UTILIZATION OF THE BREEDING TERRITORY IN THE BLACK-CAPPED CHICKADEE

RAYMOND A. STEFANSKI

Breeding territorial behavior in birds is manifested in self-advertisement, localization of activity, increased conspicuousness, threatening postures, pursuit, or actual physical combat. These activities represent a considerable expenditure of energy by the males. The function and significance of this behavior has been inferred from many studies in the past 35 years (Hinde, 1956), but until recently (Stenger, 1958; Delius, 1965; Weeden, 1965) no attempts have been made to explain this phenomenon quantitatively from empirical data.

The fascination of Noble's (1939) definition of territory (*i.e.*, "any defended area") has conventionalized and limited thinking in this area of ornithology for the past several decades (Emlen, 1957:352). The adherence to this definition resulted in an intensive search for a single function for all types of territoriality. Recent reviews (Hinde, 1956; Kuroda, 1960) have indicated a growing awareness of the futility of seeking a single explanation for this complex social behavior.

The disagreement concerning the biological significance of territorial behavior stems partly from the lack of quantitative studies. This deficiency prompted Hinde (1956) to conclude that no real progress had been made in this area since Howard brought the concept of territoriality to the attention of ornithologists in 1920.

A study to determine quantitatively the differential utilization of space at successive stages of the nesting cycle (*i.e.*, prenesting, nest-building, egg-laying, incubation, nestling, and fledgling) and to compare this utilization to the degree of territorial defense exhibited by the owners at each stage could provide insight into the adaptive significance of territorial behavior. The Black-capped Chickadee, *Parus atricapillus*, was selected for such a study because it is easily observed and is relatively conspicuous in its behavior.

THE STUDY AREA

The study was conducted at Malibu–Guinavah Forest Camp (Cache National Forest), seven miles east of Logan, Cache County, Utah. The area, at 5000 feet elevation, is located on the flat bottom of Logan Canyon, with the Logan River cutting diagonally across the eastern section. The vegetation here is discontinuous deciduous woodland, which is characterized by a heavy growth of grasses in the open areas and a dense understory of wild rose (*Rosa woodsii*), blueberry elder (*Sambucus coerulea*), hawthorn (*Crataegus rivularis*), chokecherry (*Prunus virginiana*), and Sierra willow (*Salix wolfii*). The dominant trees on the area are box elder (*Acer negundo*), dusky willow (*Salix melanopsis*), and river birch (*Betula fontinalis*). Numerous alders (*Alnus tenuifolia*) can be found along the stream banks with occasional narrow-leaf cottonwood (*Populus angustifolia*) and green ash (*Fraxinus lanceolata*) dispersed over the area. Because of recreational improvements by U.S. Forest Service personnel, the canopy is discontinuous.

METHODS

A study of this nature requires repeated observations of a number of birds in a limited area. An attempt was made to follow seven pairs of chickadees through a complete nesting cycle in each of two breeding seasons, 1964 and 1965. At least

three hours per week were spent on each territory, in observation periods of one hour during the mornings (0500–1100) on alternate days. A total of 251 hours was spent in the field during this study.

Chickadees were trapped at long-established elevated stations baited with walnut meat. The traps used were a modification of the drop-door, wire-cloth type, described by Dixon (1963). Two colored-plastic bands and an aluminum band were placed on the tarsi of each captured bird, and various patterns were painted on the rectrices with Testor's airplane dope to facilitate individual recognition. Histories were known for most individuals from previous studies (K. L. Dixon and M. J. Frydendall, personal communication). Some of these birds had been banded for two years prior to the initiation of this study.

The birds were observed for periods of one hour, and all locations they visited were plotted accurately on field maps. Intervals during which birds were not under observation were excluded from computations. Since the nest cavities are excavated near to the ground (average elevation of 12 nests was 1.9 meters with a range of 0.5 to 5.0 meters), it was possible to determine accurately the stage of the nesting cycle in nearly every pair. A small flashlight and a dental mirror were used to inspect the nest cavities.

The territories in each stage of nesting were determined from the field maps on which the sites of all boundary conflicts were accurately plotted. If a part of a territory could not be determined by observation of boundary disputes, the outermost points of utilization were connected by straight lines to form a polygon of maximum size. Only in the nest-building stage were enough boundary disputes noted to determine a territory as a defended area. In some instances (for example, where a boundary abutted the mountain slope) during this stage, no contests were noted because there were no neighboring pairs. These boundaries were represented by dotted lines and the defended boundaries by solid lines. In practice, then, territories measured in stages other than nest-building represent utilized rather than defended areas. Territory sizes were determined from these maps by use of a compensating planimeter.

RESULTS

Prenesting stage. During the period from late March to mid-April, the pairs that had formed during the winter flocking period separated from the winter flocks and ranged over part of the winter-flock area in what appeared to be an attempt to isolate themselves from other chickadees. These "selected areas" were generally a part of the winter-flock range. The birds wandered over these areas and engaged in such activities as feeding, preening, resting, and early prospecting for possible nest sites. Because of the small size of the areas, there were frequent encounters between pairs, and these resulted in conflicts over area boundaries and defense of mates. The males attempted to establish a territory as well as to defend their mates during this period by excluding other flock members and unmated newcomers from the area. These encounters were initiated by song, aggressive calls, or both, and may also serve to establish dominance between two males. The females often took an active part in these skirmishes. In the combined data for the two years, these conflicts occupied an average of 42 per cent of the birds' time (table 1). Defense of mate ("sexual territory" of Odum, 1941:326) was an important factor because unmated birds sought mates and the pair bond was still relatively loose during the prenesting period. Exchanges of mates were noted in four instances. Older males (pairs 1, 3,

TABLE 1

TERRITORIAL ACTIVITIES FOR EACH OF THE STAGES OF THE NESTING CYCLE IN 1964 AND 1965

	Prenesting				Nest-building				Egg-laying				Incubation				Nestling				Fledgling			
Pair	A[a]	N	O	D	A	N	O	D	A	N	O	D	A	N	O	D	A	N	O	D	A	N	O	D
												1964												
1	2.2	3	97	27	2.3	12	81	26	0.2	1	93	0	0.1	1	84	21	0.1	2	88	1	0.5	7	36	3
2	0.5	1	100	48	1.5	1	66	95																
3	4.4	2	100	84	2.7	11	58	40	0.1	1	23	21	0.1	1	50	3								
4	2.4	3	89	63	3.2	10	94	20	1.3	1	97	3	0.2	1	35	0	0.5	3	64	0	1.0	4	87	0
5	0.4	1	100	11	0.4	4	62	9																
6					2.2	9	80	15	0.8	1	98	5												
7	1.2	3	96	35	1.6	1	100	79					0.1	1	100	0	0.4	5	88	0	0.9	4	74	9
Means	1.8	2.1	97	45	2.0	6.8	81	40	0.6	1.0	78	7	0.1	1.0	67	6	0.3	3.3	80	0.3	0.8	5.0	66	4
												1965												
8	3.4	9	74	25	3.2	9	74	19	1.3	2	44	11	0.2	6	41	0	1.2	6	71	5				
9	1.9	2	89		1.6	8	72	21																
10	1.0	2	89	57	2.7	12	59	18	1.5	3	35	21	0.7	1	52	22	1.9	5	66	3				
11	3.9	9	51	36	2.9	7	81	9	1.4	3	78	0	0.1	1	36	0	0.1	1	61	0				
12	1.2	6	45	37	2.9	11	68	34	0.5	3	87	5	0.2	1	87	3								
13	5.3	7	48	42	5.1	13	63	27	2.1	2	67	2	0.4	4	40	6	0.5	2	54	0				
14	1.8	5	72	48	0.3	11	35	30	0.5	3	28	0	0.1	3	45	0								
Means	2.6	5.7	67	41	2.7	11.6	66	23	1.2	2.6	56	6	0.3	2.6	50	5	0.7	3.5	63	2				

[a] Designation of columns: A = area of territory, in hectares; N = number of observation periods in the territory; O = per cent of time that the birds were under observation; D = per cent of time that the birds spent in defense of area.

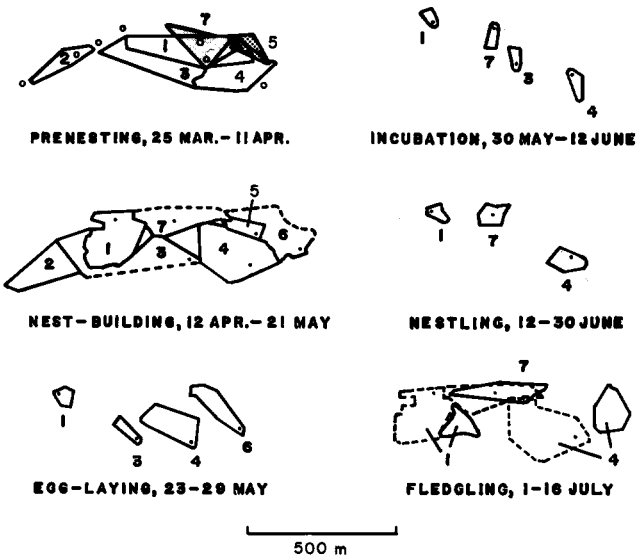

Figure 1. Disposition of territories and utilized areas in the different stages of the 1964 nesting cycle. Circles represent established feeding stations. Black dots show nest sites. In the fledgling stage the dotted lines represent the extent of boundaries in the nest-building period. The numerals denote the pairs identified in table 1.

and 4), each accompanied by his mate, frequented and established much larger areas than did younger males (fig. 1). The utilized areas of males two or three years old (six individuals) averaged 0.7 hectares larger than those of first-year birds (three individuals).

The occupied areas at this stage ranged from 0.4 to 5.3 hectares, with averages of 1.8 and 2.6 hectares in 1964 and 1965, respectively (table 1). In 1964 the birds used the winter feeding stations well into this period, and these "selected areas" were determined to a certain extent by the locations of these sites. As a consequence, some overlap in space utilization occurred (fig. 1). Considerable trespassing occurred since the boundaries were vague and varied from day to day.

Nest-building stage. Contiguous boundaries were more clearly defined during this stage than in the previous one. The selection of a nest site by the female greatly influenced the shifting of boundaries during this period (fig. 1). Territorial fights were more vigorous, and actual body contact occurred during combat (six instances). These conflicts occupied 31 per cent (average of data shown in table 1) of the birds' time and were clearly related to territorial boundaries. If the female chose a nest site well inside the "selected area," little shifting of boundaries occurred. If the female chose a nest site outside the "selected area," the male enlarged the territory to include the nest (six instances). This encroachment caused a marked increase in frequency of territorial skirmishes between the pairs concerned. Thus territorial skirmishes resulted in a firmer establishment of boundaries as compared with the prenesting period, and the "selected areas" gradually changed into territories (*i.e.*, defended areas) in the classical sense.

Territory size increased slightly (fig. 2) during this stage, but this increase was not statistically significant. The nest-building territory ranged in size from 0.3

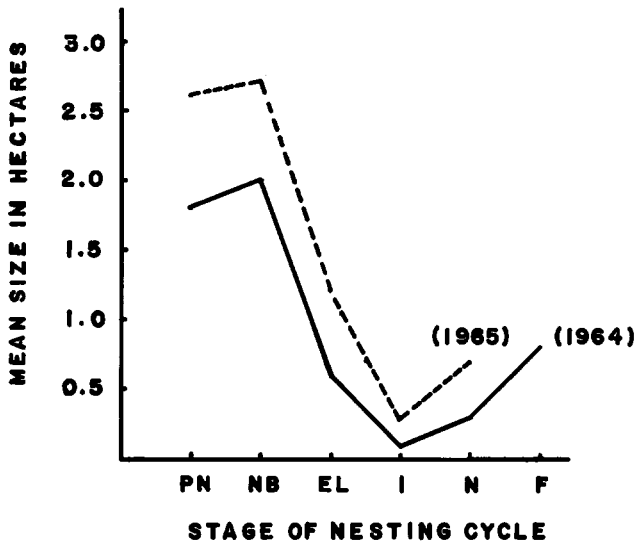

Figure 2. Mean territory sizes in different stages of the nesting cycle. Compare with figure 1. Sizes of samples are indicated in table 1.

to 5.1 hectares, with averages of 2.0 and 2.7 hectares in 1964 and 1965, respectively (table 1).

Trespass was less tolerated during this period (mid-April to late May), and all intruders were promptly evicted.

Egg-laying stage. The area utilized by chickadees during this stage (20 to 27 May) decreased markedly from that originally established during the nest-building period (fig. 2). The birds occupied only 39 per cent of the area established during nest-building. Territorial encounters also decreased precipitantly (fig. 3) and occupied only 6 per cent of the time that the birds were under observation (table 1). Only four pairs were observed at this stage in 1964 and six in 1965. The female of Pair 5 disappeared and observations of this pair were discontinued. Because of the difficulty of working in their areas, Pairs 2, 7, and 9 were not observed. The areas utilized were not centered about the nest (fig. 1), but, rather, the birds seemed to prefer to carry out their daily activities in certain areas within their own territories. The male spent considerable time feeding the female on the nest during this period.

Occupied areas ranged from 0.2 to 2.1 hectares, with averages of 0.6 and 1.2 hectares in 1964 and 1965, respectively (table 1).

Incubation stage. Four pairs were observed during this stage in 1964, and six pairs in 1965; a similar decrease in area utilized was noted in both years (fig. 2). These areas were the smallest of any found in the nesting cycle and averaged only 9 per cent of the area of those originally established during nest-building. Few territorial skirmishes were noted (fig. 3), and in five pairs they were never observed. These conflicts occupied only 5 per cent of the birds' time. A similar decline in territorial defense was noted by Odum (1941:328). Territory sizes ranged from 0.1 to 0.7 hectares, with averages of 0.1 and 0.3 hectares in 1964 and 1965, respectively (table 1). Pairs 3 and 14 disappeared during this stage, and the nests were abandoned. The nest of Pair 12 was flooded during this stage.

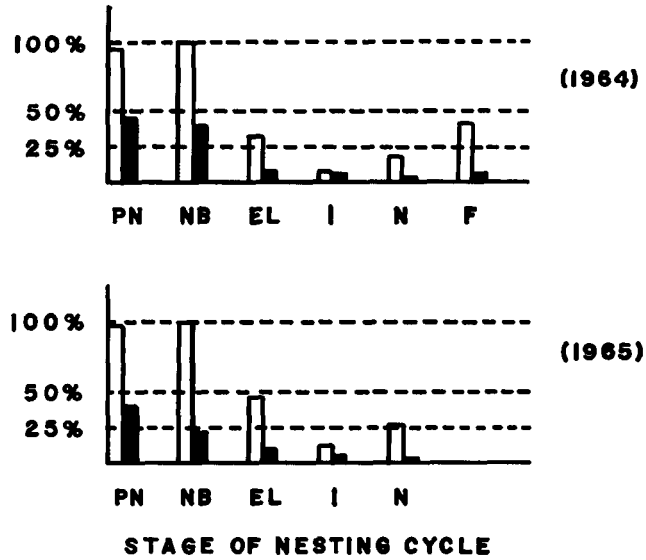

Figure 3. Size of territory related to time spent in defense during the nesting cycle. Unshaded bars show area as a percentage of nest-building size. Shaded bars show time spent in defense expressed as a percentage of the actual observation time.

The behavior of chickadees during this period (28 May to 10 June) was very similar to that of the previous stage. The male fed the female on or near the nest and frequently moved over the territory, foraging alone. The male either called the female off the nest to forage, or the female left on her own accord and spent inattentive periods alone.

Nesting stage. The utilized area increased during this stage (fig. 2) but remained only a small fraction of the original area defended while nest-building was in progress (fig. 1). Territorial conflict was infrequently noted (fig. 3), and in four pairs it was never observed. These territorial contests occupied about 1 per cent of the birds' time (table 1). Occupied areas ranged from 0.1 to 1.2 hectares, with averages of 0.3 and 0.7 hectares in 1964 and 1965, respectively (table 1). These utilized areas were only 18 and 26 per cent of the nest-building territory in 1964 and 1965, respectively. The female of Pair 11 disappeared three days after the young hatched, and the male abandoned the young. Unknown predators ate the nestlings of Pairs 10 and 13 shortly before they would have fledged. During the early part of this stage (10 to 28 June), the female brooded the nestlings while the male fed her on the nest. In the latter part of this period, both individuals fed the nestlings.

Fledgling stage. The "territory" disintegrated during this stage (28 June to 16 July). Only three pairs were observed in 1964, and two of these pairs permanently left their territories (fig. 1). Only Pair 7 remained on its territory. In 1965 Pair 8 permanently left its territory and was not located again.

The utilized area increased sharply during this period as compared with the nestling stage (fig. 2). These areas were 42 per cent as large as those originally established during the nest-building stage. Aggressive behavior was noted only where the broods accidentally met while foraging, and these skirmishes occupied, on the

average, 4 per cent of the adults' time (table 1 and fig. 3). Occupied areas ranged from 0.5 to 1.0 hectares, with an average of 0.8 hectares in 1964 (table 1).

DISCUSSION

The establishment of the nesting territory in the Black-capped Chickadee is strikingly similar to that of the Great Tit (*Parus major*), in which Hinde (1952) found the process to be a gradual one. He used the term "preferred stations" to include the area utilized by these birds before the onset of nest-building activities. Territorial conflict increased during the nest-building stage, and the boundaries (in most cases) were well defined. Thus the "preferred stations" gradually changed into territories. Territorial boundaries became vague in later stages, and the territory disintegrated during the fledgling stage.

In the Black-capped Chickadee birds separated from the winter flocks and frequented "selected areas" during the prenesting stage. Older males frequented larger areas than did younger males. The "preferred stations" of Hinde are not directly comparable to the "selected areas" because Black-capped Chickadees, as noted by Odum (1941:327), do not establish song posts as do Great Tits. The behavior of the chickadees was characterized by a large amount of time spent in boundary quarrels and in fighting related to defense of mates.

After nest-building had been initiated by the female, this pattern of space utilization changed considerably. The birds spent less time in antagonistic skirmishes, but these contests occurred with strict regard to boundaries. Gradually, the vague, shifting boundaries became clear-cut lines, especially when two nests were close to each other. Thus territories in the classical sense were established from the "selected areas" during the nest-building stage.

The space actually utilized decreased during the egg-laying and incubation stages. Territorial contests were infrequent and usually short. In terms of the resources required to insure nesting success, the nestling stage is the most critical part of the breeding cycle. During this interval the birds utilized, on an average, only 22 per cent of the area established during nest-building.

After leaving the nest the broods moved with or were divided between the two parents. Most adults left the territory and frequented areas with dense undergrowth, adjacent to the nest-building territory. If the foraging broods met accidentally, skirmishes between the adults occurred but without apparent regard to former boundaries.

The data of this study indicate that the area established initially during the nest-building stage by Black-capped Chickadees is much larger than that utilized at the most critical stage (nestling) of the nesting cycle. Also only the nest-building stage is considered to involve a territory, and the remaining stages are associated with "utilized areas."

Stenger and Falls (1959) found that the sizes of territories in Ovenbirds (*Seiurus aurocapillus*) were not fixed during the nesting cycle, but instead varied considerably from stage to stage. The utilized areas decreased after the establishment of the territory but generally increased during the nestling stage. This was also found to be the case in the Black-capped Chickadee. Older males established larger territories than did younger males less familiar with the area. Territory sizes of two- and three-year-old birds averaged 0.7 hectares larger than those of first-year birds. Since only a small part is actually utilized, it would appear that these territories could have been compressed to accommodate additional birds. This observation agrees with

Tompa's (1962) conclusion from his work on the Song Sparrow (*Melospiza melodia*). Such a conclusion was also indicated in Weeden's (1965) study of the Tree Sparrow (*Spizella arborea*).

However, there probably is a minimum size below which a territory cannot be compressed. In the Black-capped Chickadee pairs holding small territories trespassed considerably (38 per cent in one case during the egg-laying stage) to compensate for lack of available foraging area. In six instances in the present study territories were reduced in size because of encroachment by neighboring males after their females selected nest sites outside their original territories.

The failure of the birds to utilize in later stages the area originally established during the nest-building period raises the obvious question regarding the value of this behavior to the population. This study indicates that territorial behavior in Black-capped Chickadees functions to regulate density of the breeding population through the exclusion of some members of the population, and to space out the remaining breeding pairs to insure a minimum of interference from neighboring individuals of the species during reproductive activites.

Recently Gibb (cited by Tompa, 1964) pointed out that the two main complementary factors limiting avian populations are territorial behavior and intraspecific competition for food. The results of this study indicate that territorial behavior was a greater limiting factor. However, this does not exclude the possibility that under different conditions on the same area intraspecific competition for food might not have had a greater influence.

SUMMARY

Differential utilization of space at various stages of the breeding season was studied in 14 pairs of Black-capped Chickadees (*Parus atricapillus*) in 1964 and 1965 at Malibu-Guinavah Forest Camp seven miles east of Logan, Utah.

The establishment of the breeding territories was a gradual process. The "selected areas" of the prenesting stage gradually changed into territories in the classical sense. The spaces frequented during the egg-laying, incubation, and nestling stages were designated as "utilized areas"; the original territory boundaries were disregarded by the birds during the fledgling stage.

Average territory sizes of the prenesting and nest-building stages were 2.2 and 2.3 hectares, respectively. The birds spent 42 per cent of their time in territorial defense and fighting related to defense of mates during the prenesting stage, and 31 per cent of their time in territorial defense during the nest-building stage. The utilized areas decreased markedly during the remaining stages (mean size, 0.8 hectares). The amount of time (4 per cent) spent in defense of these utilized areas was minimal.

During the most critical stage (while feeding nestlings), the birds utilized only 22 per cent of the area originally established in the nest-building stage. Thus territorial behavior contributed to the regulation of breeding-population density through the acquisition by a few individuals of more space than they apparently needed.

ACKNOWLEDGMENTS

I am grateful to Keith L. Dixon for his very able assistance throughout the course of this study and for his critical editing of the manuscript. I also wish to thank Merrill J. Frydendall for helpful suggestions and Karen Frydendall for aid in the

preparation of the manuscript. Financial support was provided by National Science Foundation Grant G-23904 to Dr. Dixon.

LITERATURE CITED

DELIUS, J. D. 1965. A population study of Skylarks (*Alauda arvensis*). Ibis, 107:466–492.

DIXON, K. L. 1963. Some aspects of social organization in the Carolina Chickadee. Proc. XIII Intern. Ornithol. Congr., pp. 240–258.

EMLEN, J. T. 1957. Defended area? A critique of the territory concept and of conventional thinking. Ibis, 99:352.

HINDE, R. A. 1952. The behaviour of the Great Tit (*Parus major*) and some other related species. Behaviour, Suppl. No. 2.

HINDE, R. A. 1956. The biological significance of the territories of birds. Ibis, 98:340–369.

HOWARD, H. E. 1920. Territory in bird life. London, John Murray.

KURODA, N. 1960. An essay on bird territoriality. Misc. Reports Yamashinas Inst. for Ornithol. and Zool., 2:133–137.

NOBLE, G. K. 1939. The role of dominance on the social life of birds. Auk, 56:263–273.

ODUM, E. P. 1941. Annual cycle of the Black-capped Chickadee—I. Auk, 58:314–333.

STENGER, J. 1958. Food habits and available food of Ovenbirds in relation to territory size. Auk, 75:335–346.

STENGER, J., and J. B. FALLS. 1959. The utilized territory of the Ovenbird. Wilson Bull., 71: 125–140.

TOMPA, F. S. 1962. Territorial behavior: the main controlling factor of a local Song Sparrow population. Auk, 79:687–697.

TOMPA, F. S. 1964. Factors determining the numbers of Song Sparrows (*Melospiza melodia*) (Wilson), on Mandarte Island, B.C., Canada. Acta Zoologica Fennica, 109:1–73.

WEEDEN, J. S. 1965. Territorial behavior of the Tree Sparrow. Condor, 67:193–209.

Department of Zoology, Utah State University, Logan, Utah. (Present address: Department of Zoology, University of Toronto, Toronto 5, Ontario, Canada.) *16 March 1966.*