SHORT COMMUNICATIONS

LEK BEHAVIOR OF THE GRAY-HOODED FLYCATCHER[1]

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Abstract. We studied the behavior of five Gray-hooded Flycatcher (*Mionectes rufiventris*) males on their display territories which were part of a dispersed lek located in a lowland Atlantic rain forest in southeast Brazil. The lek was active from the end of the short dry season in August to the following January. The number of territory-holding males fluctuated between four and nine. Calls were the main form of long-distance advertisement by males on display territories. These calls predominated in the morning, which corresponded to the period of greatest vocal and display activity by males. Aggressive "wiib" notes predominated in the afternoon. Call rate, which may affect mating success, varied among males. The lek behavior of the Gray-hooded Flycatcher showed similarities to and important differences from such behavior in the Ochre-bellied (*M. oleagineus*) and McConnell's Flycatchers (*M. macconnelli*).

Key words: Atlantic forest, Gray-hooded Flycatcher, lek behavior, Mionectes rufiventris, Tyrannidae.

Among tyrannids whose behavior is known, the genus *Mionectes* is unique because its members have a lek mating system (Willis et al. 1978, Snow and Snow 1979, Westcott and Smith 1994). Males of *Mionectes* species persistently call from individual territories that are either solitary or aggregated into groups of two to six (Snow and Snow 1979, Westcott and Smith 1994). Females are presumed to visit male territories for mating.

The lek behavior of the Ochre-bellied Flycatcher (*M. oleagineus*) has been well studied (Snow and Snow 1979, Westcott 1992, 1993, Westcott and Smith 1994), whereas that of McConnell's Flycatcher (*M. macconnelli*) has been studied to a lesser extent (Willis et al. 1978). Only limited observations are available for a third member of the genus, the Gray-hooded Flycatcher (*M. rufiventris*; Willis et al. 1978, Bencke 1995). Here we report on the lek behavior of five

males of the Gray-hooded Flycatcher, as well as on the characteristics of their territories, at a lowland Atlantic rain forest site in southeast Brazil.

According to Ridgely and Tudor (1994), Gray-hooded Flycatchers (14 g body mass; Pizo and Aleixo, unpubl. data) occur in southeast Brazil, eastern Paraguay, and northeast Argentina, occupying the understory of humid forests, secondary woodlands, and forest borders. Like other *Mionectes*, the plumage of the Gray-hooded Flycatcher is plain, olive green above, with a gray head and richly ochraceous lower underparts (Ridgely and Tudor 1994). The sexes are indistinguishable by plumage. *Mionectes* species, including the Gray-hooded Flycatcher (pers. observ.), are among the most frugivorous tyrannids (Traylor and Fitzpatrick 1982, Ridgely and Tudor 1994).

METHODS

The study was conducted between October 1995 and January 1996 at the Saibadela Research Station in Parque Estadual Intervales (24°16′S, 48°25′W), a 490-km² reserve in the Serra de Paranapiacaba mountains of São Paulo State, southeast Brazil. The study site ranges in elevation from 70 to 150 m. From a topographic map we estimated that approximately 50% of the area that we searched for lekking birds was composed of flat terrain, the remaining being hilly areas with ridges and pronounced slopes. The vegetation is chiefly old-growth forest (sensu Clark 1996) with trees reaching to 30 m and an open understory. Mean annual rainfall between 1994–1996 was 4,216 mm. Mean annual temperature for the same period was 23.6°C. Rains are distributed throughout the year with no month receiving less than 100 mm. However, rains are less intense and less frequent from April to August. The Gray-hooded Flycatcher is a common understory bird of the Saibadela Station, where it frequently joins mixed-species flocks (Pizo and Aleixo, unpubl. data).

Using mist-nets and playbacks of the Gray-hooded Flycatcher song, we captured and color-banded five territory owners (four clumped and one solitary). We assumed these individuals to be males because in lek-breeding birds only males defend territories on leks (see Westcott and Smith 1994). We monitored the behavior of banded males on their display territories during 1-hr observation periods between 06:00 and 17:00 for a total of 60 hr of observation (12 hr observation/
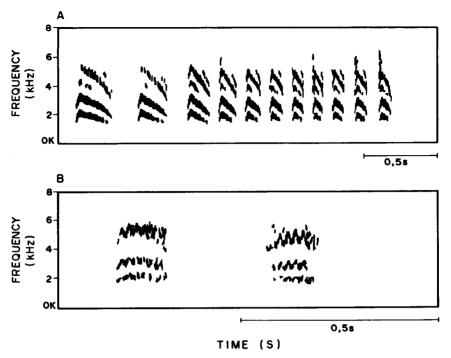
FIGURE 1.   Sonograms of the (A) advertisement and (B) aggressive calls emitted by male Gray-hooded Fly-catchers at their display territories. Recordings are deposited in the Library of Neotropical Songs (ASN) at the Bioacoustical Laboratory of the Universidade Estadual de Campinas, Campinas-SP, Brazil.

male × 5 males). The sequence of males observed and the time of observations on each male were randomly set. During each observation period, we recorded (1) the time spent by a male on its territory, (2) the time spent calling and the types of vocalizations, (3) the number of advertisement calls emitted during 1 min recorded at 5-min intervals, (4) the number and heights (visually estimated to the nearest 0.1 m) of perches used for advertisement calling (song posts), (5) the presence of intruders inside the territories, and (6) the behavior of the territory owner toward intruders. We applied the Kruskal-Wallis statistic (H) with normal approximation (Zar 1984) to test for interindividual and temporal variations in both the attendance of males at their territories and in call rate. Spearman rank correlations were used to test for associations between individual behavioral parameters (e.g., attendance at territories, mean call rate, percentage of time calling) and the number of conspecific intrusions into territories. In all tests, $P < 0.05$ was used to denote statistical significance. Values presented correspond to mean ± SE.

At the end of the study, we measured the area of each display territory considering them rectangular and taking the outermost song posts used by the owners as boundaries.

Vocalizations were recorded using an Uher 4400 IC tape recorder and a Sennheiser ME88 microphone. Sonograms were processed in a Macintosh Classic with the Mac Record Sound System 2.0.5.

RESULTS

Males started singing on their territories at the end of the short dry season (August 1995) and sang until the following January. Initially there were five birds defending territories in an area of approximately 30 ha. This number peaked in December when nine birds defended territories on the same area, and decreased to four territory owners in January. The nine territory owners recorded in December were clumped into two groups of three, and the remaining individuals (33.3 %) displayed solitarily, i.e., out of earshot of the others. The distance between the core areas of neighboring territories ranged from 20 m for clumped territories to approximately 300 m. Mean territory size was 961.5 ± 146.5 m² (range 658–1,456 m², $n = 5$). One out of the nine territories recorded in the study site was located on a ridge, whereas the others were in flat areas.

VOCALIZATIONS

As in other *Mionectes* species, song is the main form of long-distance advertisement by Gray-hooded Flycatcher males on display territories. The advertisement call consists of a series of "nasal notes that start slowly and then accelerate before abruptly stopping" (Ridgely and Tudor 1994; Fig. 1A). Willis et al. (1978) described this song as a series of "rin" notes, being "ant-bird-like" (i.e., similar to the songs of some *Thamnophilus*) or "nuthatch-like." This call is audible at distances of 50–60 m.
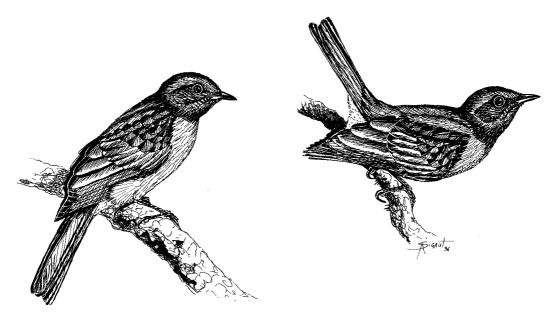
FIGURE 2. The "tail-cocked" display, a presumed courtship display involving a territory owner (right), and an intruder (left; presumed female). Territory owner raises his tail showing the ochraceous undertail coverts to the intruder while dropping and vibrating his wings.

A second type of vocalization consists of a series of "wiib," "thrush-like" notes, similar to alarm calls given by the Pale-breasted Thrush (*Turdus leucomelas*; Willis et al. 1978), and spaced at irregular intervals (Fig. 1B). This harsh call, which territory owners directed toward conspecific intruders, seems to play an aggressive role in the vocal repertoire of the Gray-hooded Flycatcher; it often preceded or followed chases involving intruders. The aggressive call, however, was not restricted to activities at the lek, being one of the vocalizations most frequently heard during the nonbreeding period when leks are deserted.

DISPLAYS

Eight of the 10 conspecific intruders recorded on display territories were promptly chased by territory owners. The remaining two intruders elicited, from two of the territory owners, a well-defined behavior that we interpret as a courtship display and named "tail-cocked" display. In these cases, recorded at 08:22 and 09:25, the territory owner approached the intruder, a presumed female, and facing the opposite direction raised its tail exposing the ochraceous undertail coverts toward it. Simultaneously, he dropped his wings and vibrated them rapidly (Fig. 2). Neither bird vocalized. The territory owner followed the intruder throughout the understory vegetation managing to keep its ochraceous underparts visible. Following this sequence, the intruder left, chased by the territory owner. The contact between the two participants inside the display territory lasted less than 1 min, and no copulatory attempt was observed.

In three instances, not related to intrusions, territory owners were observed performing a second silent solitary display that consisted of a series of "jumps" 20–30 cm high. The bird jumped and returned to the same position on a horizontal twig no more than 1 m above the ground. Birds spent no more than 30 sec jumping, and no special body posture could be observed.

BEHAVIOR OF MALES ON THEIR TERRITORIES

Daily attendance of males at territories on the lek varied greatly ($H_{11} = 38.9$, $P < 0.001$; Fig. 3). The morning corresponded to the period of greatest vocal and display activity by males. Between 06:00 and 10:00 males were on their territories 52.3% to 89.8% of the observation time, mainly calling, but sometimes preening and sallying out to capture insects from the living foliage. Between 11:00 and 13:00, absences became longer, and birds left their territories between 13:00 and 16:00, making only occasional, brief visits to the territories. Attendance increased between 16:00 and 18:00 (Fig. 3). Males moved widely throughout their territories using a mean of 10.2 ± 1.4 different song posts per observation period (range 1–34 song posts, $n = 29$). These posts were invariably slender horizontal branches 0.3 to 6.0 m above the ground (3.0 ± 0.1 m, $n = 102$).

Advertisement calls (Fig. 1A) were the chief vocalization emitted by territory owners between 06:00 and 12:00 (Fig. 4). Aggressive calls (Fig. 1B) emitted during this period generally were a response to the presence of a conspecific inside or near the territory. From 12:00 until 18:00, advertisement calls were rarely heard, and aggressive calls were the dominant vocalization in the territories (Fig. 4). During the afternoon, aggressive calls were emitted even in the absence of intruders.
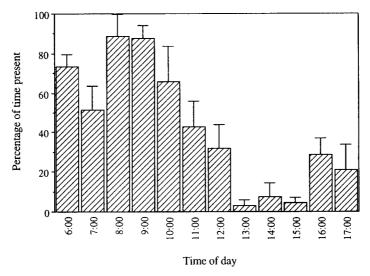
FIGURE 3.   Mean ($\pm$ SE) percentage of time males (n = 5) were present at territories throughout the day.

Advertisement calls were emitted at a mean rate of 2.6 $\pm$ 0.9 min^{-1} (range 0–5 calls min^{-1}, n = 178). However, the rate varied throughout the morning (H_6 = 60.8, P < 0.001) with a pronounced decrease between 11:00 and 12:00 (Fig. 5). Overall, territory owners gave advertisement and aggressive calls more frequently when returning from a chase. Advertisement call rate also varied among males (range 2.2–3.5 calls min^{-1}; H_4 = 17.3, P = 0.001). In addition, we detected a marginally significant interindividual difference in the percentage of time males dedicated to advertisement calling between 06:00 and 10:00, which corre-

sponded to the period of greatest vocal activity on the lek (range 54.3–98.7% of observation time; H_4 = 8.9, P = 0.06).

Nine of the 10 territory intrusions observed occurred between 06:00 and 10:00. Unfortunately, we were unable to distinguish between male and female intruders. The number of intrusions was negatively although not significantly correlated with the attendance at territories during the period of greatest activity on the lek (06:00–10:00), the percent of time males spent emitting the advertisement call, and their mean call rate (Table 1). The unique parameter marginally correlated
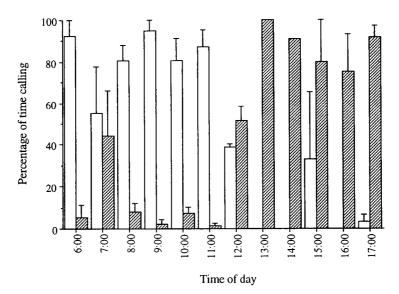

FIGURE 4.   Mean ($\pm$ SE) percentage of time during which males (n = 5) emitted their advertisement (open bars), and aggressive calls (hatched bars) throughout the day.
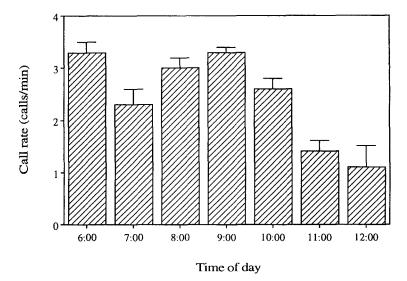
FIGURE 5. Mean (± SE) advertisement call rate of males throughout the morning. Call rates were recorded during 1 min at 5-min intervals.

with the number of intrusions was the attendance of males at their territories throughout the day (Table 1), which varied slightly although not significantly among males (range 30.4–47.0% of observation time; $H_4 = 2.1, P = 0.71$).

DISCUSSION

Although the lek behavior of male Gray-hooded Flycatchers is similar to the behavior of the other *Mionectes* species studied to date, important differences also were detected. Some of these similarities and differences in lek behavior are noteworthy because they may actually reflect phylogenetic relationships in this taxa (see Prum 1990, 1994). First, 33% of the Gray-hooded Flycatchers maintained solitary territories throughout the breeding season. Westcott and Smith (1994) found 22% and 28% of Ochre-bellied Flycatcher males ($n = 27$ and 21, respectively) displaying solitarily during their two-year study in Costa Rica. These figures taken together agree with the impression of

TABLE 1. Spearman rank correlations (r_s) between number of intrusions to male display territories ($n = 5$ males) and some behavioral variables of territory owners.

Variables	Total number of intrustions (r_s)
Attendance at territories (06:00–17:00)	−0.82[a]
Attendance at territories (06:00–10:00)[b]	−0.56
Mean call rate[c]	−0.56
Percentage of time calling[c]	−0.35

[a] $P = 0.06$; all other correlations are nonsignificant.
[b] Attendance at territories during the period of intense activity on the leks when most of the intrusions occurred.
[c] Mean call rate and percentage of time calling refer to the advertisment call.

Ridgely and Tudor (1994) that displaying males of the Gray-hooded Flycatcher are more solitary than Ochre-bellied males. The occurrence of males displaying solitarily is not unusual among lek-breeding birds, including *Mionectes* flycatchers (Willis et al. 1978, Westcott and Smith 1994 and references therein). This situation led Westcott and Smith (1994) to classify the Ochre-bellied Flycatcher as a lekking species with variable male display spacing. Based upon our observation of males holding solitary territories throughout the breeding season, whereas others held clumped territories, we suspect that this classification fits the Gray-hooded Flycatcher as well. In contrast to the Ochre-bellied Flycatcher in Costa Rica (Westcott 1993), Gray-hooded Flycatchers did not establish their territories at Saibadela Station along mountain ridges, and avoided pronounced slopes despite the general availability of both.

Although a male Gray-hooded Flycatcher occasionally emits the advertisement call from a perch near the ground, its song posts are, as noted by Willis et al. (1978), higher in the vegetation and more similar to those of the Ochre-bellied Flycatcher than to the McConnell's Flycatcher which "sings and displays near the ground, often near the base of a buttressed tree" (Willis et al. 1978). The fact that these *Mionectes* species are forest-dwelling birds, and that Willis et al. (1978) observed sympatric males of Ochre-bellied and McConnell's Flycatchers, supports the idea that differences in song post heights reflect actual differences in lek behavior rather than constraints imposed by vegetation structure. Observations on other populations of these *Mionectes* species will be required to confirm the generality of these differences.

The "jump" display of the Gray-hooded Flycatcher is not likely to correspond to the hovering display described for the Ochre-bellied (Westcott and Smith

1994) and McConnell's Flycatchers (Willis et al. 1978). Contrary to these species, the "jump" display of the Gray-hooded Flycatcher did not involve a hovering phase, and we did not observe any other bird in close proximity to the displaying male. The "tail-cocked" display (Fig. 2) apparently is not performed by either of the two other *Mionectes* species. In addition, we did not record the wing-flicking described for displaying males of the Ochre-bellied and McConnell's Flycatchers (Willis et al. 1978, Snow and Snow 1979, Ridgely and Tudor 1994). In fact, the absence of wing-flicking in the lek behavior of the Gray-hooded Flycatcher only reflects the absence (or rarity relative to the other *Mionectes* species) of these wing movements in its behavioral repertoire as a whole (pers. observ.). For the Ochre-bellied Flycatcher, in contrast, wing flicking is one of the most striking characteristics, even for individuals not involved in lekking activities (Skutch 1960).

The overall pattern of daily activity of Gray-hooded Flycatchers on their display territories was similar to that described by Westcott and Smith (1994) for the Ochre-bellied Flycatcher in Costa Rica. Advertisement calls that predominate in the morning period of intense vocal and display activity gave way to harsh, apparently aggressive, "wiib" vocalizations in the afternoon. Similar harsh calls are emitted by the Ochre-bellied and McConnell's Flycatchers and, at least for the former, these calls also seem to play an aggressive role because chasing between individuals is involved (Willis et al. 1978, Snow and Snow 1979). Although the "wiib" notes play a clear aggressive role related to the maintenance of territories on the lek, other functions can not be ruled out because this vocalization also is emitted during the nonbreeding period. Males vary in the advertisement call rate and probably also in the amount of time they dedicate to singing. If, as suggested for the Ochre-bellied Flycatcher (Westcott 1992) and other birds (Höglund and Alatalo 1995), male mating success is somehow positively correlated with song characteristics, then future investigations addressing this issue in the Gray-hooded Flycatcher should pay special attention to individual variation in song rate and time spent singing.

Westcott (1992) observed that experimentally muted males of the Ochre-bellied Flycatcher suffered an intrusion rate 22 times greater than that experienced by control males. The former invariably lost all or part of their territories to competing males. For the Gray-hooded Flycatcher, intrusions tended to be negatively correlated with the attendance of males at their territories. Thus it seems that for *Mionectes* flycatchers, intruders are especially attracted by territories that become silent, either because territory owners have left their territories unoccupied frequently or because they do not sing persistently. Both these possibilities point to the potential importance of song in the interactions of territory owners on the leks of *Mionectes* species.

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