

THE ROLE OF CHIP CALLS IN WINTER TERRITORIALITY OF YELLOW WARBLERS

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Abstract.—The role of chip calls in the winter territoriality of Yellow Warblers (*Dendroica petechia*) was studied in the Republic of Panama. There was extensive variation through the day in chip rates and time spent chipping, with vocalizations greatest in the morning (0630–0830 h) and at dusk (1730–1830 h). A bout of rapid chipping at dusk was observed in several birds. Individuals responded aggressively to playbacks of chip calls by increasing chip rate and flying close to playback speakers. Yellow Warblers responded significantly more aggressively to chip calls of conspecifics than those of a control (Northern Waterthrush, *Seiurus noveboracensis*). Results suggest that Yellow Warbler chip vocalizations function in defense of winter territories. The role of the conspicuous dusk chipping bout remains to be determined.

EL ROL DE LAS LLAMADAS “CHIP” EN LA TERRITORIALIDAD INVERNAL DE *DENDROICA PETECHIA*

Sinopsis.—Se estudió el rol de las llamadas “chip” en el territorialismo invernal de *Dendroica petechia* en la República de Panamá. Se notó una gran variación tanto en las tasas de llamadas “chip” a través del día como en el tiempo invertido en esas llamadas, con más vocalizaciones en las mañanas (0630–0830) y al atardecer (1730–1830). Se notó una emisión de “chips” rápidos en ciertas aves. Las aves respondieron agresivamente al exponerse a las grabaciones de “chips” mediante el aumento en las tasas de emisión de “chips” y volando cerca de las bocinas. La especie respondió significativamente más agresiva a los “chips” de sus conspecificos que a los de una especie control (*Seiurus noveboracensis*). Los resultados sugieren que las vocalizaciones de *Dendroica petechia* sirven para defender territorios invernales. El rol del coro conspicuo de “chips” al atardecer queda por ser descifrado.

Most passerine species that breed in the temperate zone migrate to tropical or sub-tropical habitats for the winter (e.g., Holmes et al 1989, Keast 1980). Many of these species defend exclusive winter feeding territories (Holmes et al. 1989, Mabey and Morton 1992, Marra et al. 1993, Rappole and Warner 1980, Stutchbury 1994). However, studies of territory defense during the nonbreeding season are often based on anecdotal observations (e.g., Eaton 1953, Greenberg 1986; reviewed by Rappole and Warner 1980). Relatively little is known about winter territoriality of Neotropical migrants (Greenberg 1986, Rappole and Warner 1980).

In many passerine species, song plays an important role in defense of breeding territories (Falls 1988, Searcy and Andersson 1986). On the wintering grounds several warbler species utter chip calls [e.g., American Redstart, *Setophaga ruticilla* and Black-throated Blue Warbler, *Dendroica caerulescens* (Holmes et al. 1989); Kentucky Warbler, *Oporornis formosus* (Mabey and Morton 1992); Hooded Warbler, *Wilsonia citrina* (Stutchbury

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1994)] that, among other roles, may function in territory defense (Rappole and Warner 1980). However, quantitative data on this behavior are scarce.

Yellow Warblers (*Dendroica petechia*) are small, insectivorous songbirds that breed throughout most of North and Central America, and into South America. They winter from Mexico south to Peru and Brazil (Godfrey 1986). Birds begin arriving at the wintering grounds in late August, where they compete for feeding territories. Greenberg and Salgado Ortiz (1994) found that Yellow Warblers in Mexico tended to use vocalizations in territorial interactions with conspecifics. We observed that male and female Yellow Warblers wintering in Panama uttered chip calls throughout the day. We tested the hypothesis that chip vocalizations function in winter territory defense. We conducted watches on territories to document temporal patterns of chipping behavior and simulated territorial intrusions using playbacks of chip calls. We predicted that Yellow Warblers would respond more intensely to chip calls of conspecifics played back on their territories than to vocalizations of another warbler species.

METHODS

This study was conducted from 16–26 Feb. 1995 and 7–10 Mar. 1996 (early dry season) in Parque Nacional de Soberania, Republic of Panama (9°N, 80°W). The study site consisted of second-growth scrub forests located in the town of Gamboa. Territories were mapped by behavioral observations and subsequently measured (Rappole and Warner 1980). Territorial boundaries were determined by observations of border disputes and responses to playbacks. Although birds were not banded, individuals could be distinguished visually by plumage brightness and degree of red streaking on breast and flanks (Studd and Robertson 1985; Greenberg and Salgado Ortiz 1994).

Watches.—In order to measure chipping behavior, 1-h watches were performed in the morning (0630–0830 h EST), midday (1130–1330 h) and at dusk (1730–1830 h) for each of 12 birds (eight males and four females). Chip rate was defined as the number of chips per minute while a bird was chipping. Time spent chipping was the total time a bird was chipping within the hour watch. With one exception, individuals were not watched for two consecutive hours during morning and midday watches to improve representation of overall chipping behavior. Each individual was observed for a total of 6 h. Dusk watches were conducted 1 h before sunset when observations suggest chipping occurred most frequently.

Playback experiment.—We performed a 5-min playback of male Yellow Warbler chip vocalizations or Northern Waterthrush calls in each of 11 territories between 1600 and 1700 h. In addition, we conducted playbacks of Yellow Warbler chip calls on 12 more territories to increase our sample sizes for comparisons of responses between the sexes. The Northern Waterthrush (*Seiurus noveboracensis*) was chosen for the control because it often occurred in similar habitats as Yellow Warblers. Thus, Yellow War-

blers should be familiar with waterthrush vocalizations. Because the Northern Waterthrush forages on the ground, it is not a direct competitor and Yellow Warblers should not respond to it aggressively.

We placed a Realistic® tape player and speaker on the ground under trees centrally located within each bird's territory. We observed Yellow Warbler responses to playbacks from a distance of 20 m or greater so as not to influence the response. One observer watched the response with binoculars while another observer timed and recorded the behaviors. Responses to playbacks were based on the following observations: latency to respond, closest approach number of perch changes, chip rate for the first minute and total time responding after the playback ended. We defined a response as the territory owner flying to within 20 m of the playback speaker and/or vocalizing. We considered a bird to have stopped responding when it flew away from the playback speaker or stopped vocalizing and began to forage. We also noted chases involving conspecifics and other species during the playbacks. For the purpose of analysis, if a bird did not respond, we assigned a value of 20 m for closest approach because subjects could be readily seen within this distance. Similarly, a value of 5 min was assigned as the latency value if Yellow Warblers did not respond. We alternated between chip recordings of two different male Yellow Warblers for playback experiments to reduce the problems associated with pseudoreplication (Kroodsma 1989), however, we had only one recording of a Northern Waterthrush. Calls were played back at a rate of 50–60 per min. We never conducted playback experiments in the same territory, or in a neighboring territory, where a dusk watch had been scheduled for a given bird.

Statistical analyses.—Nonparametric tests were used because data were not normally distributed. Friedman tests were used for comparisons of chipping behavior at the three observation times. If the Friedman test was significant, Wilcoxon signed-rank tests were used to compare chipping behavior between different times of day. Wilcoxon signed-rank tests were used to compare responses of Yellow Warblers to calls of conspecifics and Northern Waterthrushes in a paired design. Male and female differences were analyzed using Mann-Whitney U-tests. Medians are given with interquartile ranges. Analyses and boxplots were performed using Stat-View® 4.51 (Abacus Concepts, Inc. 1992).

RESULTS

Daily patterns.—There was no significant difference between males and females in chip rates ($Z < 1.8$, $P > 0.05$) or time spent chipping ($Z < 1.2$, $P > 0.24$) throughout the day, thus the sexes were combined for the following analyses. Considerable variation in chip rates and time spent chipping existed among individuals (Figs. 1, 2). Rate of chipping differed significantly among time periods ($\chi^2 = 11.0$, $df = 2$, $P = 0.004$). Morning and dusk chip rates were significantly higher than midday ($Z = -2.4$, $P < 0.017$, for both comparisons; Fig. 1). Dusk chip rates (median = 26.9) were higher than morning rates (median = 17.2), but not signifi-

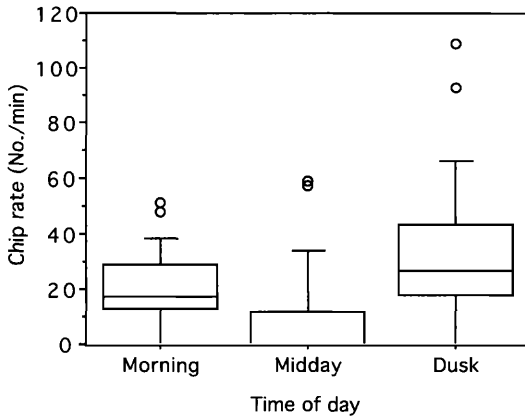


FIGURE 1. Boxplots of the chip rate of Yellow Warblers ($n = 12$) throughout the day in Gamboa, Republic of Panama, during 16–26 Feb. 1995. The boxplot shows the median, interquartile range, and the 10th and 90th percentiles. Observations beyond these limits are indicated by open circles.

cantly so ($Z = -1.8$, $P = 0.07$). Time spent chipping also differed significantly throughout the day ($\chi^2 = 15.5$, $df = 2$, $P = 0.0004$). Chipping occurred significantly more frequently during morning and dusk than at midday ($Z = -3.1$, $P < 0.003$, for both comparisons; Fig. 2). There was no significant difference in the amount of time spent chipping in the morning compared with dusk ($Z = -0.2$, $P > 0.8$).

Playback experiment.—Yellow Warblers responded significantly more intensely to chip vocalizations of conspecifics than to those of the control (Table 1). Yellow Warblers typically responded to playbacks of Yellow War-

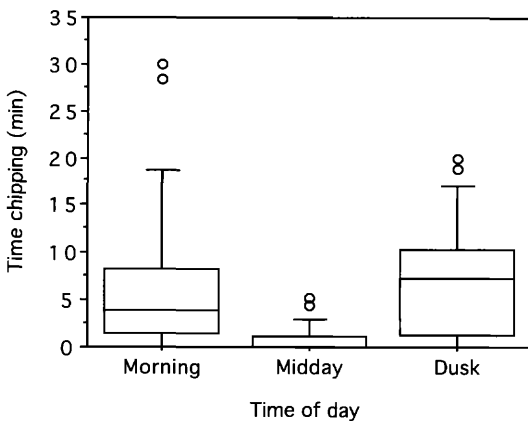


FIGURE 2. Boxplots of the time spent chipping by Yellow Warblers ($n = 12$) throughout the day in Gamboa, Republic of Panama, during 16–26 Feb. 1995.

TABLE 1. Comparison of the median (and interquartile range) responses of Yellow Warblers ($n = 11$) to playbacks of Yellow Warbler and Northern Waterthrush vocalizations from 7–10 Mar. 1996.

Response	Yellow Warbler	Northern Waterthrush	<i>P</i>
Distance at start (m)	25 (10)	20 (12)	0.18
Latency to respond (min)	0.5 (0.5)	3.5 (3.4)	0.05
Closest approach (m)	10 (12)	20 (4.5)	0.01
Perch changes	22 (23.5)	0 (0)	0.008
Response after playback (min)	3 (1.4)	0 (0.8)	0.03
Chip rate during playback (No./min)	72 (34)	0 (31.6)	0.02
Chip rate after playback (No./min)	49.5 (41.3)	0 (6.8)	0.008

bler chip calls on their territories with close approaches, perch changes and rapid chipping (Table 1). Yellow Warblers responded significantly more quickly and approached more closely to conspecific playbacks than the control. Perch changes and chip rates (both during and after the playback) were significantly greater in response to conspecific playbacks than the control. Only Yellow Warbler playbacks attracted neighboring conspecifics and resulted in chases between the resident and intruder ($n = 7$). There were no significant differences in how males and females responded to playbacks for any of the response variables tested ($Z < -1.6$, $P > 0.10$).

Ad hoc behavioral observations.—Yellow Warbler territory size averaged 1671.6 m² ($n = 9$). Territories were defended by single individuals and intrusions were frequent. Twenty-one chases were observed during daily watches, involving both males and females. In 15/21 (71%) chases, a Yellow Warbler territory owner was the aggressor; 6/21 (29%) involved conspecifics. Yellow Warblers were observed chasing Tennessee Warblers (*Vermivora peregrina*) and Blue-gray Tanagers (*Thraupis episcopus*) and were chased by Lesser Kiskadees (*Philohydor lictor*), Yellow-green Vireos (*Vireo flavoviridis*) and Orchard Orioles (*Icterus spurius*).

DISCUSSION

Chip calling by Yellow Warblers showed a daily pattern with more frequent and rapid vocalizations occurring in the morning and at dusk (Figs. 1, 2). Although not significant, chip rates were 50% faster at dusk than in the morning (Fig. 1). Chip calls appear to function in defense of winter territories in a similar manner to the functions of song on breeding territories. The increased rate of chipping at dusk could be analogous to the dusk choruses reported for many species on the breeding grounds (Armstrong 1963, Kacelnik and Krebs 1982, Slagsvold et al. 1994 for reviews). Many of the Yellow Warblers we watched chipped rapidly at dusk, sometimes uttering 100 calls per minute. Unlike other times of the day when chipping was less frequent, Yellow Warblers did not feed when they chipped rapidly. Perhaps territorial intrusions are more frequent at this

time causing Yellow Warblers to guard their territories more intensely. Rappole and Warner (1980) reported that Wood Thrushes (*Hylocichla mustelina*) utter call notes throughout the day, but most frequently under low light conditions.

Our results support those of Greenberg and Salgado Ortiz (1994), who found that territorial interactions between conspecific Yellow Warblers often involved vocalizations. Similarly to Greenberg and Salgado Ortiz (1994) we observed numerous interspecific interactions, which involved chases, but usually not chipping. Thus, Yellow Warbler chipping appears to function more in intraspecific rather than interspecific territoriality.

Yellow Warblers clearly distinguished between the calls of conspecifics and those of the Northern Waterthrush (Table 1). The intense behavioral responses of Yellow Warblers to playbacks of conspecific chip calls suggests that such calls function in defense of winter territories. In other studies, migratory songbirds such as the White-eyed Vireo (*Vireo griseus*), Worm-eating Warbler (*Helmitheros vermivorous*) and Wilson's Warbler (*Wilsonia pusilla*) also respond aggressively to playbacks (Greenberg et al. 1993, Rappole and Warner 1980). Similarly, Mabey and Morton (1992) reported that Kentucky Warblers responded aggressively to playbacks of conspecifics in Panama, with territory owners responding within one minute of the start of playback trials, similar to the results of our study.

Chipping behavior of Yellow Warblers apparently functions in territorial defense, but the purpose of the rapid dusk chipping bout requires further testing. Quantification of chipping behavior of Yellow Warblers at the time of territory establishment, as well as later in the season, and observations of intrusion rates throughout the day may shed some light on this question. The extent to which this behavior occurs in other migrant warblers remains to be determined.

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