feeding, as well as the rate of fecal sac removal, at this time. At first the male does most of the feeding and may continue to do so through fledging; however, in the last 3 or 4 days before fledging, both adults may share equally in feeding.

When a male and female arrive at the nest together, both wing-flutter but usually do not call. Either may enter the nest first, and the other waits for the first to emerge before entering. When the male arrives alone, he often

TABLE 2

CARE OF NESTLINGS BY ADULTS

	Stage of nestling life and sample size					
	Days 1–5	Hours of observation	Days 6–10	Hours of observation	Days 11–18	Hours of observation
Total feedings per hour[1]	9.1	53	12.2	129	13.9	60
Feedings per hour per chick[1]	1.7	40	2.2	27	2.8	45
Percent of feedings by male	73.2	53	62.8	65	56.9	45
Fecal sacs removed per hour per chick[1]	0.03	40	0.24	27	0.34	45

[1] By both adults.

gives soft calls; on the other hand, the female rarely calls as she approaches the nest. If a bird flies directly into a nest already occupied by its mate, the former bird immediately comes out again and waits for the mate to emerge.

The modal length of the nestling period is 18 days. Again this is longer than 17 (Bent 1946) or 13 to 14 (Dixon 1961) days for the Carolina Chickadee or 16 days for the Black-capped Chickadee (Odum 1941b). The young cannot fly earlier than this, although by the 15th day they can flutter-walk (run along the ground and sometimes up tree trunks while flapping their wings) well enough to make their capture (by a human) difficult. At least 4 young (out of a brood of unknown size) that fledged on the 15th day survived to at least 10 days after fledging.

In 3 cases in which fledging was actually observed, it took place in the morning; these fledglings could fly at least 3 m on their first attempt. During fledging, both parents flew or hopped rapidly about the nest area, giving frequent soft calls. If there was a lag between the fledging of various of the young, the adults continued to feed those still in the nest. The earliest fledging took place 22 June 1971 while the latest was 3 July 1972. Once all the young had fledged the family departed the vicinity of the nest.

Dispersal of the young.—For the first 2 weeks after fledging, the family essentially stays within the boundaries of the nesting territory. During this time the young are fed with decreasing frequency by their parents. For the first few days the young do not move about much, spending most of their time sitting quietly and giving occasional begging calls. The volume and frequency of these calls increases as an adult approaches. In time the fledglings increasingly forage on their own, with a concomitant decrease in

begging. Within a week after fledging, the fledglings seemingly fly as well as adults. By 3 weeks after fledging the young have left the territory.

SUMMARY

The breeding biology of the Boreal Chickadee was studied in the summers of 1971 and 1972 in Algonquin Park, Nipissing District, Ontario.

Pair formation develops gradually, beginning while birds are still in the flock. Male-female chases (3 types) and hole-inspection may play a part in pair formation, but this is not certain. Begging behavior apparently does not play an important role in pair formation in this species, as it does not occur until after the pair has been associated for 2 to 3 weeks and has established a territory. Excavation of cavities may occur at several holes before a nest site is chosen. Although both sexes excavate, the female alone builds the nest, which consists of soft plant and animal material. The cavity forms the structural part of the nest. Copulation may be initiated by either sex, and the calls given by the male while mounted suggest an aggressive component to this activity. The female alone incubates and is fed largely by the male. She incubates for shorter attentive periods when called from the nest by the male than when terminating an attentive period spontaneously. Hatching occurs about the 15th day. Both parents feed the young, with the male feeding more at the beginning of the nestling period; both sexes feed more or less equally by fledging. Some females show a behavior not reported in other parids, i.e. "nest watching." The young fledge on about the 18th day of life and are fed with decreasing frequency for about 2 weeks. After this they are no longer found regularly in the nesting territory.

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NEW LIFE MEMBER

Eric G. Bolen has recently become a life member of the Wilson Ornithological Society. Dr. Bolen is presently assistant director of the Welder Wildlife Foundation, Sinton, Texas, and has just recently been named editor of the Wildlife Society Bulletin. Dr. Bolen is interested in waterfowl ecology, endangered species, and eagle-livestock predator-prey relationships as well as the general ecology of birds. He has published nearly 50 papers resulting from his research. In addition to his professional interests, Dr. Bolen collects antiques, especially decoys. He is married and has one son.