BEHAVIOUR AND SOCIAL ORGANIZATION DURING THE BREEDING SEASON IN <u>MIONECTES</u> <u>OLEAGINEUS</u> (AVES, TYRANNIDAE).

by

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B.Sc. (Hons.), Australian National University, 1987

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF MASTERS IN SCIENCE

in

THE DEPARTMENT OF ZOOLOGY

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

May 1991

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Date _22/5/91_

Abstract:

Mionectes oleagineus (Aves, Tyrannidae) is a small, sexually monomorphic, lek breeding bird. The behaviour and mating system of this species were studied on Costa Rica's Osa Peninsula over two years. In this thesis I ask three questions: 1) What kind of social organization does M. oleagineus exhibit? 2) Does habitat influence male display dispersion? and 3) What is the function of song in attracting mates and in male-male interactions?

In Chapter 2, I describe M. oleagineus' social organization. There were three categories of males: territory owners, satellites and floaters. The latter 2 categories were non-territorial and represented half of the male population. I describe interactions between displaying males and visitors to their territories, including courtship display and aggressive interactions between males. Male display dispersion was highly variable in the study area, including classical leks, in which territories shared contiguous boundaries, an exploded lek, where the territories did not share boundaries, and solitary display territories.

In Chapter 3, I test the hypothesis that the number of males that can settle in an area, and their subsequent display dispersion, is determined by the availability and dispersion of suitable habitat. Discriminant function analysis of measures of vegetation structure from both territories and non-territory sample plots showed that territory habitat could be distinguished from non-territory habitat. Eleven percent of the sample plots were described as suitable habitat in the analysis. Given that half the male population is non-territorial, the existence of unoccupied, suitable habitat makes it unlikely that habitat availability determines the number of males settling, or their display dispersion.

The major occupation of males on their display territories is singing. In Chapter 4, I investigate the function of song for M. oleagineus using behavioural observation and an experiment involving temporary muting. Males which sang at higher rates received more visitors of both sexes. The territories of most muted territorial males were rapidly usurped by other males. Two of the muted males regained their territories upon regaining the ability to sing. This study is the first to directly demonstrate a key role for song in male-male interactions on leks. It also provides evidence that females use song in mate assessment.

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Acknowledgements

I owe thanks to many individuals, probably too many to mention. Probably too many for me to remember them all.

First I must thank Robin and Laurie who have yet to say anything. I must also thank Louise who was instrumental in making this thesis happen.

At U.B.C. I have been priviledged in the company that I have been able to keep. In particular Jamie Smith has been a generous advisor. The calm reception he extended to my many extraordinary propositions was totally disconcerting. The members of my committee, Lee Gass, Charlie Krebs, Dolph Schluter, and Ron Ydenberg all provided much needed and helpful comments, discussion, and advice. I usually bounced my ideas off Wes Hochachka first. Though he eventually sought refuge in Toronto, he was always willing to listen to me. A variety of people read parts of my thesis or my proposals, or discussed my research with me they included; Lance Barrett-Lenard, Nick Folkard, Todd Hatfield, Trevor Price, and Dick Repasky. Alistair Blachford, Marc Labelle, Xavier Lambin, Joerg Messner, Dick Repasky and Wes Hochachka all helped me meet the challenge of my computing and analysis problems. Many others were good company.

In Sirena, Christine Chesson and Arne Mooers graciously endured primitive living conditions, low pay, extreme boredom, lots of nasties, endless rice and beans, and me. They were cheerful, interested, and dilligent workers. They made the field work pleasant and possible. Los trabajadores del Servicio de Parques Nacionales, Christina, Don Felix, Don Hector, y Adrian Arias Navarro fueron buenos amigos. Les agradezco por su hospitalidad. Gracias al pueblo y gobierno de Costa Rica, especialmente al Servicio de Parques Nacionales de Costa Rica, por el permiso para trabajar en su pais.

Chapter One

General Introduction

In lek mating systems males hold small display territories and these are clustered together onto "leks" (Selous 1906-1907). Females do not obtain resources on the display territories of males, and a male's sole contribution to the female and their joint offspring is sperm. Consequently, females visit leks only to choose mates and to copulate. In most polygynous mating systems, males gain reproductive access to females by defending resources, females, or both from other males (Oring 1982). Because males on leks defend neither females nor resources (Snow 1976; Bradbury 1981), females are able to choose their mates free of male coercion.

Lek mating systems present two major questions, both of which I address in this thesis. The first is: what factors determine the dispersion of males and lead to the evolution of leks? Though lek mating systems are generally rare in any single taxon, e.g. they are known to occur in only 1% of bird species (Trail 1990), they are found in most higher animal taxa, e.g. birds, mammals, fish, anurans, and many insect groups. Despite this general distribution and the interest of many theoreticians and empiricists (e.g. Snow 1962; Koivisto 1965; Hjorth 1970; Snow 1976; Bradbury 1981; Bradbury et al. 1986; Beehler and Foster 1988), the answer to this first question remains elusive. The second question raised by leks concerns the basis of female mate choice. On leks, females are free to choose their mates, and receive only sperm from them. This means that female mate choice can be studied free of the effects of material benefits from the male (sensu Borgia 1979) that may mask the effects of any genetic benefits. Thus, leks are ideal systems for studying the basis and consequences of mate choice.

Typically, studies of lek mating systems have documented the behaviour of highly sexually dimorphic species on large, dense leks. Almost without exception, they have considered only a single, or a very few (Lill 1974; Gibson and Bradbury 1987), large leks within a population. Thus our knowledge of lek mating systems is based on a

set of extreme examples. There are several problems with this. First, while the extremes are spectacular and bizarre, they inadequately represent a large proportion of known lek mating systems. Second, processes that seem important on large leks, and for strongly dimorphic species, are not necessarily the important processes in the evolution of the mating system. Thus, we risk being blinded to other processes that may better further our knowledge (Höglund and Robertson 1990; Trail 1990). Finally, by ignoring intra-specific variation in mating systems, we forego the opportunity to compare the costs and benefits of particular mating strategies, and the chance to explore the factors that shape lek systems.

In this thesis I examine the lek mating system of the ochre-bellied flycatcher, Mionectes oleagineus. My aims are to provide background natural history on a species that has variable display dispersion and that is monomorphic in size and plumage, and to examine aspects of its social organization. In Chapter 2, I describe: social organization; behaviour related to reproduction; and the dynamics in of the social system. In Chapter 3, I ask whether the availability of suitable habitat limits the number of males that settle, and whether the distribution of suitable habitat determines the display dispersion of males. In Chapter 4, I use both behavioural observations and a field experiment to explore the role of song on leks in: 1) attracting mates and 2) territorial interactions between males.

Chapter Two

Behaviour and Social Organization during the Breeding Season

Introduction.

The ochre-bellied flycatcher, Mionectes oleagineus (Aves, Tyrannidae), is a small (12 gm), olive-green bird with a black bill and an ochre-coloured belly. It is usually a solitary species (Skutch 1960; Slud 1964) and resides in the understory of wet lowland forests from Mexico to southern Amazonia, including Trinidad and Tobago (Meyer de Schauensee 1966). Skutch (1960) described the species as an outstanding example of a bird with no distinguishing physical features; however, it is distinct from other tyrannids in several ways. In a family well known for its radiation and specialization, M. oleagineus is intermediate and unspecialized in morphology (Keast 1971). This is perhaps because it has an unusual diet for a tyrannid, most of which is fruit (Sherry 1983, and references therein). Also, in a family thought to be almost exclusively monogamous, M. oleagineus has a lek mating system (Skutch 1960: Snow and Snow 1979).

Skutch (1960) and Snow and Snow (1979) provided some information concerning morphology, nesting, diet, song, and the social organization of M. oleagineus. Sherry (1983) reviewed these and other scattered references to the species. In this chapter I add to this previous work by providing the first detailed information concerning demography, social organization and behaviour of a population of M. oleagineus. I also provide the first description of display behaviour for the species.

Methods.

The study was conducted between May and August 1989 and March and July 1990 at Estacion Sirena (lat. 8° 29' N, long. 83° 36' W) in Corcovado National Park, Costa Rica (Figure 2.1). The study site is approximately 1 km^2 in area and is divided

between low rugged hills (to approximately 130 m in height) and flat areas (Figure 2.2). The area receives a mean annual rainfall of 5305 mm (S.D. = 953 mm, n = 10 years; data from the records of the Servicio de Parques Nacionales de Costa Rica). There is a distinct wet season between May and November, with peak rainfall occurring in September and November. The vegetation is tropical, pre-montane, wet forest (Tosi 1969) and approximately 80% of it is primary forest with a canopy height of approximately 35 m. The remainder is 15 year-old second growth with a variable canopy height.

Birds were caught using mist-nets placed in the forest understory. Most mist-netting was conducted at leks. However, I also netted at other locations on the study site in an attempt to catch individuals that might not have been visiting leks. In hilly areas, nets were placed on ridges, particularly in saddles on ridge lines, and at the heads and mouths of valleys and gullies. In flat areas nets were placed randomly. Upon capture, the following morphological data were collected for each bird: mass, tarsus length, flattened wing chord, tail length, and culmen length, width and depth. Each bird was also given a unique colour band combination.

All male display territories on the study site (n = 27 in 1989 and n = 24 in 1990) were located and plotted onto a map (1:5000) of the study site. The behaviour of males and their visitors on these display sites was recorded during two-hour observation periods. Each male was observed at least once a week. During these observation periods, I made maps of the display territories of the focal males.

M. oleagineus is a sexually monomorphic species 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-like mating system, I assumed 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 classified as males. Once a sufficiently large sample of behaviourally sexed individuals was obtained, I used canonical discriminant function analysis to derive a discriminant rule by which to sex the remaining banded but unsexed birds.

Results.

In total, 130 birds were banded during the two field seasons. Forty-one of these (12 females and 29 males) were sexed by their behaviour. Using the morphological data from each of these individuals, a discriminant rule for sexing was constructed (Figure 2.3). The traits and their means and standard deviations for each sex are given in Table 2.1, as is the standardized discriminant function coefficient. This value indicates the contribution of each trait to the construction of the discriminant function. Significant differences were found only in wing chord and tail length.

The discriminant function was then used to assign the remaining birds to either the male or female categories. This analysis showed that of the total of 130 individual birds banded, 73 were males and 31 were females. Twenty six 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).

The gape colour of the sexes did not differ. Both males and females had both yellow and brown gapes. Furthermore, the gape colour of 2 birds of each sex changed from yellow to tan or brown between the two years.

Male Behaviour and Territoriality.

Observations at leks revealed 3 classes of males. Below I outline each of these classes and their distinguishing traits:

Territorial Males.

These individuals defended display territories at leks throughout the breeding season, from March through to the onset of the heaviest rains of the wet season in early August. These territories had defined boundaries within which males displayed and attempted to displace intruding males. The average territory size over both field seasons was 763 m^2 ($\pm$ 595 S.D., n = 46). This is about the area of a circle with a 15 m radius, though all territories were irregularly shaped. The boundaries of territories corresponded with the outermost song posts used by the territorial males. At leks, neighbouring males often countersang from songposts located on either side of these boundaries. Even vigorous aggressive chases of intruders did not usually cross territorial boundaries, though the territory owner sometimes followed the intruder into the adjacent territory. Intrusion, generally by non-territorial males, was common (mean # of intruders = 1.2, $\pm$ 2.08 S.D. per 2 hour observation period). The territory owner was nearly always dominant to intruders and chased them from the territory.

Though territorial males often preened, they spent most of their time on their territories in display, i.e. singing. Territories were seldom used for other purposes. In over 400 hours of observation, males foraged for insects only 21 times, although, occasionally, males fed on the fruit of plants growing on their territories. Usually the plant was a small bush (e.g.. Psycotria spp.) or an 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 3 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 4 territories. The males on these territories remained on the 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 known banded females that fed at the tree.

Floaters.

These males neither defended nor regularly associated with territories on the study site. Though they might have held territories elsewhere, searches at leks 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 hours. Floaters were generally seen on the territory only briefly before being chased away by the territorial male. Though floaters sometimes visited a display territory repeatedly in one observation period, they did not do so on a daily basis. When at a lek, they sometimes visited all of the display territories. Floaters behaved as if they were sampling the status of territories and their owners' ability to defend them.

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, appeared two weeks later as a satellite on a territory at a lek of 5 males. Over the next one and a half months he was resighted repeatedly during every observation period and recaptured there 5 times. He was not sighted or recaptured on any other territory at the lek or elsewhere on the study site. Over the two years, 7 males (9% of all banded males) behaved as satellites.

The relationship between the satellite and the territory owner was an evolving one. All 7 satellites initially appeared simply to be persistent floaters. However, unlike floaters, they were seen day after day, and restricted their activities to single territories. At first, satellites were completely subordinate to the territorial males; they skulked around low down on the territory, and were seldom seen when the territorial male was present. If the territorial male discovered a satellite he quickly chased it from the territory. In the absence of territorial males, satellites sang and displayed in the presence of females. However, they quickly desisted from display or song upon the return of the territorial male. The longer satellites remained on territories, the more assertive they became. They ceased to skulk on the territories and returned to the territory quickly after being chased. Eventually territorial males tolerated satellites, even when the territory owners were displaying to females. In advanced stages of the relationship satellites began to sing and display even in the presence of territorial males. Once the relationship reached this stage, a territory takeover usually occurred soon after.

How long satellites remained as satellites varied greatly, and was apparently a function of the ability of the territorial male to resist intrusion and/or expulsion. In 1989, the mean tenure as a satellite was 37 days (SD = 6.8, n = 3 different satellites). This figure, however, is probably conservative, due to the shorter field season that year. In 1990, the mean tenure as a satellite was 67.5 days (SD = 30, n = 4). In 1990, 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 7 satellites evicted their territory owners prior to the end of the breeding season, and the remaining 4 took over the territory at the end of the breeding season. Of the 3 satellites present on the study site at the end of the 1989 breeding season, 2 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 wet season.

Changes in Male Status.

Thirty-one males defended a total of 27 display territories during the two breeding seasons. Changes in territory ownership occurred as a result of: abandonment; males being forced off by a floater or a territorial male; and by losses to satellites (Table 2.2). 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 (U = 621.5, p = 0.007, n = 4). Males that were forced off their territories by males other than satellites experienced 1 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 period of the study, 42.5% of banded males were territory owners at some point, 9.5% were satellites and later territory owners, and 48% were only floaters.

Song.

Display by males when alone on territories was composed entirely of advertisement song. Snow and Snow (1979) describe 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 my study site, song could also be divided into three types which I have termed "ipp", "eek" and "sweet" (Figure 2.4). 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 I 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 was extremely variable. Over the course of the study the average number of songs during a 2 hour observation period was 1302 (SD = 1240, n = 201), or one song every 5.5 seconds. The most recorded in a single observation period was 4006, or 1 song every 1.8 seconds.

Dispersion of Territories.

Males defended display territories both solitarily and at leks. The mean number of males displaying at a lek in this population was 2.1 (range 1 - 6, SD = 1.44, n = 46). In 1989 there were 6 solitary display sites and 7 leks, and in 1990 there were 6 solitary display sites and 6 leks found on the study area. Though the leks were at the same sites 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.

Although 22% of the males displayed solitarily, a Clark and Evans nearest neighbour test shows that the distribution of display territories over the study site differed significantly from random (Index of Aggregation R = 0.383, z =-5.53, p << 0.05) and was obviously clumped (Figure 2.1). The distribution of leks (i.e. any location where one or more display territories can be found) did not differ from random (R = 1.068, z = 0.47, p > 0.05).

Three types of lek were observed on the study site. Seven were classical leks where males held territories that were separated by common, defended boundaries. These individuals were in both visual and vocal contact from within their territories. One lek was an exploded lek with the display territories of the two males being separated by approximately 40 m. At this distance song of M. oleagineus is audible to the human ear only under permissive environmental conditions. Finally, 6 territories were solitary.

Interactions at Display Territories.

On average, displaying males received 1.5 visitors per 2 hour observation period (SD = 1.99, n = 201): 0.3 females (SD = 0.42, n = 201) and 1.2 males (SD = 1.2, n = 201). Below I describe the "typical" interactions between territorial males and visitors of both sexes to their display territories.

Male-Male Interactions.

Interactions between a territory owner and an intruding male were almost all 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 neighbouring territory owners when a territorial male was displaying to a female.

Territorial defense was achieved through a combination of song and physical threat. Males prevented from singing could not prevent other males from taking over their territories (Chapter 4). Physical threat usually involved chases and sometimes actual strikes. The typical response of territorial males to male intruders, 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 to sing constantly, 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 seconds, and 1 or 2 chases were usually all that was required before

the intruder left. If an intruder was persistent, chases sometimes extended well beyond the boundaries of the territory.

Male-Female Interactions.

Initially, female visitors provoked similar reactions from territorial males as did male visitors. Once a male detected a female, he increased his song rate. While the female was present, he leaned forward, held his head as if looking up, and held his tail slightly lower than horizontal. He also greatly increased both the rate and the exaggeration of his wing flicking. Females, too, maintained high rates of wing flicking during visits.

As the female moved toward the centre 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 minutes duration each. If the female left during trailing the male generally gave chase, though without the "chur" sounds that accompanied 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 1 of 3 kinds of flight displays. Though all males apparently used all 3 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 metres 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 seconds.

The second display was the "flutter" flight. This also involved a flight between two perches approximately 2 metres 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 (D.B. McDonald 1989 b).

The final display was the "hover" flight. This was performed either between two very close perches, or by returning to the same perch. The female was usually within a metre 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 could be performed at any stage. As display became more intense, the pair generally moved to a location with close perches, such as inside the crown of an understory tree or bush.

Only 1 definite and 1 probable copulation were observed. The definite copulation was performed by a male at a lek, while the probable copulation was performed by a solitarily displaying male. In each case, the female indicated her preparedness to copulate by crouching down on the branch with her tail raised and her

head forward. 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 pre-copulatory 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 seconds. The female left the territory immediately. The definite copulation lasted for 36 seconds. After the male dismounted both birds flew to low perches and preened briefly. The female left the territory within 1 minute. In all, this visit lasted for 3 minutes and 40 seconds and was the last of 4 visits by the female during the observation period.

Female Mimicry by Males.

Mimicry of female visitors by males was observed on 12 occasions. I was alerted to this by the chases accompanied by "chur" calls that terminated some visits by "females". The sex of these birds was later confirmed using morphological data. In 4 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 the authors of the 2 previous studies of M. oleagineus, I found no readily identifiable, sexually dimorphic traits. Snow and Snow (1979) noted that male M. oleagineus pallidiventris from Trinidad showed emargination of the outer 4 primaries,

whereas the females did not. M. oleagineus dyscola, the race I studied, showed no sex differences in the emargination of primaries. Nor did I note the sex related differences in gape colour reported by Skutch (1960). Skutch described the yellow gape as a persistent juvenile trait found only in males, but it appears to be highly variable over the species' range. Lovejoy (in Willis et al. 1978) noted a yellow gape in birds at Belém, Brazil, while it is absent in Trinidadian birds (Snow and Snow 1979). In the population I studied at Sirena, gape colour varied: individuals of both sexes had yellow or brown gapes. Over the period of my study, the gapes of some individuals, including nesting females and territorial males, changed from yellow to brown. This suggests that gape colour is related to age or to the sexual status of the individual.

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. However, he also found that if phylogenetic trees are examined, dimorphism in size and/or plumage often arises prior to lekking. Additionally, the number of independent origins of lekking is far fewer than the observed instances of lekking. Thus, the correlation between lek mating systems and sexual dimorphism disappears (Höglund 1989). Further, approximately 25% of known avian lek-breeding species are monomorphic in colour and size (Trail 1990). Trail suggests that monomorphism in lek breeding birds may be due to: a) phylogenetic inertia, b) sexual selection focusing on behaviour rather than morphological traits, or c) to "social' selection (Crook 1972; West-Eberhard 1983) favouring monomorphism due to advantages in social interactions, e.g. deceitful behaviour. Of these three hypotheses, Trail (1990) suggests that for M. oleagineus, phylogenetic constraints may be the most reasonable explanation. However, my observation of female mimicry by males and the use of song by females as a mate choice cue (Chapter 4), suggest that any or all of Trail's hypotheses may explain the persistence of monomorphism in this species.

Sexual monomorphism allows effective inter-sexual mimicry (though mimicry does not necessarily require that the mimic look like a member of the opposite sex, e.g. Trail (1985 b)). For all categories of males, mimicry both delayed chases of the mimics by the territory owners, and increased the proximity of the mimics to the territory owners. Benefits for inexperienced males might include the opportunity to observe display behaviour at close range, and a chance for the mimic to assess the vigor of the territory owner safely. 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 subrufficolis_, (Myers 1979) and was suspected on leks of capuchinbird, _Perissocephalus tricolor_, by Trail (1990). This same advantage has also been hypothesised to explain delayed plumage maturation in many avian species (Foster 1987).

Mating System.

My observations of behaviour at display sites indicate that _M. oleagineus_ has a true lek mating system, _sensu_ Bradbury (1981). Males defended spatially clumped display territories. Males provide no assistance to females in rearing their young in this species (Skutch 1960; unpubl. data) and are unable to force females to remain on their territories to mate. Consequently, females can choose their mates. Finally, display territories do not contain resources that females require. The three occasions when fruiting trees were observed on display territories appear to have been purely coincidental: the males did not try to exclude other males, nor did they display to females visiting the trees. The lack of territorial defense at such times may be due to high

intrusion pressure making territorial 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 thus went unrecognized.

With 3 categories of male, M. oleagineus has a complicated male social organization for a lek-breeding bird. Though several categories of male have been reported for other lekking birds, this has usually been in association with some factor limiting the male's options for breeding, e.g. cooperative display (D.B. McDonald 1989 a), genetically distinct mating strategies (Van Rhijn 1983), or changing female behaviour and numbers (Lank and Smith 1987). In M. oleagineus, I could not identify a factor that limited the ability of satellites and floaters to defend display territories. In Chapter 3, I consider the possibility that there is insufficient suitable display habitat available, but I found that this was not the case. Alternatively, through interference, territorial males may deter non-territorial males from establishing display territories. Aggressive responses by territorial males to new males singing on unoccupied areas adjacent to their territories suggest that such aggression prevents males from settling at leks. The appropriate response by males unable to resist such aggression may be to wait, as satellites or floaters. Finally, the costs of territorial defense, display and foraging may simply be too great for subordinate males.

Previous authors have 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). My study indicates that, at least at Sirena, small classical leks are common. I suggest that this is so elsewhere. The failure of other authors to note leks could be due to limited sampling, since previous workers have studied only a small

number of males (Skutch 1960; Snow and Snow 1979). Since males defend display territories with radii of approximately 10 - 15 m, often only one displaying male is visible from a given point. Also, the display dispersion within the population is extremely variable. Consequently, classical leks in this species are easily overlooked.

I 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, I 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.

Table 2.1: 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 millimetres.

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

Table 2.2: 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		Force		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		

Figure 2.1: Map of the Republic of Costa Rica, showing the location of Corcovado National Park and Sirena.

Figure 2.2: Map of the Sirena area. The study site comprises the middle band of the map. The filled triangles are the display sites of individual males. Dashed lines are trails. Solid lines are creeks and contour lines. Contour lines are spaced at 20 m intervals.

Figure 2.3: Contours describing the probability of being male and female derived from the discriminant function analysis.

Figure 2.4: Sonograms of the three song types. Due to the amount of background noise from insects and other animals tracings of the original sonograms are presented here. From left to right they are: ipp, eek, sweet. The intervals between the songs have been adjusted for the figure.

Chapter Three

Habitat Characteristics of Lek Sites and Their Availability.

Introduction

One of the most conspicuous characteristics of lek mating systems is the leks themselves. Leks are aggregations of small male display territories that contain no resources required by females. Consequently, they are defended by males for display to females. Females visit leks to choose mates and to copulate. After copulation, females leave and care for the offspring alone , while males remain at the lek displaying. In some species, leks of up to several dozen males defend display territories that are clumped together (e.g. sage grouse, Centrocercus urophasianus, Gibson and Bradbury 1987; cock-of-the-rock, Rupicola rupicola, Trail 1985a), while in other species leks may consist of only 1 or 2 males (e.g. three-wattled bellbird, Procnias tricarunculata, Snow 1976; Lawe's parotia, Parotia lawesii, Beehler and Pruett-Jones 1983). Not surprisingly, the question of why male distribution is clumped has attracted much attention from both empiricists and theorists (e.g. Snow 1962; Koivisto 1965; Hjorth 1970; Snow 1976; Bradbury 1981; Beehler and Foster 1988).

Males are generally believed to cluster their display territories onto leks for one of three non-exclusive reasons: 1) females prefer clustered males (Alexander 1975; Bradbury 1981; Wrangham 1981; Avery 1984), 2) males that are unsuccessful in attracting females and obtaining matings cluster around attractive, successful males (Beehler and Foster 1988; Höglund and Robertson 1990), 3) males cluster where female densities are highest (Bradbury 1981). Although, these hypotheses have generated a great deal of interest, few researchers ha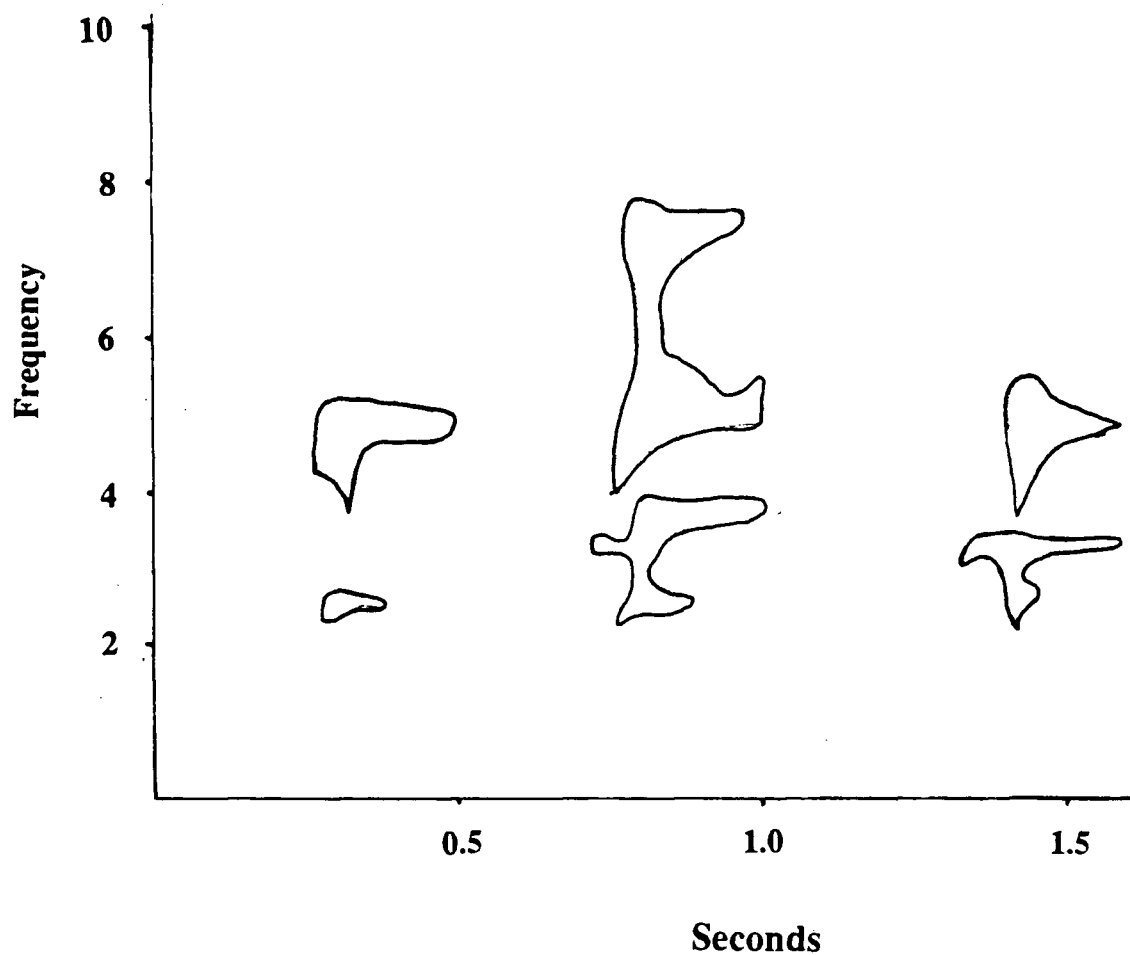ve considered the possibility that simple environmental limitations may influence the display dispersion of males. This chapter considers the hypothesis that male display dispersion is determined by the availability and distribution of suitable display habitat (Snow 1974; Gullion 1976; Boag and Sumanik 1969; Bradbury 1981).

The "habitat limitation" hypothesis suggests that males require a certain habitat type for display territories. For leks to form, this habitat type should be sufficiently limiting that males are obliged to aggregate in the available patches. Several authors have noted a preference by males for a specific display habitat, and some have confirmed this with both mensurative (Hamerstrom and Hamerstrom 1957) and manipulative (Anderson 1969) experiments. Few authors have attempted to quantify the differences between the characteristics of lek and non-lek sites (but see Boag and Sumanik 1969, and Pruett-Jones and Pruett-Jones 1986). To my knowledge no-one has attempted to determine the effect of the availability and distribution of suitable display habitat on male dispersion.

This study addressed habitat selection and the availability and distribution of suitable display habitat for the lek mating ochre-bellied flycatcher, <u>Mionectes oleagineus</u>. My aims were to determine:

a) whether display territories differed in terms of vegetation structure or in topographical placement from randomly chosen plots.

b) whether suitable display habitat was limiting.

c) whether the distribution of apparently suitable display habitat and male display territories suggests an influence of habitat on the male display dispersion observed.

Methods

Data Collection and Analysis: An Overview.

This analysis was conducted in two stages. The first was a descriptive stage in which data were collected and analysed to determine whether "territory habitat"

could be distinguished from "non-territory habitat". In the second stage a new data set was collected and the discrimination technique obtained in the first section was used to assign the new observations to either the territory or non-territory categories. The aim of the second stage was to determine the availability and distribution of apparently suitable habitat. This process is outlined in greater detail below.

Habitat Description.

I first asked whether leks are distinguishable from randomly chosen plots on the basis of topographical location and vegetation structure. To do this, measures of vegetation structure (listed and defined in Table 3.1) were taken on 25 display territories and 27 non-territory plots. The 27 non-territory plots were chosen by generating 27 sets of random x and y co-ordinates. These co-ordinates were then marked on a map of the study site and located on the ground using angles and distance from known locations. None of the plots was located within 50 metres of the edge of a lek.

A sampling quadrat, consisting of a circle with a 5 metre radius (78 m^2), was laid out on each territory and plot . On display territories this quadrat was positioned over the owner's centre of activity on the territory (based on maps of male movements made during behavioural observations; see Chapter 2).

Analysis was performed using canonical discriminant function analysis. This is a descriptive multivariate technique that highlights the differences between two sets of observations, in this case territories and plots. It then calculates a linear function which allows discrimination between the two groups. Discriminant function analysis assumes multivariate normality, which is unlikely in this case. However the technique is robust to violations of this assumption, even to the extreme of handling binary data

(Titterington et al 1981; Vlanchonikolis and Marriott 1982). When necessary, log transformation was performed to ensure homogeneity of variances.

The effectiveness of the analysis in distinguishing between the groups can be assessed by several error estimation techniques. Resubstitution error estimates are obtained by examining the derived function's error rate in re-assigning the observations used to derive the discriminant rule. This results in downward biasing of the error estimation (Solow 1990). Cross-validation error estimates are obtained using a jackknife procedure and are consequently unbiased. The statistical significance of these error estimates was assessed by randomization tests (Solow 1990). In these tests each observation was randomly assigned to either the territory or the plot category. When all observations had been assigned, the discriminant function analysis was performed and the resulting error estimate recorded. This process was repeated 1000 times. The results were then plotted in frequency histograms and the fifth percentile calculated. If the error estimates calculated in the original discriminant function analysis fall within the fifth percentile, they are considered likely to have resulted from chance alone in only one in twenty trials. In other words, they are considered statistically significant according to current conventions.

Habitat Prediction.

The second question addressed in this study was the possibility that suitable display habitat may limit male settlement patterns. To examine this question I collected data on 135 quadrats, in addition to the original 52 territories and plots. The additional data were collected on 2 transects with a total length of 3375 m (Figure 3.1). In hilly areas males tend to locate their display territories on ridge lines. Since the aim of this section of the analysis was to sample the availability of suitable habitat, in the hilly sections of the study site the transects were run along ridge lines. On the flat section of

the study site the transect in part paralleled a trail, and then followed a randomly chosen compass bearing from the end of the trail. The end of this random section of the transect was then joined to the end of a ridge line transect.

Since sampling the full set of 19 variables involved in the initial descriptive analysis was not feasible, only the 6 variables that made a significant or nearly significant contribution in the descriptive analysis were used in the predictive analysis. To verify that the discrimination obtained with 19 variables was similar to that obtained using only 6 variables, a second descriptive canonical discriminant function analysis was performed using these 6 variables. These variables proved sufficient to discriminate and are listed in Table 3.5 and defined in Table 3.1. In the "predictive" analysis the discrimination rule obtained in the descriptive analysis was used to categorize each of the new observations. The categorization describes each observation as either fitting or not fitting the description of a display territory.

In the analysis of the spatial distribution of suitable habitat a runs test was used. For this analysis the two transects were joined by deleting the last quadrat of one transect (to provide an open end that was a known distance from a territory or suitable plot) and joining it to the other transect at an end with a known distance to a territory or a suitable quadrat, the end of the loop in Figure 3.1.

Results

Habitat Description.

In the initial descriptive analysis 19 variables were measured on 25 territories and 27 plots. The analysis showed significant separation between the two categories (Table 3.3). The number of observations correctly assigned, and the

corresponding error rates are given in the first column of Table 3.2. Due to the downward biasing associated with the resubstitution error estimation, the more conservative cross-validation estimates are given more weight here. In the randomization test, the results of the initial descriptive analysis fell within the fifth percentile for both the resubstitution and the cross-validation estimates, indicating that the discrimination result was unlikely to have arisen by chance alone.

The discriminant function coefficients (Table 3.3) indicate the relative contribution of each variable to the discrimination function. Those variables which contributed significantly are stems <5 cm in diameter and between 1 and 2, and 2 and 3 metres tall, and the percentage cover provided by the lower canopy. Comparison of the group means (Table 3.3) shows that males tended to select sites with fewer saplings and greater lower canopy closure than on the randomly chosen plots. Analysis of the placement of territories and random plots with reference to topography, shows that males were most likely to select ridge top locations in hilly terrain (Table 3.4).

Habitat Prediction.

The predictive discriminant function analysis used 6 measures of vegetation structure (Table 3.5). Again the two categories were significantly separated. In this analysis the resubstitution error estimate increased significantly over that of the original descriptive discriminant function analysis (Table 3.2). However, the cross-validation error estimate showed no change. Thus, reducing the number of variables had little effect on the ability to discriminate between the two categories. In the randomization test the error estimation rates again fell within the lower 5th percentile, therefore the results were unlikely to have arisen by chance alone.

In the subsequent predictive analysis, the 135 transect plots were classified as either territory or non-territory habitat. Fifteen of the 135 plots (11%) were classified as territories, while the remaining 120 (89%) were classified as non-territory habitat. Of the 15 classified as territories habitat, 7 were located immediately adjacent to a territory, i.e. within 25 m of a territory boundary. This represents 46% of all the plots classified as similar to territories and 23% of the 30 transect plots located adjacent to an active display territory. This suggests that display habitat represents only a small to moderate proportion of the available habitat, and that unutilized display habitat is not rare.

The third aim of the study was to examine possible effects of the distribution of suitable habitat on male distribution, i.e. do males clump their territories because of the distribution of available, suitable habitat? Since territories tend to be placed on ridge lines, the transects represent a reasonable sample of the appropriate available habitat. The transect plots were regularly spaced with one every 25 metres, thus the distribution of display territories and suitable plots could be analyzed using a runs test. The distribution of suitable habitat did not differ significantly from random (p = 0.534). Thus, males are not obliged to clump because of the spatial distribution of suitable display habitat.

Discussion

The first aim of this study was to determine whether a particular "territory habitat" could be identified. The initial canonical discriminant function analysis showed that the vegetation structure of territories was different to that of randomly chosen plots. Males tended to choose sites with fewer plants between 1 and 3 metres tall (the height at which most male activity on the display territory occurs), and with greater closure of the

lower canopy than was found on randomly chosen plots. Although it is uncertain why males prefer this vegetation structure, several plausible explanations exist. Choosing sites with few saplings may reduce the extent of obstruction of both visual and auditory display signals by vegetation (Boag and Sumanik 1969), and may enhance the male's ability to detect approaching visitors or predators. Another possibility is that male display requirements may set habitat preferences. M. oleagineus displays involve several different display flights (Chapter 2). A subset of these involve 2 metre long flights which may be most easily performed in areas with few saplings.

The preference for sites with greater canopy closure is perhaps most easily explained by predation risk (Boag and Sumanik 1969). A wide variety of potential predators occured on the study site, and predation attempts were observed by raptors (tiny hawks, Accipiter superciliosus, and collared forest falcons, Micrastur semitorquatus). In each case the raptor dashed from cover in the upper canopy to attack the male. Sites with a relatively closed lower canopy would provide a barrier between displaying males and predators attacking from the upper canopy.

Males also tended to locate territories on ridge lines when these were available, rather than on slopes or in gullies. Preference for ridge top display sites occurs in several other lek-mating frugivores (Macgregor's bowerbird, Amblyornis macgregoriae Pruett-Jones and Pruett-Jones 1986; red-crowned and blue-capped manakins, Pipra mentalis, and P. coronata, unpubl. data). Possible explanations for this phenomenon are that ridges provide sites that enhance signal transmission, and that ridge tops allow simultaneous transmission into more than one valley. In some cases, valleys are large relative to the ability of males to broadcast display signals. In these instances, leks on ridge tops may expose males to females crossing between valleys. It is also

possible that habitat with appropriate vegetation structure is found predominantly on ridge tops (Pruett-Jones and Pruett-Jones 1986).

Though this analysis resulted in significant discrimination between territory and non-territory habitat, there is an important caveat to accepting the results at face value. This is that humans and male M. oleagineus may perceive environments very differently. Consequently, without experimentation we cannot be certain that what we measure is indeed what the birds consider important in their habitat selection. However, I am satisfied that I have at least measured features that are significantly correlated with those characteristics used by males to select display habitat.

Assuming that males do indeed select territories on the basis of the habitat characteristics listed in Tables 3.3 and 3.5, we can ask whether suitable habitat is sufficiently limiting that males are obliged to aggregate onto leks located in this habitat. Slightly more than 10% of all the 135 transect plots were identified as suitable, but unoccupied, territory habitat. If suitable sites were actually limiting the settlement of males, it is unlikely that such a large percentage of apparently suitable sites would be vacant, since a approximately 50% of males in this population do not hold territories and competition for display sites is intense (Chapter 2, Chapter 4). Under these conditions subordinate males might be expected to defend territories in any habitat that appeared suitable. In many avian mating systems subordinate males will attempt to join the breeding population by defending even unsuitable habitat (Korpimäki 1988; Ficken and Ficken 1966). This does not seem to be occurring in this case, since not only were apparently suitable plots vacant, but 23% of these plots were immediately adjacent to leks and therefore apparently in prime locations. Consequently, I conclude that suitable habitat does not limit male settlement.

Even if the availability of suitable display habitat does not limit male display dispersion, its distribution could. However, the analysis of the distribution of suitable plots and territories along the transect did not detect significant clumping, as would be expected if the distribution of suitable habitat was indeed driving male clustering. Additionally, if all males currently displaying along the transect preferred to display solitarily, it appears that they could. In total 15 males displayed at a total of 9 leks and solitary display sites. The discriminant function analysis identified a further 8 unused solitary and suitable plots. This makes a total of 17 distinct potential display sites, or 2 more than required for all males to display solitarily. Alternatively, might some males be obliged to display solitarily by the lack of suitable habitat at leks? Again, the answer appears to be no. There were 7 suitable but vacant plots identified immediately adjacent to display territories, but only 4 males displayed solitarily.

Taken together, these results suggest that, though males do select a certain type of display habitat, this habitat is neither sufficiently limiting, nor distributed so as to oblige males to cluster into leks. This evidence is contrary to the hypothesis that habitat availability and distribution drives the evolution of leks, and suggests that alternative hypotheses explain the evolution and maintenance of lekking in this species.

Table 3.1: Habitat characteristics measured at each display territory and on randomly chosen plots. With the exception of topography, a categorical variable, all were used in the discriminant function analysis. All measurements were taken by one person to reduce error.

Characteristic	Symbol	Definition
Topography		- location on a ridge top, the side of a slope, or on flat terrain.
Number of Stems	<1 <2 <2 <2 <3 <2 >3 <2 <1 <5 <2 <5 <3 <5 >3 <5 <1 <10 <2 <10 <3 <10 >3 <10 <2 >10 <3 >10 >3 >10	- less than x metres tall and y cm in diameter.
Canopy cover	%lc	- Percentage cover of the lower canopy. Estimated visually through a 5 cm^2 hole in a card held up at arms length.
	%uc	- Percentage cover of the upper canopy
Canopy height	htlc htuc	- Height of the lower canopy - Height of the upper canopy

Table 3.2: A comparison of the resubstitution and cross-validation error estimation rates obtained using the full data set (the initial predictive analysis) and the partial data set (the second descriptive analysis, see the text for details). Both the number of misclassified observations and the corresponding error rate (or proportion misclassified) are presented. The full data set comprised 16 variables while the partial data set comprised 6 variables. Both sets of estimation rates were obtained from a canonical discriminant function analysis.

Estimation Technique	Full Data Set #	rate	Partial Data Set #	rate
Resubstitution	5	.09	14	.26
Cross-validation	18	.34	18	.34

Table 3.3: Summary of the discriminant function analysis using 19 measures of vegetation structure on territories and randomly-chosen plots. Definitions of the characteristics are given in table 3.1.

Characteristic	Group means, ± S.E.				Standardized Discriminant Function Coefficients
	Lek		Plot		
<1 <2	20.88	1.70	24.22	3.50	0.2156
<2 <2	21.92	2.66	31.15	6.41	0.4283
<3 <2	15.88	1.73	18.15	4.15	0.0938
>3 <2	18.16	3.44	11.63	3.70	-1.1510
<1 <5	2.20	0.60	3.15	0.60	-0.1040
<2 <5 **	2.70	0.59	7.77	1.21	0.7520
<3 <5 *	1.64	0.30	3.11	0.61	0.4060
>3 <5	11.68	1.03	9.15	1.80	0.3333
<1 <10	0.04	0.04	0.11	0.66	0.2210
<2 <10	0.56	0.26	0.37	0.17	-0.1440
<3 <10	0.24	0.13	1.30	0.89	0.1520
>3 <10	3.68	0.49	5.48	2.60	1.1880
<2 >10	0.04	0.04	0.04	0.04	0.3780
<3 >10	0.04	0.04	0.15	0.09	-0.2980
>3 >10	4.72	0.37	4.55	0.45	0.2870
%lc *	42.12	2.91	33.37	2.69	-1.0390
%uc	41.32	3.11	48.37	3.22	0.5060
htlc	13.37	11.01	11.84	1.09	0.2340
htuc	24.64	1.03	27.16	0.94	0.3640

** means differ at p < 0.001   * means differ at p < 0.05

Table 3.4: Comparison of the distribution of territories and randomly-chosen plots across the different topographical categories (G-test chi^2 = 24.71, df = 3, p < .00002).

	Flat	Ridge Line	Slope
Territory	8	16	1
Random Plot	6	6	15

Table 3.5: Summary of the discriminant function analysis using 6 measures of vegetation structure on territories and randomly chosen plots. Definitions of the characteristics are given in table 3.1.

Character	Group means +/- S.E.		Standardized Discriminant Function Coefficients
	Lek	Plot	
<2 <2	15.88 1.73	18.15 4.15	0.2019
>3 <2	18.16 3.44	11.63 3.70	0.2317
<2 <5 ***	2.70 0.59	7.77 1.21	0.8917
<3 <5 *	1.64 0.30	3.11 0.61	0.2609
>3 <5	11.68 1.03	9.15 1.80	-0.2663
%lc *	42.12 2.91	33.37 2.69	0.4055

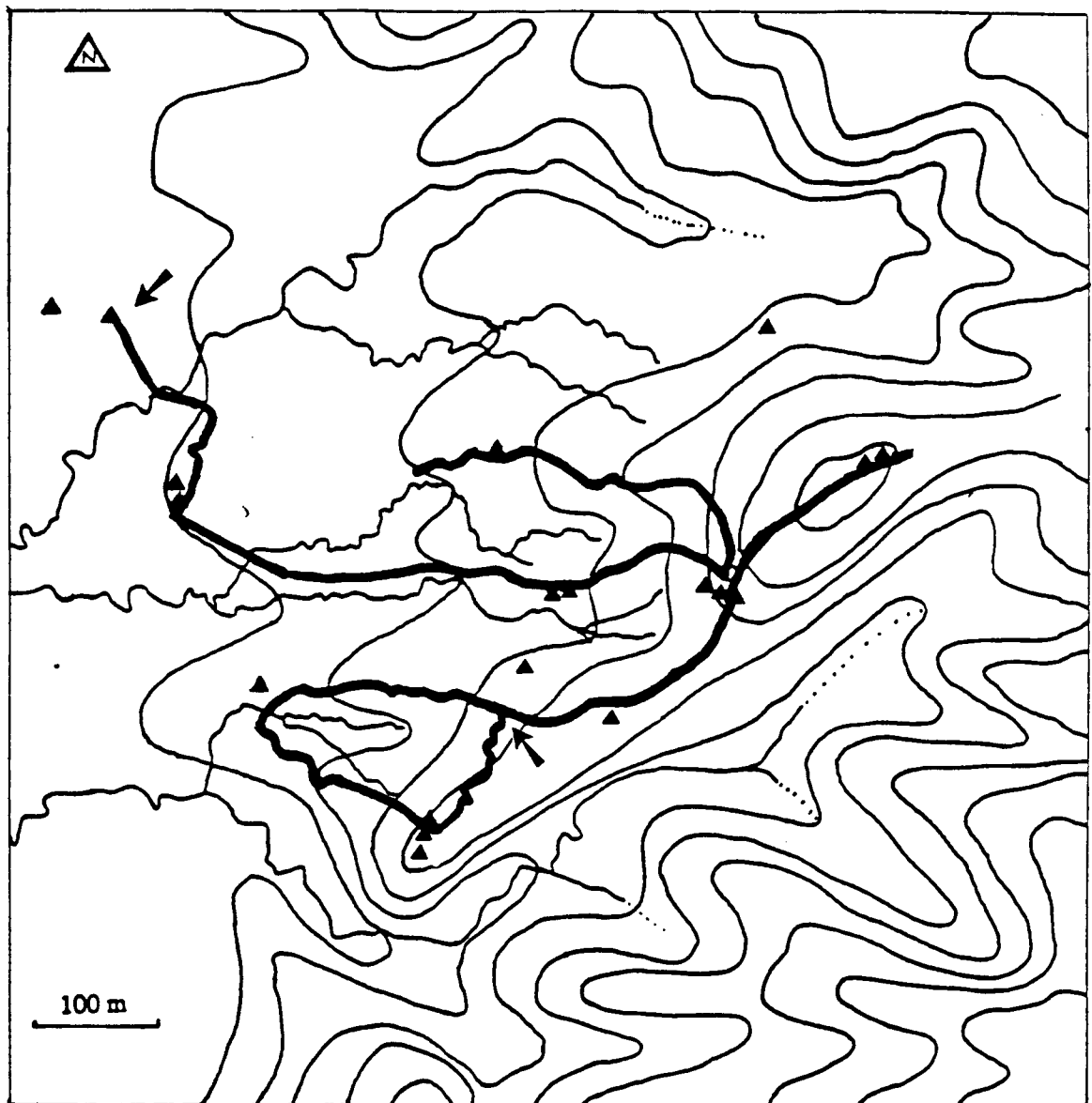*** means differ at p < 0.0001   * means differ at p < 0.05

Figure 3.1: Map of the study site showing the two transects. The filled triangles indicate male display territories. The arrows indicate the points at which the two transects were joined for the analysis.

Chapter Four

Inter- and Intra-Sexual Selection: the Role of Song in a Lek Mating System.

Introduction

Bird song has many potential functions: territory defense, mate attraction, individual and species recognition, coordination of reproductive activity, and signalling of intent and motivation (authors in Kroodsma and Miller 1982; Searcy and Andersson 1986). The strong positive correlation between the onset of breeding and the peak of song activity suggests that song functions primarily in territory defense and mate attraction (Thorpe 1961; Armstrong 1973; Catchpole 1982; Searcy and Andersson 1986). However, there is surprisingly little experimental evidence relating song and these two functions, although available experimental data support both hypotheses (territory retention: Peek 1972; Smith 1976, 1979; Krebs 1977; mate attraction: Erickson and Wallin 1986; Gibson 1989; Alatalo et al. 1990; both simultaneously M.V. McDonald 1989).

Despite the fact that song, and other auditory displays, are used extensively in avian lek mating systems, almost all relevant evidence concerning the role of song comes from resource-based mating systems. Since the goal of most recent studies of lek mating systems has been to determine the basis of female mate choice (e.g., Gibson and Bradbury 1985; Höglund and Lundberg 1987), song in these systems has been interpreted almost entirely within a "female mate choice" context (Beehler and Foster 1988). This has not been without cause. When correlates of female mate choice have been identified, one has usually been a song or auditory display characteristic (e.g.. Gibson and Bradbury 1985; Höglund and Lundberg 1987; D.B. McDonald 1989b). Gibson (1989) showed experimentally that, when the song output of a male sage grouse was supplemented by song playback, more females visited his territory. Thus, it is not surprising that mate attraction is seen as the pre-eminent function of song in lek systems. However, little consideration has been given to other roles that song may be performing.

Alternatively, song may function in male-male competition in intra-sexual interactions (Foster 1983; Beehler and Foster 1988). Interactions among males often take the form of overt aggression or disruption of display to females (Trail 1985 a; Lill 1976; Robel and Ballard 1974; Wiley 1973; Clutton-Brock et al. 1989), or result in dominance hierarchies (Foster 1981; D.B. McDonald 1989 a). Song, including audible display, functioning as a subtle form of male-male competition has rarely been explicitly considered in lek mating systems (but see Avery and Sherwood 1982).

In this chapter, I describe an experimental study of the role of song in the lek mating system of the tyrannid flycatcher, Mionectes oleagineus. Investigating the function of song requires distinguishing the effect of the male's presence from the effect of his song (M.V. McDonald 1989). This can be done in the field by removing the male while maintaining his song using playbacks (e.g. Krebs 1977). Alternatively, one may leave the male on his territory and manipulate his song either by supplementing it with playbacks (e.g.. Gibson 1989), or by removing it through muting (e.g.. Smith 1976, 1979; M.V. McDonald 1989). Because of the difficulties of keeping wild birds in captivity at a remote location, and the adverse reaction of males to song supplementation in pilot trials, I used the temporary muting technique developed by Smith (1976) and M.V. McDonald (1989). Data presented here suggest song plays both an inter- and an intra-sexual role. Females tended to visit those males which sang the most, and the muting experiment demonstrates a crucial role for song in territory defense.

Methods

Behavioural Observations.

Each male was watched for 2 hours at least once a week; the sequence of males was chosen each week using a random number table. Observations were conducted between 0530 and 1130, the period of greatest display activity. Observation periods started 10 minutes after the arrival of the observer. The observer remained still and quiet, and neither the male, nor visitors to the territory, showed any apparent response to being observed. On several occasions, males displayed to females as little as 2 metres from the observer. Behaviour was recorded using continuous sampling (Altmann 1974; see Table 4.1 for a list and definition of the behaviours). In 1989 I recorded behaviour onto paper in 90 second blocks, using a time signal from a pre-recorded tape played in a cassette recorder. In 1990 I used a Radio Shack TRS-80 portable computer as an event recorder; each behaviour was recorded along with the number of seconds elapsed since the beginning of the observation period.

Muting Experiment.

The temporary muting procedure used in this experiment was a minor modification of that used by M.V. McDonald (1989). The technique was performed as follows:

1) The feathers and skin of the fulcrum and neck area were swabbed with an antiseptic solution.

2) A water soluble gel (K-Y gel, ®™) was then applied to the feathers of this region to hold them out of the way.

3) At this point the intra-clavicular air sac was clearly visible through the skin. A 5 mm incision was then made in the skin over the airsac.

4) A small incision was then made in the airsac with the point of a scalpel. This hole was then enlarged as much as the exterior hole would allow, to between 3 and 4 mm, using either the scalpel or a pair of forceps.

5) The exterior incision was then completely sealed using a veterinary tissue adhesive, Vetbond ®™.

6) The feathers and skin around the incision were again swabbed with an antiseptic solution.

7) The bird was released.

I used no anaesthetic due to the difficulties of safely dosing small birds in the field, and the increased risk of predation and injury after release due to the effects of residual anaesthetic. I also wished to minimize the duration of the male's absence from his territory (since even brief captivity might result in territory loss).

The entire procedure took less than 6 minutes, and no problems were encountered. On no occasion did birds bleed. The procedure seemed to involve minimal stress; individuals remained alert during the procedure, and did not struggle, call or show any signs of shock (e.g. drooping eyelids or heads).

Upon release, experimental birds behaved identically to control birds. They flew strongly, preened briefly on a nearby branch and then moved off. One male attacked an intruder 10 minutes after being muted and another was seen flycatching 20 minutes after being muted. The effects of the muting lasted between 10 and 14 days. All sham-experimental and experimental birds were alive and apparently healthy 2 weeks or more after the manipulation.

Experimental Design.

The experimental design was based on that used by M.V. McDonald (1989). At the beginning of the experiment, males were assigned semi-randomly (see below) to one of three treatments: Control (caught, banded and released); Experimental (caught, muted, and then released); Sham-experimental (caught and the muting procedure carried out as above, except that instead of puncturing the intra-clavicular airsac, the airsac was simply picked up with a pair of forceps and then released). The last treatment controlled for possible effects of the surgical procedure. Only one experimental or sham-experimental male was allowed at any lek, and all other males at the lek were assigned to the control treatment. Consequently, there resulted a bias in the number of control males that eventually entered the experiment. The final tally included 12 control males, 6 experimentally muted males and 3 sham-experimental males.

Behavioural observations of males in all three treatment groups were conducted for one month prior to the manipulation period, during the manipulation period, and for one month after the manipulation period.

Results

I examined whether there was a relationship between the advertisement effort of males and the number of visitors to their territories. In both 1989 and 1990 there was a significant positive correlation between the average total advertisement effort and the average frequency of female visits per observation period to a given male's territory (Table 4.2). The contribution of each of the song types to this correlation varied between years. In both years the singing rates of all three song types were significantly correlated with female visitation (Table 4.2). The mean number of male intrusions per observation

period was also significantly correlated with mean total advertisement effort, and all three component song types in both years (Table 4.2).

The Muting Experiment.

Territory Size.

There were no differences in the sizes of the territories of control and sham-experimental males either before or during the manipulation periods (before: Mann-Whitney U-test, U = 19.00, p = 0.88; during: U = 23.0, p = 0.47, Figure 4.1). This indicates that other than actual puncturing of the airsac, the experimental procedure per se produced no strong effects on male behaviour. During the pre-manipulation period the mean territory sizes of the control and the experimental males did not differ (U = 24.0, p = 0.53). However, they differed markedly during the manipulation period (U = 62.00, p = 0.014, Figure 4.1), primarily because of territory loss by experimental males. The only experimental male to retain any of his territory during the manipulation period lost approximately 65% of its pre-manipulation area.

Territory Retention.

None of the 12 control males nor any of the sham- experimental males (including one which had a satellite on his territory throughout the term of the experiment) lost their territories during the manipulation period. Thus, capturing and handling had no effect on the ability to retain territories. Experimental males were more likely to lose their territories than controls (Fisher Exact Test (2-tailed) p = 0.013). Five of the 6 experimental males lost their territories during the manipulation period (3 within one day, and 2 after 3 days), and one male regained his after regaining his song. Experimental males with satellites took longer to lose their territories than males without satellites(U = 0.0, p = 0.05). The sole experimental male who retained part of his

territory throughout the manipulation also regained the remainder of it once he regained his song. The 6 muted males lost their territories to 3 floaters, 2 satellites and 1 territory owner.

Frequency of Visitors.

Territories in the three groups received the same frequency of visitation during the pre-manipulation period (Mann-Whitney U-test p = 0.34). The control and sham experimental males did not differ during the manipulation period (Mann-Whitney U-test p = 0.11), but the experimental males received markedly higher visitation rates during the manipulation period (control mean = 0.683, visits/ 2 hour observation period, ± 0.144 S.E., and experimental mean = 3.027, visits/ 2 hour observation period, ± 0.775 S.E., U = 9.5, p = 0.023). This increase in visitation rate was due entirely to an increase in the number of male intruders.

During the pre-manipulation period there was no difference between the control and the experimental males in the number of male intruders (Kruskal-Wallis Test = 30.0, p = 0.57, Figure 4.2). However, the sham-experimental males had more male intruders than did control males prior to the experiment (U = 4.5, p = 0.05, Figure 4.2). This was primarily due to two high means resulting from the presence of a satellite male on the territory of one sham male, and two observation periods when 11 and 9 intruders were seen on another sham male's territory. During the experimental period the control and sham-experimental males did not differ (U = 9.5, p = 0.14). However, the experimental males suffered intrusion rates approximately 22 times greater than those of the control males during the same period (control mean = 0.15 visits/observation period, experimental mean = 3.3 visits/observation period, U = 7.5, p = 0.0001, n = 21 males, Figure 4.2).

Due to the extremely short tenure of the experimental males during the manipulation period, it was impossible to detect any changes in the frequency of visitation by females.

Male-Male Interactions.

There were no differences in the number of trails or chases per visitor (see Chapter 2 and Table 4.1 for definitions) between the control category and the two experimental categories during the pre-manipulation period (control vs sham-experimental: $U = 14.0$, $p = 0.93$; control vs experimental: $U = 42.0$, $p = 0.20$). During the manipulation period, experimental males did not differ from the control and sham-experimental males in the number of trails per intruder ($U = 7.5$, $p = 0.12$).

There were no significant differences between the control category and the two experimental categories in the number of chases per visitor during the pre-manipulation period (control vs sham-experimental: $U = 14.5$, $p = 0.93$; control vs experimental: $U = 35.5$, $p = 0.76$). During the manipulation period, experimental males were more likely to chase intruders than the control and sham-experimental males ($U = 0$, $p = 0.046$).

Discussion

Song and Female Mate Choice.

Covariance between the mating success of males and their phenotypic traits results in sexual selection (Arnold 1983; Wade 1987). An initial aim of this study was to identify males who successfully mated, and then to determine whether song covaried with male mating success differences. Because so few copulations were observed (1 definite and 1 probable) this was not possible. However, the positive

correlation between song and female visitation suggests song influences female mate choice. In studies of manakins (Pipridae), which are ecologically similar to M. oleagineus, both Lill (1976) and D.B. McDonald (1989 b) found that female visitation rates to a male's territory and that male's mating success were highly correlated. This may be the case for M. oleagineus since both of the males thought to have copulated had high levels of female visitation. If female visitation is an index of male mating success, then M. oleagineus is an example of a sexually monomorphic species in which female mate choice is based on behavioural rather than morphological traits of males.

At the outset, I expected the muting experiment to provide direct evidence for or against an inter-sexual role for song. However, males lost their territories so rapidly that I could collect no relevant data. A more appropriate way to address this question for this species may be to playback male song at non-territory sites and compare the capture rate of females with that at non-territory sites without playback (e.g. Erickson and Wallin 1986).

Song and Male-Male Interactions.

The possibility of an intra-sexual role for song in lek systems has largely been ignored, perhaps because of the belief that leks represent model systems for examining female mate choice (e.g. Emlen and Oring 1977; Bradbury and Gibson 1983). However, no consensus has been reached even when this possibility has been considered. Lill (1976) noted that male golden-headed manakins, Pipra erythrocephala, seldom sang when females were present on the lek, and never sang if females were present on their display territories. This, he suggested, indicated an intra-sexual role for song. D.B. McDonald (1989 b) concluded from his study of the long-tailed manakin, Chiroxiphia linearis, that song played an inter-sexual role, being important in attracting females to the display territory, whereupon females based their decisions of whether to mate on the

quality of the dance display they observed there. Avery and Sherwood (1982) noted that male great snipe, Gallinago media, always faced each other when calling, that the call was unlikely to carry very far, and that the peak in song rates occured prior to the arrival of females on the lek. From this they concluded that song played an intra-sexual role. Höglund and Lundberg (1987) also studied G. media. They found that song rate was correlated with male mating success, but they did not test the possibility of an intra-sexual role for song.

Perhaps because of the inter-sexual emphasis in studies of lek systems, the results of my muting experiment were surprising. Without exception, the territories held by experimental males shrank after muting and all but one male completely lost his territory. The lack of any such effects for either the control or the sham-experimental males clearly establishes that song plays a major intra-sexual role in the lek mating system of M. oleagineus. This argument is strengthened by the fact that two of the experimental males ousted their usurpers after regaining the ability to sing and regained control of all of their lost territory.

It is not necessarily the loss of song, per se, that led to the changes that I observed. Alternatively, males that are rendered incapable of singing lose or abandon their territories simply because of the psychological effect of the loss of song on them. If this hypothesis is correct, males should lose their territories irrespective of the intrusion rates they experience and experimental males should decrease their response to intruding males. The intrusion rate data showed that muted males suffered far higher levels of intrusion after muting than before. They also suffered levels of intrusion 22 times that experienced by control males during the experimental period. Muted males showed no decrease in their reaction to intruding males in either the number of trails per intruder, nor in the number of chases per intruder. Indeed the latter increased. It is unlikely,

therefore, that muted males abandoned their territories. Rather, they were simply unable to exclude intruders. The intruders, however, were able to exclude them.

Two experimental males entered the experiment with satellites on their territories. Both took significantly longer to lose their territories (to the satellites) than did those males that entered the experiment without satellites. This suggests that a previously established relationship between males entails some kind of inertia that must be overcome before a satellite can assume ownership of a territory. This result is reminiscent of the reluctance of beta males to assume the alpha position on Chiroxiphia linearis leks when the alpha male disappears (Foster 1981).

The Effect of Male Competition on Female Mate Choice.

In some respects this experiment functioned as a removal experiment. It confirmed the existence of a large population of mature, non-territorial males. I previously suspected this due to the high rate of intrusion by males, and because approximately 50% of banded males were not known to hold display sites either on or off the study site (Chapter 2). Such a large non-territorial male population is surprising in a lekking species, since available habitat is not saturated. On my study site apparently suitable, vacant sites existed, both generally over the study site and immediately adjacent to leks (Chapter 3). This apparent reluctance of sexually mature males to settle at available and apparently suitable sites suggests that male settlement is determined at more than one level. First, the presence of vacant sites away from currently active territories suggests that current territories are favoured over other sites, perhaps because of their history or some attribute such as their spatial relation to some resource (e.g. female, Bradbury et al. 1986). Second, the failure of non-territorial males to settle immediately adjacent to existing leks suggests that they were excluded by the territorial males that were already present.

Although females are potentially free to choose mates at leks without coercion by males, male-male competition is a common element of lek systems and may limit the extent of female choice (Foster 1983). For example, aggressive interactions may modify female choice either by physical interruption of copulation (Trail 1985a), or by distracting either the male or the female, such that the female leaves or avoids a particular territory (Lill 1976; Trail 1985a; Clutton-Brock et al 1989). Though distraction and physical disruption do occur in M. oleagineus' mating system, their importance is unclear. However, male-male competition may also influence female mate choice more subtly. For example, male-male interactions may result in only a subset of the available males being eligible to attract females (Foster 1983; Beehler and Foster 1988). If we assume that nearly all matings take place on display territories, this scenario is quite likely for M. oleagineus. I found no evidence that males and females associate away from display sites, nor that males display away from established sites. Also, males appear to make a huge investment in time, energy and perhaps risk in obtaining, defending, and displaying on territories. Given this investment, it is likely that if matings were to occur away from leks regularly, the lek system would break down (Gibson and Bradbury 1987). Thus males without territories are effectively invisible to female mate choice. Since current display territories are apparently limiting (see above) and their ownership is determined through male-male competition, the invisibility of non-territorial males has arisen as a direct consequence of intra-sexual selection. How important is this effect? Banding data and the results of searches for floaters displaying off the study site suggest that as much as 50% of the male population falls into one of the non-territorial categories, satellite and floater (Chapter 2). If this is the case, intra-sexual selection may be a potent force in this mating system.

However, the importance of intra-sexual selection in this system is dependent on females mating only with males that have territories. If territory ownership is not a pre-requisite for being chosen for mating (in this instance, if females ignore non-territorial males even if they do hold a territory) the scope for inter-sexual selection cannot be limited by prior intra-sexual selection. Thus, to argue that intra-sexual selection is important we need to show that floater males are eligible to be chosen as mates if they obtain territories. They did obtain territories in this experiment. In one case a floater that usurped an experimental male's territory sang at very high rates, received an above average female visitation rate, and copulated several days after gaining control of the territory. This male was subsequently displaced by the experimental male after the latter recovered and began to sing again. The high song rates and the high female visitation rates received by two other floaters which displaced experimental males also provide support to this argument. Thus, I conclude that if all matings do occur at the lek, prior male-male interactions can greatly reduce the scope of female mate choice to the set of males that hold display territories. In this case, this set contained less than 50% of all males.

This study has shown that song functions both in the attraction of mates and in territorial defense in the lek mating system of M. oleagineus. The results emphasize the importance of considering both intra- and inter-sexual selection in lek mating systems (Bradbury and Davies 1987). I caution against dismissing a role for intra-sexual selection without data that specifically address the question. The role played by intra-sexual selection may not be obvious simply from observation of copulations at leks.

Table 4.1: A description of all of the behaviours recorded during observations of displaying males. The behaviours were recorded at all stages of the experiment.

Behaviour	Description
Ipp	Song type.
Eek	Song type.
Sweet	Song type.
Total Song	Sum of ipp, eek, and sweet.
Move	Any movement from a perch, usually involved flight
Feed	A feeding event, food type was recorded where possible, i.e.. fruit or arthropod.
Preen	Preening.
Rest	Male present on territory but inactive.
Visitor	A visitor of either sex present on the territory. Visitors were sexed immediately by behaviour (see text) or subsequently using banding data.
Trail	Male closely follows a visitor. This often resulted in the visitor leaving the territory. If not, and the visitor was a female, the male sometimes displayed. If the visitor was a male, the owner attacked it.
Chase	The owner attacks and chases a visitor. These chases were violent and occasionally led to the loss of feathers.
Bash	The visitor attacks the territory owner.
Hover	Display.
Hop	Display. Male flies rapidly between several, usually vertical, perches. Males often gave an eek call during these flights.
Butterfly	Display. Male flies between perches in a slow, fluttering manner.
Copulate	Male mounts a crouching female, pushing his tail down and under her up-raised tail.

Table 4.2: Relationship between the average number of visitors to a male display territory per observation period and the male's average song effort per observation period. Spearman Rank Correlation Coefficients are given and all are significant at p = 0.001. Sample sizes were 27 and 25 males for 1989 and 1990 respectively.

1989

Song Category	Female Visitors r_s	Male Visitors r_s
total song	0.380	0.236
ipp	0.375	0.251
eek	0.387	0.174
sweet	0.386	0.244

1990

Song Category	Female Visitors r_s	Male Visitors r_s
total song	0.298	0.165
ipp	0.340	0.130
eek	0.259	0.208
sweet	0.190	0.280

Figure 4.1: Mean territory sizes of males of each category during the three phases of the experiment: before, during and after manipulation. Data shown are means, ± standard errors. For the experimental category, sample sizes for the 3 phases of the experiment were; before = 6, during = 1, and after = 2. The control and sham categories sample sizes were 12 and 3 respectively. They were constant throughout the experiment.
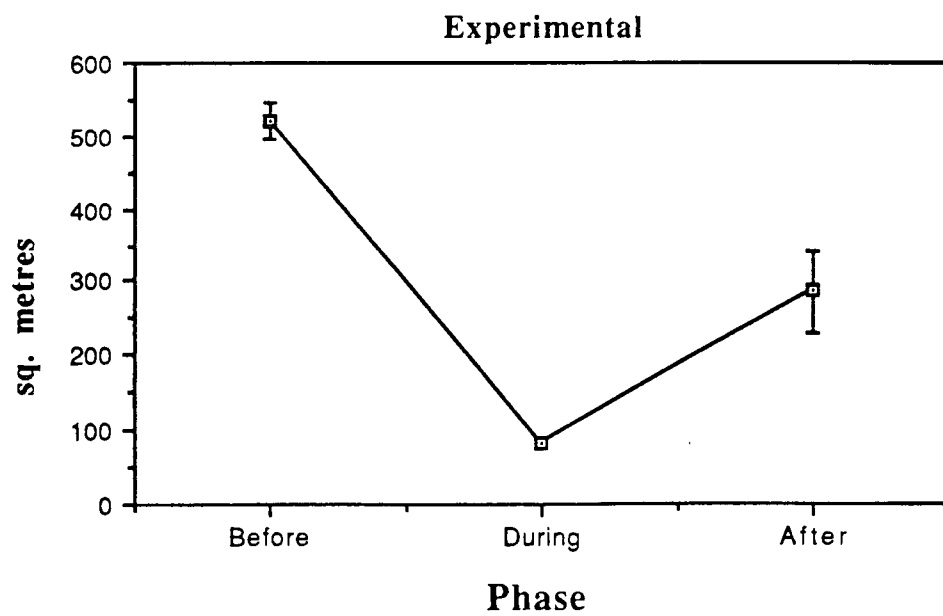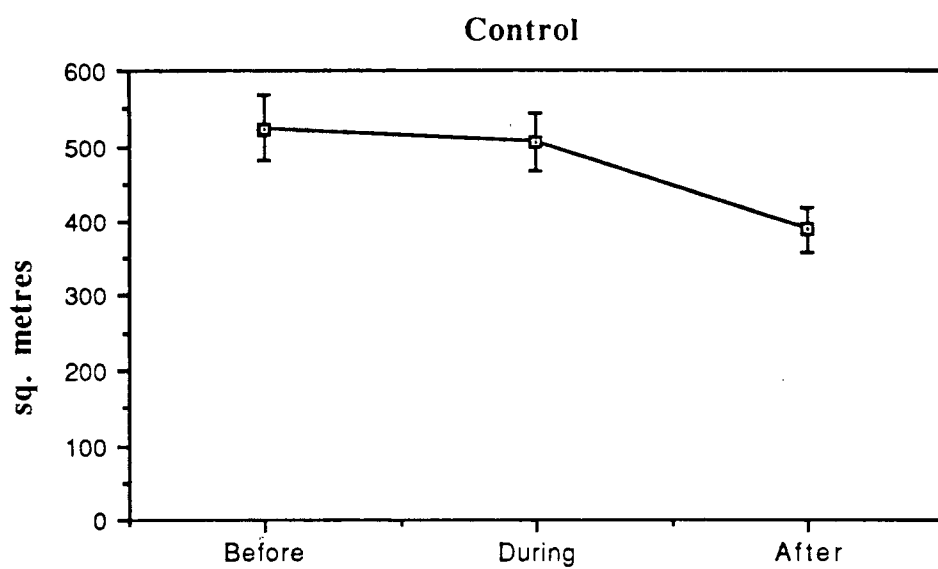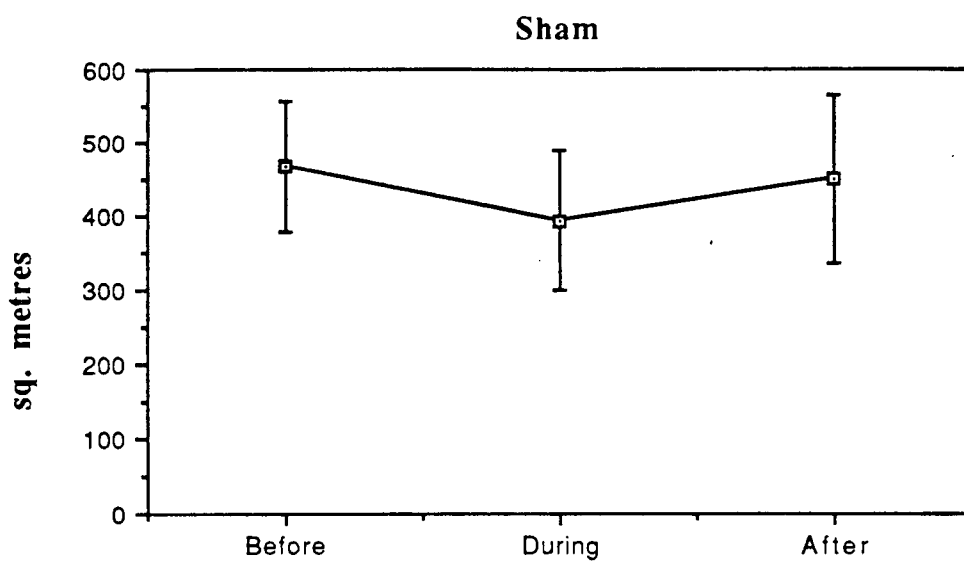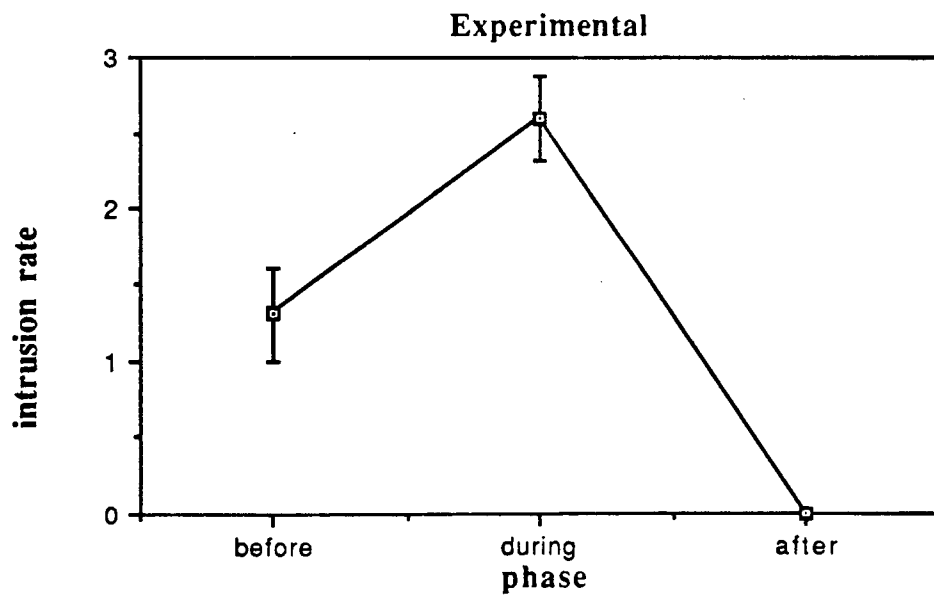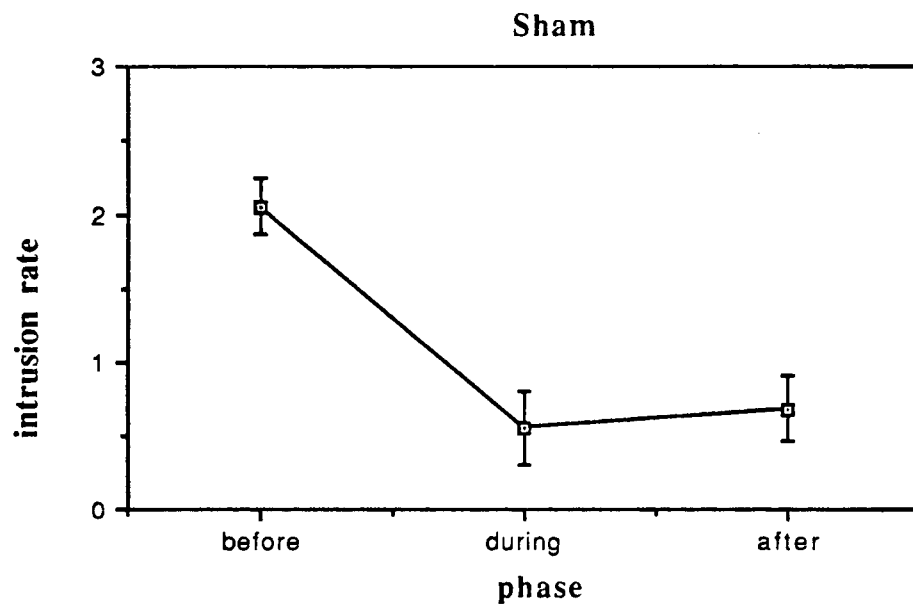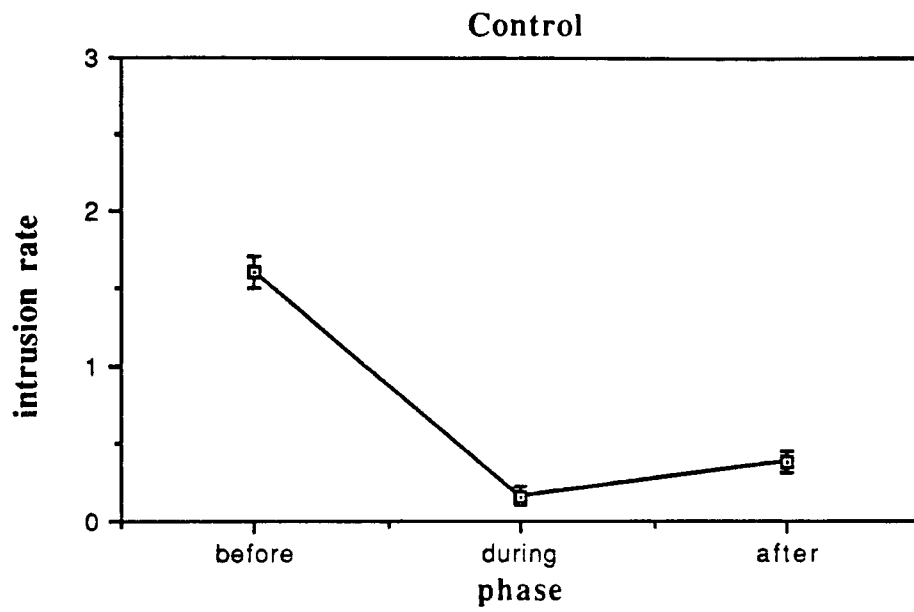
Sham

Control

Experimental

Phase

Figure 4.2: The mean intrusion rate by males per 2 hour observation period for each category of male during each phase of the experiment: before, during and after manipulation. The error bars are standard errors.

Control

Sham

Experimental

Chapter Five

General Conclusions

Taken together, my work indicates that the leks of M. oleagineus are the sites of intense competition between males. This competition is both indirect, through female mate choice, and direct, through aggressive male-male interactions. In Chapter 2, I described the social organization of M. oleagineus. Many males in the population studied did not hold display territories, but instead adopted one of two non-territorial strategies, being satellites or floaters. Non-territorial individuals were not apparently limited by the availability of suitable display habitat (Chapter 3). Instead they seemed to follow a waiting strategy in the face of competition for currently active display sites. When the owners of display territories were muted, they were quickly subjected to extremely high intrusion rates and were rapidly forced from their territories (Chapter 4). This result confirms both that non-territorial individuals are deterred from settling at leks by intra-sexual interactions, and that the degree of competition for currently available display territories is intense. The value of the territories currently defended over that of locations immediately adjacent to them is unclear. This result also clearly demonstrates the key role played by song in male-male competition in this mating system and suggests that male-male interactions limit the extent of female mate choice.

With the exception of Chapter 3, I have paid little attention to hypotheses for the evolution of leks. Therefore, I briefly discuss here the relevance of some of my findings to these hypotheses. As I noted in Chapter 3, males are generally believed to cluster their display territories onto leks for one of the following reasons: 1) females prefer clustered males (Alexander 1975; Bradbury 1981; Wrangham 1981; Avery 1984); 2) males that are unsuccessful in attracting females and obtaining matings cluster around attractive, successful males (Beehler and Foster 1988; Höglund and Robertson 1990); 3) males cluster where female densities are highest (Bradbury 1981).

The first of these hypotheses, the "female preference" hypothesis, predicts that since females prefer clustered males, solitary males should be unsuccessful in their attempts to attract, or copulate with females. My observations that some solitarily displaying males received many female visitors, and that one of them probably copulated, run counter to this prediction (Chapter 2). If females do not distinguish between a solitary male and a lek of 3 or 5 males, it seems unlikely that female choice will be sufficient to select for clustered male display.

Beehler and Foster's (1988) "attractive male" hypothesis predicts that male-male interactions structure the mating system, and that unsuccessful males cluster around successful individuals. While the data from my muting experiment indicate the importance of male-male interactions in shaping the mating system (Chapter 4), the hypothesis' prediction that successful males will attract other males was not met. As I noted above, several solitary males were successful in attracting females (one of which probably copulated), but remained solitary (Chapter 2). In two of these cases, the males were successful over the whole two years of the study. It is uncertain, however, whether they did not attract other males because the attractive male hypothesis does not apply (attractive males are insufficient to cause a lek to form), or whether some other factor, such as interference by the male that had already settled, prevented subsequent males from settling.

The final major hypothesis is Bradbury's (1988) "hotspot" hypothesis. This hypothesis suggests that males settle according to female distribution and densities. The only observation from my study that supports this hypothesis is the movement of an active male from a display site where few female visitors were seen, to a display site where more females were seen. However, this only weakly supports the hotspot hypothesis since I have not distinguished the effect of the current or previous territory

owner from that of the location of the territory relative to female densities on this visitation rate.

While my results do not provide strong evidence for any of the major hypotheses, the results of the study do suggest that this is a good system for examining this question further. The existence of both lekking and non-lekking males in the population (Chapter 2) allows a comparison of the pay-offs of these two apparent strategies. Additionally, the variation in display dispersion provides an excellent situation for examining the location and size of leks relative to the distribution and movements of females. Further work should also consider more closely the factors affecting mate choice in this mating system. Females appear to prefer the males which sing the most. Experimental manipulation of males, e.g. treatment of parasites and addition of weights, will allow description of the relationship between male condition, male parasitemias, song rates, and female mate choice. Additionally, the relationship between the traits preferred by females and those that make males successful in male-male competition could be usefully explored. Though females seem to prefer males that sing at high rates, a significant number of territory owners do not do so. In the muting experiment, some of these males were replaced by males with higher song rates, suggesting that the different sexes may use different traits when assessing males.

M. oleagineus has proven to be a tractable and informative species with which to work. It is, however, appropriate to consider some of the shortcomings of this species for this kind of study, and some of the shortcomings of study. The most problematic of these is the small number of observed copulations. This small sample size is probably a function of the great length of the breeding season (c.f. Pruett-Jones and Pruett-Jones (1990)) and the large area within which males can display. One of the consequences of the difficulty of observing copulations is that I have been forced to use

an indirect measure of reproductive success for males, the number of female visitors. Though I believe this to be an accurate index of reproductive success, it is not as satisfactory as the number of copulations obtained, or ideally the number of offspring feldged. This problem could be overcome with the determination of the paternity of nestlings through DNA finger-printing.

A second shortcoming is that it is difficult to examine the female perspective of the mating system adequately. Though I can document some females' visits to territories, and sometimes the males with which they copulate, I cannot look at the process of the mate choice of individual females, either among or within leks. Finally, as was the case with males, it is impossible to evaluate female reproductive success with respect to mate choice without being able to observe a larger number of copulations.

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