BLACK-CAPPED AND CAROLINA CHICKADEES IN THE SOUTHERN APPALACHIAN MOUNTAINS

BY JAMES T. TANNER

INTRODUCTION

THE Black-capped Chickadee, *Parus atricapillus*, and Carolina Chickadee, *Parus carolinensis*, are two closely related and very similar but distinct species of birds. The ranges of the two are different but contiguous and, in the non-breeding season, occasionally overlapping. Both species are found in the southern Appalachians, where their nesting ranges differ in altitude and where they may nest within a mile of each other. This situation provided an excellent opportunity to study the relations between these two species and to attempt to answer the following questions: Do the two species intermingle and perhaps interbreed? If they remain separate, what factors operate to keep them separate? Is there competition between the two species?

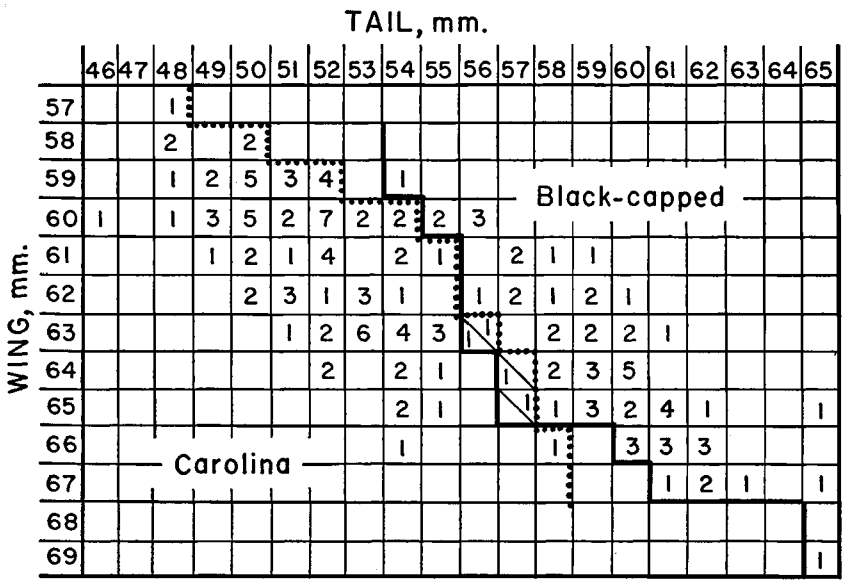
Most of the field work for this study was carried on in the Great Smoky Mountains National Park, and there I was greatly helped by the full cooperation of the Park Naturalist, Arthur Stupka. Specimens for this study were obligingly loaned from the collections of the United States National Museum, the Museum of Comparative Zoology, Albert F. Ganier, and George M. Sutton.

CHARACTERISTICS OF THE TWO SPECIES

Measurements.—The most obvious, though not the most consistent, difference between the two species is in size, the Black-capped Chickadee being the larger of the two. Table 1 shows the distribution of tail and wing lengths in the two species, regardless of sex, and illustrates the considerable overlap in each of these two measurements when taken alone, and the small overlap when the two are considered together. In both species males average larger than females, but their measurements overlap as can be seen from Table 3. Tail length was measured from the insertion in the skin of the two central tail feathers to the tip of the longest tail feather. Wing length was measured from the bend of the wing to the tip of the longest primary, with the feathers flattened. Only specimens collected in the months of September through March are included here, to eliminate the possible error caused by heavy wear during the nesting season. The Black-capped Chickadees whose measurements are recorded here were from the southern Appalachians, and the Carolina Chickadees were from the states containing these mountains, *i. e.* West Virginia, Kentucky,

TABLE 1

FREQUENCY OF BLACK-CAPPED AND CAROLINA CHICKADEES POSSESSING EACH COMBINATION OF TAIL AND WING LENGTH*



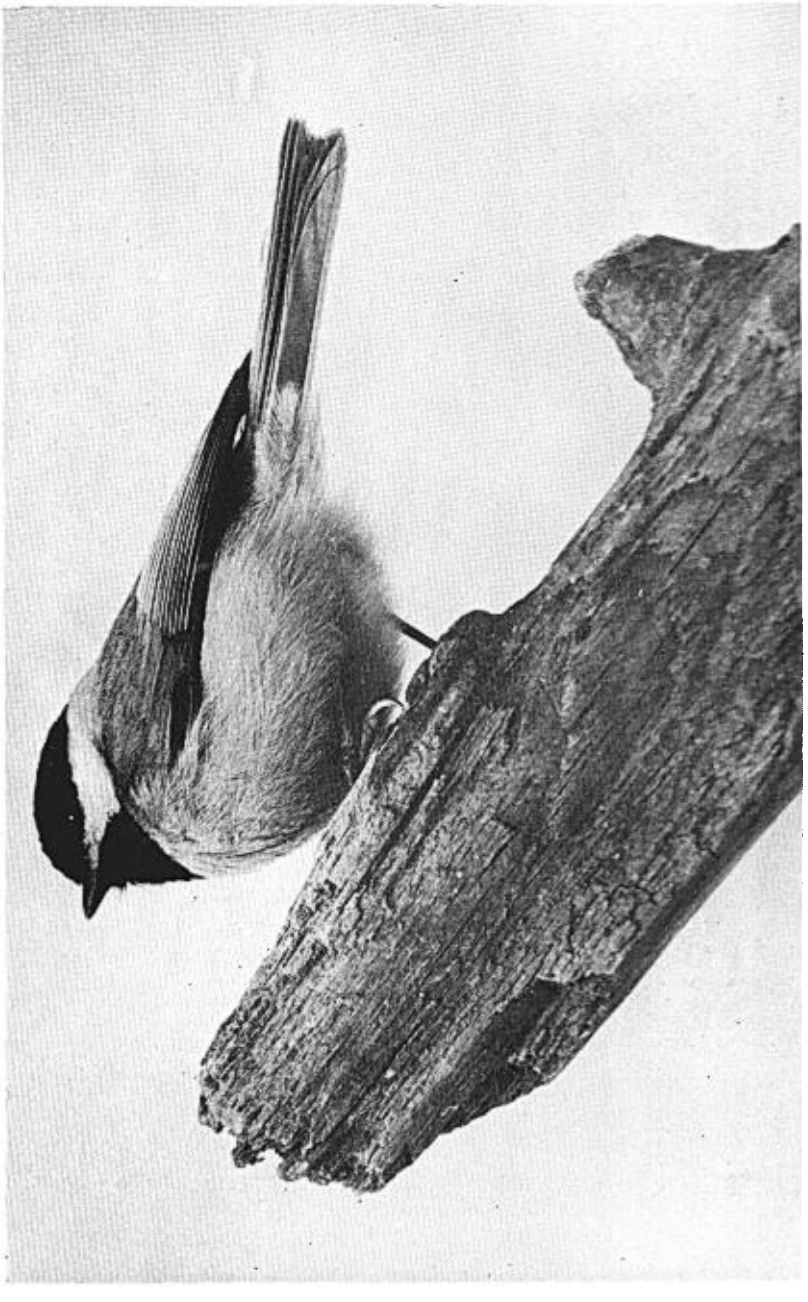
WING, mm.	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65
57			1																	
58			2		2															
59			1	2	5	3	4		1											
60	1		1	3	5	2	7	2	2	2	3									
61				1	2	1	4		2	1		2	1	1						
62					2	3	1	3	1		1	2	1	2	1					
63						1	2	6	4	3	1	1	2	2	2	1				
64							2		2	1		1	2	3	5					
65									2	1		1	1	3	2	4	1			1
66									1				1		3	3	3			
67																1	2	1		1
68																				
69																				1

* Black-capped Chickadees are all above and to the right of the solid line, and Carolinas are below and to the left of the dotted line. In the region of overlap, the numbers of Black-caps are in the upper right and of Carolinas in the lower left of each square.

Virginia, Tennessee, and North Carolina. The two Black-caps in the region of overlap came from the Plott Balsam Mountains in North Carolina where some hybridization had evidently occurred.

The most consistent difference found between the measurements of the two species is the greater tail length as compared with wing length of the Black-capped Chickadees. This characteristic is expressed as the tail-wing ratio (tail length divided by wing length). Statistical analysis of this ratio showed that it was independent of sex, so that the ratios from male and female specimens could be combined, and likewise that there were no significant differences between the ratios obtained from worn and non-worn specimens. This makes it possible to combine the data on tail-wing ratio from all specimens of one species from one area, which results in the statistical advantage of more data for the comparison of one group with another. The mean, standard deviation, and range of this ratio are included in Table 2.

Culmen and tarsus measurements average larger for Black-capped Chickadees than for Carolinas, but the difficulty of getting consistent measurements of these make them of little use in analysis.



CAROLINA CHICKADEE. PHOTOGRAPHED JANUARY 15, 1950, ON THE CARL KRIPPENDORFF FARM NEAR GLEN ESTE, CLERMONT COUNTY, OHIO, BY KARL MASLOWSKI AND WOODROW GOODPASTER.

Black-capped Chickadees usually average heavier in weight than do Carolina Chickadees.

Plumage.—Plumage differences are small, but are sometimes useful in identifying specimens. The most characteristic difference is that Black-capped Chickadees have wider and whiter edging to the secondaries than do Carolina Chickadees. The edging on the wing feathers of Carolinas is grayish or even brownish. Many, but not all, Black-capped Chickadees have a distinct white edge to the outer vane of the outer tail feathers, while in Carolinas this is at most only a gray edge. In many Black-capped Chickadees of the southern Appalachians the brown of the sides and flanks contrasts well with the gray mid-breast and belly, a pattern that is very rare in Carolinas where the underparts tend to be uniform gray or brownish gray. All these plumage differences are most pronounced in fall specimens and tend to disappear in worn, breeding individuals.

Voice.—To most observers the difference in song has appeared to be the best way to distinguish between the two species in the field. The song of the Black-capped Chickadee is usually a clear, whistled '*phe-bee-ee,*' or less often, '*phe-bee.*' The typical song of the Carolina is a thinner, higher pitched, four-noted '*se-fee-se-fu,*' but I have heard frequent variations, including a two-noted song very similar to some songs of the Black-capped. In the early morning of April 18, 1949, in the Great Smoky Mountains at an elevation of about 2800 feet, I heard a chickadee rapidly repeating a fairly typical Carolina song, and then suddenly it changed to a typical Black-capped song, pitched much lower. It continued this song as it moved rapidly up the slope. From subsequent observations and collections of birds in that area, I suspect that it was a young Black-capped Chickadee that had wintered at that elevation or lower in company with Carolina Chickadees. With one exception, singing birds collected were males; the exception was a solitary female Carolina Chickadee collected on April 20, 1950, that was singing a weak, atypical song.

The call notes of Carolina Chickadees are higher pitched and thinner than those of Black-caps, and the '*dee-dee-dee*' note of the former is given more rapidly. This difference in the rate of calls was measured crudely but effectively by counting the individual '*dee*' notes as a bird called '*dee-dee-dee- . . .*' and continuing counting at the same rate for a total time of five seconds, timing the period by the second-hand of my watch. The count thus obtained was the number of '*dee*' notes per five seconds, even though most calls last one second or less, and was a measure of the rate of calling. The mean rate for 179 records of

calls of known Carolina Chickadees was 38.9 (*dees* per five seconds) with a range from 25 to 52 and a standard deviation of 5.5. The mean rate for 183 records of calls of known Black-capped Chickadees was 23.6 with a range from 17 to 32 and a standard deviation of 2.8. Both species called more rapidly when excited. This method of measuring the rate of calling proved useful in identifying birds in the field.

Behavior.—The behavior of the two species, at least in the Great Smoky Mountains area, differs in one respect; the Black-capped Chickadee is more curious and less timid than the Carolina. Black-capped Chickadees frequently approached me closely and were relatively easily decoyed by squeaking noises or a whistled imitation of their song; Carolinas were more shy or less curious, and I was never able to call them to me.

The nesting habits of the two species are very similar. Most of my observations on nesting chickadees happened to be of Carolinas, and their behavior was essentially similar to that described for the Black-capped Chickadee in New York state by Odum (1941a, 1941b, 1942).

The six Carolina Chickadee nests found were in dead trunks of silverbell trees, *Halesia carolina* L. Nest digging began by April 1 or earlier. Incubation began between April 20 and May 6. At one nest the incubation period was apparently 12 days (May 6 to 18). One nest contained five eggs, another seven, and a third held six young. One pair that was color-banded by being trapped at the nest in 1949 nested in the same stub in a different hole in 1950, and in 1951 they nested again in the second hole. Of a second pair color-banded in 1949, one bird nested in the same territory in 1950, but its mate this year was unbanded.

All four of the Black-capped Chickadee nests observed were in dead trunks of yellow birch, *Betula lutea* Michx., from 5 to 60 feet above ground. Nest digging was observed in late April and early May. Comparison of the dates of nesting of the two species shows that in the Great Smoky Mountains area the Carolinas nest two to three weeks earlier than do the Black-caps.

In the winter both species associated in loose flocks with other small, tree-feeding birds. In the Great Smoky Mountains, Black-capped Chickadees have been observed flocking with Red-breasted Nuthatches, Golden-crowned Kinglets, Downy Woodpeckers, and Tufted Titmice; Carolina Chickadees have been seen with Tufted Titmice and Golden-crowned Kinglets. The two species occasionally join in the same flock. On February 16, 1950, I collected a Black-capped Chickadee from a flock containing Carolina Chickadees iden-

TABLE 2

TAIL TO WING RATIO OF BLACK-CAPPED AND CAROLINA CHICKADEES

	Number of specimens	*Mean ratio*	*Standard deviation*	*Range*	*Significance of difference*
All BLACK-CAPPED	116	.926	.022	.88–1.00	Very significant
All CAROLINA	152	.850	.028	.77–0.92	(P < 1%)
BLACK-CAPPED from:					
West Virginia Area*	54	.932	.021	.89–1.00	Not significant
Great Smoky Mtns.	45	.926	.022	.89–0.97	(P = 20%)
Plott Balsams	13	.909	.018	.88–0.94	Significant (P < 2%)
CAROLINA from:					
Great Smoky Mtns.	17	.852	.017	.82–0.88	Not significant
Western and middle Tennessee and Kentucky	38	.850	.028	.77–0.89	(P = 40%)

* The West Virginia area includes the Appalachians of West Virginia, western Virginia, western Maryland, and southwestern Pennsylvania.

tified by their call notes and song. Dr. Alexander Wetmore reported (verbally) collecting a Black-capped Chickadee from a flock of Carolina Chickadees in the Shenandoah Mountains of Virginia in the winter.

The feeding habits of the two species appear to be identical; members of both species feed by gleaning twigs, leaves, buds, and bark for insects. Seeds are occasionally eaten. The stomach contents of all collected specimens contained fragments of small insects.

Evidence of hybridization.—During this study no specimen was examined that could not be assigned to one or the other species. No obvious hybrids were found. Evidence of hybridization was looked for in another way—by seeing if populations of either species adjacent to populations of the other showed any trend in measurements towards those of the opposite species. The tail-wing ratio, being the most consistent difference between the two species, was used for this test. The data are presented in Table 2.

The tail-wing ratio of Black-capped Chickadees from the Great Smoky Mountains, an isolated population of this species surrounded by Carolina Chickadees, is less than that of Black-capped Chickadees from West Virginia and neighboring areas (southwestern Pennsylvania, western Maryland, extreme western Virginia) which are not an isolated group, but there is no statistical significance to the difference. There is then no acceptable evidence of hybridization having affected the characteristics of the Black-caps in the Great Smoky Mountains. This is especially interesting as the Black-caps from this area average smaller than do those from the West Virginia area; Table 3, comparing the measurements of wing and tail lengths, shows that with one exception there are significant differences in wing length and in tail length between the birds of these two areas.

TABLE 3

WING AND TAIL LENGTHS OF BLACK-CAPPED AND CAROLINA CHICKADEES IN MILLIMETERS (SEPTEMBER THROUGH MARCH)

	Number of specimens	*Mean length*	*Standard deviation*	*Range*	*Significance of difference**
BLACK-CAPPED, WING—MALES					
West Virginia area	14	65.8	1.55	63–69	Significant ($P < 5\%$)
Great Smokies	13	64.6	1.39	62–66	
Plott Balsams	4	64.5		63–66	
BLACK-CAPPED, WING—FEMALES					
West Virginia area	13	63.6	1.61	61–66	Very significant ($P < 1\%$)
Great Smokies	9	61.3	1.73	59–64	
Plott Balsams	3	61.3		60–63	
BLACK-CAPPED, TAIL—MALES					
West Virginia area	14	61.6	2.21	58–65	Questionable (P = about 7%)
Great Smokies	13	60.3	1.24	58–62	
Plott Balsams	4	58.8		56–60	
BLACK-CAPPED, TAIL—FEMALES					
West Virginia area	13	59.8	1.30	57–62	Very significant ($P < 1\%$)
Great Smokies	9	57.2	2.05	54–60	
Plott Balsams	3	56.7		56–68	
CAROLINA CHICKADEE					
Wing—Males	52	61.9	1.79	59–66	
Wing—Females	37	60.0	1.59	57–64	
Tail—Males	52	52.3	2.86	46–58	
Tail—Females	37	51.2	2.07	48–55	

* The significance of the difference was measured by the t test. There were too few specimens from the Plott Balsams for statistical comparison with birds from the Great Smoky Mountains.

A comparison of Carolina Chickadees from the Great Smoky Mountains with others from central and western Kentucky and Tennessee likewise shows no evidence of the former being affected by hybridization with Black-capped Chickadees (Table 2). This does not mean that there is never any hybridization between the two species in this area, but that, even if there is, it has not occurred frequently enough to affect significantly the characteristics of these populations.

A different picture is presented, however, by specimens of Black-capped Chickadees collected from the Plott Balsams, North Carolina, a line of mountains about 20 miles southeast of the center of the Great Smoky Mountains (Fig. 1). Thirteen specimens were available from these mountains—12 collected by Charles F. Batchelder in the winter of 1885–86 and one I collected in June, 1950. The tail-wing ratio of these birds is significantly less than that of the Black-caps of the Great Smoky Mountains (Table 2). These birds do show evidence of what may be occasional hybridization between the two species because they have a tail-wing ratio tending toward that of Carolina Chickadees, discussed in a later section of this paper.

DISTRIBUTION OF THE TWO SPECIES IN THE SOUTHERN APPALACHIANS

The Black-capped Chickadee is found throughout the northern states and north of the United States from coast to coast, while the Carolina Chickadee is only in the southeastern part of the continent. The boundary where the two species meet, as determined from the ranges described by Bent (1946) and omitting the southern Appalachians, runs from northern New Jersey to southwestern Pennsylvania, then across central Ohio, Indiana, Illinois, and Missouri to central or southeastern Kansas. This boundary is not sharply defined, for there is little information about the abundance and even the identity of the chickadees from localities along this line. In the wintertime Black-capped Chickadees may wander southward into the breeding range of Carolina Chickadees.

Black-capped Chickadee.—The distribution of the Black-capped Chickadee during the nesting season in the southern Appalachians is shown in Figure 1. In southwestern Pennsylvania, western Maryland, and northeastern West Virginia, Black-capped Chickadees are found below 3000 feet in elevation. In most of the West Virginia mountains they are found only above 3000 feet. In the Great Smoky Mountains and neighboring mountains in North Carolina they are found almost exclusively above 4000 feet.

Carolina Chickadee.—Throughout the lowlands of the area covered by Figure 1 Carolina Chickadees are common. For this species, Figure 1 shows only the locations of nesting season records that are above 3000 feet elevation in the northern part of the area and above 4000 feet in the southern part. Carolinas are, almost without exception, absent from these higher elevations where Black-capped Chickadees are present. But there are about 14 localities at these higher elevations where Black-capped Chickadees are absent and Carolinas are present. On several of these mountains Carolina Chickadees have been found nesting at or near the tops of the mountains in forests of spruce and northern hardwoods. Here they are rare and widely scattered, compared with their density at low elevations, but the important point is that they do live and nest successfully on some of the higher mountains.

The one area shown in Figure 1 where Black-capped and Carolina chickadee records are from the same area above 4000 feet elevation is the Black Mountains or Mt. Mitchell area of North Carolina. William Brewster visited these mountains before they were logged over and reported (1886) that Black-capped Chickadees were fairly common in the "balsam belt," mingling with Carolina Chickadees along the lower

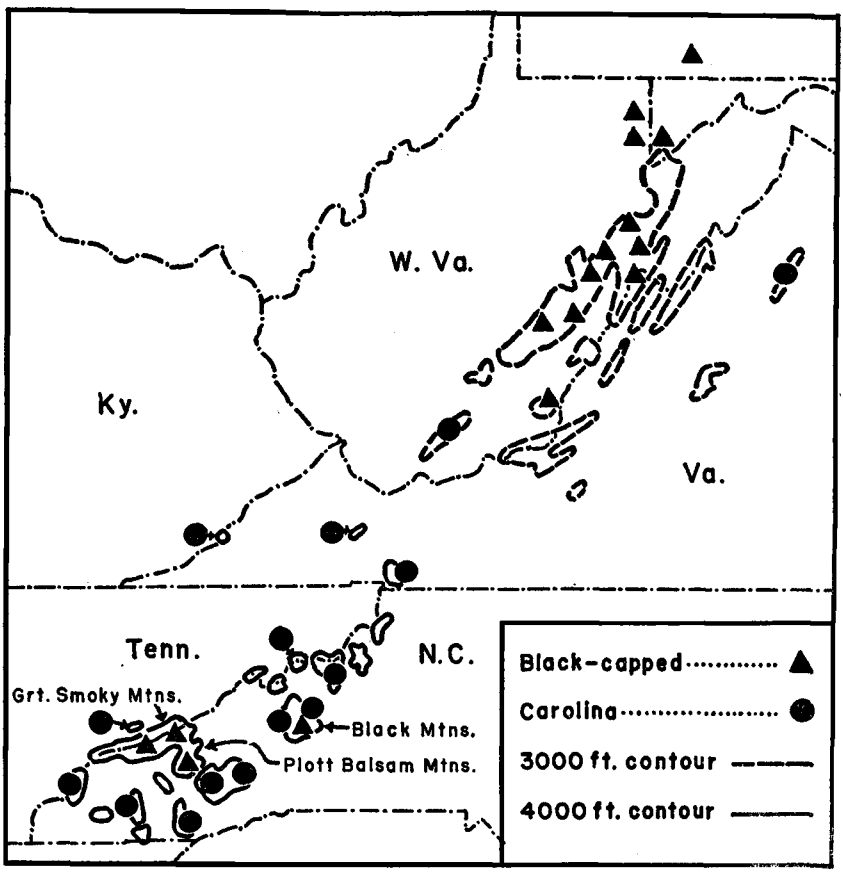


FIGURE 1. Nesting season records for Black-capped and Carolina chickadees in the Southern Appalachians. Locations of Carolina Chickadees are shown only when they are above 3000 feet elevation in the northern part of the map or above 4000 feet elevation in the southern part. Carolina Chickadees are common residents in the lowlands of the area covered by this map. The records indicated on this map are all based upon collected specimens.

edge of this, the spruce-fir forest. This same area was studied extensively by Thomas Burleigh in the years 1930 through 1934, after these mountains had been logged and repeatedly burned over. He reported (1941) Carolina Chickadees at an elevation of 5000 feet; he saw only two Black-capped Chickadees, one of which was collected, on May 8, 1930, and considered these birds to be accidental. In a brief trip to these mountains in June, 1950, I found no Black-capped Chickadees, but did find a pair of Carolinas nesting at an elevation of 4800 feet in a forest of spruce, birch, and other mountain trees.

The presence of Carolina Chickadees on some high mountains where there are no Black-caps and their absence from the higher parts of those mountains where Black-capped Chickadees are present are perhaps evidence for the hypothesis that there is competition between the two species and that in some mountains the Black-capped prevent the Carolina Chickadees from extending their range to the higher elevations. In the Mt. Mitchell area Black-capped Chickadees have disappeared since Brewster's time, and Carolina Chickadees have since invaded the spruce-fir zone. Further evidence for the hypothesis of competition is presented in a later section of this paper.

Absence of Black-capped Chickadees from certain areas.—From the southernmost locality in West Virginia where Black-capped Chickadees are present to the Great Smoky Mountains is a gap of about 200 miles wherein there are, to my knowledge, no records authenticated by collected specimens of nesting Black-capped Chickadees. There are in this gap several mountains containing what appears to be suitable habitat for Black-caps—forests of spruce, fir, birch, beech, and maples where live such northern species of birds as Red-breasted Nuthatch, Golden-crowned Kinglet, Winter Wren, and Junco. There is then no apparent absence of suitable habitat or of climate.

Two hypotheses to explain the absence of Black-capped Chickadees from these mountains are suggested here. The first is based upon the fact that in the Great Smoky Mountains all the nests of Black-capped Chickadees I observed were dug by the birds in yellow birch trees, an abundant tree there. In trips to other mountains where Black-capped Chickadees are absent, I observed that yellow birch trees, although present, are not nearly as abundant as in the Great Smokies. In the Mt. Mitchell area, where Black-caps have disappeared since Brewster's time, mature yellow birch is practically absent, apparently a victim of the logging and repeated fires on those mountains. This hypothesis is, then, that the Black-capped Chickadees of this part of the Appalachians require yellow birch trees for nesting sites and are found only where mature trees of this species are abundant. Although this hypothesis is one of the simplest to explain the disappearance of the birds from the Mt. Mitchell area, it has the apparently unanswerable objection that farther north Black-capped Chickadees use a variety of nesting sites and also use abandoned woodpecker nests and similar cavities (Odum, 1941b; Bent, 1946).

The second hypothesis is that isolated populations of Black-capped Chickadees, when surrounded by Carolina Chickadees, can exist only if their numbers are above a certain minimum; and when their numbers

are below this minimum, hybridization between the two species results in the elimination of the isolated population. The evidence in support of this hypothesis is, first, that the Great Smoky Mountains provide the largest, high, mountain area, supposedly capable of supporting the largest population of mountain birds, in the Appalachians south of West Virginia, as can be seen from Figure 1; and as reported in a previous section, the Black-capped Chickadees found in the Great Smokies show no acceptable evidence of having been affected by hybridization. Secondly, the Black-capped Chickadees of the Plott Balsams, a much smaller area, do show evidence of hybridization between the two species, by tending toward the proportions of Carolina Chickadees.

Hybridization between two species will have a harmful effect on a small, isolated population if any of the three following conditions occur: if matings between the two species are relatively infertile; if hybrids themselves are less fertile than typical members of either species; or if the hybrids are less successful and therefore shorter lived. Any one of these three conditions would result in lessening the reproductive potential of a population, but the effects would be much greater on a small population than on a large, for the proportion of hybridization, or of matings between species to matings within the species, will be greater in a smaller population than in a larger.

To state the second hypothesis: An isolated population of Black-capped Chickadees surrounded by Carolina Chickadees can exist only if the population is above some minimum size; below that minimum, hybridization between the two species occurs often enough to reduce the reproductive potential of the isolated population sufficiently to cause its elimination.

The evidence for hybridization affecting an isolated population is based upon the measurements of the Plott Balsam chickadees, which give no clue as to the frequency of hybridization. And there is no proof that hybridization produces harmful effects. If the hypothesis were proven to be true, then it could be said that south of West Virginia only the Great Smoky Mountains are large enough to support a population of Black-capped Chickadees, except for the Plott Balsams where the population is apparently just above the minimum size, that several other mountains are too small even though they have suitable habitat, and that the Black Mountains of North Carolina formerly held a population of Black-capped Chickadees but that this population was reduced below the minimum size, probably by the adverse effects of logging and fires. All five Black-capped Chickadee specimens that I examined from the Black Mountains were collected in the months of May and June and thus their wing and tail measurements cannot be

used with confidence, but in all of them the tail-wing ratio is at the lower end of the range for the species, possibly indicating that there was a considerable amount of hybridization.

DISTRIBUTION OF THE TWO SPECIES IN THE GREAT SMOKY MOUNTAINS

The distribution of the two species of chickadees in the Great Smoky Mountains was worked out during the winter and spring of 1948, 1949, and 1950. Most of my field work was concentrated on the northwestern slopes of Mt. LeConte; trips were made to other areas of the Smokies to see if the pattern of distribution appeared to be uniform, which it did with certain exceptions described later. Mt. LeConte is typical of the Smokies in that its slopes are heavily forested, mostly in virgin forest, and the forest varies from oak-chestnut at the lower elevations to spruce-fir at the summit. As many areas as possible were covered in the early morning, for males of both species sing regularly just at dawn during late winter and early spring, and in the absence of wind and other noises, these songs can be heard for a considerable distance. Singing becomes less regular after sunrise and almost ceases by mid-morning. The regularity of song in the early morning made it possible to decide definitely where chickadees were present, and, in some ways more important, where they were absent. The winter distribution of the two species was worked out by collecting specimens, and collecting was used to check the identification of questionable individuals during the nesting season.

Figure 2 shows the distribution of the two species in a portion of the Great Smokies. Nests of Black-capped Chickadees have been found from an elevation of (rarely) 3400 feet to the tops of the mountains. On the same mountains where Black-caps are present, Carolina Chickadees nested up to an elevation of about 2800 feet. This left a gap of about 600 feet in elevation between the two; on the comparatively steep slopes of Mt. LeConte this is a distance of about one mile. An estimated 35 miles were walked during the nesting season in this gap, much of this in the early morning, without finding any chickadees there. In the winter Black-caps moved down the slopes as low as 2000 feet, thus mingling with Carolinas which wintered in their breeding range. Occasionally Carolina Chickadees wandered to higher elevations in wintertime, shown by a specimen collected by Thomas Burleigh near Indian Gap at 5500 feet on November 30, 1930.

Some Black-capped Chickadees remained at elevations of about 3000 feet, which is below their nesting range, until after Carolina Chickadees were nesting and other members of their own species had begun to dig nest cavities. The latest date that this was observed

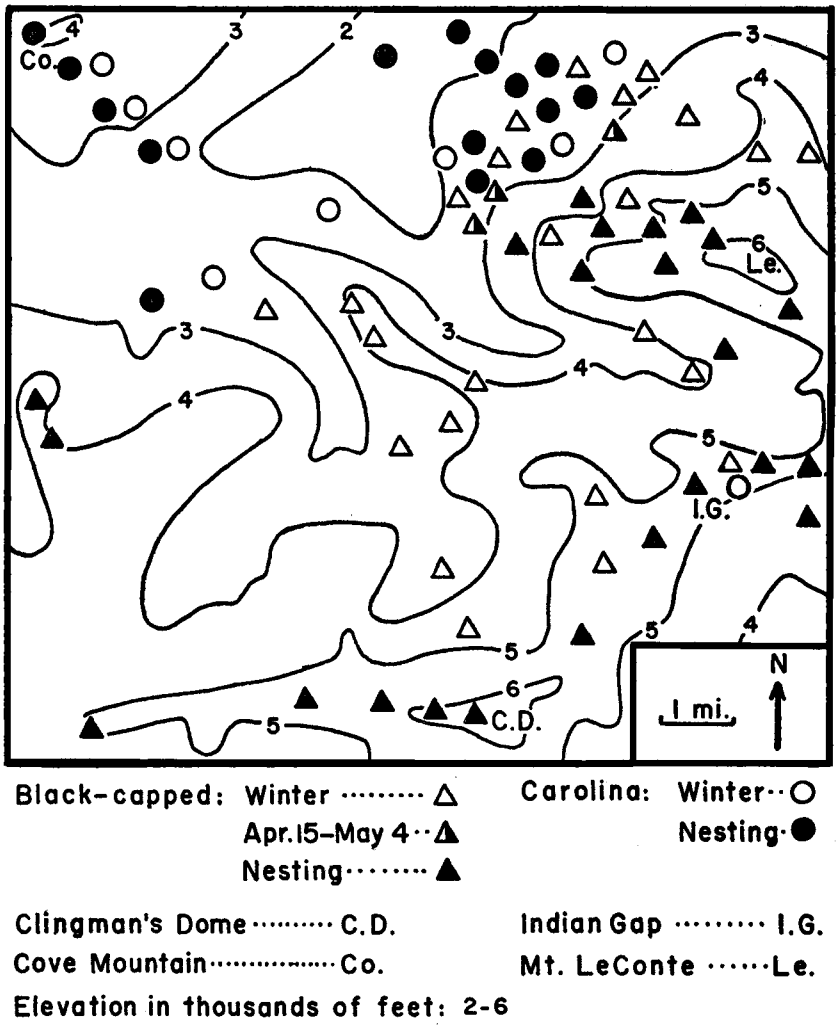


FIGURE 2. Records of Black-capped and Carolina chickadees in a portion of the Great Smoky Mountains of Tennessee and North Carolina.

was May 4. These birds sang regularly in the early morning, frequently were paired, and in general behaved as if they were going to nest. But I never observed them digging nest cavities, and I did not find them at those elevations during or after the middle of May when nesting activities should have been in full swing; presumably they had by then moved higher in the mountains. These birds may have been young of the preceding year, because some of the songs these chicka-

dees sang were not typical; one bird in particular changed from a song sounding like that of a Carolina Chickadee to a typical Black-capped song. I do not doubt the identification of these birds as Black-caps, because the five specimens collected from these elevations proved to be Black-capped Chickadees. The unusual songs were probably learned from Carolina Chickadees by young Black-caps wintering at low elevations.

TABLE 4

COMPARATIVE ABUNDANCE OF CHICKADEES IN EACH FOREST TYPE IN THE GREAT SMOKY MOUNTAINS*

	Black-capped Chickadees		*Carolina Chickadees*
	Nesting season	*Winter season*	*All seasons*
Spruce-fir	64	28	0
Northern hardwoods	29	56	7
Southern hardwoods	7	16	93

* Based on the number of contacts per mile walked in each forest type. Each contact was counted as a single contact regardless of whether it was with a single bird or a flock. Contacts with Black-capped Chickadees made in the months of May, June, and July were counted as nesting season contacts.

The comparative abundance of the two species in the different types of forest is shown in Table 4. During their nesting and post-nesting season, Black-capped Chickadees are most abundant in the spruce-fir forest (red spruce, *Picea rubens* Sarg.; southern balsam fir, *Abies fraseri* (Pursh) Poir.; yellow birch, *Betula lutea* Michx.). In winter they are commonest in northern hardwoods (yellow birch; beech, *Fagus grandifolia* Ehrh.; sugar maple, *Acer saccharum* Marsh.; frequently with hemlock, *Tsuga canadensis* (L.) Carr.), probably because of movement down the mountains. Carolina Chickadees in the Smokies are practically confined to two or more forest types here combined and designated as southern hardwoods (tulip tree, *Liriodendron tulipifera* L.; yellow buckeye, *Aesculus octandra* Marsh.; silverbell, *Halesia carolina* L.; chestnut, *Castanea dentata* (Marsh.) Borkh.; various oaks; frequently with pines). Just as nesting Black-capped Chickadees become scarcer and more widely scattered toward the lower limit of their nesting range, nesting Carolina Chickadees become scarcer toward the upper limit of their nesting range. In an area near Knoxville, Tennessee, about 30 miles from the Smokies, the distance between centers of eight adjacent territories of Carolina Chickadees averaged less than one-quarter mile, while at the upper edge of the nesting range of Carolinas in the Smokies this distance for four territories averaged almost one-half mile.

The above discussion of the distribution of the two species in the Great Smokies has considered only mountains like Mt. LeConte where

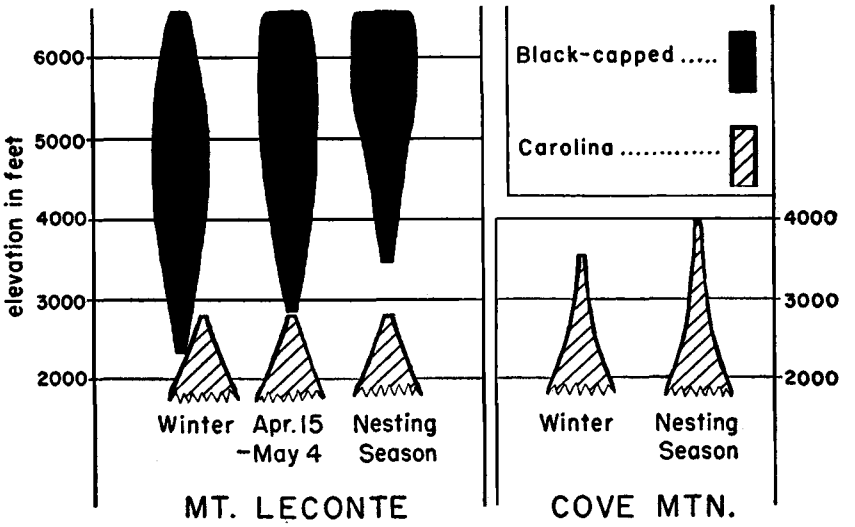


FIGURE 3. Diagram of altitudinal distribution of chickadees on two different mountains in the Great Smoky Mountains. The width of each symbol approximates the relative abundance of the chickadees at the different elevations.

both species are present. The situation is different wherever Black-capped Chickadees are absent. This is illustrated by conditions on Cove Mountain, about eight miles west-northwest of Mt. LeConte (Fig. 2). The summit of this mountain is just above 4000 feet in elevation. The forest on Cove Mountain is similar to that on Mt. LeConte at comparable elevations and exposures. Black-capped Chickadees were absent from Cove Mountain, and Carolina Chickadees were found to the top of the mountain in summer and up to at least 3700 feet in winter. This relationship agrees with that described earlier for the entire southern Appalachian region—that Carolinas are found at higher elevations wherever Black-caps are absent.

The distributions of the two species on Mt. LeConte and Cove Mountain are diagrammed in Figure 3 which graphically shows the changes occurring between winter and nesting seasons and the differences between the two mountains.

Competition affecting the distribution of Carolina Chickadees.—The distribution of the two species on mountains like Mt. LeConte may supply further evidence for there being competition between the two. The Black-capped Chickadees inhabit the higher parts of the mountain. As shown by Table 4, they were most abundant during the nesting season in the spruce-fir forest at the top, but nesting birds were found downwards in smaller numbers to elevations of about 3400 feet

on Mt. LeConte, which is in the upper edge of the southern hardwoods. It seems that they are better adapted to some conditions found at the higher elevations; the question of what limits their downward distribution is discussed in the following section.

During the winter Black-capped Chickadees moved down to lower elevations, some of them mingling with Carolina Chickadees. As the nesting season approached the Black-caps withdrew up the slopes, but some remained behind, as described above, and behaved as if they were going to nest at elevations of about 3000 feet. About May 1 or soon after, these Black-caps disappeared from these places.

On Mt. LeConte, Carolina Chickadees were not found nesting above 2800 feet. There is ample evidence that the habitat does not limit their upward distribution. On several mountains outside the Smokies where Black-caps were absent, Carolinas were found nesting at elevations of almost 5000 feet in northern hardwoods, spruce, and similar trees, and on Cove Mountain, only a few miles away from Mt. LeConte, Carolinas were found on the 4000 foot summit (Fig. 1). Their upward limit was apparently determined by the presence of Black-capped Chickadees at elevations of around 3000 feet during the early part of the Carolinas' nesting period. Even though the Black-caps did not nest this low, they did not withdraw from these elevations until after May 1, when Carolina Chickadees were laying or incubating. This resulted in leaving on Mt. LeConte a gap of about 600 feet in elevation (2800 to 3400) in which no nesting chickadees of either species could be found. There is, then, this evidence for competition between the two species, in which the Black-capped Chickadee is the dominant or successful species at higher elevations since its presence determines the absence of nesting Carolina Chickadees at these elevations. The evidence indicates that the competition exists during the early nesting season or at the time territories are established, because the two species will mingle in winter flocks, and because of the sequence of events resulting in a gap in elevation between the nesting distribution of the two species. The fact that Black-capped Chickadees are larger than Carolinas may be significant. Despite the many hours I have spent looking for and watching chickadees, I have never observed any kind of interspecific conflict, display, or territorial defense in these species.

Some observations which are interesting, but do not shed much light on the problem, were made on April 16, 1950, and were almost duplicated on May 3, 1951. On the earlier date a pair of Carolina Chickadees had a newly completed nest at an elevation of about 2300 feet. Two Black-capped Chickadees, one singing, were found about 40 yards from this nest; I followed them for about 20 minutes as they fed

through the trees, then lost them. They were neither seen nor heard again on this or following days, even though I looked for them several times. Apparently they had just wandered through that area. On May 3, 1951, when the same pair of Carolina Chickadees had a nest with eggs, three Black-capped Chickadees, one singing and the others giving typical calls, were found again about 40 yards from the nest. They moved off and were lost, and I did not see or hear them again in the next two hours I spent in that area. On neither occasion did I see or hear a Carolina Chickadee near the Black-caps; there certainly was no attempt by the nesting Carolina to drive the Black-caps away. This may not be significant because there was no way to tell if the Black-caps were trespassing on the territory of the nesting Carolina Chickadees; there were no neighboring Carolinas so there were no combats to reveal the boundaries of the territory of the male Carolina in question, and there were two other Carolina nests located 30 yards or less from the boundaries of the respective territories.

Why did not the presence of these Black-caps prevent the nesting of Carolina Chickadees at 2300 feet? In both 1949 and 1950 I was in this area several times before and during the early nesting season, looking for and observing the nest of the Carolina Chickadees there; in 1951 I only drove through the area a few times during this season. The two incidents described above were the only times when Black-caps were observed anywhere in this vicinity. In contrast, at this same time of the spring, Black-caps were found repeatedly at elevations of around 3000 feet, behaving as if they were on their territory until they disappeared about the first week of May, and it was in these areas that no Carolina Chickadees were found nesting. The observations made at 2300 feet indicate that the Black-caps seen there were wandering birds, not behaving as territorial birds, and they had no more effect on the resident Carolinas than the Black-caps that winter as low as 2000 feet.

Lower limit to the distribution of Black-capped Chickadees. The presence of Black-capped Chickadees apparently determines the upper limit of Carolina Chickadees in the southern Appalachians, but there remains the question of what determines the lower limit of the Black-capped Chickadees. What keeps them from nesting farther down the slopes of the mountains than they do? The fact that many Black-caps remained at lower elevations until about the first of May, and then disappeared from there, probably moving farther upwards, indicates that whatever factor determines their lower limit operates at about this time of the year. Three possible answers to this question were investigated, all with negative results; they are summarized below.

Because all of the nests of Black-capped Chickadees I found in the Great Smoky Mountains were in yellow birch trees, it seemed possible that the lack of this kind of tree or of a suitable substitute at lower elevations limited their nesting distribution. Yellow birch trees, however, are found along streams at elevations considerably below the lowest nesting Black-capped Chickadees. A further test of this idea was the placing of 24 nest boxes, of a kind suitable for chickadees, at various elevations from 2600 to 6000 feet with the largest number below 4000 feet. Some of these boxes remained up through three nesting seasons. None of these boxes were used. One pair of Black-caps nested in a yellow birch stub within 70 feet of a nest box.

Temperature is a factor that might limit the distribution, and a test of this was made by searching for a temperature condition that was the same for the southern limit of the distribution of Black-capped Chickadees in non-mountainous areas (see the description of the range of this species in an earlier part of this paper) and for the lower limit of their nesting range in the Great Smoky Mountains. A fair number of temperature data was available for this comparison; several kinds of measurements were investigated, such as the average daily maximum dry bulb and wet bulb temperatures for both the beginning of the nesting season and the hottest time of the year, extremes of high temperature, duration of hot weather, etc. In none of these was the correlation between temperature and the limits of the nesting range close enough to show that temperature determined the limit of the range.

On the northwestern slopes of Mt. LeConte, where most of the field work in the Great Smokies was done, the lower limit of Black-capped Chickadee nests coincided with the upper limit of Tufted Titmouse nests, suggesting competition between these two species. This idea is contradicted by the large overlap in the ranges of the two species in non-mountainous areas, *e. g.*, the Great Lakes area.

SUMMARY

The Black-capped and Carolina chickadees are closely related species that are similar in appearance and habits but which have fairly constant differences in measurements, plumage, and voice. Hybridization, if such actually occurs, is so rare as to have little effect on the characteristics of either species except for small, isolated populations such as the Black-capped Chickadees of the Plott Balsams, North Carolina; here hybridization may have occurred often enough to change the characteristics of the Black-caps of these mountains.

In the southern Appalachians, Black-capped Chickadees are found in the mountains of West Virginia nesting mostly above an elevation

of 3000 feet and in the Great Smoky Mountains and the neighboring Plott Balsams nesting mostly above 4000 feet. They are more abundant at higher elevations, apparently being better adapted to conditions found there. Carolina Chickadees are found at lower elevations; they do not nest at higher elevations wherever Black-capped Chickadees are present; but where the latter are absent, Carolinas nest sparsely as high as 5000 feet. In the Great Smoky Mountains there is a gap between the nesting range of the two species, wherein neither one nests. In the spring, this gap is occupied by Black-capped Chickadees which behave as if they are going to nest, but which disappear from these areas about the time that Carolina Chickadees begin incubation. These facts indicate: 1) that there is some form of competition between the two species, that operates during the early nesting season; and 2) that the presence of Black-capped Chickadees prevents the Carolinas from inhabiting the higher parts of these mountains.

Why Black-capped Chickadees are absent from certain mountains that appear to possess suitable habitat and the problem of factors determining the lower limit in the mountains of the nesting range of Black-capped Chickadees are discussed. Satisfactory answers to these problems were not found.

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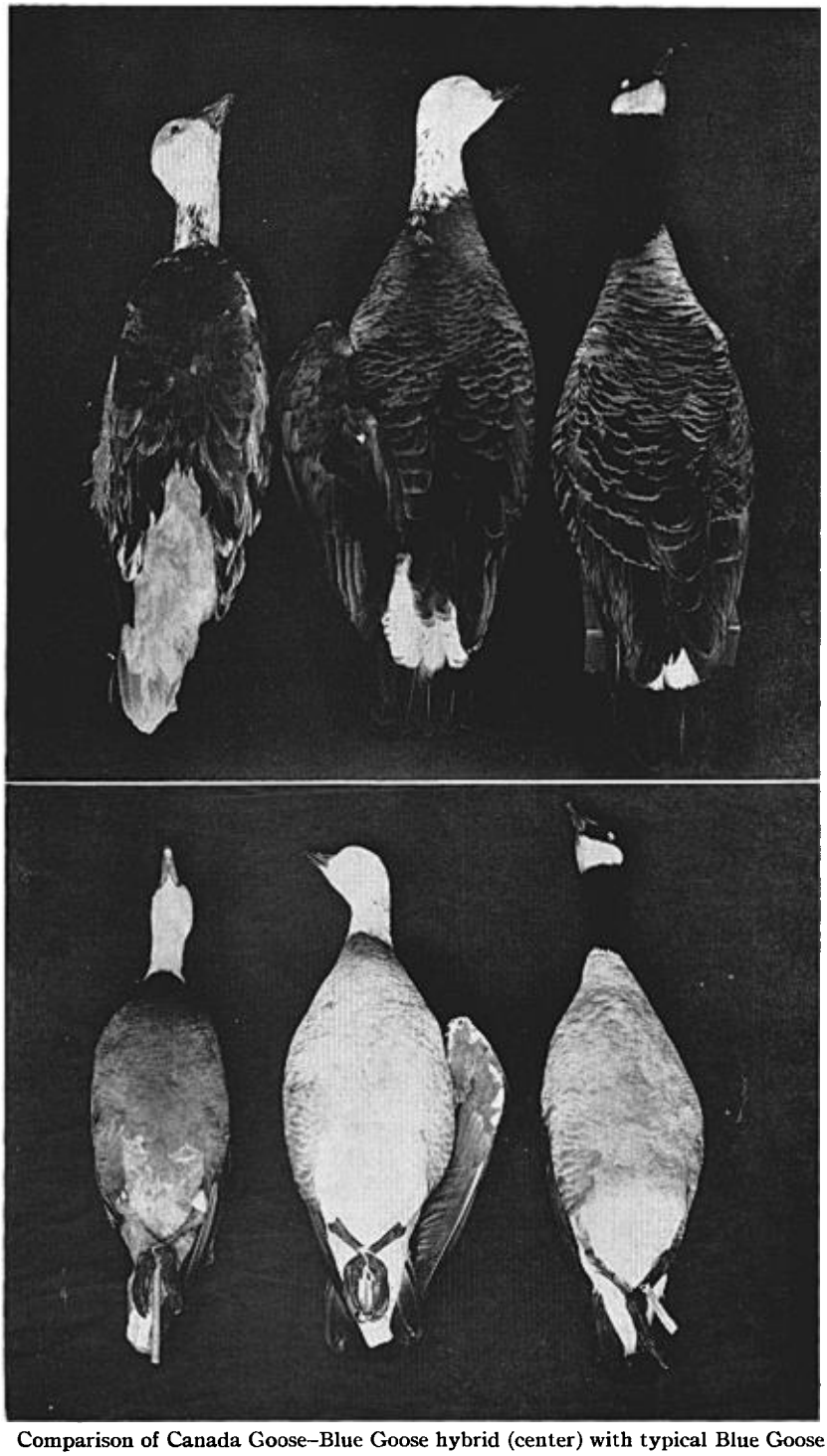

Comparison of Canada Goose–Blue Goose hybrid (center) with typical Blue Goose (left) and Richardson's Goose (right). (*Top*) Dorsal view. (*Bottom*) Ventral view. Photographs by Harvey L. Gunderson.