AN APPRAISAL OF THE SONG OF THE BLACK-CAPPED CHICKADEE

KEITH L. DIXON AND RAYMOND A. STEFANSKI

THE songs of most species of birds are distinguished from call notes by the restriction of the former to one sex, and by the differences in the functions served by the two classes of sounds (Tinbergen, 1939:73–74; Thorpe, 1961:15). Song usually is confined to the mating season, and is associated with occupancy of a breeding territory. The vocalization considered to be the song of the Black-capped Chickadee (*Parus atricapillus*) often is transliterated as *fee-bee* or *phoebe*. The usual form is a sequence of two pure, whistle-like notes, the second lower in pitch (Fig. 1A). This vocalization is categorized as a song according to Tinbergen's definition ". . . those loud sounds that are given by birds of one sex especially at the beginning of the reproductive period." The restriction of loud singing to males during the breeding season, and the manner of delivery, as described by Bradford Torrey (quoted by Tyler, 1946), support this view.

In other respects this vocalization of the Black-capped Chickadee does not conform to the concept of "advertising" song as it is exemplified by other passerines. The *phoebe* song is not complex in its physical structure, as Bremond (1963) would require, and it is not delivered regularly from an exposed perch by males during the breeding season (Odum, 1941:327). These notes are not restricted to the breeding season (Bicknell, 1884:135; Saunders, 1947), and their functions may differ with the seasons. This unique song clearly warranted further study, some aspects of which we were able to pursue as a facet of a population study.

METHODS

Observations of behavior associated with singing were made in a population of color-banded chickadees whose nesting progress was known (Stefanski, 1967). Approximately 400 hours were spent in the field, principally in 1964 and 1965, in a deciduous woodland in the floor of Logan Canyon, 7 miles east of Logan, Cache Co., Utah, at an elevation of 5,000 feet. Some of the marked individuals were observed for short intervals in January and early February in a room 7 × 10 feet in area. After being conditioned to the room individually, they were confined by twos for a period of several days, and their behavior observed through simulated one-way glass windows. Vocalizations were recorded in the field and indoors with a Nagra IIIB tape recorder, and analyzed with a Kay Electric Company Sona-Graph. Playback experiments were conducted with breeding individuals of this population when the birds were known to be within hearing range. Either the playback system of the Nagra or a battery-powered amplifier-speaker system with a Transflyweight recorder was used. The tape recordings broadcast consisted either of songs or call notes of the flock integration ("chickadee dee") sort.

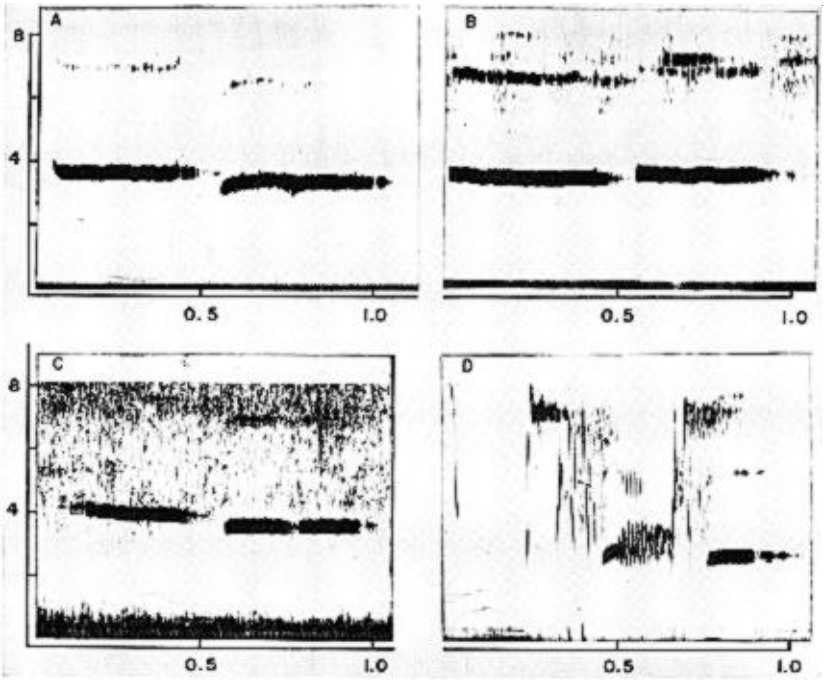

FIG. 1. Sound spectrographs of vocalizations of *Parus atricapillus*. Vertical scale, frequency in kilocycles per second; horizontal, time in seconds. A, typical song. B, song pattern with second note higher pitched. C, "signal" song of male approaching nest. D, fighting call uttered while supplanting a rival.

CONTEXTS OF SINGING BY MALES

The *phoebe* song is uttered infrequently in fall and winter, but the incidence increases with the weakening of flocking tendencies in early spring (Odum, 1941:322; Johnston, 1942). In late March and early April in northern Utah (the pre-nesting stage), exchanges of song occur in obvious relation to particular areas frequented by rival males. Most of these males already are paired. During this interval territorial boundaries are established, and these normally are altered only if the female selects a nest site outside the original territory.

Loud singing occupies a relatively small amount of the territory-holding male's time during the breeding cycle (Table 1). However, the higher incidence prior to incubation coincides with the maximum extent of breeding territory (Stefanski, 1967:Fig. 2), after which defended areas diminish in size. During this interval singing may begin without evident external stimulus.

TABLE 1

AN INDEX TO SEASONAL CHANGES IN INCIDENCE OF SINGING OF BLACK-CAPPED CHICKADEES IN 1965

Stage:	Pre-nesting	Nest-building	Egg-laying	Incubation	Nestling
Inclusive dates:	27 Mch–15 Ap	16 Ap–17 My	18–25 My	26 My–8 Jn	9–29 Jn
Observer hours:	39	70	15	15	13
Incidence[1]	1.8	7.3	5.7	3.7	2.6

[1] Percentage of observer's time on a territory during which that particular male sang.

However, the sporadic nature of the singing and the size of territory occupied make it difficult to ascertain the circumstances of initiation in many instances.

Male Black-capped Chickadees exhibit a strong tendency to answer the songs of other males with song, and to approach singing rivals. The data presented in Table 2 reflect this disposition (singer approached in 18 of 26 incidents of categories 1A, B; and in all 11 experiments in which song was

TABLE 2

SUMMARY OF ENCOUNTERS OF BLACK-CAPPED CHICKADEES

I.	Incidents initiated by distant detection of a singing rival		
	A. Song exchanges by neighboring territorial males	17	
	1. singers remained in stationary positions		8
	2. singers approached one another; confrontation ensued		9
	B. Song not answered but singer was approached; skirmish followed	8	
II.	Contests initiated at close range		
	A. Confrontations during which the intruder sang	11	
	1. defender responded with aggressive calls only		5
	2. defender responded with song		3
	3. defender evicted the intruder silently		3
	B. Incidents in which the defender alone sang	2	
III.	Encounters involving pursuit or physical contact by combatants	28	
	A. Aggressive calls but no song uttered while contestants were sparring		26
	B. Song uttered during skirmish		2
	C. Singing occurred subsequent to clash		6
IV.	Simulated violation of the territory		
	A. Playback of flock integration calls	12	
	Defender perched above speaker and sang		9
	B. Playback of song	11	
	Defender responded by singing while perched above speaker		11
V.	Attacks on a trapped chickadee by a free-ranging individual (winter)	28	
	Number in which either participant sang		0

broadcast in the territory). In a pattern typical for the pre-nesting and nest-building stages, males approach one another while singing loudly and steadily, accompanied by their mates. They meet at a point on a common, tentative boundary and engage in a sparring match involving supplanting attacks and short pursuits of one another. Once visual contact is established as the birds are in proximity, song is replaced by a variety of sibilant, sputtery calls, one of which is illustrated in Fig. 1D. Following this sparring, which may involve the females also, the participants withdraw gradually. When no longer in proximity one or both males may sing, although this is infrequent (Table 2, III C). Such boundary contests are not always preceded by countersinging, but the delivery of song by one of the males usually is effective in precipitating a skirmish. Thus, singing does not repel an established rival, but rather serves to attract rivals to sites at which territorial boundaries are reaffirmed. The system of establishment and maintenance of territorial boundaries, then, does not involve distant vocal threat, and thus it differs from that of most songbirds.

The role of song in attracting males to the territorial boundary has not been emphasized previously, although Odum (1941:324) described loud singing as a part of the "challenge" and ". . . preceding the actual chase." However, the responsiveness of chickadees to imitations of their song is well known ("quickest summons in the bird world," according to Dawson, 1923: 610), and the broadcasting of song usually attracts a singing male to the site (Table 2, IV B). In most of the simulated intrusions the responding male appeared to be searching for the rival.

We noted singing during a territorial skirmish on only two occasions. Brewer (1961:365), referring to this species and to *P. carolinensis*, stated that ". . . if close distance conflicts take place, they appear about the same as fights at any other season." We infer from this statement that he did not note singing as part of the contest.

Unmated males.—Loud singing by male chickadees is heard upon the temporary disappearance of their mates, and males that are unmated sing much more persistently than do territory holders. They tend to wander randomly, and to intersperse among their songs some calls that ordinarily are delivered only during skirmishes. This latter response was noted infrequently in mated males in the absence of a rival.

Two males lost their mates in the course of this study. Both abandoned their territories and wandered widely, giving songs intermingled with "fighting calls." The male widowed at a later stage of the cycle (hatching) sang less frequently and continuously. When they were intruding, both males were intimidated easily but they usually resumed singing after being "escorted"

to the boundary. We witnessed the expulsion of a singing transient chickadee by a resident male as late as 30 June, a date when some broods have fledged.

On 11 and 12 May 1965, the singing of an unmated (but banded) male precipitated a clash between two territory-holding pairs, and the contest was renewed repeatedly upon the resumption of singing by the non-participant. On several subsequent occasions this unmated male ceased singing when answered by a territory holder. This unmated male remained in the vicinity, and nested nearby in each of the two following seasons.

Low-volume singing.—Song of low volume occurs in a variety of situations involving intrapair communication. One of these is the "signal" song uttered by the male as he approaches the nest in which the female is incubating or brooding. Spectrographs (Fig. 1C) support the structural identity of this utterance to the "territorial" song.

Males frequently deliver songs of moderate to loud volume in an apparent attempt to lead their fledglings away from a source of disturbance. One brood, 3 days out of the nest on 6 July 1964, flew 40 feet through dense willow growth to the source of broadcast of tape-recorded songs. (Odum's observation of subdued singing by both parents as the brood was leaving the nest cavity may be interpreted similarly.) On 15 July 1964, a male answered a song played back in his vicinity, and the fledglings (one week out of the nest) appeared agitated by the singing. The male retained his perch, and the response of the fledglings diminished.

Low-volume songs differ markedly in context from the "whisper songs" of parulids, such as *Dendroica kirtlandii* (Mayfield, 1960:127).

SINGING BY FEMALES

Singing by female Black-capped Chickadees has been reported by several authors (Dwight, 1897; Odum, 1942). It usually is of low volume, and we noted it only under unusual circumstances.

On two occasions a particular male interrupted his participation in the excavation of the nest cavity to fly to the boundary and begin singing. His challenge was not answered, and his mate approached, sang softly, and "led" him back to the cavity on both occasions.

A female whose mate was killed by a Sharp-shinned Hawk (*Accipiter striatus*) on 6 April 1965, sang intermittently for several hours thereafter.

In one case, in which the brood was divided between the two parents, the female (known to be in her third breeding season) sang to lead the brood. Such singing by the female was not noted when both parents remained with the brood. In the following year this female's new mate, a second-year male, was not notably aggressive, and this female sang steadily at the territory boundary for 7 minutes. Her mate did not sing during this interval, and

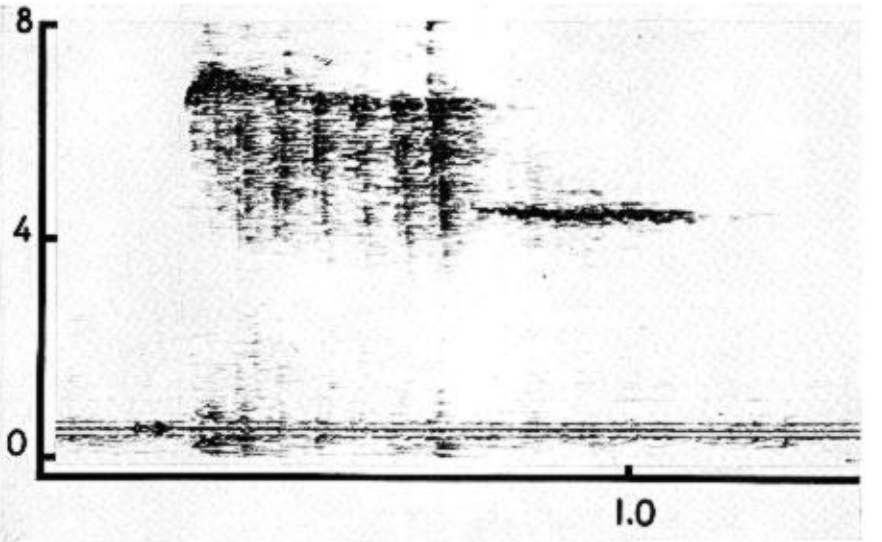

FIG. 2. "Chatter-fee" sequence uttered by a captive Black-capped Chickadee following separation from a social companion.

the "challenge" was not answered by any neighboring male. One female, known to be in her second nesting season, sang on several occasions in the temporary absence of her mate, and even answered his song softly at times during the nest-building and egg-laying stages. Another female delivered a "signal" song while approaching the nest 10 days after hatching. Thus, singing by females normally serves in intrapair or parent-offspring signalling.

OBSERVATIONS OF CAPTIVES

After two captive chickadees had been confined together in an observation room for one and one-half days or longer, a single-cell wire trap was placed on the floor. The member of the "couple" that was trapped effectively "disappeared," and the other bird usually paid little or no attention to the trap. Soon after the male of one couple was so trapped on 31 January his female companion, which had dominated him for the five days of their association, uttered a "chatter" similar to that denoting "disturbance" in other contexts, then a song note (Fig. 2). Similar sequences of softly-uttered song notes in a separation context were given by two males on 4 occasions when their partners were trapped or removed from the room. One female gave such a sequence twice, and a bird of undetermined sex did so once. The males sang at the "disappearance" of both male and female partners, and the female uttered song notes following the removal of both male and

female companions. On two other occasions females were silent and otherwise appeared unperturbed.

Although the absence of the mate has been suggested as a proximate cause for singing in many passerines (Andrew, 1961), three aspects of these observations of captives seem noteworthy. These are the short duration of acquaintance, the mid-winter condition, and the either-sex relationship.

DISCUSSION

Whether loudly or softly uttered, the song notes or *phoebe* whistles of Black-capped Chickadees serve as signals that function in attracting the recipient to the vicinity of the signaller. This "beckoning" function appears in the close-quarters intrapair signalling of either male or female (leading the mate to or from the nest, leading the brood, attraction of neighbors to a common territorial boundary). Even in the last context the mate as well as the rival may be "beckoned," thus facilitating defense of mate.

With the onset of the breeding season loud singing becomes associated with particular sites (although song is not delivered from an exposed perch). The possession of and tendency to defend an area is evident in the use of song by the territory holder in 20 of 23 simulated intrusions (Table 2, IV A, B). Further, the proclivity to answer the songs of other individuals is characteristic of this season. Possibly the "awakening song" (see Davis, 1958:327) serves also in the announcement of occupancy. However, "concern" with general area rather than precise territorial boundaries seems evident from our observations and those of Odum (1942:526).

The use of the *phoebe* notes by male and female in separation context, as "signal" song, and in leading the mate or brood, suggest the origin of this song as an intrapair signal, denoting a particular social relationship. The essential restriction of loud singing to breeding males, and in relation to occupancy of a particular area, suggest that the original intrapair signal was enhanced under hormonal influence. The disposition to *answer* a rival doubtless reflects a lowering of a threshold for aggression facilitated by androgens (see Marler and Hamilton, 1966:175). Although accompanied by ". . . a tendency for dominance to be linked with environmental references such as a territory" (Marler and Hamilton, loc. cit.), the song exchange in *Parus atricapillus* does not express as high a level of aggression as that found in boundary skirmishes.

The *phoebe* song seems to function as a means of locating the rival, challenging and beckoning him to a meeting site rather than as a means of repelling him from a fixed boundary. Individual recognition probably plays a role in such contests. For example, in the encounters observed on 11 and 12 May 1965, the mated territory holders clashed with one another, virtually ignoring

the unmated male whose singing had precipitated the contest. This specialized system of *atricapillus* relates to the transitory territorial boundaries (Stefanski, 1967) and to "sexual" territory (Odum, 1941:326), seasonally more extended than in Odum's original view. In the latter interpretation (defense of mate by confrontation rather than indirectly by the maintenance of precise boundaries), Mrs. Louise deK. Lawrence concurs (pers. comm., 1967). Thus the song of the Black-capped Chickadee does not serve as a distant threat or as a substitute for fighting as do the songs of most passerines (Thorpe, 1961: 43). In view of the postulated origin from contact calls rather than threat notes, and the unique territorial system of this species, these differences in function are not unexpected.

The proximate cause of singing in this species is not clear. In some situations (temporary separation, dawn singing) absence of the mate is the evident external stimulus. Immediately following a skirmish the withdrawal of the rival from the boundary may evoke singing, a point noted for *Parus major* by Hinde (1952:68), and for some other passerines by Andrew (1961:552). On several occasions during the nest-building phase we gained the impression that the males were "seeking" song exchange. Incidents such as that described under "Singing by Females" did not seem to represent a carryover from previous boundary confrontations. If the song were answered the initiator often was brought into a different stimulus situation, a skirmish in which further singing was replaced by more complex vocalizations reflecting stronger attack tendencies (see Fig. 1D).

A similar conclusion was reached for the Chaffinch (*Fringilla coelebs*) by Marler (1956:88). He stated that ". . . as soon as the conflict increases song stops" . . . and that ". . . it seems that song only accompanies the mildest tendency to attack." In these two species, then, song does not appear strongly aggressive in nature. However, in some other passerines, such as the Song Sparrow (*Melospiza melodia*) (Nice, 1943:154–156; J. A. Mulligan, pers. comm.), the American Robin (*Turdus migratorius*) (Young, 1951), and Rufous-sided Towhee (*Pipilo erythrophthalmus*) (Davis, 1958:317), low-volume, rapidly uttered versions of advertising song motifs are uttered during confrontations. Further, in the Plain Titmouse (*Parus inornatus*) (Dixon, 1949:117, 1969:96), singing may occur in the course of fighting, and may be directed at trapped conspecifics that are being attacked. In contrast (Table 2, IIIA, V) "fighting" calls rather than *phoebe* songs are uttered by Black-capped Chickadees in such skirmishes and attacks. Thus among the passerines there appear marked differences in the relationship of advertising song motifs to the threat or fighting calls that are uttered during confrontations.

Presumably the acoustic properties of the pure tones of intermediate

frequency (Fig. 1 A–C) are better suited to transmission in the dense swamp woodlands inhabited by many populations of this chickadee than are the fighting calls of varying frequency (see Marler, 1955:6). Hence the *phoebe* whistle has been enhanced as a distant signal denoting occupancy of an area, but the original valence in evoking an approach to the signaller has persisted.

SUMMARY

The contexts of singing were studied in a population of marked individuals of *Parus atricapillus*, and in short-term captives confined as couples. Exchange of the "whistled" song attracts rivals to a common boundary where a skirmish, accompanied by calls of varying frequency, may occur. Thus the song attracts rivals rather than repelling them. Songs of low volume are uttered by males when approaching the nest and when leading the mate or fledglings. Females sing softly in similar contexts of intrapair signalling. Captives of either sex delivered primitive song notes when separated from a partner of a few days' acquaintance.

In most contexts song seems to function as a summons. The origin appears to be from an intrapair signal enchanced by hormonal influence, and related to occupancy of an area. This song is not as indicative of a tendency to attack as are the fighting calls of varying frequency. The *phoebe* song does not function as a distant threat, and relates more to the defense of the mate than to defense of fixed boundaries. The structure of this song is such that it may be detected in dense woodlands at greater distances than the fighting calls.

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DEPARTMENT OF ZOOLOGY, UTAH STATE UNIVERSITY, LOGAN, UTAH 84321 (PRESENT ADDRESS, R.A.S.: DEPARTMENT OF ZOOLOGY, UNIVERSITY OF TORONTO, TORONTO, ONTARIO), 22 MAY 1968.

ANNOUNCEMENT

A symposium, "Distributional History of the Biota of the Southern Appalachians: Part 3, Vertebrates" is scheduled to be held at Virginia Polytechnic Institute, 25–27 June 1970, and will include the discussion of birds. Those interested may write for a program to: Jerry Hargis, Continuing Education Center, VPI, Blacksburg, Virginia 24061.