BEHAVIOR AND SOCIAL ORGANIZATION DURING THE BREEDING SEASON IN *MIONECTES OLEAGINEUS,* A LEKKING FLYCATCHER[1]

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Abstract. The social systems and behavior of Tyrannids are best known for the North American representatives, a small percentage of a large and diverse family. In this paper, we describe the breeding season social organization and behavior of the Ochre-bellied Flycatcher, *Mionectes oleagineus,* a lek-breeding Neotropical Tyrannid. We describe three distinct categories of males. Territory owners defended display territories either solitarily or at small leks of two to six males. Territories at leks shared common defended boundaries and, overall, territories averaged 763 m² in size. About 10% of banded males behaved as subordinate satellites on the territories of other males. These individuals eventually replaced the owner on the territory. Forty-eight percent of banded males did not hold or associate with a display territory. Instead, these individuals behaved as floaters and moved widely over the study site. The majority of visitors at display territories were males, despite an apparently even sex ratio in the population. Interactions between individuals, including display and copulation, are described.

Key words: Tyrannidae; Mionectes oleagineus; *lekking; behavior; social organization.*

Resumen. La gran mayoria de los Tyrannidos son Neotropicales y son poco conocidos. Aquí se describe el comportamiento y sistema social del mosquerito aceitunado, *Mionectes oleagineus,* un Tyrannido Neotropical con un sistema social de lek. Se describe tres tipos de machos. Machos territoriales defienden territorios en leks o territorios solitarios. Territorios en leks comparten sus fronteras con sus vecinos. Aproximadamente 10% de los machos viven en territorios de otros machos como "satélites." Los satélites estan subordinados a los dueños de los territorios y reemplazan a los dueños cuando estos desaparecen del territorio. Los demás machos (48% de la poblacion de machos) no tienen territorio y se mueven por todas partes a menudo visitando territorios como intrusos. La mayoria de los visitantes de los territorios son machos, a pesar de una proporción sexual igual en la poblacion. Se describen las interaciones entre individuos, incluyendo despliegue y copula.

Palabras claves: Tyrannidae; Mionectes oleagineus; *leks, comportamiento; organización social.*

INTRODUCTION

With about 384 species, the family Tyrannidae is the largest avian family endemic to the Americas. Tyrannids are found throughout the Americas and in nearly every land habitat of the region (Keast 1972). Despite remarkable divergence in ecology, morphology and behavior in South America, the family is known almost entirely from the 32 very similar species that have invaded North America (Keast 1972, Traylor and Fitzpatrick 1982). Given the size and the diver-

sity of the family there is a need for better descriptions of all aspects of the natural history of Central and South American species. This basic information is lacking or incomplete even for many of the more common species.

The Ochre-bellied Flycatcher, *Mionectes oleagineus,* is one of these common but poorly known species. Found throughout the wet, lowland Neotropics (Meyer de Schauensee 1966), *M. oleagineus* is a resident of the lower levels of closed forest, occasionally venturing into adjacent woodland and clearings. In many areas, *M. oleagineus* is one of the more abundant understory species of primary forest (unpubl. data, Loiselle and Blake 1991, Karr 1982). However, in areas

where it occurs with other lowland congeners it may be restricted to second growth adjacent to primary forest (Willis et al. 1978).

A small (12 g), unpatterned, olive-green Tyrannid with an ochre-colored belly, *M. oleagineus* has been described by Skutch (1960) as ". . . one of the least prepossessing feathered creatures. . . ." Described by Keast (1972) as intermediate and unspecialized in foraging morphology, *M. oleagineus'* bill is long and narrow relative to those of species with similar diets (e.g., Piprids) and lacks the rictal bristles well developed in most other Tyrannids.

In two important traits, members of the genus *Mionectes* are divergent from other Tyrannids and appear more similar instead to manakins (Pipridae). First, while many Tyrannids include some fruit in their diets, *M. oleagineus* and its congeners are truly frugivorous (Traylor and Fitzpatrick 1982), taking a wide variety of fruits, berries and arils (Skutch 1960; Sherry 1983 and references therein). Second, members of the genus *Mionectes* are the only Tyrannids known to have a lek mating system (Skutch 1960, Snow and Snow 1979). In this paper, we concentrate on this latter trait, providing the first detailed information concerning the demography, social organization and male behavior of a population of *M. oleagineus*. We also provide the first description of display behavior for the species.

MATERIALS AND METHODS

The study was conducted between May and August 1989 and March and August 1990 at Estación Sirena (lat. 8°29'N, long. 83°36'W) in Corcovado National Park, Costa Rica. The study area is divided between low rugged hills (to 140 m in height) and flat areas (Fig. 1). The area receives a mean annual rainfall of 5,305 ± 301 mm, $n = 10$ years (Servicio de Parques Nacionales de Costa Rica). There is a distinct wet season between May and November, with peak rainfall occurring between September and November. The vegetation is tropical, pre-montane, wet forest (Tosi 1969) approximately 80% being primary forest while the remainder is 15 year-old second growth.

Birds were caught using mist-nets both at leks and at other locations on the study site. Upon capture, the following morphological data were collected for each bird: mass (to 0.25 g), tarsus length (to 0.02 mm), flattened wing chord, tail length (both to 0.5 mm), and culmen length, width

and depth (all three to 0.02 mm). Each bird was also given a unique color band combination.

The behavior of males on their display territories and that of their visitors was recorded during two-hour observation periods. Each male was observed at least once a week. During these observation periods, maps of the focal males' display territories were made. Territory boundaries corresponded with the outermost song posts used by the owner. The location of each male's display territory on the study site was subsequently plotted onto a topographical map (1:5000) of the study site (Fig. 1).

M. oleagineus is sexually monomorphic, with the sexes being indistinguishable, even in the hand. Two methods were used to assign a sex to each individual. Since *M. oleagineus* has a lek mating system, we assumed that all individuals trapped at nests, and subsequently observed caring for young, were females. All individuals that defended display territories by singing and chasing intruders were classed as males. The sample of individuals behaviorally sexed using these criteria was then used to calculate a canonical discriminant function to assign the sex of the remaining banded but unsexed birds.

RESULTS

We banded 130 birds, forty-one of which (12 females and 29 males) were sexed by their behavior. Using the morphological data from each of these individuals, a discriminant rule for sexing was constructed (Fig. 2). The trait means and standard deviations for each sex are given in Table 1, as is the standardized discriminant function coefficient. This value indicates the contribution of each trait to the construction of the discriminant function. Significant sex differences were found only in wing chord and tail length.

The discriminant function was then used to assign the sex of the remaining birds. Of these, 73 were males and 31 were females. The remaining 26 birds could not be sexed due to incomplete data resulting from molt, missing or broken feathers and escapes. The sex ratio at leks was highly skewed in favor of males (3:1) while an even sex ratio was observed away from leks (12 females and 11 males).

Skutch (1960) suggested that in *M. oleagineus*, gape color may be a sexually dimorphic trait with the gape of females being brown and that of males yellow. We found that in the Sirena population the gape color of the sexes did not differ. Both
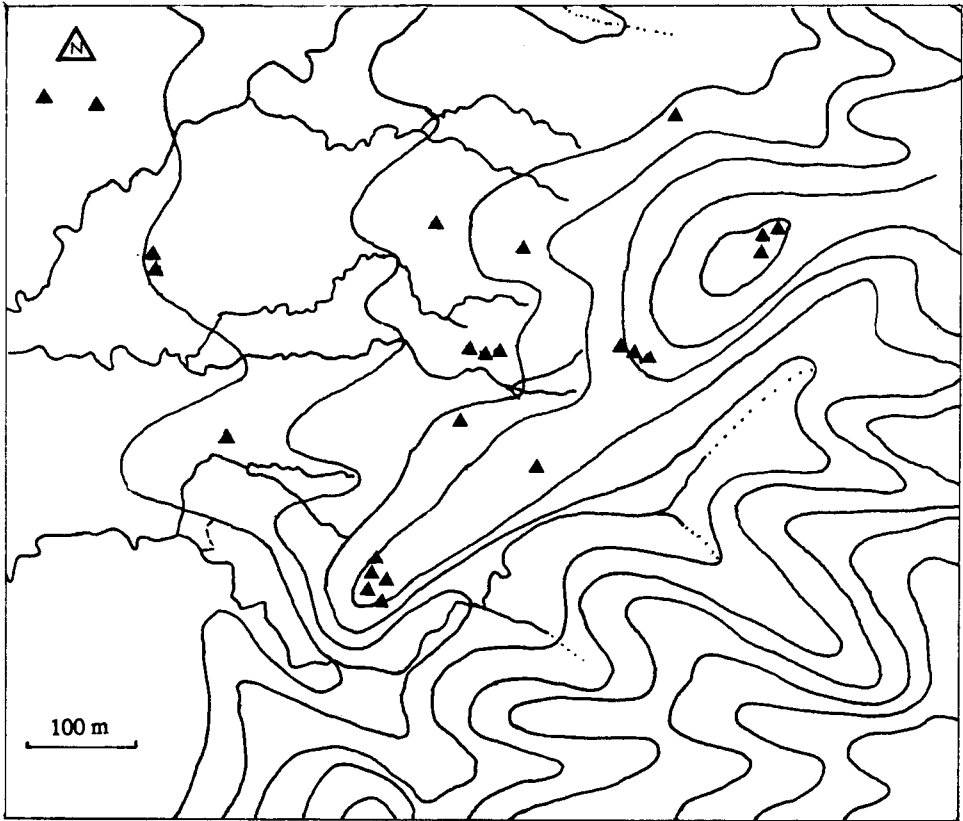
FIGURE 1. Map of the study site in 1989. The filled triangles are the display sites of individual males. Solid lines are creeks and contour lines. Contour lines are spaced at 20 m intervals.

males and females had both yellow and brown gapes. Furthermore, the gape color of two birds of each sex changed from yellow to tan to brown between the two years. No change from brown to yellow was observed.

MALE BEHAVIOR AND TERRITORIALITY

Observations at leks revealed three classes of males. We outline these classes and their distinguishing traits below.

TERRITORIAL MALES

These individuals defended display territories, at leks and in some cases solitarily, throughout the breeding season, from March to the onset of the heaviest rains of the wet season in early August (Fig. 3). Within these territories, territorial males displayed and attempted to displace other intruding males. The average territory size over both field seasons was 763 + 88 m² SE, $n = 46$ (median = 477 m²). At leks, neighboring males

often countersang from song posts located on or near either side of the territories' boundaries.

Intrusion, by both territorial neighbors and non-territorial males, was common (mean number of intruders = 0.6, ± 0.07 SE per observation period). The territory owner was nearly always dominant to intruders and chased them from the territory. In general, these chases terminated near the territory boundary and the owner would resume singing. Occasionally, however, an intruder would return repeatedly. These persistent intruders were always either non-territorial males attempting to usurp the territory owner or neighbors. The vigorous and aggressive chase of such intruders continued into neighboring territories and unoccupied habitat. The owner of a territory so invaded, if not already involved, often joined the chase. After such a chase territory owners often returned to their territory and remained quiet near the boundary, apparently waiting to surprise any new intrusion attempt.
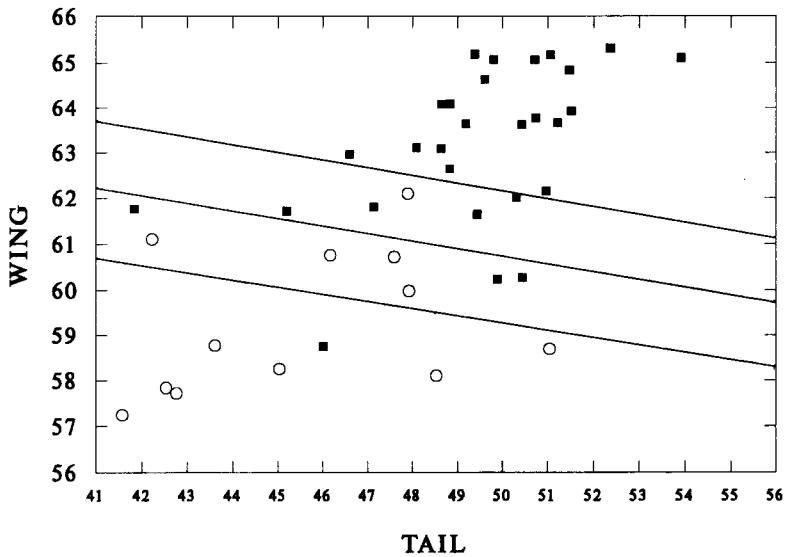
FIGURE 2. Contours describing the probability of being male and female derived from the discriminant function analysis: the upper line is the p(male) = 0.9 contour, the middle the p(female) = 0.5 contour, the bottom the p(female) = 0.9 contour. Plotted with the contours are the data used in the analysis; filled squares—males, open circles—females. The resubstitution error rate associated with the discriminant function was 0.14 for males and 0.08 for females.

Territorial males spent most of their time on their territories singing and preening (Fig. 4). Territories were seldom used for other purposes. Males did forage opportunistically on insects, hovering to take them in the air or to glean them from the undersides of leaves. On occasion, males also fed on the fruit of plants growing on their territories. Usually the plant was a small bush (e.g., *Psychotria* spp.) or epiphyte (e.g., a Bromeliad) which presented only a few fruits and consequently provided only a small part of the male's daily food intake. On three occasions, trees (*Clusea tovomitosis*, Cluseaceae) large enough to provide a significant proportion of a male's daily fruit intake, fruited on the territory. These fruiting events affected four territories. The males on these territories remained on territory and fed extensively at the tree. However, they did not attempt to exclude birds of either sex from their territories or the fruiting tree, nor did they display to either known banded or suspected females that fed at the tree.

SATELLITES

Though these individuals did not "own" territories, they associated almost exclusively with a single territory. For example, one male who was

banded initially as a floater (see below), appeared two weeks later as a satellite on a territory at a lek of five males. Over the next one and a half months he was resighted repeatedly during every observation period and recaptured five times on the same territory. He was neither sighted nor recaptured on any other territory at the lek nor elsewhere on the study site. Over the two years, seven males (9% of all banded males) behaved as satellites.

The relationship between the satellite and the territory owner was evolving. Initially, all satellites appeared simply to be persistent floaters. However, unlike floaters, they were seen day after day on the same territory and appeared to restrict their activities to that territory. Initially, satellites were completely subordinate to territorial males; they skulked near the ground, and were seldom seen when the territorial male was present. If such a satellite was discovered by a territorial male, it was quickly chased from the territory. In the absence of territorial males, satellites behaved as if they themselves owned the territory, singing, chasing intruders and, in the presence of females, displaying. However, they quickly desisted from these activities upon the return of the territory owner. The longer satellites
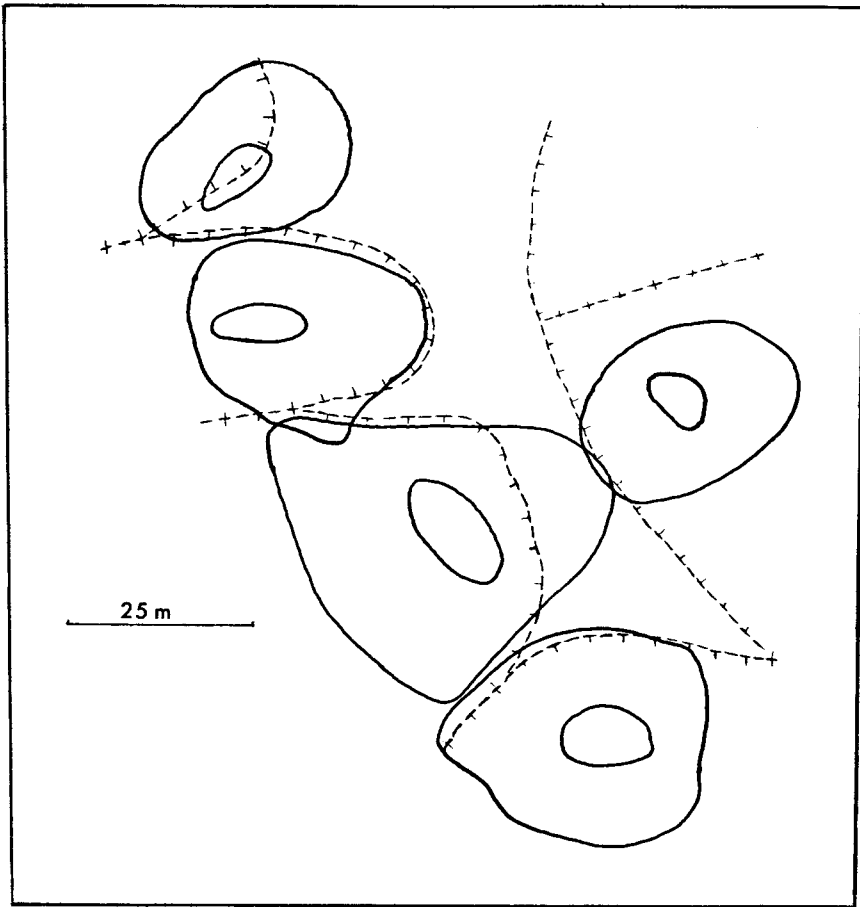
FIGURE 3. A map of a lek of five males. The heavy outer circles represent the boundaries of the display territory of each male. These boundaries correspond to the outermost song posts used by the territory owners. The inner most circles enclose the territories core area (where males spent 50% of their time). The dashed lines represent ridgelines, the terrain drops sharply on the side of the hatching. Note the corrrespondence between territory shape and topography.

remained on territories, the more assertive they became. They ceased to skulk on the territories and returned quickly after being chased. Eventually territorial males began to tolerate satellites and though satellites were not less likely to be present on the territory during the second half of their tenure (four of seven were seen more often, Sign Test, $P = 1.00$, $n = 7$), they were all chased by the territorial males less often (Sign Test, $P = 0.016$, $n = 7$). When attacked, five of seven satellites were more likely to return the attack in the second half of their tenure than in the first (Sign Test, $P = 0.125$, $n = 7$). Finally, in the second half of their tenure, all satellites sang and displayed more often in the owner's presence (Sign Test, $P = 0.016$, $n = 7$). A territory takeover usually occurred soon after the satellite began displaying in the territorial male's presence (mean = 16.6 days, $\pm$ 3.6 SE, $n = 7$).

The tenure of satellites varied greatly, presumably as a function of the ability of the territorial male to resist intrusion and expulsion. The mean satellite tenure prior to territory takeover was 53.5 days, $\pm$ 9.9 days SE, $n = 7$. Satellites appeared on territories in the first half of the breeding season and remained there until the territorial male was forced off, or abandoned the territory at the end of the breeding season. Three of seven satellites evicted their territory owners prior to the end of the breeding season, the re-
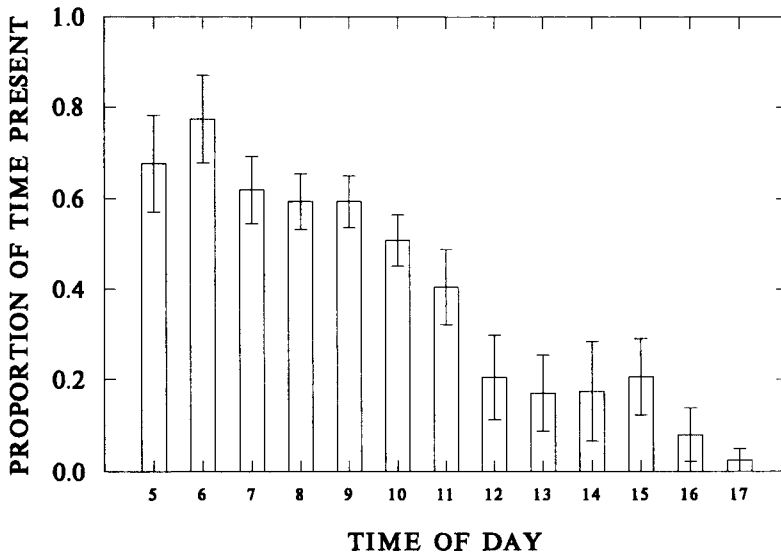
FIGURE 4.   The male daily time budget in terms of the average proportion of time (±SE) males were active on their territories during observations. The x axis refers to the hour during which the observations were begun.

maining four acquired the territory at the end of the breeding season. Of the three satellites present on the study site at the end of the 1989 breeding season, two were the territory owners at the beginning of the 1990 breeding season. The third was a floater, its territory having been destroyed by a tree fall during the non-breeding season.

FLOATERS

These males neither defended nor associated regularly with specific territories on the study site. Though they might have held territories elsewhere, searches at leks near but off the study site failed to locate territories held by apparent floaters. Floaters moved widely over the study site, presumably as part of their daily foraging movements. During these movements they were often seen as intruders on display territories at leks. Marked individuals were observed as intruders at leks as far apart as 700 m within 1.5 hr. Floaters were generally seen on the territory only briefly before being chased away by the territorial male. While individual floaters sometimes visited a display territory repeatedly in one observation period, they were not observed to do so on a daily basis. When at a lek, floaters sometimes visited all of the display territories. Floaters thus behaved as if they were sampling the ability of owners to defend their territories.

CHANGES IN MALE STATUS

Thirty-one males defended a total of 27 display territories during the two breeding seasons. Changes in territory ownership occurred by abandonment, and by eviction by another male (Table 2). Territories that were abandoned were either destroyed by treefalls ($n = 3$), or received few visitors compared to territories that were retained till the end of the breeding season (median number of visitors/observation period of retained territories = 2.063, of abandoned territories = 0.332, $U = 101.0$, $P = 0.003$). Males that were forced off their territories by males other than satellites experienced one to several days of continual intrusion and harassment. The territorial male eventually abandoned the attempt to exclude the intruder and left. Males that lost their territories were either not seen again (8 of 17), and presumably left the study site or died, were resighted as floaters (6 of 17), or moved to new territories (3 of 17). Over the study period, 42.5% of banded males were territory owners at some point, 9.5% were satellites and later territory owners, and 48% were only recorded as floaters.

DISPERSION OF TERRITORIES

Males defended display territories both solitarily and at leks (Table 3). These were "classical" leks

TABLE 1. Morphological measurements of males and females. Starred traits were significantly different between females and males at $P = 0.001$. Mass is measured in grams, all other traits are measured in millimeters. Sample sizes are, females $n = 12$, males $n = 29$.

Character	Female		Male		Standardized discriminant function coefficient
	Mean	SD	Mean	SD	
Mass	12.25	0.88	12.15	0.81	−0.0922
Tarsus	14.47	0.28	14.51	0.24	0.3388
Wing*	59.33	2.61	63.25	2.86	1.2914
Tail*	45.58	9.17	49.39	5.58	0.4020
Culmen length	9.10	0.22	9.18	0.10	−0.1605
Culmen width	8.30	2.16	8.92	1.38	−0.0276
Culmen depth	3.43	0.02	3.39	0.02	0.1348

(sensu Bradbury 1981) in that males held territories that were separated by common, defended boundaries and that these individuals were in both visual and vocal contact from within their territories (Fig. 3). Though lek arena locations were the same in both years, their sizes varied. In 1990, two solitary display territories were abandoned entirely during the breeding season. The male from one was not resighted while the male from the second forced a male off a solitary display territory 200 m away.

A Clark and Evans' Index of Aggregation (with Donnelly modification, Krebs 1989) showed that the distribution of display sites (i.e., any location with one or more display territories), across the study site was random in both years of the study (1989: Index of Aggregation $R = 1.031, P < 0.05$, $n = 14, z = -0.386$; 1990: $R = 0.91, P < 0.05$, $n = 12, z = -1.16$). Although 22% and 28% of males displayed solitarily in 1989 and 1990 respectively (Table 3), the distribution of display territories showed significant clumping (1989: R

$= 0.377, n = 27, z = -5.45, P < 0.05$; 1990: $R = 0.335, n = 21, z = -5.044, P < 0.05$; Fig. 1).

SONG

Display by males when alone on their territories, i.e., not in the presence of a female or an intruder, was composed entirely of advertisement song. Snow and Snow (1979) describe the song of *M. oleagineus* in Trinidad as falling into three types: "*chup*," "*up*" and "*char*." They describe the sequence of songs as being "*chup up*" repeated and interspersed with sets of char songs. On our study site, song could also be divided into three types which we have termed "*ipp*," "*eek*" and "*sweet*" (Fig. 5). These categories correspond to those of Snow and Snow (*chup = ipp, up = eek, char = sweet*). However, song in this population, particularly the sweet song, had a thin whistle-like quality that is not suggested by Snow and Snow's terms. In the population we studied, advertisement song consisted of a long series of ipps interspersed with sets of several sweets and an occasional eek. The rate at which males sang and the sequence of song types was extremely variable. Over the course of the study the average number of songs during a 2 hr observation period was 1,302 (SD = 1,240, $n = 201$), or one song every 5.5 sec. The most recorded in a single observation period was 4,006, or one song every 1.8 seconds.

INTERACTIONS AT DISPLAY TERRITORIES

On average, displaying males received 1.5 visitors per observation period (± 0.14 SE, $n = 201$): 0.3 females (± 0.03, $n = 201$) and 1.2 males (± 0.08 SE, $n = 201$). Below we describe the ("typical") interactions between territorial males and visitors of both sexes to their display territories.

TABLE 2. Summary of the circumstances under which territories were left by their owners. The "abandoned" category refers to males that left their territories due to tree falls, or for an undetermined reason. The "forced" category refers to males that lost their territories to males other than satellites. The "satellite" category refers to males that lost their territories to satellites from their territory.

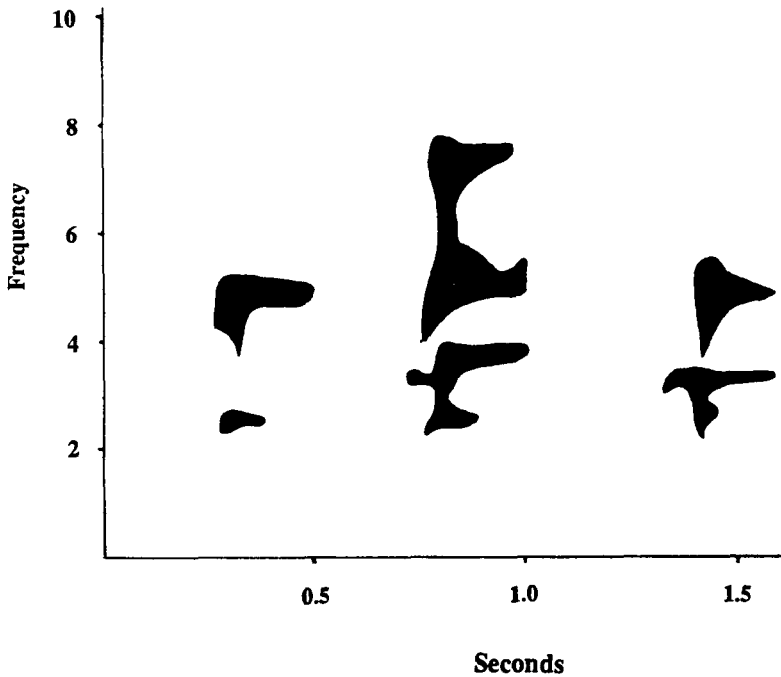| Year	Abandoned		Forced		Satellite		Total
	n	%	n	%	n	%	
1989	2	33	1	16	3	50	6
Between years	3	100	—	—	—	—	3
1990	2	25	2	25	4	50	8
Total	7		3		7		17

FIGURE 5. Sonograms of the three song types. Due to the amount of background noise from wind and insects tracing of the originals are presented. From left to right they are: *"ipp," "eek," "sweet."* The intervals between the song types have been adjusted for the figure.

MALE-MALE INTERACTIONS

Interactions between a territory owner and an intruding male were almost always aggressive, and resulted in the expulsion of one of them from the territory. Intrusion by males occurred both when a male was alone and singing on his territory, and as apparent interference by neighboring territory owners during display to a female.

Territorial defense was achieved through a combination of song and physical threat. Males prevented from singing lost their territories to other males (Westcott 1992). Physical threat usually involved chases and sometimes actual strikes. The typical response of territorial males to an intruder, either on or near their territories was to increase song rate. If the intruder remained on the territory, the male then began to *"trail"* him. Trailing involved following the intruder from a distance of 1–2 m. As the territorial male got closer to the intruder, the latter moved to a new perch. During trails, the territorial male typically ceased singing, though it was not unusual for occasional soft *"ipp"* calls to be given. The trail sequence was sometimes terminated by the intruder leaving the territory without a chase. More often the male, having landed close to the intruder, suddenly chased him. Chases generally lasted for only 2–3 sec. With persistent intruders, chases sometimes extended well beyond the boundaries of the territory into a neighboring territory or undefended forest.

MALE-FEMALE INTERACTIONS

Initially, female visitors provoked reactions from territorial males similar to male visitors. Once a male detected a female, he increased his song rate. While the female was present, he crouched and leaned forward, held his head tilted to one side, and his tail slightly lower than horizontal. He also greatly increased both the rate and the exaggeration of his wing flicking. Females also wing flicked constantly during visits.

As the female moved toward the center of the display territory, the male *"trailed"* her much as he would a male visitor. Display sequences sometimes contained several bouts of trailing of up to 3 min duration each. If the female left during trailing the male generally gave chase, though without the *"chur"* sounds that accom-

TABLE 3. Summary of the distribution of territorial males across display sites in the two years. Display site refers to any site where one or more display territories are located, lek arena refers to any display site where two or more males display.

Category	Year	
	1989	1990
No. of territories on the study site	27	21
No. solitary	7	6
No. of lek arenas	7	6
Mean territories/lek arena	3	2.5
Mean territories/display site	2.07	1.75

panied the chase of a male. The male then quickly returned to the territory and sang at an elevated rate for several minutes.

If a female remained on the territory, the male began one of three kinds of flight displays. Though all males apparently used all three displays, the sequence in which they were used, and the length of each display, varied depending on the male. If the female began to move away during these flight displays, the male reverted to trailing, or even to singing.

The first display was a "*hop*" between perches. In the early stages this consisted simply of a fast straight flight from one perch to a second, about 2 m distant, and then back. As the male landed, he simultaneously gave an "*eek*" call, hopped and flew back to his previous perch, or to one near by. This hop gave the impression that the male had bounced off the perch. As the male's display became more excited, the hops became repeated dashes between closer perches, often only separated by as little as 30 cm. Up to 10 hops were performed in 8 sec.

The second display was the "*flutter*" flight. This also involved a flight between two perches approximately 2 m apart. Rather than flying quickly between the perches, however, the male held his body vertically and flew in a slow, fluttering manner, describing a steep arc between the two perches. This flight is like the butterfly flight described for the manakin *Chiroxiphia linearis* (McDonald 1989a).

The final display, the "*hover*" flight, was performed either between two very close perches, or by returning to the same perch. The female was usually within a meter of the male. The male began to hover, rising 15–20 cm off his perch for several seconds before landing. If two perches were involved, the male performed a slow arc between them.

Though there was no set sequence to these displays, flight display tended to begin with hops, and if the female was still present, to terminate with hover displays. However, displays were performed at all stages.

Only one definite and one probable copulation were observed in 566 hr of observation. The definite copulation was performed by a male at a lek, while the probable copulation was performed by a solitary male. In each case, the female indicated her preparedness to copulate by crouching down on the branch with her tail raised. The male immediately landed next to her and mounted her, covering her with his wings. On one occasion the male had been performing a hover display when the female adopted this precopulatory pose. On the other, the male was performing a short flutter flight. During the probable copulation the male was not settled stably on the female and the copulation lasted for only 10 sec. The female left the territory immediately. The definite copulation lasted for 36 sec. After the male dismounted both birds flew to low perches and preened briefly. The female left the territory within 1 min. In all, this visit lasted for 3 min and 40 sec and was the last of four visits by the female during that observation period.

FEMALE MIMICRY BY MALES

Apparent mimicry of female visitors by males was observed on 12 occasions. We were alerted to this behavior by the chases accompanied by "*chur*" calls that terminated some visits by females. These *chur* calls were usually associated with chases of male intruders. The sex of these birds was later confirmed using morphological data. In four cases, the mimic was present during a visit by a female. In each case, the interaction between the mimic and the territorial male resembled that usually seen between a male and a female, with the exception of the final chase accompanied by "*chur*" calls. These interactions sometimes only included trails, but also included flight displays. In one such instance, the mimicking male was the owner of the territory next to that of the displaying male.

DISCUSSION

SEX DETERMINATION AND MONOMORPHISM

Unlike two previous studies of *M. oleagineus*, we found no readily identifiable, sexually di-

morphic traits in our population. Snow and Snow (1979) noted that male *M. oleagineus pallidiventris* from Trinidad showed emargination of the outer four primaries, whereas the females did not. *M. oleagineus dyscola,* the race we studied, showed no sex differences in primary emargination nor in the gape color, as reported by Skutch (1960). This latter trait, however, appears to be highly variable over the species' range. While present in birds at Belém, Brazil (Lovejoy in Willis et al. 1978), it is absent in Trinidadian birds (Snow and Snow 1979). In the population we studied at Sirena, gape color varied: individuals of both sexes had yellow or brown gapes. Over the period of our study, the gapes of some individuals, including nesting females and territorial males, changed from yellow to brown. This suggests that gape color is related to age or to the sexual status of the individual rather than to its sex per se.

Avian lek mating systems are usually thought to be associated with striking sexual dimorphism in size and or plumage traits. Höglund (1989) showed that lekking and sexual dimorphism are positively correlated in birds. However, he also found that if phylogenetic trees are examined, dimorphism in size or plumage often arises prior to lekking. Additionally, because the number of independent origins of lekking is far fewer than the observed instances of the behavior, the correlation between lek mating systems and the degree of sexual dimorphism disappears (Höglund 1989). Further, approximately 25% of known avian lek-breeding species are monomorphic in color and size (Trail 1990). Trail (1990) suggests that monomorphism in lek breeding birds may be due to (1) phylogenetic constraints; (2) sexual selection focusing on behavior rather than morphological traits; or (3) to social selection (Crook 1972, West-Eberhard 1979) favoring monomorphism due to advantages in social interactions, e.g., deceitful behavior. Of these three hypotheses, Trail (1990) suggests that for *M. oleagineus,* phylogenetic constraints may be the most reasonable explanation. Our observations of female mimicry by males and particularly the use of song by females as a mate choice cue (Westcott 1992), suggest that any, or all, of Trail's hypotheses may explain the persistence of monomorphism in this species. This question has yet to be adequately addressed for *M. oleagineus.*

Sexual monomorphism allows effective intersexual mimicry (though mimicry does not nec-essarily require that the mimic look like a member of the opposite sex, e.g., Trail [1985]). For all categories of males, mimicry both delayed chases of the mimics, and increased the proximity of the mimics to the territory owners. Benefits for inexperienced males might include the opportunity to observe display behavior at close range, and a chance for the mimic to safely assess the vigor of the territory owner. Mimicry during a visit by a female might allow intruders to interfere in the territory owner's display and/or his attempts to copulate. More importantly, mimicry might give males the opportunity to obtain copulations when females visit the territory of another male. A combination of female mimicry and attempted copulation by males on the territories of other males has been reported on leks of buff-breasted sandpiper, *Tryngites subruffi-colis* (Myers 1979), and was suspected on leks of the capuchinbird, *Perissocephalus tricolor,* by Trail (1990).

MATING SYSTEM

Our observations of behavior at display sites indicate that *M. oleagineus* has a true lek mating system, sensu Bradbury (1981). Display territories are spatially clumped. Males provide no assistance to females in rearing their young in this species (Skutch 1960; unpubl. data) and females choose their mates. Finally, display territories do not contain resources that females cannot obtain elsewhere. The three occasions when fruiting trees were observed on display territories appear to have been purely coincidental: the territorial males did not try to exclude other males from fruiting trees, nor did they display to females that visited the trees. The odd lack of territorial defense at such times may be due to high intrusion pressure making such defense uneconomical (Davies and Houston 1984). The lack of display to females is more difficult to explain, unless foraging females simply did not provide males with any cues for sexual identity and went unrecognized or weren't receptive at the time.

With three categories of male, *M. oleagineus* has a complex male social organization for a lek-breeding bird. Though several social categories have been reported for males in other lekking species, this has usually been in association with some factor limiting male options for breeding, e.g., cooperative display (McDonald 1989b), genetically distinct mating strategies (Van Rhijn 1983), or unpredictable female behavior and

numbers (Lank and Smith 1987). In *M. oleagineus,* we could not identify any factor that limited the ability of satellites and floaters to defend display territories. Limited habitat availability was considered as a factor influencing male settlement, but had no effect (Westcott 1993). Through interference, territorial males may deter nonterritorial males from establishing display territories. Observations of aggressive responses by territory owners to new males singing from unoccupied adjacent areas suggest that such aggression could prevent males from settling at leks (unpubl. data). The appropriate response by males unable to resist such aggression may be to postpone settlement. Another possibility is that the combined costs of territorial defense, display and foraging may simply be too great for subordinate or inexperienced males, forcing them to delay their settlement.

While either of these hypotheses may explain the floaters' decision not to settle, explaining satelliting is more problematical. The behavior of satellites indicates that they are capable not only of balancing the costs of display, defence and foraging but also of weathering the aggression of owners. Since all seven satellites we observed eventually became territory owners, it seems reasonable to interpret their behavior as a waiting strategy that insures territory ownership once the current owner leaves. Among the benefits of such a strategy is the inheritance of a territory whose value is known to both the satellite and to females. Also, tenure as a satellite allows a male to advertise himself as a potential mate prior to becoming a territory owner. Both possibilities may be advantageous in species where females return to the same territory or to the same male to mate (e.g., Kruijt and de Vos 1988, Lill 1976, Trail and Adams 1989, Pruett-Jones and Pruett-Jones 1990). Does the territory owner benefit from the presence of the satellite? In the absence of the owner the satellite both sings and defends the territory. Both these activities may benefit the owner, since, even in his absence, his territory remains attractive to females that can potentially be courted upon his return.

The relations between territory owners and satellites in this species are reminiscent of those of cooperatively displaying species, e.g., manakins, *Chiroxiphia* spp. (Foster 1981, McDonald 1989) and *Pipra fascicauda* (Robbins 1985). While those between *M. oleagineus* males are much shorter and not cooperative, they possibly represent a precursor to full cooperation between males. The nature of these relationships and the pay-offs for the participants warrants further investigation.

Previous authors reported that *M. oleagineus* males display at exploded leks or as dispersed individuals (Skutch 1960, Slud 1964, Meyer de Schauensee 1966, Snow and Snow 1979), although a single case of a classical lek in Costa Rica was reported by Sherry (1983). Our study indicates that, at least at Sirena, small classical leks are common. We suggest that this is so elsewhere. The failure of others to note leks could be due to limited sampling; previous workers have studied only a small number of males (Skutch 1960, Snow and Snow 1979). Given the within population variation in display dispersion and that only a single male is usually visible from a single location, classical leks in this species are easily overlooked.

We documented the entire range of possible male display dispersions, solitary, exploded and classical (Bradbury 1981) at Sirena. Though such extreme variation in male display dispersion is not commonly associated with lek mating systems, solitarily displaying males have been reported in a variety of species where most males display at leks (manakins, Snow 1962, Lill 1976; grouse, Kruijt and Hogan 1967; bulbuls, Brossett 1982; birds of paradise, Pruett-Jones and Pruett-Jones 1990). Kruijt and Hogan (1967) showed that in black grouse, *Lyrurus tetrix,* such solitary males were juveniles or subordinates. Brossett (1982) suggested that this was also true for the yellow-whiskered greenbul, *Andropadus latirostris,* since solitary display sites lasted for only a few days. In *M. oleagineus,* solitary display territories remained occupied by the same male, and in some instances by several males in succession over both breeding seasons. These territories were subjected to forced take-overs, and some attracted satellites. Also, solitary males successfully attracted female visitors, and the presumed copulation was performed by a solitarily displaying male. It seems unlikely, then, that solitary display is a temporary strategy. Therefore, we follow Pruett-Jones and Pruett-Jones' (1990) terminology and describe the mating system of *M. oleagineus* as a lek mating system with variable male display dispersion.

ACKNOWLEDGMENTS

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