

LEKKING IN THE OCHRE-BELLIED FLYCATCHER, MIONECTES OLEAGINEUS

by

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ABSTRACT

In this thesis, I examine the social and ecological pressures that have resulted in the evolution and maintenance of lekking in the ochre-bellied flycatcher, Mionectes oleagineus. I do this by asking two general questions: i) where should leks occur, and ii) how many males should settle at a site.

I begin by considering the influence of female distributions on male settlement patterns. The "hotspot" hypothesis suggests that population level patterns of female movement and/or dispersion determine male settlement patterns. Leks occur due to marked heterogeneities in these distributions. I confirmed three novel, interspecific predictions of the hotspot hypothesis: 1) leks of ecologically similar, sympatric species are clustered; 2) the degree of clustering is related to the degree of similarity in diet between the species; and, 3) species with similar diets show correlated changes in the sizes of neighbouring leks.

If, as suggested by this interspecific comparison, hotspot mechanisms are involved in lek evolution, then leks should be associated with some aspect of female distribution. Using radio-telemetry I found that females use identifiable and discrete routes when travelling through their environment. Lek location was strongly associated with these routes and tended to be associated with areas where the most females could be encountered.

I also examined the consequences of variation in lek size. Females visited and mated at both leks and solitary territories. While female visitation rates increased with lek size, they did so in proportion to the number of males present. Thus not only did females not show a preference for larger leks, but there were no identifiable benefits to males of display at larger leks. There was, however, a cost. At leks, 28% of displays to females were interrupted by intruders, such interruption did not occur at solitary display sites. These results contradict the predictions of "preference" hypotheses and at least one version of the hotshot hypothesis.

Finally, I investigated the hypothesis that males attempt to limit lek size due to the costs associated with display at larger leks. This was confirmed in a playback experiment. This experiment also demonstrated that males can distinguish neighbours from strangers using song.

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CHAPTER ONE.

INTRODUCTION.

What are lek mating systems?

Leka is a Swedish word meaning to play. The term lek was first used in reference to aggregations of displaying male ruff, Philomachus pugnax, by Edward Selous (1906). Generally the term has been used to describe species in which males cluster together to display to attract mates. Bradbury (1977) set out four defining characteristics of a lek mating system:

- 1) there is no male parental care; males contribute only sperm to a reproductive attempt.
- 2) the display territories of males are spatially aggregated and fill only a small part of the available habitat.
- 3) the display territories contain no significant resources required by females other than the males themselves.
- 4) females visiting the lek can choose their mates (Bradbury 1977; 1981).

Lek mating systems are known from a very small number of taxa; they represent less than 0.5% of known avian, and fewer than 0.2% of known mammalian mating systems (Davies 1991). Despite their rarity, lek systems have inspired a rich literature that dates back to the beginning of the century (Selous 1906, 1927; Bradbury 1981; Bradbury and Gibson 1983; Wiley 1991). The fascination that lek mating systems hold for behavioral and evolutionary ecologists stems from three questions raised by the mating system. First, what factors determine male display dispersion, in particular, what mechanisms drive clustered male display? Second, given that females of lekking species receive only sperm from their mates, how do females choose their mates and do they benefit from exerting that choice? Third, what factors are involved in the evolution of the elaborate secondary sexual traits and displays of many lekking species.

Within the scope of Bradbury's four characteristics, lek mating systems show a great deal of variation on several levels. Perhaps the best documented aspect of this variation is that

encountered in male display dispersion. Contrary to popular belief, lek mating systems are not a discrete category consisting only of large, tightly clustered groups of males. Rather, the mating system includes a continuum of male display dispersions, ranging from only slightly to highly clustered aggregations.

For convenience, two categories of leks are referred to: exploded and classical leks. The most dispersed lek systems are "exploded leks" (Bradbury 1981). Exploded leks differ from the closest non-lek mating systems, in which males are dispersed uniformly (Beehler and Pruett-Jones 1983; Beehler and Foster 1988), in that display territories fill only a small part of the available habitat and are spatially clustered. On exploded leks, the territories of neighbouring males do not share contiguous boundaries, and males are usually in vocal rather than visual contact, e.g. the epomorphine bat Epopomops franqueti (Bradbury 1977), the king bird of paradise, Ciccinurus regius (Beehler and Pruett-Jones 1983), capercaillie, Tetrao urogallus (Lumsden 1961), and McConnell's flycatcher, Mionectes macconnelli (Willis et al. 1978). In some species the clustered nature of male display dispersion may only be apparent at a population level. For example in the bearded bellbird Procnias averano (Snow B.K. 1970) the display territories of males at an exploded lek are separated by as much as several hundred metres.

Classical leks, where males are clustered tightly together on small, contiguous display territories, have been the focus of most lek research. These leks may consist of as few as 2 displaying males, as in Lawe's parotia, Parotia lawesii (Pruett-Jones and Pruett-Jones 1990), or up to several hundred as in sage grouse, Centrocercus urophasianus (Scott 1942).

More Variations on the Lek Theme

While individual species can be categorized as falling into one of the above groups, variation in lekking can also be found within a species, or even within a population. In the buff-breasted sandpiper, Tryngites subruficollis, males shift from display at leks to solitary display as the breeding season progresses (Pruett-Jones 1988). In other species while some males display at

leks others display solitarily, e.g. Lawe's parotia (Pruett-Jones and Pruett-Jones 1990), fallow deer, Dama dama, (Apollonio et al. 1992), white-bearded manakins, Manacus manacus (Lill 1974), and capercaillie, Tetrao urogallus (Wegge and Rolstad 1986). In a number of ungulate species lekking can occur simultaneously in the same population with resource-defense territoriality (Clutton-Brock et al. 1988; Gosling et al. 1987; Balmford and Turyaho 1992). Variation in lek behaviour can also be genetically determined. In the ruff, in addition to a number of behavioural strategies (Lank and Smith 1987), there are two genetically distinct types of males: dark coloured territory owners and light coloured males that display on the territories of other males (van Rhijn 1983).

Finally, though males at leks are engaged in the seemingly competitive activity of attracting mates, males of a few species cooperate in their display to females, e.g. manakins of the genera Chiroxiphia (Foster 1977; 1981) and Pipra (Robbins 1985; Schwartz and Snow 1975). Chiroxiphia lineata males display cooperatively on leks which are functionally a single territory. Though multiple males are required both to attract females to the territory and for effective display, only the alpha male ever mates (McDonald 1989a). Subordinate males must wait for their turn at the top, a wait that typically lasts 8 years (McDonald 1989b).

The Taxonomic Distribution of Lekking

Despite its overall rarity, the taxonomic distribution of lekking is as varied as its forms. In birds, the mating system is known from at least 12 families. In some avian families lekking occurs only in a single species, e.g. among the Psittacidae only the kakapo, Strigops habrotilus (Merton et al. 1975) leks, while in others it is the rule, e.g. Pipridae (Sick 1967; Prum 1994). Amongst mammals lekking is known from the marsupial mouse Antechinus stuartii (Lazenby-Cohen and Cockburn 1988), from old world ungulates (Clutton-Brock 1989), and bats Bradbury (1977). To date, only one species of frog, Ololygon rubra, has been shown to have a lek mating system (Bourne 1992). Amongst the insects lekking is known from a wide variety of Hymenopterans, Dipterans and from the Lepidoptera (Campanella and Wolf 1974; Alexander

1975; Parsons 1977; Alcock 1987).

Aims of this thesis

In this thesis, I address the question of what determines male display dispersion in the lek mating system of the ochre-bellied flycatcher, Mionectes oleagineus (Aves: Tyrannidae). This species has a lek mating system in which some males defend solitary display territories while others defend territories at small leks. A large proportion of males do not hold territories at all (Westcott and Smith 1994). I focus on two major questions: i) what determines where leks occur?, and ii) what determines the size of leks? Under the umbrella of these two questions I have addressed a number of related issues.

I begin in Chapter 2 (Westcott 1994) by comparing the locations and sizes of leks of the understory lek breeding species that occur on my study site. My aim here is to document the community level patterns of lekking and to provide a test of predictions of the hotspot hypothesis using inter-specific comparisons.

In Chapter 3, I again examine the hotspot hypothesis but in this instance I shift from the community level to focus specifically on M. oleagineus. The aim of this chapter is to examine whether lek locations are associated with some aspect of female distributions.

In Chapter 4, I address the question of what determines lek size. I use data collected during behaviour observations over three breeding seasons to address two further hypotheses for lek evolution: the preference hypotheses and the hotshot hypothesis.

In Chapter 5, I use a song playback experiment to determine whether male-male interactions influence male settlement patterns, in particular, how many males settle at a site and whether males are capable of distinguishing between neighbours and strangers on the basis of song.

CHAPTER TWO

LEKS OF LEKS: A ROLE FOR HOTSPOTS IN LEK EVOLUTION ?

ABSTRACT

A lek is a cluster of males on display territories. Despite the attention that lek mating systems have received, the factors involved in lek evolution are still poorly understood. The "hotspot" hypothesis suggests that population level patterns of female movement and/or dispersion determine male settlement patterns. Males, it is argued, should settle where females are most likely to be encountered or where female densities are greatest. Leks occur due to marked heterogeneities in female distributions. I tested three novel interspecific predictions of the hotspot hypothesis: 1) the leks of ecologically similar, sympatric species should be clustered; 2) the degree of this clustering should be related to the degree of similarity in diet between the species; and, 3) species with similar diets should show correlated changes in the sizes of neighbouring leks. I documented the size and locations of leks of four Neotropical bird species over four years. All three of the predictions were confirmed. The interspecific aggregation of leks strongly suggests a role of hotspot mechanisms in the evolution of lekking in these species.

INTRODUCTION

In lek mating systems, males gather into aggregations, called leks, and display to prospective mates. Within a lek each male defends a display territory. Display territories contain no significant resources and it is assumed that females visit leks solely to assess potential mates and for copulation (Bradbury 1981; Wiley 1991). Because females at leks can choose their mates relatively free of coercion by males, much interest in lek mating systems has focused on female mate choice (Balmford 1991). Recently attention has again focused on the pressures leading males to aggregate (e.g., Alatalo et al. 1992; Stillman et al. 1993; Théry 1992). Despite this, the mechanisms responsible for the evolution of leks themselves are still unclear (Clutton-Brock 1989; Balmford et al. 1993).

Hypotheses for the evolution of leks fall into three general categories. 1) The 'preference' hypotheses propose that males and/or females prefer mating at leks because of the advantages they gain compared to mating at solitary sites. Leks might be preferred because: i) they reduce the risk of predation (Koivisto 1965; Hjorth 1970; Wittenberger 1978; Gosling 1986); ii) they reduce mate search costs (Alexander 1975); iii) they allow a more efficient comparison of more males (Emlen and Oring 1977; Parker 1978); iv) lek size acts as an arbitrary Fisherian trait (Queller 1987); or, v) receptive females at leks are better able to avoid harassment by males and males are better able to attract and retain receptive females (Clutton-Brock et al. 1993; Stillman et al. 1993). 2) The 'hotshot' and 'attractiveness' hypotheses suggest that leks form as a result of high variance in male mating success. Males that obtain few copulations cluster around those that are successful (Arak 1983; Beehler and Foster 1988; Höglund and Robertson 1990a). 3) The 'hotspot' hypothesis (Lill 1976; Bradbury and Gibson 1983; Bradbury et al. 1986) suggests that patterns of female movement and/or dispersion determine where males settle: leks should form where female densities are highest or where females are most likely to be encountered.

Of these three ideas, the hotspot hypothesis is appealing simply because its

underlying mechanism, that male dispersion is a function of female distributions, is fundamental to our ideas about mating systems evolution in general (Vehrencamp and Bradbury 1984; Davies 1991). Because males in lek mating systems males provide only sperm in a reproductive attempt, they are freed from the constraints of parental care and are able to pursue those options that maximize their reproductive success. Consequently, it is in lek mating systems that the effects of hotspots should be most apparent. It is, therefore, surprising that with a few notable exceptions (see, for example, Pruett-Jones 1988; Théry 1992; Schroeder and White 1993) there has been little empirical support for the role of hotspots in lek evolution. In this study, I assess the plausibility of the hotspot hypothesis in explaining the evolution of leks in a group of Neotropical birds. I develop and test three predictions concerning the interspecific patterns of lek distribution of sympatric species that might be expected when hotspot mechanisms underlie lek evolution.

The Hotspot Hypothesis: the Interspecific Case.

To extend the hotspot hypothesis to several species, I begin by considering a suite of sympatric, lekking bird species. These species are similar in size and use similarly distributed resources. If ranging patterns are determined primarily by resources (Emlen and Oring 1977; Davies and Lundberg 1984; Wimberger 1988; Hews 1993) the females of these species should exhibit similar ranging patterns. Furthermore, if these species have similar environmental constraints on their movements, both the routes they use to travel to resources and the points at which their movements are concentrated should be in roughly the same locations.

Males should then settle where their exposure to the greatest number of potential mates is maximized. This is usually thought to be where female densities are highest (Höglund and Robertson 1990b; Théry 1992; Balmford et al. 1993). However, female home range use is often heterogeneous because the locations of resources vary over the breeding season (Höglund and Robertson 1990b; Bradbury et al. 1989a; Worthington 1982). Males may therefore do best by settling at sites where females' movements are channelled by environmental features. Males can then be certain that females will pass near these points as they move between resource

patches, irrespective of the patches' exact locations.

Given the above scenario, three predictions follow if hotspot mechanisms are involved in lek evolution. First, because females of all the species face similar constraints on movement, leks of the different species should be clustered. Second, because resources determine ranging patterns, the strength of this clustering should be related to the degree of diet similarity between the species. Finally, the hotspot hypothesis suggests that the number of males in an area should change to track the number of females using that area. Consequently, species with similar diets should exhibit correlated changes in the sizes (number of males) of neighbouring leks.

METHODS.

This study was conducted at Estación Sirena (lat. 8° 29' N, long. 83° 36' W) in Corcovado National Park, Costa Rica, from 1989 through 1992. The study area is 1.15 km² and is divided between low rugged hills (to approximately 140 m in height) and an alluvial plain. The area receives a mean annual rainfall of $5,305 \pm 301$ mm, $n = 10$ years (Servicio de Parques Nacionales de Costa Rica) with a distinct wet season between May and November. The vegetation is tropical, pre-montane, wet forest (Tosi 1969) and approximately 80% is primary forest with a canopy height of approximately 35 m. The remainder is 15 year-old second growth with a variable canopy height, roughly between 15 - 25m.

On the study site, four bird species, the ochre-bellied flycatcher (Mionectes oleagineus), the red-capped manakin (Pipra mentalis), the blue-crowned manakin (Pipra coronata), and the long-tailed hermit hummingbird (Phaethornis superciliosus), form leks in the forest understory. The first three of these birds are 11- 15 g frugivores that show broad overlap in resource use (Leck 1972; Flemming 1979; Skutch 1980; Loiselle and Blake 1990; pers. obs.). Local abundance of these three species is known to change in response to changes in fruit availability (Levey 1988; Blake et al. 1990). The fourth species is a 6 g, trap-lining nectarivore.

All four species move large distances (as much as 1 km, pers. obs.) within the forest understory between dispersed resource patches and thus probably face similar environmental constraints on their movements.

Each year I conducted exhaustive searches of the study site. During 1989 all areas were visited repeatedly to map the study site, make trails and survey vegetation. I checked the trunk of every canopy tree once every two weeks in 1990 and once every month in 1991 and 1992 in searches for nests and displaying males. Additional visits to all areas of the study site were made in the course of concurrent work in all years.

During searches I determined lek locations, the number of displaying males and the location of each lek centre. Lek centres were then plotted onto a map of the study site and a Donnelly modification of the Clarke and Evans test (Krebs 1989) was used to describe lek distribution quantitatively. This technique tests for deviations from a random distribution by comparing observed and expected nearest-neighbour distances in populations whose densities are known. An index of aggregation of $R = 1.0$ indicates a random distribution. Scores lower than and greater than $R = 1.0$ indicate deviations towards clumped and uniform distributions respectively.

I also used the Clarke and Evans test to identify any clustering of leks around topographical features that might be expected to channel movements. Such topographical features included: i) confluences of drainages, ii) saddles in ridgelines, iii) the ends of ridgelines, and, iv) in flat areas, watercourses. Using the 1992 data, I identified areas where more than one species lekked and determined the centre of the combined leks in each of these areas. The distance to the nearest topographical feature was then determined from the study site map.

RESULTS

Figure 2.1 summarizes the numbers of leks and males as well as lek locations for the

four species in each year of the study. Because *P. superciliosus* were not individually marked, no data on numbers of males were recorded for this species.

In all four years, the leks of the four species were significantly clumped (Figure 2.1, Table 2.1 i). At some sites, this clumping was so extreme that all four species could be encountered displaying simultaneously on partially overlapping leks. More commonly, however, leks were located short distances from each other (Figure 2.2). Leks were also significantly aggregated with topographic features (Clarke and Evans Test, $R=0.77$, $n=38$, $z=-3.15$, $P<0.05$).

While the leks of all four species were clustered, the nectarivore leks showed the least clustering (Table 2.1 i, Figure 2.2). Significant differences across all species in mean distance to nearest heterospecific lek were found in only one year (Table 2.1 ii). In each year, however, nectarivore leks had larger mean distances to the nearest heterospecific lek than did the frugivores (Table 2.1 iii). There were no significant differences in mean distance to the nearest heterospecific lek among the three frugivores in any year (Table 2.1 iv).

Monitoring changes in lek sizes from one breeding season to the next showed that neighbouring frugivore leks tended to change size in the same direction (Table 2.2). Because of movements of males among leks within or between years, lek sizes are not independent of each other. Consequently, simple correlations between the sizes of neighbouring leks were not calculated. At sites where more than one frugivore species lekked, I scored each possible species pair at the site as follows: +1 if their lek sizes changed in the same direction (both increase or both decrease); -1 if they changed in opposite directions (one increases while the other decreases); and, 0 if one changed size while the other remained constant. If neither lek showed any change in size they were both dropped from the analysis. The mean of these scores was then calculated. A positive mean score indicates that average lek sizes changed in the same direction, a negative mean score that they changed in opposite directions. Though the mean scores were low in individual comparisons between years, the results were consistent across the three comparisons. The mean score over the three years, 0.118, is significantly greater than zero (one sample, one-tailed t-test $t=15.72$, $d.f.=2$, $P<0.05$).

DISCUSSION

The clustering of leks documented here argues for the action of some common factor on all species. Under my starting assumptions, the effects of environmental features, e.g. topography and vegetation, on movement are likely candidates. This scenario suggested that the same environmental features will act to constrain the movements of all four species at the same locations because they all move long distances and do so through the forest understory. This process should result in interspecific foci of female movements. According to the hotspot hypothesis, males should settle at these sites, thus producing the observed clusters of leks.

My suggestion that the interspecific clustering of leks is due to the shared influence of environmental features on female movements is supported by several observations. First, leks are significantly associated with topographical features that would channel movements through a particular area. Other environmental features, such as boundaries between different vegetation types, might also have an effect. In addition, radio-telemetry data from M. oleagineus indicates that topographical influences on movement are strong and that features like those listed above do indeed channel female movements (Chapter 3).

Can the clustering of leks be explained through other mechanisms? One alternative might be that the four species share preferences for a particular display habitat of limited availability. This is unlikely. M. oleagineus males do show preferences for a particular display habitat. However, the distribution of the preferred display habitat does not appear to influence male distribution and much similar habitat away from current leks is vacant, 11% of that sampled (Westcott 1993). In addition, though all four species often occur in one area, within that area they choose different levels of the understory for their displays. This results in marked differences across the species in the microhabitat types selected.

Alternatively, lek clustering might be due to decreased predation risk associated with

the interspecific clusters. Potential predators are common on the study site. However, in over 500 hours of observations at leks, only two predation attempts, both unsuccessful, were observed (unpubl. data). In both instances, neither conspecifics nor heterospecifics in adjacent territories appeared to notice the incidents and display continued uninterrupted. Alarm calls eliciting general responses to predators were not recorded at the leks of any of the species. In addition, predators were not more or less common at leks than elsewhere on the study site (unpubl. data). These observations cannot rule out an influence of predation on lekking. However, they do suggest that predation is probably not the primary force in the production and maintenance of leks (Lill 1976; Beehler and Pruett-Jones 1983; Deutsch and Weeks 1992; Balmford and Turyaho 1992).

Another alternative is that lek sites are chosen because they are very close to, or even within, resource patches. Several observations argue against resource patch location as the major determinant of lek location. First, resource patches are relatively short lived and their exact locations vary both within and between years. In contrast, lek locations remain constant within, and with some exceptions, between years (Figure 2.1). There is little indication for any of these species that males shift lek locations within years to track changes in resource distributions. Second, if leks are located near or within resource patches both males and females should feed close to leks. Two M. oleagineus males radio-tagged in 1990 foraged large distances from their leks, even going to foraging sites beyond other conspecific leks. Recaptures of foraging males long distances from their display territory were also not unusual. Finally, radio-tagged female M. oleagineus do most of their foraging at sites that are no more or less associated with leks than expected by chance (Chapter 3). This is not to say that resources cannot sometimes be found on leks. Insectivory by lek attending males of all four species was common. However, frugivory at leks was rarer (Westcott and Smith 1994) and nectar feeding was not observed.

As predicted, the sizes of the leks of the frugivores at a given site tended to change in the same direction. Although the overall mean change score was positive, correlated changes in lek size were by no means the rule. This suggests that mechanisms other than hotspots probably

also influence lek size (Bradbury et al. 1986; Beehler and Foster 1988; Alatalo et al. 1992; Balmford et al. 1993). If this is the case, then the best interpretation of the observations presented here is that hotspots provide the initial impetus for male aggregation and determine lek location. Additional factors then modify lek size.

This report of "leks of leks" suggests that the hotspot hypothesis is a plausible explanation for lek evolution. My results raise several interesting points. First, a criticism of the hotspot hypothesis has been that areas of high female density are unlikely to be small enough to produce the clusters of males that characterize many lek systems (Bradbury et al. 1986; Alatalo et al. 1992). If environmental constraints on movement in given locations are severe, however, females' movements may be sufficiently channeled to produce tightly clustered leks through hotspot mechanisms alone. Second, the questions of why lek?, where should a lek form?, and how many males should settle at a lek? may all require separate consideration.

Table 2.1. Summary of the statistics relating to i) the aggregation of leks and ii -iv) distances between heterospecific leks. In part i), R is the Index of Aggregation from the Clarke and Evans test, see text, n is the number of leks included in the analysis, and z is the test statistic.

YEAR	TEST			
i	Index of Aggregation of leks			
1989	R=0.57	n=44	z=-4.55	P<0.05
1990	R=0.59	n=42	z=-4.19	P<0.05
1991	R=0.58	n=42	z=-4.22	P<0.05
1992	R= 0.57	n=48	z=-4.69	P<0.05
ii	One-way ANOVA with prior comparisons: across all species			
1989	F=3.249	d.f.=3	P=0.032	
1990	F=2.658	d.f.=3	P=0.062	
1991	F=2.406	d.f.=3	P=0.083	
1992	F=1.557	d.f.=3	P=0.21	
iii	between nectarivore and the grouped frugivores			
1989	F=5.200	d.f.=1	P<0.05	
1990	F=5.818	d.f.=1	P<0.025	
1991	F=5.254	d.f.=1	P<0.05	
1992	F=7.29	d.f.=1	P<0.025	
iv	within the frugivores			
1989	F=0.197	d.f.=2	P>0.05	
1990	F=0.829	d.f.=2	P>0.05	
1991	F=1.928	d.f.=2	P>0.05	
1992	F=0.538	d.f.=2	P>0.05	

Table 2.2:

Summary of lek size changes (# of display territories) for each of the species pairs. The means are presented for each species pair within a year, for all pairs within a year, and for all pairs in all years. See Text for explanation.

Species pair	Score			Mean	
	1		-1	within pairs	all pairs
	0				
89/90					
M. oleagineus/P. mentalis	2	5	2	0.0	0.115
M. oleagineus/P. coronata	1	5	1	0.0	
P. coronata/P. mentalis	3	7	0	0.3	
90/91					
M. oleagineus/P. mentalis	3	7	1	0.18	0.107
M. oleagineus/P. coronata	2	4	2	0.0	
P. coronata/P. mentalis	2	6	1	0.11	
91/92					
M. oleagineus/P. mentalis	2	5	4	-0.18	0.133
M. oleagineus/P. coronata	3	4	2	0.11	
P. coronata/P. mentalis	7	1	2	0.5	
					0.118

Figure 2.1:

A map of the locations of the centres of the leks of each the four species in each year from 1989 to 1992: diamond = M. oleagineus; square = P. mentalis; triangle = P. coronata; circle = P. superciliosus. The dotted lines are creeks. The number of leks, number of territorial males and territorial males/ha for each species in each year are as follows: M. oleagineus - 1989: 15, 26, 0.22; 1990: 13, 22, 0.19; 1991: 12, 20, 0.17; 1992: 15, 29, 0.25; P. mentalis - 1989: 9, 28, 0.24; 1990: 11, 24, 0.21; 1991: 10, 22, 0.19; 1992: 14, 25, 0.22; P. coronata - 1989: 12, 35, 0.3; 1990: 11, 30, 0.26; 1991: 12, 27, 0.23; 1992: 12, 30, 0.26; P. superciliosus (number of leks only) - 1989: 8; 1990: 7; 1991: 8; 1992: 7.

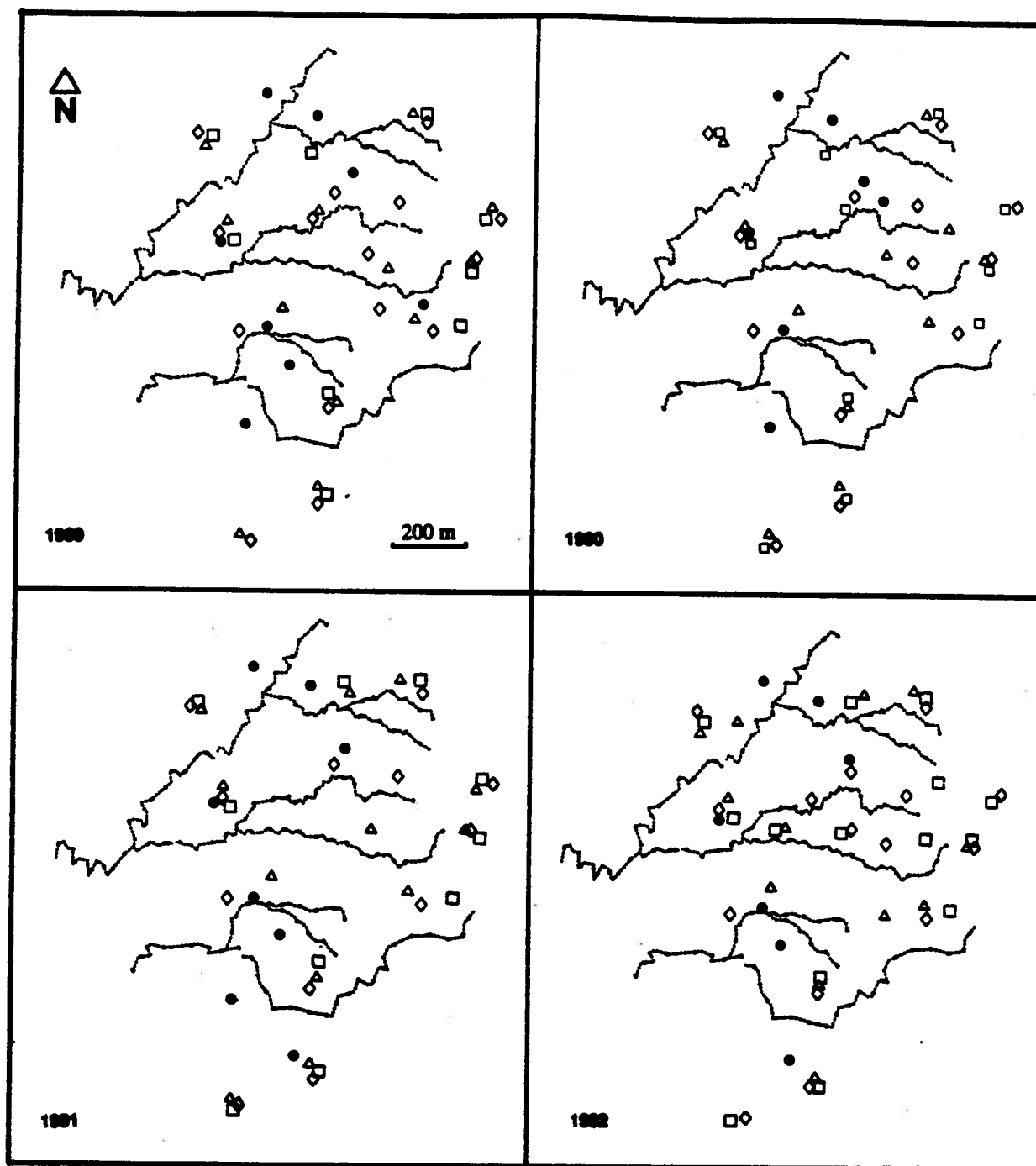
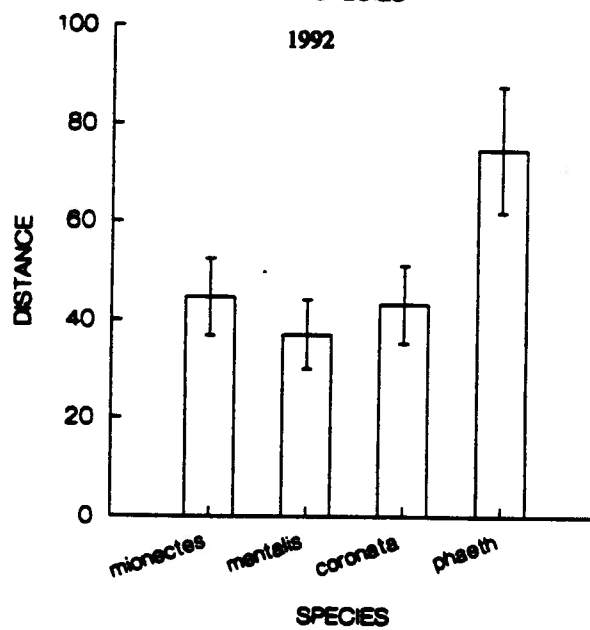
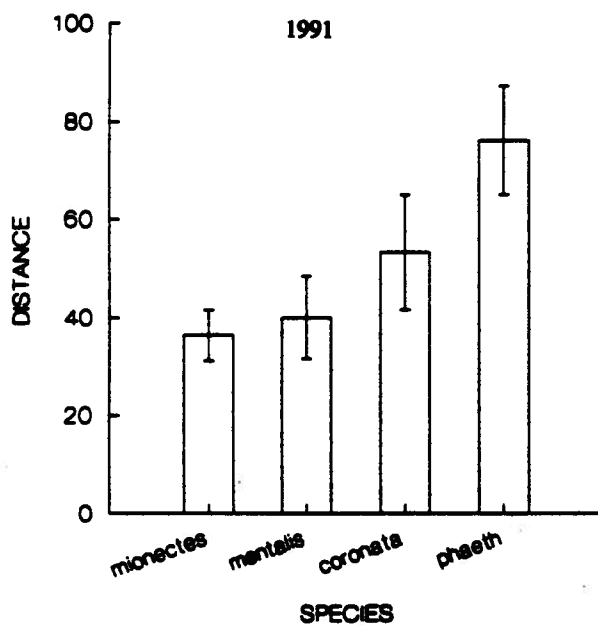
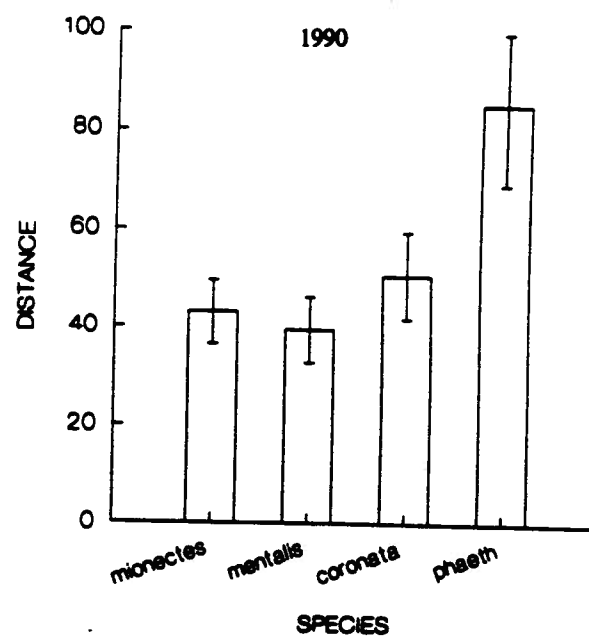
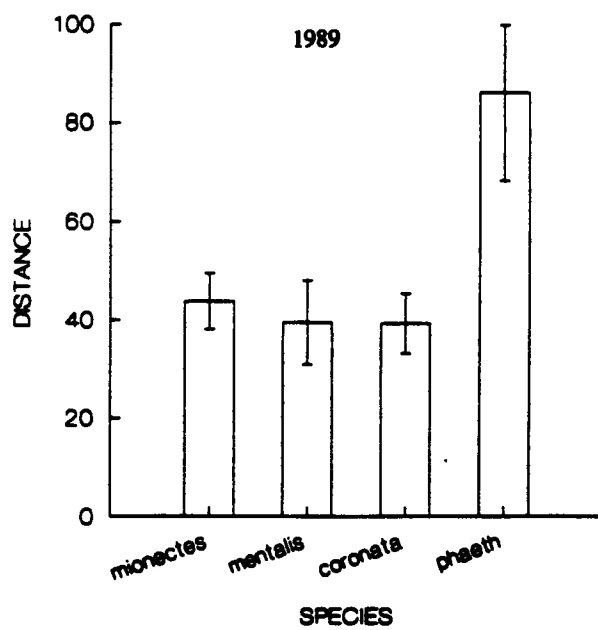


Figure 2.2:

Mean distances (in m, \pm S.E.) from the leks of each of the species to their nearest heterospecific neighbor lek in meters, for each of the four years.



CHAPTER THREE.

THE RELATIONSHIP BETWEEN LEK LOCATIONS AND PATTERNS OF FEMALE MOVEMENT AND DISTRIBUTION IN A NEOTROPICAL FRUGIVOROUS BIRD.

ABSTRACT

The different versions of the hotspot hypothesis for the evolution of leks variously suggest that leks should form either in areas 1) where there is a high degree of overlap of female home ranges, 2) where females spend most of their time, 3) where the most females can be encountered, 4) or in areas where there is high female traffic. The notion underlying these predictions, that males adjust their behaviour according to that of females, is basic to how we think about the evolution of mating systems in general. I monitored female movements using radio-telemetry to test the various predictions of the hotspot hypothesis in the lek mating system of the ochre-bellied flycatcher, Mionectes oleagineus (Aves: Tyrannidae). I found that females use identifiable routes when travelling through their environment. Each route was used by several females. Lek locations were strongly associated with these routes, and tended to be in areas where the most females could be encountered. Leks were not located in areas where females spent the most time. These results support the female traffic version of the hotspot hypothesis for the evolution of leks in this species.

INTRODUCTION

The most recognizable aspects of lek mating systems are the leks themselves. Leks are clusters of displaying males attempting to attract potential mates. Determining the nature of the pressures that result in the formation of leks has been a primary focus of research into lek mating systems. Hypotheses for lek evolution can be divided into three general categories. In the 'preference' hypotheses, males and/or females prefer mating at leks because of the advantages they gain, compared to mating in other male display dispersions. Leks might be preferred because: i) they reduce the risk of predation (Koivisto 1965; Hjorth 1970; Wittenberger 1978; Gosling 1986); ii) they reduce mate search costs (Alexander 1975); iii) they allow a more efficient comparison of more males (Emlen and Oring 1977; Parker 1978); iv) lek size acts as an arbitrary Fisherian trait (Queller 1987); or, v) receptive females at leks are better able to avoid harassment by males, and males are better able to attract and retain receptive females (Clutton-Brock et al. 1993; Stillman et al. 1993). In the second category are the 'hotshot' hypotheses. These suggest that leks form as a result of high variance in male mating success. Males that obtain few copulations cluster around those that are more successful (Arak 1983; Beehler and Foster 1988; Höglund and Robertson 1990a). Finally, the 'hotspot' hypothesis (Alexander 1975; Bradbury 1981; Bradbury et al. 1986) suggests that patterns of female movement and/or dispersion determine where males settle: leks form where female densities are highest or where females are most likely to be encountered.

The appeal of the hotspot hypothesis lies in the fact that its underlying mechanism, that male dispersion is a function of female distributions, is fundamental to our ideas about the evolution of mating systems in general (Crook 1965; Emlen and Oring 1977; Vehrencamp and Bradbury 1984; Davies 1991). Males in lek mating systems are freed from the constraints of parental care and, therefore, are able to pursue other options to maximize their reproductive success. These options include moving to display at sites where their exposure to potential mates is maximized. Consequently, it is reasonable to expect that hotspot effects should be apparent in

lek mating systems, and indeed several studies have provided some support for the hypothesis (Pruett-Jones 1988; Théry 1992; Schroeder and White 1993; Westcott 1994, Chapter 2).

The hotspot hypothesis has been proposed in a number of different formats. Following from Kruijt et al.'s (1972) observations of the formation of a black grouse lek, Lill (1976) suggested that leks form when males "'solve' the problem of meeting receptive hens...by using a fixed display site at a location favoured by feeding females" (p. 72). Bradbury (1981) suggested that leks should form at locations where females were most likely to pass, i.e. at hotspots in female traffic. The first formal version of the hotspot hypothesis was provided by Bradbury and Gibson (1983) and developed later by Bradbury et al. (1986). They proposed that males settle at those sites where female densities are the greatest. In their models, these authors used as their measure of female density the extent of female home range overlap. Most subsequent tests of the hotspot hypothesis have been based on the results of Bradbury et al.'s (1986) simulations (Bradbury et al. 1989a; Höglund and Robertson 1990b; Théry 1992; Schroeder and White 1993; Balmford et al. 1993).

Empirical tests of the hotspot hypothesis have had mixed results. Leks can be located at sites with apparently high female traffic, e.g. along a route travelled by females as part of their daily movements (Appolonio et al. 1990), and in locations with high female densities (Clutton-Brock et al. 1988; Pruett-Jones 1988; Apollonio 1989; Gosling and Petrie 1990), though in sage grouse, Centrocercus urophasianus, this is only apparent at a coarse grain (Bradbury et al. 1989a). Similarly, Schroeder and White (1993) found that in greater prairie chicken, Tympanuchus cupido, males settled in areas where their "breeding potential" was maximised. The hotspot prediction, that female home range size and the degree of male clustering should be positively correlated, has been supported in studies of both mammals (Bradbury 1981; Balmford et al. 1993) and birds (Bradbury et al. 1986; Théry 1992). However, this prediction is also shared with other hypotheses for lek evolution (Emlen and Oring 1977; Bradbury 1981; Beehler and Foster 1988). Finally, Westcott (1994; Chapter 2) found that the leks of sympatric lekking bird species were clustered, as would be predicted from the hotspot hypothesis if we assume similar

movements and similar constraints on movement within and across species.

In contrast, several studies have failed to confirm the hypothesis' predictions. There was no association between lek location and areas of greatest female densities in three species of ungulate (Balmford et al. 1993), or in the small heath butterfly, Coenonympha pamphilus (Wickman et al. 1995). Nor were leks located in the areas of the highest female home range overlap in capercaillie (Wegge and Rolstad 1986) or great snipe, Gallinago media (Höglund and Robertson 1990b). In addition, inter-lek distances in these species appear to be greater than predicted by the hypothesis, i.e. less than the average female's home range diameter (Wegge and Rolstad 1986; Höglund and Robertson 1990b). However, this prediction is also shared with female preference models (Bradbury et al. 1986; Gibson et al. 1990).

In the work I report here I provide a direct test of the hotspot hypothesis' most basic prediction, that the distributions of leks is related to some aspect of female distribution or movement patterns. I monitored movements of female ochre-bellied flycatchers, Mionectes oleagineus (Aves: Tyrannidae), by radio-telemetry to examine three different formulations of the hotspot hypothesis:

- 1) Males settle where females spend the most time, e.g. at resting and/or feeding sites, the time/resource model (Kruijt et al. 1972; Lill 1976; Gosling and Petrie 1990).
- 2) Males settle in those areas which are used by the greatest number of females, i.e. have the highest female densities.
- 3) Males settle at hotspots in female traffic.

METHODS

Study Species

Mionectes oleagineus is a resident of the understory of lowland, wet forests throughout the Neotropics. It is a small bird (11-12 g) and the sexes are monomorphic, being

dull, olive green in colour with a slight ochre wash on the belly. M. oleagineus is a frugivore that takes a variety of small arils, fruits etc. (Sherry 1983) and supplements this diet with arthropods (pers. obs.).

From roughly late January to August, male M. oleagineus defend small display territories in the forest understory (median size 477 m², Westcott and Smith 1994). Territorial males attempt to attract mates and defend their territory using song (Westcott 1992). Approximately 30% of territorial males hold solitary display territories while the remainder are found in small leks of 2 - 6 individuals. Only half the male population is territorial, however, and the remainder behave either as floaters or as satellites on the territories of other males (Westcott and Smith 1994).

Females build nests and care for the young alone. Eggs are incubated for about 21 days and the nestling stage lasts approximately 18 days. Eighty six percent of nests fail prior to fledging, usually due to predation (Westcott, unpubl. data). Because the breeding season can last up to 8 months in a good year, females have the opportunity for renesting and may rear more than one brood per year. I have recorded renesting within a breeding season occurring only after nest failure, though it is possible that renesting might also occur after successful attempts. Females are rare visitors to leks (Westcott and Smith 1994).

Study Site

This study was conducted between May 1991 and December 1992 at Estacion Sirena in Corcovado National Park, Costa Rica (lat. 8° 29' N, long. 83° 36' W). The study area is 1.15 km² and is divided between low rugged hills (to approximately 140 m in height) and an alluvial plain. The area receives a mean annual rainfall of 5,305 mm, \pm 301, n = 10 years (Servicio de Parques Nacionales de Costa Rica). The majority of this rain falls between late June and November. The vegetation is tropical, pre-montane, wet forest (Tosi 1969) and approximately 80% is primary forest, the remainder being 17 year-old second growth.

I laid out a trail system following each of the ridge lines and creeks on the study site.

Every 25 m along each trail I placed a permanent, numbered, reference marker. I then surveyed the study site and made a topographical map on which these trails and permanent markers were plotted.

Telemetry

Birds were captured using mist nets, weighed, measured and each individual was given a unique combination of coloured leg bands. Females were identified from the morphometric data (see Westcott and Smith 1994). Radios (0.8g when mounted) from Biotrack and Holohil Systems Ltd. were attached to females using harnesses made from gauze. All birds flew strongly upon release and appeared not to be bothered nor hindered by the radios. In all cases where birds were recaptured or resighted 6 weeks after being tagged, $n=6$, the radio had and harness been dropped.

Since my aim was to identify correlations between lek location and female distributions and movements, it was necessary to control for any influence of males or leks on females' movements. An obvious way of doing this was to track females only during the non-breeding season. The short duration of the non-breeding season, the heavy rainfall (as much as a metre per month), and the fact that males are present, though not necessarily actively displaying, on their display territories all year round, all conspired to make this a less than satisfactory approach. Consequently, I did what telemetry was possible during the non-breeding season, a quarter of my total sample, and did the remainder during the breeding season.

To avoid any confounding effects resulting from the presence of males on display territories, only non-breeding females were selected for telemetry during the breeding season. Females were selected if they met the following criteria: i) were known to have recently bred successfully within the previous month, so presumably were unlikely to reneest, or, ii) showed no sign of tail feather wear indicative of ongoing incubation, iii) did not differ from the non-breeding female mean mass, and iv) did not have an enlarged brood patch. This procedure was successful in selecting non-breeding females. Only 3 of 25 tagged females showed any sign of

breeding activity during this work. One female made repeated visits to leks over a period of several days, one visited a lek and subsequently laid a clutch, and another was already incubating when tagged. These females were excluded from the analysis. I sampled four females during the non-breeding season.

With the exception of two birds early in the study, I followed only one female at a time. As far as possible, I followed the females continuously from prior to their leaving their roost site in the morning until they settled down again in the evening. Location fixes were made by triangulation, using bearings taken from the permanent markers along the trails. A new fix was determined whenever a change in the bird's location could be detected. Triangulations were analyzed using "Locate II" (Nams 1990). Mean 95%-error ellipses (Maximum Likelihood Estimator) on triangulation fixes were 282 ± 78 S.E. m², n=4060.

Radio-telemetry data was analysed in the following manner. A grid of 25 m² cells was laid out over the map of the study site. Within each of these cells, all occurrences of the female distribution parameter under consideration were tallied. These distribution parameters included: i) total number of fixes from all females recorded in that cell, ii) total number of females recorded in the cell, and iii) number of instances of travel through the cell (outlined in more detail in the results section). This resulted in matrices of scores that were overlaid on the map of the study site. Randomization tests were then used to analyze the distribution of leks relative to these female distribution parameters.

Randomization tests were performed as follows. There were 13 leks on the study site during the period of the study. For each of the three distribution parameters, the score for the cell in which each lek's centre occurred was determined and the mean for all 13 leks calculated, the observed mean lek score. Thirteen computer "leks" were then randomly settled onto the pattern in question and their mean score was determined and recorded. This process was repeated 5000 times. The location of the observed mean lek score in the distribution of simulated mean lek scores was then determined. An observed lek score that lay in either the upper or lower 2.5% tails of the distribution indicated that leks were either more or less associated with a pattern of

female distribution than would be expected by chance alone.

RESULTS

In total, 16 females, or approximately 25% of the estimated female population (unpubl. data), are included once in this analysis. Four of these were followed during the non-breeding season. A further 6 tagged females were not included in the analysis because they were followed for less than 4 days. This occurred due to presumed radio failure (dropped radio or battery failure, $n=3$), the female leaving the study site ($n=1$), being taken by a raptor (Acipiter superciliosus, $n=1$), or by a snake at night ($n=1$). Three additional females were excluded because they showed signs of breeding activity during the time they were being tracked (see above). Females were tracked for a mean of 8 days, the range being 4-16 days.

The mean female home range size was 28.4 ha, ± 3.7 S.E., and included 4.7, ± 0.5 S.E., leks. Home range size increased with each additional day of tracking ($r=0.6$, $n=16$, $P=0.016$), though the strength of the correlation was due largely to a single female. Though still a trend, the correlation was no longer significant when this female was removed ($r=0.46$, $n=15$, $P=0.096$). There was no correlation between the date on which tracking of a female commenced and the size of her home range ($r=-0.19$, $n=16$, $P=0.49$), nor did home range size vary with season ($t=-0.02$, d.f.=14, $P=0.984$). Neither the number of leks within a female's home range ($t=0.066$, d.f.=14, $P=0.948$), nor the mean proportion of time that females spent at leks (Mann-Whitney $U=38$, $n=16$, $P=0.488$) differed between the breeding and non-breeding seasons. Indeed, even during the breeding season females' visits to leks appeared not to be concerned with males; they simply passed through the territory, and males were often not even present.

The pattern of use of the study site by the females is shown in Figure 3.1. Use of the area was extremely heterogeneous. Females spent a higher proportion of their time in areas where fruiting plants were plentiful. Areas of extremely high usage were localized and

associated with fruiting events of long duration, e.g. fruiting by the tree Clusia tovomitosis. In the randomization test 48% of the 5000 iterations had mean lek scores higher than that observed in the field. Thus leks were not associated with areas where females spent their time than would be expected by chance ($P = 0.96$), a result that is inconsistent with the time/resource model of the hotspot hypothesis.

The distribution of female densities, i.e. the number of different females recorded at least once in each cell, is shown in Figure 3.2. The greatest female densities tended to be found in the gullies. In the randomization test only 3.4 % of the simulated mean lek scores were higher than that observed for leks in the field. Thus, leks tended to be associated with areas of high female densities ($P = 0.068$).

In general, females tended to spend relatively long periods of time, sometimes almost entire days, in a single area, e.g. in a patch of fruiting bushes or at a large fruiting tree, before moving on to a new area. Movement between such "patches" took two forms. In the first, females moved in a stop-start fashion, often changing direction. This pattern of movement was suggestive of exploration or foraging and such behaviour was confirmed by direct observation. This first movement type was similar to the circumscribed within-patch movements, which would re-cover the same ground. The second form was characterised by movement with a relatively constant speed and heading, and is hereafter called directional movement. In the following analysis I have extracted all recorded instances of directional movement. Each occurrence of directional movement was plotted as a vector on the map of the study site. In order to analyze their distribution, the directional movements traversing each cell were tallied.

Movement between patches followed distinct routes and such routes were documented in all areas of the study site (Figures 3.3, 3.4). Each route was used by several females and also used repeatedly by individual females. Routes tended to follow lines of least topographical resistance, e.g. to run along drainages and to cross ridges at cols (Figure 3.4). In the randomization test, only 43, or 0.0086 % of the 5000 mean lek scores were greater than those observed in the field. Thus, leks are very significantly associated with areas of high female

traffic ($P = 0.0172$).

DISCUSSION

The Influence of Males on Female Movement

When attempting to document the effect of female movement on male distributions, it is important that the males are not themselves influencing female movements. This possibility represents the major potential shortcoming of this study as most females were tracked during the breeding season. Even though some females were tracked during the non-breeding season this was not a complete solution to the problem. First, males maintain their territories and sing through out the year (pers. obs.), though active display is rare during the non-breeding season. Second, adverse weather conditions severely reduced both the time available and the quality of the work that could be done during the non-breeding season. To minimise the effect of the presence of males during the breeding season, I selected and used data from non-breeding females only. This approach was permitted by the fact that for a significant proportion of the long breeding season females are in non-breeding condition. The marked influence of topography on movements (Figure 3.4) and the lack of differences between the breeding and non-breeding season in female movement patterns, e.g. home range sizes, number of leks per female home range and the proportion of time that females spend at leks, suggest that the influence of males was successfully controlled.

Female Distributions and the Hotspot Hypothesis

My telemetry results support several predictions of the hotspot hypothesis. Both verbal and simulation models (Bradbury and Gibson 1983; Bradbury et al. 1986) suggest that if hotspot mechanisms are involved in lek evolution, inter-lek distances should be less than the average female home range diameter, and females should visit more than one lek prior to mating.

Though the irregular shape of home ranges here makes the concept of "average home range diameters" difficult to deal with, the presence of 4.7 display sites within the average female home range is consistent with the prediction. Since females regularly passed more than one lek in a day's foraging, it seems likely that they would visit more than one lek prior to mating.

Observations of the same individual females being displayed to by males at different leks on the same and subsequent days (unpubl. data), and of the one radio-tagged female visiting multiple leks (n=3) confirm this.

My most important result is the support for the hotspot hypothesis' more general prediction; that male settlement patterns are a function of female distributions. Leks were most strongly associated with the routes that females use to travel through their environment (Figure 3.3). Leks tended to occur where the greatest numbers of different females were recorded (Figure 3.2). Leks were not associated with areas used heavily by females, such as fruiting plants (Figure 3.1).

To understand why males might distribute themselves based on traffic routes, rather than some other aspect of female distribution, requires consideration of the circumstances under which they are attempting to meet receptive females. Three points are important. First, receptive females are spread unpredictably and sparsely through time. Not only is M. oleagineus' breeding season long, but females are also highly asynchronous, with nesting occurring throughout this period. Second, female mate choice appears to be based on long-term sampling of males rather than on song performance on the day of a visit (Westcott 1992, Chapter 4). Third, the locations of fruiting events varies both within and between breeding seasons (Worthington 1982; D. Graham, pers. comm.). Males must, therefore, approximate the optimal solution to several conflicting demands. Ideally, they should maintain the maximum exposure to females, and be readily locatable by females over the entire length of the breeding season, both for assessment for mate choice and for subsequent copulations. However, the locations where females can be found, e.g. at fruiting plants, will be unpredictable both within and between breeding seasons.

Males will benefit from displaying at a fixed location when females need to reliably

relocate them. This will occur when mate choice is based on information gathered over a long period of time. It will also be the case if females return to a male to copy the mate choice of others (Wade and Pruett-Jones 1990), or to remate either within (Kruijt and Vos 1988; McDonald 1989a; Trail and Adams 1989; Balmford 1990) or between breeding seasons (McDonald 1989a; Pruett-Jones and Pruett-Jones 1990; Lill 1974a). When females do need to relocate mates, it is unlikely that for males settlement at sites where females spend time, i.e. feeding sites, would provide an adequate solution to the problem of display site selection. The ephemeral nature of fruiting events (Worthington 1982; D. Graham, pers. comm.) means that it will be difficult to choose a single site which remains close to good feeding habitat throughout the breeding season. A second problem with this strategy is that settlement at resources exposes males only to the females that use that particular patch; potentially only a small fraction of the females in an area (compare Figures 3.1 and 3.2). Males at these sites will maximize their exposure to females in terms of total time, but not always in terms of the number of receptive females encountered.

Under the second hotspot formulation, males attempt to settle at those sites where they can encounter the greatest number of females. While leks showed some association with this pattern of distribution (Figure 3.2), this result was not quite significant, nor was it the distribution pattern to show the strongest association with leks. Given the expectation that lek-breeding males are attempting to maximize the number of potential mates they encounter, this result is surprising. This result may, however, be a function of the nature of the "site" rather than of the logic that lead to the expectation of males settling in areas of high female densities. While many of the sites with high numbers of females are located along travel routes (see below), others are located at fruiting plants. Once again, the variability in the location of these fruiting sites over time probably makes them a poor choice for display site location.

Leks were most strongly associated with areas used by females traveling between sites (Figure 3.3). Settlement along travel routes is an appropriate solution only when their use by females is predictable. In this study, females traveled along these routes and through particular points irrespective of precisely where they had come from in one area or where they

were going to in another (Figure 3.5). Such predictability is most likely to arise when environmental conditions restrict female movements to certain sites (e.g. Apollonio et al. 1990). However, such strong constraint is unlikely to have been involved in the case of M. oleagineus. For M. oleagineus the predictability of female movements through particular sites appears to have more to do with travel along lines of least resistance, e.g. moving around the end of a ridge rather than climbing over it (Figure 3.4). In other cases, females appear to cross ridges at certain points simply because the gullies and associated small ridge lines that originate at these points focus and channel, rather than constrain, movement.

Previous Tests of The Hotspot Hypothesis

Based on the mixed results of tests of the hotspot hypothesis, Gibson (1992) and Balmford et al. (1993) argued that if hotspot mechanisms are involved in lek evolution, they operate only at a very coarse level. Two observations from my study suggest that such a general conclusion is premature. Following Bradbury and Gibson's (1983) statement that the hotspot hypothesis would be falsified if it was found that leks did not occur in areas where the greatest number of female home ranges overlap, several studies have concentrated on female home range size and distributions. However, in my study home ranges commonly encompassed areas that the individual did not actually use and some areas of very high home range overlap were not recorded being used by some or all of the females in whose home ranges they occurred. This is an artifact of standard home range estimation procedures. So, firstly, estimates of home range overlap may be of limited value when an accurate assessment of female distributions is required. Secondly, few studies have considered more than one measure of female distribution; different aspects of female distribution may be relevant under different conditions. For example, Bradbury et al. (1989) concluded that, while female densities could predict lek location on a coarse level in sage grouse, they failed to do so on a fine scale. These authors suggested that this was possibly due to the over-riding influence of specific habitat preferences of males at this level. In my study, the three female distribution parameters showed very different associations with

leks. If male sage grouse face a similar set of conditions to male M. oleagineus, an alternative hypothesis might be that they are settling according to local female travel routes (pers. comm.).

Summary

In summary, hotspot mechanisms appear to affect lekking in M. oleagineus. In particular, my study identifies a clear role for hotspot mechanisms in determining the precise location of leks of M. oleagineus. Leks were most strongly associated with travel routes. I interpret this pattern to be a result of the males' solution to the "mate encounter problem" (Lill 1976). Females nest asynchronously and assess males and mate throughout the long breeding season. Individual males then, need to be easily relocatable and, therefore, should display from a single location. This location, however, cannot be at feeding areas because these are both ephemeral and unpredictable within and between breeding seasons. Males may settle along travel routes because all females use these routes and route locations remain constant over time. My results suggest that it is too early to write the hotspot hypothesis off as responsible only for minor background variation in lek mating systems. Ephemeral and unpredictable resources, large daily movements, a long breeding season, and low female synchrony are characteristic of many other tropical, lek-breeding, frugivorous birds. I suggest that the hotspot hypothesis may still prove to be useful for explaining lekking in these species.

Figure 3.1:

Distribution of use of the study site in terms of time spent in each 25 m² cell by all females. Leks are shown as hollow diamonds, creeks as black lines. Females spent less than 58 minutes in white areas. The time spent in each cell increases as the shading darkens. There is no association between leks and areas of high female use ($P=0.96$).

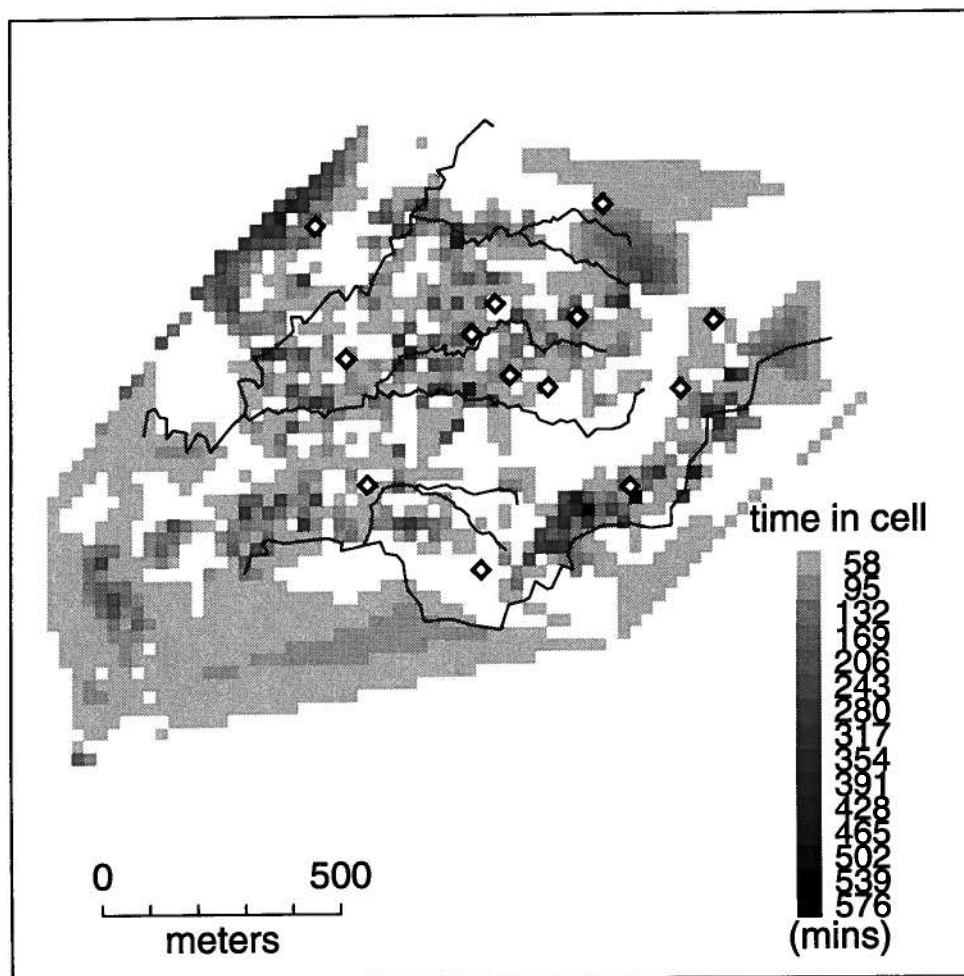


Figure 3.2:

Female distribution in terms of the number of individual females recorded in each 25 m² cell.

Leks are shown as hollow diamonds, creeks as black lines. White shading represents cells where fewer than 2 females were recorded. Leks showed slight association with areas with high numbers of different individual females ($P=0.068$).

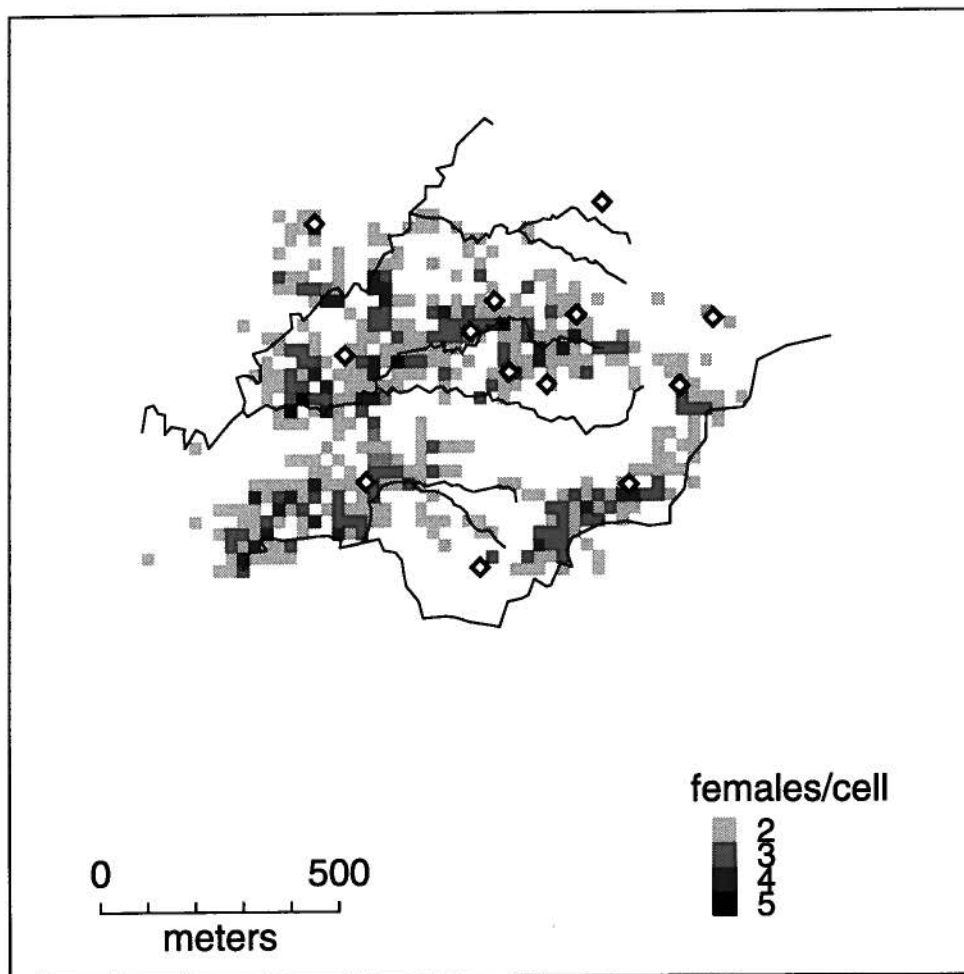


Figure 3.3:

Distribution of travel routes over the study site, see text. Leks are shown as hollow diamonds, creeks as black lines. Leks showed a significant association with areas with high female traffic ($P=0.0172$). White shaded areas were transected by <4 paths.

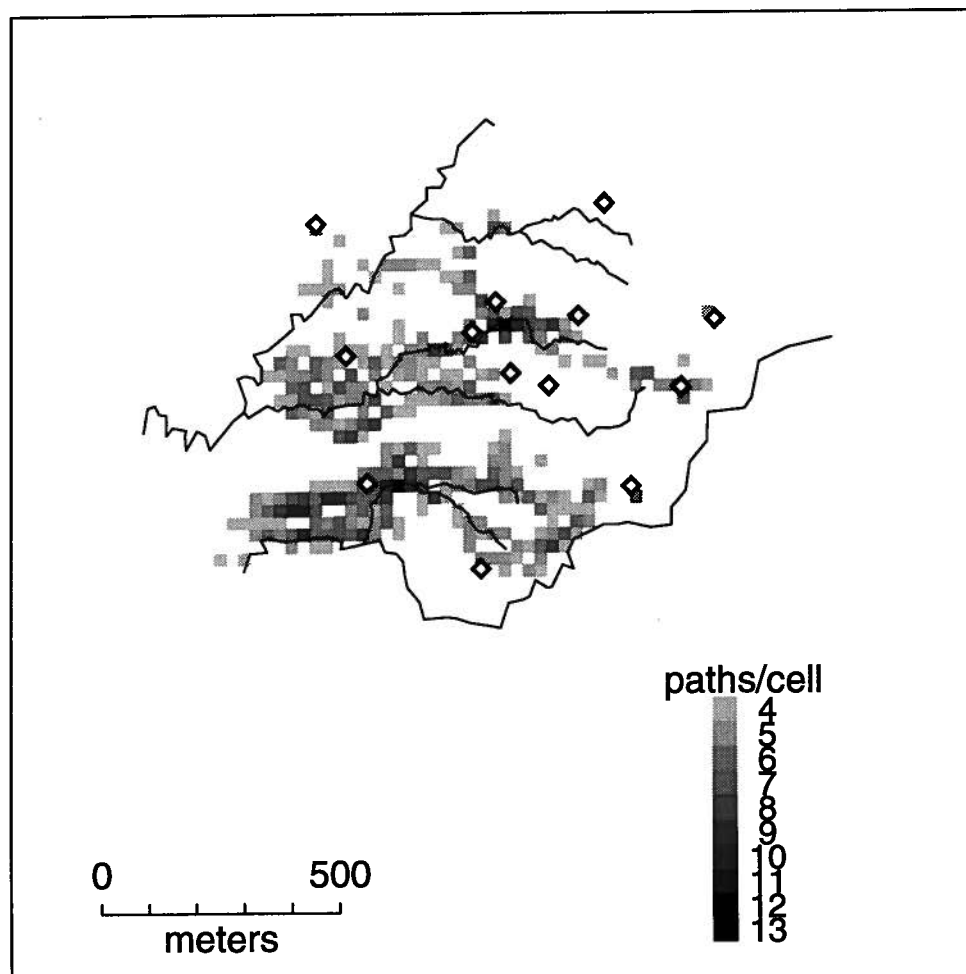


Figure 3.4:

Travel routes used by females in relation to topography. a) tracing of travel routes, dark line, over the travel routes of females weighted by the number of females recorded in a cell (# of paths transecting cell/# of females recorded in cell). b) the same tracing of travel routes superimposed on the topographical map. Darker shading represents increased altitude, maximum altitude is 150m.

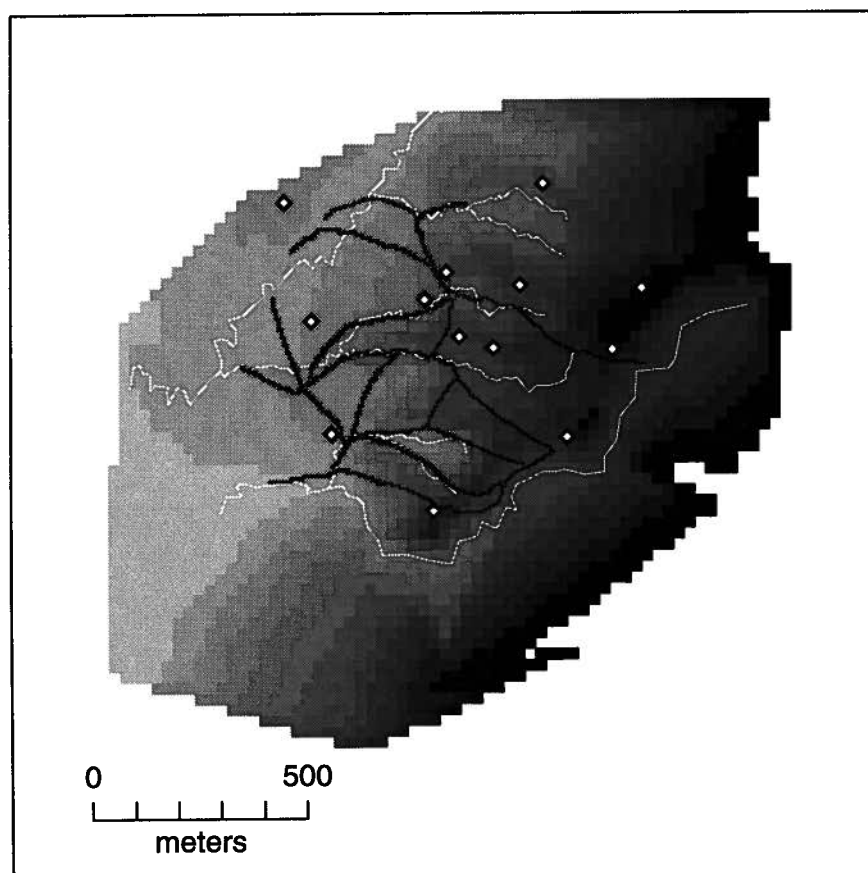
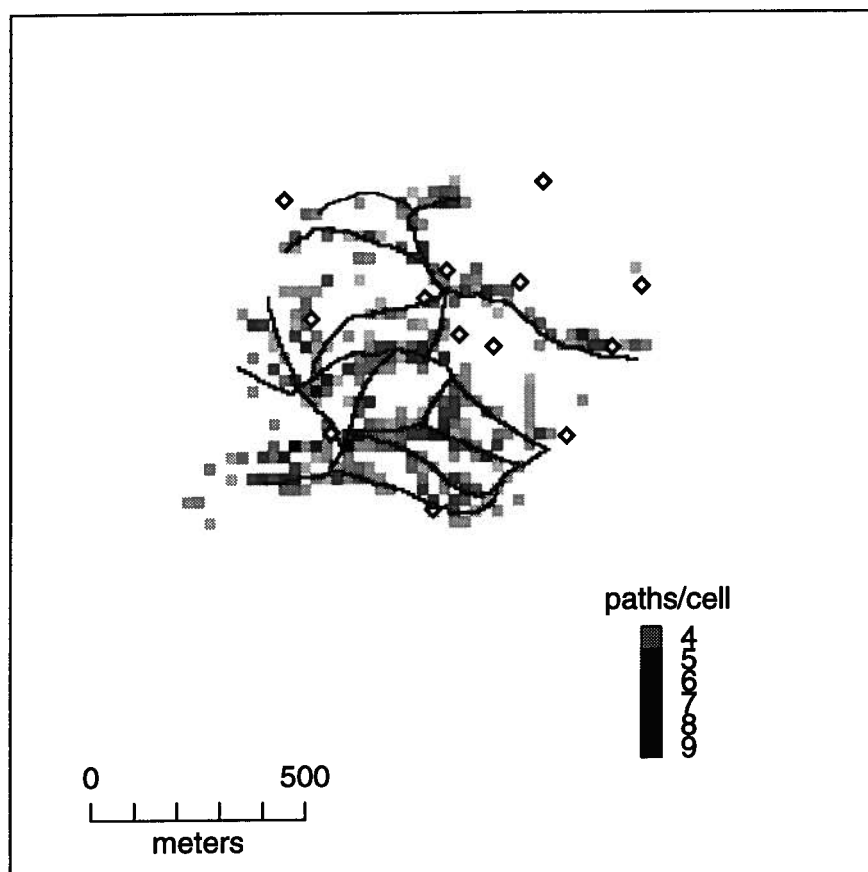
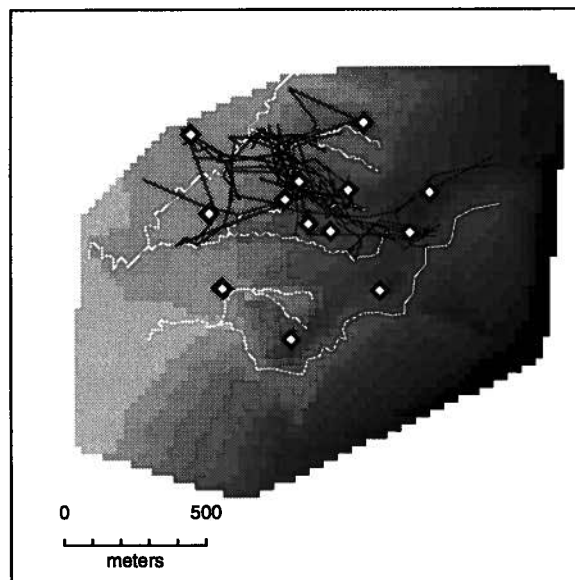
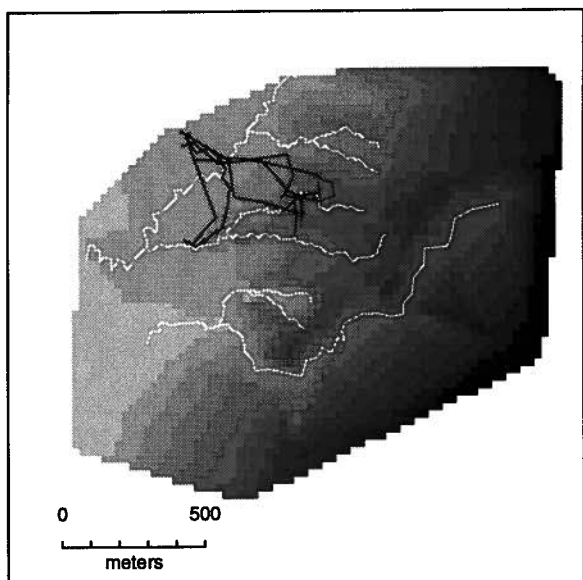
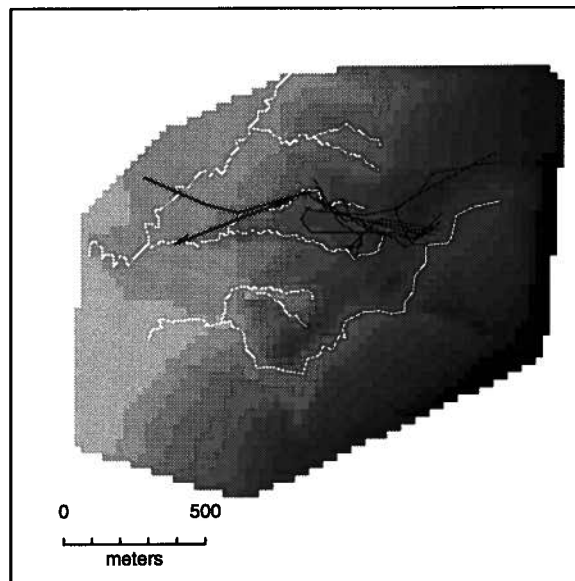
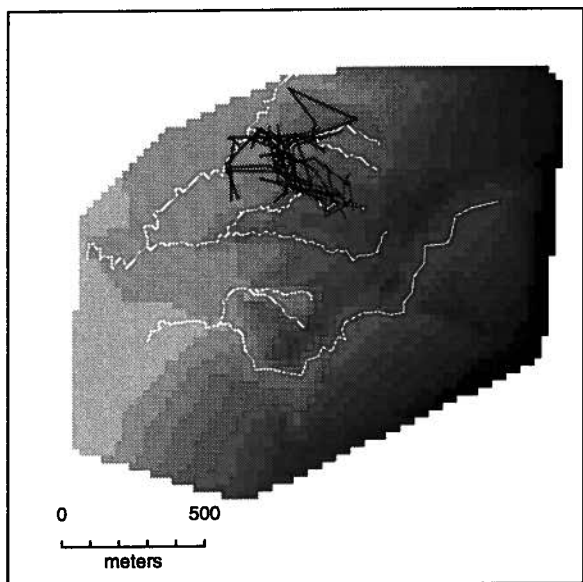


Figure 3.5:

Examples of the travel routes of three females that used the same part of the study site. (a) Female 18, non-breeding season, (b) female 9, breeding season, (c) female 6, breeding season, (d) all three combined. Note that the leks are associated with junctions in the travel routes and that females tend to travel around rather than over the ridge to the east of the two leks in the centre of the map. Shading indicates topography, pale lines are creeks and the hollow diamonds are leks. Darker shading represents increased altitude.



CHAPTER FOUR.

CONSEQUENCES OF VARIATION IN LEK SIZE IN THE OCHRE-BELLIED FLYCATCHER, MIONECTES OLEAGINEUS.

ABSTRACT

Several hypotheses suggest that the costs and benefits of display in aggregations of different sizes play a major role in both the evolution of leks and the patterns of distribution of males across leks of different sizes. I examined the consequences of variation in lek size for both males and females in a study of the ochre-bellied flycatcher, Mionectes oleagineus. In total 41 solitary display sites and leks, ranging in size from 1 - 5 males, were observed over three breeding seasons. Although mean visitation rate by females was positively correlated with lek size, female visitation rate per male remained constant across lek sizes. The rate at which females visited the male with the highest female visitation rate at each lek was positively correlated with lek size. Neither mean nor per capita intrusion rates were correlated with lek size. For the top ranked male, however, there was a significant correlation between intrusion rates and the size of the lek at which he displayed. Intrusion at leks may be costly, since 28% of female visits were interrupted by intruders. Solitary males suffered no such interference. Females show no preferences for larger leks, visiting and mating at solitary sites as well as at leks. However, females preferentially visit males with high singing rates and this male trait may determine visitation patterns. My data argue that preferences for larger leks are not important in the evolution of lekking in this species, nor do they affect lek size. Instead, males settle according to the distribution of female movement, while females choose mates without consideration of lek size.

INTRODUCTION

In lek mating systems, the number of males displaying at a site can vary from just a single individual, as in some birds of paradise (Pruett-Jones and Pruett-Jones 1990) and manakins (Lill 1974, 1977; Théry 1990, 1992), to over 400 males in the most extreme example, sage grouse, Centrocercus urophasianus (Scott 1942). Marked variation in lek size occurs within as well as between species. Within a single population it is common to find that some males display solitarily while others display at leks (Kruijt et al. 1972; Lill 1974; Sexton 1979; de Vos 1983; Rolstad and Wegge 1987; Höglund et al. 1993; Westcott and Smith 1994). In recent years there has been increased interest in the costs and benefits associated with variation in lek size. This shift in emphasis away from studies of within-lek dynamics has been prompted by the realization that the variation in payoffs between leks may be a function of lek size and might provide insights into the processes underlying lek evolution. A number of hypotheses attribute lek evolution to an increase in benefits with increased lek size for one or both sexes. These hypotheses, referred to as "preference" hypotheses, suggest a number of ways in which a positive relationship between reproductive success and lek size may evolve.

Preference hypotheses suggest that females have a specific preference for mating at larger leks. This could occur if increased lek size was positively associated with factors such as i) decreased predation rates (Koivisto 1965; Hjorth 1970; Wittenberger 1978; Gosling 1986), ii) an increase in the ease or probability of detecting the lek (Otte 1974; Alexander 1975), iii) more efficient comparisons of mates (Emlen and Oring 1977; Parker 1978), or, iv) decreased harassment by males (Clutton-Brock et al. 1993; Stillman et al. 1993). Preferences for larger leks may also occur if lek size functions as a male secondary sexual characteristic (Queller 1987), perhaps in a manner similar to the bowers of bowerbirds (Borgia 1985; Borgia et al. 1985) and widowbirds (Andersson 1991). The reasons for using leks as secondary sexual traits would be the same as those suggested for the evolution of other epigamic traits, because males at leks are more attractive (Lande 1981; Kirkpatrick 1982) or viable (Zahavi 1975; Hamilton and Zuk 1982;

Andersson 1986).

Other preference models rely on indirect mechanisms to produce preferences for larger leks. A preference of females for mating with specific individual males may result in unsuccessful males clustering around those preferred individuals in an attempt to parasitize their success (Beehler and Foster 1988; Höglund and Robertson 1990a). Because females mate preferentially with these "hotshot" males, irrespective of the number of other males present at the lek, and because the number of males around a successful individual should reflect the quality of that individual, females will appear to show a preference for larger leks. Although the various preference hypotheses differ in mechanism, they all share two predictions: 1) one or both sexes benefit from mating at larger aggregations, and, 2) one or both sexes show a preference for larger leks.

Variation in the costs and benefits associated with attendance at leks of different sizes is an important assumption not only of preference models of lekking. Such variation may affect the settlement decisions of individual males even when these decisions are made according to the physical distribution of receptive females, i.e. the hotspot hypothesis (Bradbury 1981; Bradbury and Gibson 1983; Bradbury et al. 1986). In the simplest versions of the hotspot hypothesis males settle over the distribution of receptive females according to ideal free distribution rules (sensu Fretwell 1972; Parker 1978). Under these conditions, male settlement should result in the mean payoff to males being equal across all lek sizes. It has also been suggested that a model assuming ideal free distribution of unequal competitors provides a more appropriate description of male settlement patterns (Sutherland and Parker 1985; Parker and Sutherland 1986; Bradbury et al. 1986; Alatalo et al. 1992; Höglund et al. 1993), given the high variance in male mating success in most lek mating systems (Bradbury and Gibson 1983). This model assumes that males distribute themselves not only according to resources, as in the ideal free case, but also according the distribution of competitors and their relative competitive abilities. Thus males should settle at leks of different sizes as a function of their competitive abilities. High quality males should be found at large leks where, despite higher costs, payoffs will be greater because of higher female

densities. Low quality males, on the other hand should settle at sites where both costs and rewards are lower. The result of this process should be that as lek size increases, so too should the mean payoffs associated with display at that lek.

To date, slightly less than half of the cases examined have failed to demonstrate increased payoffs associated with larger leks (Hammerstrom and Hammerstrom 1955; Koivisto 1965; Lill 1976; Pruett-Jones 1985; Bradbury et al. 1989b; Deutsch 1994). Conversely, the remaining experimental (Kruijt et al. 1972; Lank and Smith 1992) and observational (Shelley 1990; Alatalo et al. 1992; Höglund et al 1993; Balmford et al. 1992) studies have found a per capita increase in female visitation or copulation rates at larger leks. The prediction of models that consider settlement by unequal competitors, that males of different competitive abilities will have preferences for different lek sizes, has also received empirical support in two studies (Alatalo et al. 1992; Widemo and Owens 1995).

In this paper I examine the consequences of variation in the size of leks of M. oleagineus, a Tyrannid flycatcher. The study had two aims. The first was to examine the costs and benefits associated with display at leks in the light of the hypotheses discussed above. The second was to explore the reasons why territorial males attempt to prevent new males from settling adjacent to their display territories. In particular I was interested in answering the following two questions: 1) are females more likely to visit males at larger leks?, and 2) do males benefit by displaying at larger, rather than smaller, leks?

METHODS

Study Species.

M. oleagineus is a small (12 g) understory resident of wet, lowland forests from southern Mexico to southern Amazonia, including Trinidad and Tobago (Meyer de Schauensee 1966). In Costa Rica it occurs at elevations of up to 1200 m on both the Pacific and Atlantic slopes (Stiles and Skutch 1989). In south-western Costa Rica the breeding season of M.

oleagineus lasts from February to August (unpublished data), though this varies with rainfall. This period spans the last half of the dry season and the beginning of the wet season.

There are three "classes" of male in my study population: territorial, satellite and floaters. Territorial males held display territories with a mean size of $763, \pm 88$ S.E., m². Display territories were both solitary or clustered into small leks (size range = 2-6 males, mean = 2.6 ± 0.83 males). With the exception of 2 two-male exploded leks, where territories were separated by an undefended interstitial buffer of 10 and 13 m respectively, display territories at leks share contiguous boundaries. The average solitary male was $114.7, \pm 28.9$ S.E., m from his nearest neighbour (Westcott and Smith 1994). In this paper I use the term "display territory" to refer to the area defended by a territorial male against other males and to which he attempts to attract females by singing. I also use the term display site to refer to any location where one or more males defend display territories.

Non-territorial males include "satellites" and "floaters" (Westcott and Smith 1994). Satellites do not "own" a territory; instead they surreptitiously use the territories of another male. When the owner is present the satellite behaves in an inconspicuous manner; when he is absent, the satellite behaves like the owner. Floaters have no territorial association; they wander widely and visit display sites at many leks. They are not tolerated by territorial males and are generally seen only briefly on display sites before being chased off by the owners.

Data Collection.

Birds were caught using mist-nets and banded with unique combinations of colour bands. All territory owners were banded. The sexes are almost entirely monomorphic and the sex of individuals was ascertained either through their behaviour or from morphometric data (see Westcott and Smith 1994).

Males were observed on their display territories, one at a time, during observation periods of either 1 (1990 and 1992) or 2 (1989) hours duration. Observations were conducted between 0530 and 1130 hours, the time of peak display activity (Westcott and Smith 1994). All

males were observed approximately once a week and both the sequence in which males were observed, and the time of day that each male was observed on was randomized. Behaviour of males and of their visitors was documented using continuous sampling (Altmann 1974) and recorded using an event recorder program running on a Tandy TRS-80 computer. The data presented in this paper were collected between May and August in 1989, and March and August in 1990 and 1992. Because much of the analysis of this data is based on rates, the underlying distributions of which are uncertain, I used non-parametric statistical methods except where parametric tests were appropriate. All rates are events per hour.

When the same individual males displayed at the same lek in two years, the data for those years were pooled. This only occurred in the case of solitary males. If the lek's size remained constant but one or more males were replaced between years, or if lek size changed, the lek was considered to have changed and was included more than once in the analysis. The outcome of the statistical tests are qualitatively identical if data from different years is combined when leks at a site remained the same size but were composed of different males.

Data Analysis.

Because a suite of *a posteriori* correlations was performed against lek size, sequential Bonferroni adjustments were used in assessing their significance level (Rice 1989). Sequential Bonferroni adjustments at $\alpha=0.05$ had no effect on the statistical significance of the results, with results significant prior to the adjustment being significant afterwards and non-significant results remaining so. Consequently, for ease of interpretation, I present only the non-adjusted P-values.

RESULTS

A total of 74 males was studied at 41 display sites over the 3 years of this study. The

number of display sites, both lekking and solitary, and the number of males studied in each year are given in Table 4.1. One to 5 males held territories at a given display site during the study.

The mean rate of visitation by females to leks was positively correlated with the size of the lek at which the territory was located ($r_s=0.42$, $n=40$, $P<0.01$; Figure 4.1.a). This increase in female visitation rate occurred in proportion to the number of males present at the lek and, consequently no significant relationship was detected between per capita rate of female visitation and lek size ($r_s = 0.24$, $n=40$, $P>0.10$; Figure 4.1.b). However, if the female visitation rates of the top ranked male (the male at each display site with the highest female visitation rates) at each display site and lek are considered alone, there is a significant correlation between female visitation rate and lek size ($r_s=0.53$, $n=40$, $P<0.001$; Figure 4.1.c). Female visitation rate to the display territories of second-ranked males was not correlated with lek size ($r_s=0.18$, $n=40$, $P>0.20$, Figure 4.1.d). There was also no significant increase in the variance in female visitation rates among the territories of a lek along with increasing lek size ($r_s=0.139$, $n=40$, $P>0.20$).

Copulations were rarely seen, but there was no detectable preference on the part of females for mating at leks over solitary display territories. In the 585 hours of observations included in this analysis, 2 copulations were observed; one involving a solitary male and the other a male at a lek of 2.

For a male, one potential result of displaying at a lek is that exposure to the stimuli of other males displaying may elevate his own display performance. Though I found a positive relationship between the rates of female visitation to a male's territory and his song rates ($r_s=0.36$, $n=74$, $P<0.002$; Figure 4.2.a), I detected no tendency for mean song rates to increase with lek size ($r_s=0.159$, $n=40$, $P>0.20$ Figure 4.2.b). Nor was tenure on a territory greater for males at leks than for solitary males; at both solitary territories and at leks the median tenure of a territorial male was 1 breeding season with a range of 0.5 - 4 breeding seasons (Mann-Whitney U-Test, $U=278$, $P=0.285$).

The males most visited by females at a lek sang more in larger leks ($r_s=0.50$, $n=40$, $P<0.002$; Figure 4.2.c). This is not to say, however, that the best solitary males have low song

rates. Song rates of more than 1500 songs/hour were recorded from just 3 males: one a solitary male, one a male at a lek of two, and one a male at a lek of five. Song rates of greater than 1000 songs/hour were recorded from all lek sizes. The mean song rate across all males was $687, \pm 40$ S.E., songs/hour. A male's song rate rank on the study site in a given year was positively correlated with his female visitation rank that year ($r=0.491$, $n=74$, $P<0.0001$; Figure 4.2.d).

Rates of intrusion on to a territory by other males are only weakly correlated with the size of the lek at which the territory was located ($r_s=0.233$, $n=40$, $P>0.10$ (Figure 4.3.a). Nor was there significant correlation between per-capita rates of intrusion and lek size ($r_s=-0.20$, $n=40$, $P>0.20$; Figure 4.3.b). As in the case of female visitation rates, however, there was a significant positive correlation between lek size and the intrusion rates on the territories of the males with the top female visitation rank ($r_s=0.46$, $n=40$, $P<0.005$; Figure 4.3.c). No correlation was detected between intrusion rates on the territories of the second ranked males and lek size ($r_s=0.21$, $n=23$, $P=0.10$; Figure 4.3.d). Males at leks were more likely to suffer intrusion during display to females than were solitary males. Intrusion occurred during 13 (28%) of 46 bouts of display to females by 9 males at leks while no intrusion occurred during 17 bouts of display by solitary males (Fisher's Exact Test, $P=0.013$).

DISCUSSION

Small Sample Sizes and Non-Significant Correlations.

As with other studies of variation in lek size, many of my reported correlation coefficients are low and non-significant. Despite my relatively large sample sizes, $n=23$ and 40 (c.f. Alatalo et al. 1992; Höglund et al. 1993; Deutsch 1994), the statistical power associated with these correlations is low, always less than 0.33 . Consequently, these correlations do not show that relationships do not exist. However, within the same system and at the same level of power, I did detect significant correlations with lek size. While these non-significant correlations may

describe real relationships, I suggest they are not dominant influences on lekking.

Do Females Prefer Leks?

Preference hypotheses suggest that there is an adaptive advantage to females from mating at leks. This advantage might accrue through improved mate choice (Otte 1974; Alexander 1975; Bradbury and Vehrencamp 1977; Bradbury 1981; Queller 1987), decreased predation (Koivisto 1965; Hjorth 1970; Wittenberger 1978) or decreased harassment (Clutton-Brock et al. 1993; Stillman et al. 1993). For *M. oleagineus*, there was no per capita increase in female visitation rates with lek size, and females visit and copulate (Westcott 1992) with solitary males. These observations suggest that females have no preferences for males at leks over solitary males, or for large over small leks. This argues against a role for female preference based models in determining lek size in *M. oleagineus*' mating system.

The lack of a preference for larger leks is probably because males with high song rates, a correlate of female visitation rates (Figures 4.2.a and 4.2.d), can be found at leks of all sizes (Figure 4.2.c). The strong correlation between a male's song rate rank and his female visitation rate rank indicates that females' preferences are for the male with the highest song rate, or for some closely correlated trait, at a lek. Given the lack of any per capita increase in mean female visitation rates with lek size, I suggest that females prefer to visit the males in their home range with the highest song rates, independently of the number of other males at the display site. Having selected a set of potential mates based on average song rate, females may then choose their mate from among these individuals on the basis of the males' complete display performance (see Westcott and Smith 1994).

The Costs and Benefits of Lekking for Males.

I found no detectable relationships between either mean intrusion rates onto display territories or per capita intrusion rates and lek size. This is surprising since the presence of a permanent pool of potential intruders in the form of neighbours at leks would seem to be the

perfect recipe for increased intruder pressure. However, the bulk of intrusion is performed by non-territorial males, and the behaviour of these individuals suggests that they visit the display territories within their home range during their daily foraging movements, apparently prospecting for potential territories (Westcott and Smith 1994). Under the maxim that any territory is better than no territory, floaters might be expected to investigate solitary and lek territories equally, thus no difference in intrusion rates across lek sizes would be expected.

Territorial intrusion, however, clearly does constitute a cost in M. oleagineus' mating system. Top-ranked males suffered higher intrusion rates when they displayed at larger leks (Figure 4.3.c). Based on this relationship, the top-ranked male at a large lek could expect double the intrusion rate of a solitary male. The costs associated with such increased intrusion are potentially large. First, increased intrusion requires a greater investment in territory defense. Costs associated with territory defense include the extra time and energy that is diverted from display and self-maintenance, and the risk of injury during encounters with intruders. This risk of injury may be significant. Twice I recorded raptor attacks on males preoccupied with intruders, though both attempts were unsuccessful. On one occasion the predator, a collared forest-falcon, Micrastur semitorquatus, was unsuccessful only because I inadvertently flushed it as it was walking up to the male and his intruder. These two were on the ground together, helplessly entangled in spider web, Nephila spp., and still completely engrossed in their mutual attack.

Second, and more importantly, intrusion results in lost copulations. This may occur in two ways. First, when a male is absent from his territory, intruders, both satellites and floaters, often sing on the territory and will even display to visiting females (Westcott and Smith 1994). It is possible that females will occasionally mate with these impostors. Second, the display of solitary males was never interrupted by intruders; at leks, however, 28% of female visits were interrupted by intruders. When a visit was interrupted, the female usually left the territory and was not seen visiting that territory again by us. This intrusion most likely decreases the net benefits to top ranked males of displaying at larger leks. For lower ranked males, interference

during display may be even more severe due to their lower female visitation rates.

Do males prefer displaying at larger leks? The lack of a detectable per capita increase in female visitation rates with lek size means that for the average male there should be no advantage in displaying at larger leks. Indeed, only the top male at a lek experienced increases in female visitation rates with lek size. Nor did lekking provide other advantages such as increased display performance, or increased tenure on a territory. Thus, I conclude that the average male gains no advantage from larger leks, and thus should have no preference for displaying at them. With no detectable advantage to larger leks for males or for females, preference hypotheses for lek evolution can be discounted as explaining lek size for M. oleagineus.

Hotshots and Lek Sizes

An alternative to the preference hypotheses is the hotshot hypothesis (Beehler and Foster 1988). This hypothesis suggests that less attractive males settle around the males preferred by females. If this is the case then lek size should increase as a function of the success in attracting females of a lek's hotshot. The correlation between lek size and female visitation rates on the territory of the male with highest female visitation rates is consistent with this prediction (Figure 4.1.c). However, two pieces of evidence run contrary to the hypothesis' predictions. First, the distribution of males did not match hotshot predictions in three regards. Not only were the highest mean female visitation rates recorded at two leks of 2 males and one of 3 males rather than at the largest leks on the study site, but males with low female visitation rates remained at some leks of two and three males despite the extremely paucity of female visitors to those leks. Also, consistently high female visitation rates at several 2-male leks did not lead to an increase in the size of these leks over the four years of the study, as predicted by the hypothesis (Beehler and Foster 1988). Second, the long breeding season and low rates of female visitation to males suggest that subordinate males should use the same cues for choosing their hotshot as do females for choosing mates, i.e. song rate, rather than direct observation of female visits. Over

the period of this study, this hotshot selection process should have resulted in the largest three leks forming around males that actually held territories at display sites of one, two and five males.

Though these results are not consistent with Beehler and Foster's (1988) version of the hotshot hypothesis, they might be expected if hotshots, unable to prevent interruption and disturbance by neighbours, attempt to circumvent the problem by preventing new males from settling nearby (Höglund and Robertson 1990a). Because males do attempt to prevent settlement adjacent to their territories (Chapter 5), the distribution of males across M. oleagineus leks may, at least partially, be explained by hotshot processes.

Female Visitation, Lek Size and Hotspots.

The hotspot hypothesis suggests that males settle according to some aspect of the distribution of females (Bradbury 1981; Bradbury and Gibson 1983). In the simplest hotspot model, male settlement occurs such that the mean access to females is constant across leks, i.e. according to ideal free distribution rules (Bradbury et al. 1986). There is good evidence from my earlier studies that hotspot mechanisms explain some aspects of male display dispersion in M. oleagineus. As predicted by the hotspot model, leks of M. oleagineus are not only clustered along with the leks of other understory lekking species, but they also show a tendency to change in size in unison with neighbouring leks of other frugivorous species (Westcott 1994). Also, leks are located along travel routes used by females and are most closely associated with locations with high female traffic (Chapter 3). The results of this study also provide support for the hotspot model. Female visitation rates increased significantly with lek size, but did so in proportion to the number of males at the lek, as would be expected if lek sizes are a function of the distribution of females.

However, this picture of males settling according to simple ideal free rules is marred by the fact that female visitation rates are not equal across the males at a lek; female visitation

rates increased with lek size for the male with the top female visitation rank at each lek but did not do so on a per male basis (Figures 4.1.a and 4.1.c). If some males are more attractive than others, an ideal free model with unequal competitors might provide a more realistic description of male settlement processes. However, the unequal competitor model predicts that, despite increased competition, high quality males should settle at larger leks because these are the sites with the highest rewards (Sutherland and Parker 1985; Parker and Sutherland 1986; Alatalo et al 1992; Höglund et al. 1993). Lower quality males should settle at smaller leks where both the costs and the rewards are lower. The absence of any detectable per-capita increase in female visitation rate with lek size suggests that current unequal competitor models cannot adequately explain male distribution in this species.

Another explanation for the unequal distribution of female visitation within leks is that the territories of the top ranking males may be located closer to, or directly on, the points of highest female traffic. If environmental features force females to pass through very small areas, e.g. a break in a thick scrub (Apollonio et al. 1990), individual males may be able to monopolize these areas. Other males at the site may have much lower visitation rates simply because their territories are located on the edge of, rather than directly over, this site. While female M. oleagineus do use habitual travel routes when moving through their environment (Chapter 3), there are no locations where either their movements or the environmental features around leks suggest such severe constraints (Chapter 3).

Alternatively, while males may settle in an ideal free manner over female distribution, all males may not be equal in the sight of those females. If females exhibit strong preferences for particular individuals, then the benefits associated with ideal free settlement patterns may not match those predicted by theory. This is probably what is happening in M. oleagineus. The observation that the female visitation rate a male receives is strongly correlated with his song rate (Figure 4.2.a) suggests that females choose males on the basis of song rate, or some closely correlated trait. If females do exhibit strong preferences within leks for this trait then a male's rank at a lek in terms of song rate should be strongly correlated with his female

visitation rate rank at that lek. This is in fact the case (Figure 4.2.d).

Summary.

The results of my study rule out the preference hypotheses for lekking: there is no increase in female visitation, or in any other possible benefits that I measured with increased lek size for the average male. Females also show no preference for males at larger aggregations. The study is not, however, so clear in distinguishing between the hotspot and the hotshot hypotheses. Given the evidence from my previous work in favour of a role for hotspot mechanisms in determining both the location and size of M. oleagineus leks, the hotshot hypothesis might be discounted on the basis of parsimony alone. However, the two hypotheses are not mutually exclusive and additional tests of their specific predictions are needed. If hotspot mechanisms are the primary determinants of lek size, then the distribution of males across display sites will be a function of the number of females passing through an area and the ability of territorial males to prevent settlement at that site by others. The existence of a large non-territorial male population suggests that despotism is an effective means of preventing settlement. While intruder pressure will eventually force many males to accept additional settlers at a lek, despotism might limit lek sizes to levels significantly below those that would be expected under simple ideal free rules.

Table 4.1:

A summary of the number of males and display sites that were present on the study site in each year of the study. In 1990 the study site was extended and included 4 additional solitary males that were not included in 1989 or 1992.

Year	1989	1990 ¹	1992
# of solitary display sites	6	9	3
# of leks	6	7	9
# of males at leks	18	16	22
mean males/lek	3	2.3	2.4
Total # of males	24	25	25

Figure 4.1:

Female visitation rates (number/hour): a) visitation to leks of various sizes, b) visitation per male, c) visitation to the territory of the male at each lek with the highest female visitation rates, d) visitation to the territory of the male at each lek with the second highest female visitation rates. To reveal overlapping points a small amount of uniform random error has been added to each point, resulting in some non-integer lek sizes and negative rates.

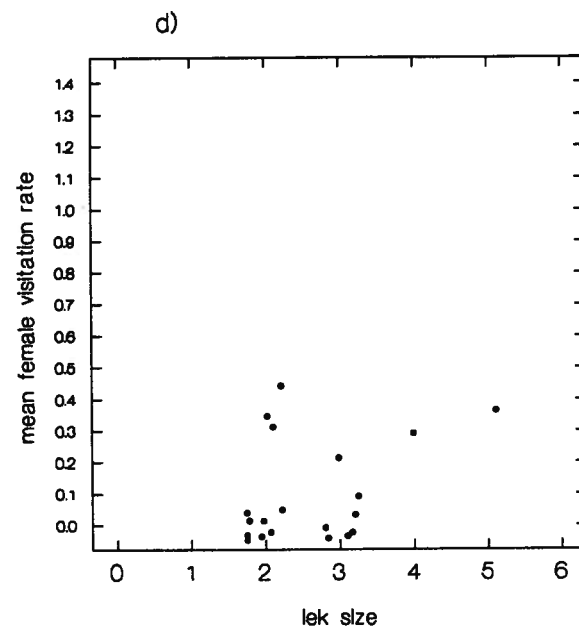
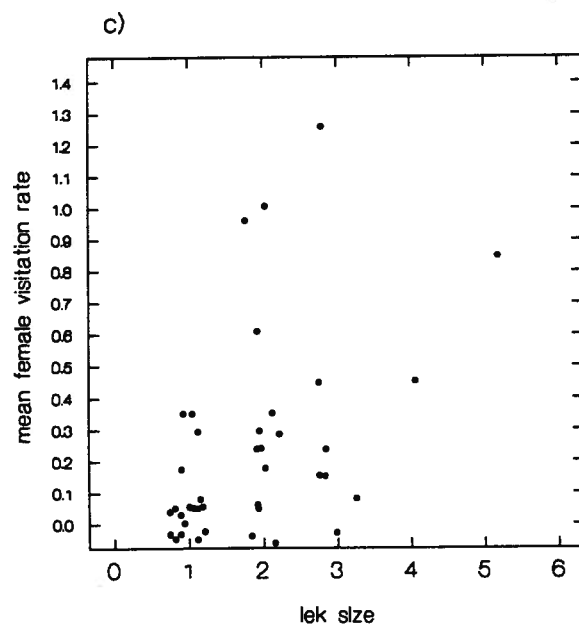
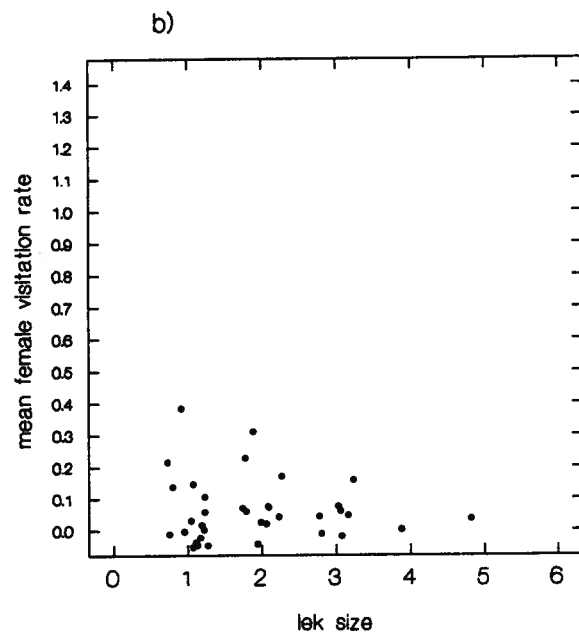
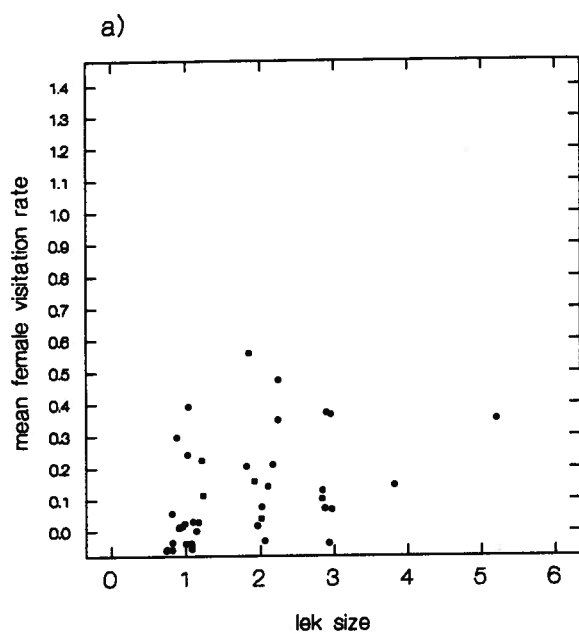


Figure 4.2:

a) Mean female visitation rate/hour for each male plotted against his mean song rate/hour: data from 1989 and 1990 from Westcott (1992). b) Mean song rate at each lek plotted against lek size. c) Mean song rate of the male at each lek with the highest female visitation rate plotted against his lek size. d) The rank, in terms of female visitation rate, of each male that held a territory at a lek in any given year plotted against his rank in terms of song rate at that lek. To reveal overlapping points a small amount of uniform random error has been added to each point, resulting in some non-integer lek sizes and negative rates.

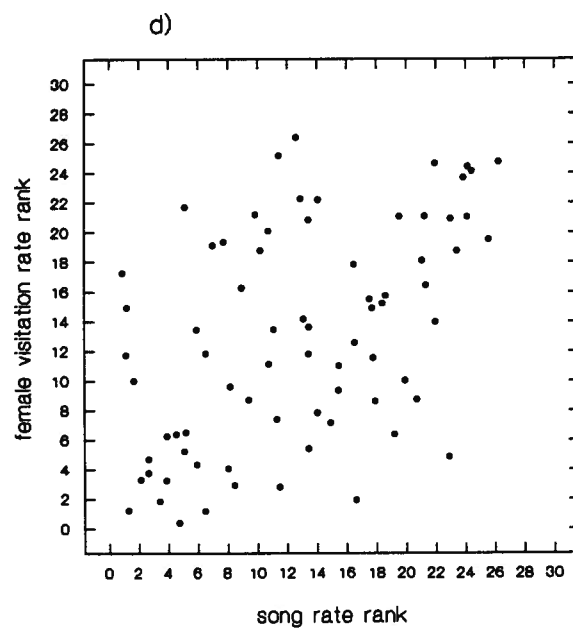
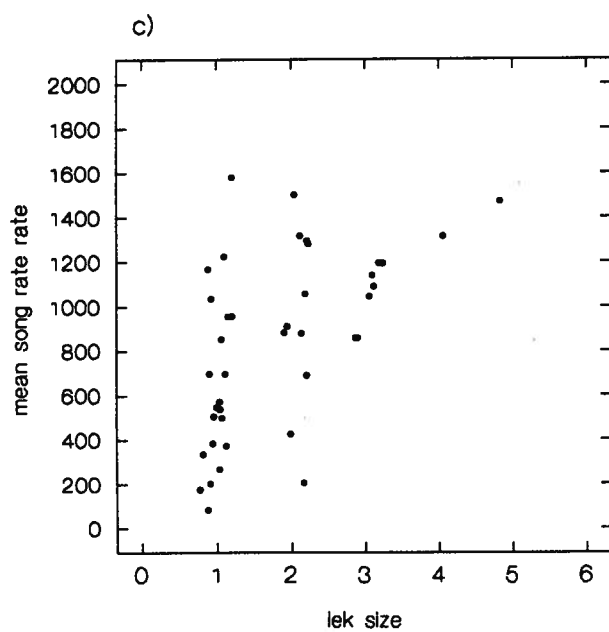
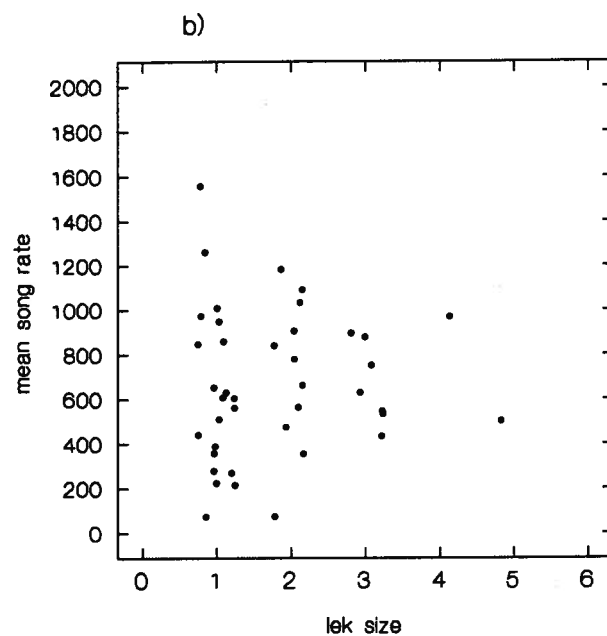
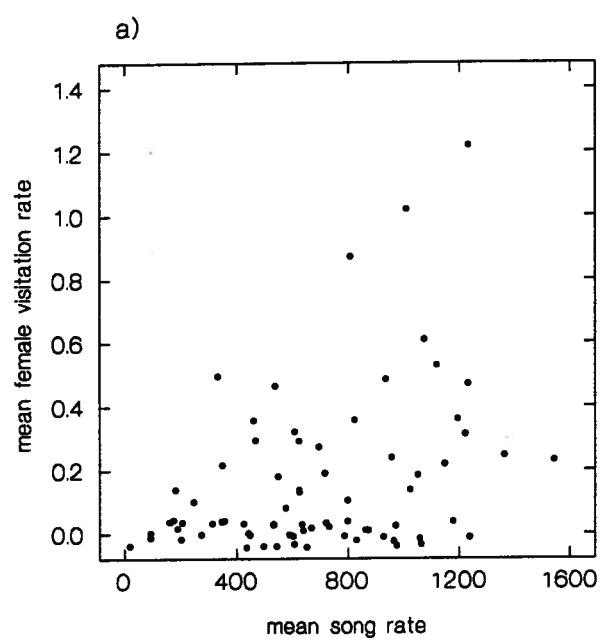


Figure 4.3:

Mean intrusion rate (number/hour): a) intrusion to territories at leks of various sizes, b) intrusion rates per male at leks, c) intrusion onto the territory of the male at each lek with the highest female visitation rates, d) intrusion on to the territory of the male at each lek with the second highest female visitation rates. To reveal overlapping points a small amount of uniform random error has been added to each point, resulting in some non-integer lek sizes and negative rates.

CHAPTER FIVE.

NEIGHBOURS, STRANGERS AND MALE-MALE AGGRESSION AS A DETERMINANT OF LEK SIZE.

ABSTRACT

Interactions between males on leks may play a role in lek formation and the regulation of lek size. In this paper I present the results of a playback experiment that simulated 'de novo' settlement at sites adjacent to currently existing display territories of the ochre-bellied flycatcher, Mionectes oleagineus. In the study population, males displayed both solitarily and at small leks. A large proportion of males held no display territory at all. A stranger's song was played to both solitary and lekking males from 10 m outside their territorial boundaries. In separate playbacks, lekking males were also played neighbour's song. Both lekking and solitary territorial males reacted to the playback by decreasing their song rate, approaching the playback speaker and, on occasion, attacking the model. Solitarily displaying males responded more aggressively to playback of stranger's song than did lek males. Lek males were able to distinguish between their neighbour's and a stranger's song and did so irrespective of whether it was played from the neighbour's territory or from outside the lek. The nature of the response to such playbacks, however, depended on where the playback originated. These results indicate that male-male interactions can be influential in structuring leks. In M. oleagineus, interactions between males are aggressive and act to limit rather than augment lek size.

INTRODUCTION

The factors that structure leks and the role of interactions between males in this process have been of interest since the earliest research on leks (Selous 1906,1927). Male-male interactions may affect lek size and structure in several ways. First, dominance hierarchies within leks, for example, are probably fundamental to lek stability in many species (Foster 1981; Avery 1984; Beehler and Foster 1988). Display is often directed towards other males (LeCroy et al. 1980; Avery and Sherwood 1982), and is necessary for territory maintenance in many lekking species; failure to display can result in increased intrusion and territory loss (Snow 1974; Westcott 1992). In some species, dominance interactions between males have been ritualised into complex, coordinated displays (Prum 1985, 1986; Théry 1990). In extreme cases, these displays have become essential components of display to females (Foster 1977, 1981). In cooperatively breeding manakins stable, long-term dominance hierarchies not only allow males to co-exist at a lek (Foster 1977, 1981; Schwartz and Snow 1978; Robbins 1985; McDonald 1989b) but are imperative for successful attraction of mates (McDonald 1989a). The breakdown of the dominance hierarchy at a lek can result in increased display disruption and can even cause the disintegration of the lek (Trail 1985; Robel and Ballard 1974). Similarly, the lack of a dominance hierarchy and the continual destruction of competitors' bowers is suspected to be responsible for the absence of lekking in bowerbirds, Ptilonorhynicidae (Pruett-Jones and Pruett-Jones 1982, 1994; Borgia 1985).

Second, males might monitor the mating success of others and modify their own behaviour at the lek correspondingly. Unsuccessful males might cluster around males that are successful in attracting females and attempt to parasitize their success (Beehler and Foster 1988; Höglund and Robertson 1990a). Finally, differences in the competitive abilities of males might determine the lek at which a male eventually settles (Alatalo et al. 1992; Höglund et al. 1993). If males of a particular competitive ability encounter higher net rewards at leks over a particular range of sizes they should move preferentially to leks of those sizes (Alatalo et al. 1992; Höglund

et al. 1993). In ruff, Philomachus pugnax, larger leks favour low-ranked males while medium-sized leks favour high-ranked males. At small leks all males attempt to attract passing males to join the lek (Hogan-Warburg 1966). Once a ruff lek reaches a medium size, about 4 males, the top ranked males cease enticement displays towards other males, low ranked males, however, continue to display (Widemo and Owens 1995).

In this paper, I consider the influence of male-male interactions on lekking in the ochre-bellied flycatcher, Mionectes oleagineus, a small, lek-breeding, Neotropical Tyrannid (Skutch 1960). Males defend display territories either solitarily or at small leks in the forest understory (Snow and Snow 1979; Westcott and Smith 1994). Song is involved in both territorial defence and mate attraction (Westcott 1992). This study was initially prompted by the puzzling observation that a large proportion of the banded male population, approximately 50%, do not hold display territories (Westcott and Smith 1994). These non-territorial males behave either as furtive satellites on the territories of other males, or as wandering floaters with no apparent territorial attachment. That such a large proportion of males are non-territorial is especially surprising given that only territorial males have been seen to display to, and copulate with, females. Non-territorial males thus appear to be foregoing current reproductive opportunities.

Why these males do not establish display territories is not immediately obvious. In M. oleagineus, and in lek mating systems in general, the majority of the habitat remains unoccupied and apparently available for settlement (Westcott 1993). There are at least 3 possible explanations for this failure of non-territorial males to establish territories. First, non-territorial males, while able to establish a territory, may not be able to bear the energetic costs of territory ownership, perhaps because they are young and inexperienced. Second, inexperienced males, though able to bear the costs of territoriality, may not garner sufficient copulations to make the effort worthwhile. In both these instances young individuals may postpone territoriality until their prospects have improved, e.g. when they are older (Wiley 1991). Third, settlement at existing display sites by non-territorial males may be resisted by the territorial males already present at the site. This is likely to be particularly important when there are preferred sites for

settlement (e.g., at traditional mating sites: Warner 1988), or locations where females are likely to pass (e.g. Westcott 1994 and Chapter 3) and can be defended by an established male as a resource.

Here I describe a playback experiment conducted to determine whether territorial males attempt to prevent the establishment of new territories, adjacent to their own. If territorial males benefit from increases in lek size, as suggested by several theories for lek evolution and a number of field studies (Kruijt et al 1972; Lank and Smith 1992; Shelley 1990; Alatalo et al. 1993; Höglund et al. 1993), then territorial males should not respond aggressively to new settlers and might actively encourage settlement. On the other hand, if increased lek confers a net cost, they should respond aggressively and try to limit lek size. I tested this hypothesis with a playback experiment. My results support the latter hypothesis. They also show that males can distinguish the songs of neighbours from those of a stranger, and that they modify their response to these different signals depending on location of the playback.

METHODS

Study Site.

The study was conducted between April and June 1992 at Estacion Sirena (lat. 8° 29' N, long. 83° 36' W) in Corcovado National Park, Costa Rica. The study site is divided between low rugged hills (to 140 m in height) and flat areas. There is a distinct wet season between May and November, with peak rainfall occurring between September and November. Mean annual rainfall is $5,305 \pm 301$ mm S.E., $n = 10$ years (Servicio de Parques Nacionales de Costa Rica). The vegetation is pre-montane, wet forest (Tosi 1969) of which 80% is primary forest, the remainder being 15 year-old second growth.

Playbacks.

Recordings for the playbacks were made during March 1992 using a Sennheiser ME-80 directional microphone and a Sony Professional Walkman WM-D6C. Each territorial male was recorded and a 2 minute section was selected for each according to the following criteria: i) the focal male was singing at a standard rate of between 18 and 20 songs/minute, ii) there was a low level of ambient noise, iii) the male had not had a visitor of either sex on his territory for at least 1 hour, and, iv) none of his neighbours were singing. The "strange" male recording was made subject to the same criteria and obtained near the junction of the Cedral and Sirena rivers, some 11 km north of the study site. It is unlikely that any of the males subjected to this playback had been previously exposed to this individual's song. All males sing the three songs recorded from M. oleagineus (Snow and Snow 1979; Westcott and Smith 1994). In all playback recordings singing occurred at a relatively constant rate throughout the playback, i.e. with no noticeable pauses.

I conducted playbacks between April 20th and June 4th 1992. I kept the duration of the experiment brief to minimize effects of stage of the breeding season on males' responses. This period represented approximately 30% of the breeding season and began after most territories had been established for 2 months.

Solitary males were subjected to a single session of playback of the stranger's song from outside their territory. Males at leks were subjected to four playback sessions; i) the stranger's song played from outside the lek, ii) the stranger's song played from within a neighbour's territory, iii) neighbour's song played from outside the lek, and iv) neighbour's song played from within that neighbour's territory. An individual lek male was played the same neighbour's song in both neighbour playbacks. Each male at a lek was played the song of a different neighbour. In addition, a random sample of solitary and lekking males was subjected to a playback of background noise. No male experienced more than one playback per week. To avoid association of my presence with the playback by the males, all focal males experienced at least two 1 hour observation periods between consecutive playback sessions. The sequence of

presentation of the different types of playbacks was random and differed between males.

Because my aim was to simulate the settlement of a new male adjacent to the focal male, playbacks were performed from a point 10 m outside the territory boundary of the focal male. This distance corresponds approximately to the radius of a circle the size of an average male display territory (760 m², Westcott and Smith 1994). Playbacks were performed only if the following conditions were met: i) there had been no visitors of either sex to the territory of the focal male within the previous half hour, ii) no other birds were currently on the territory, iii) the focal male was in the centre of his territory, iv) his neighbours were not singing and, if it was a neighbour playback that was to be performed, his neighbour was not present on his territory, and finally, v) ambient noise levels were low. I considered these restrictive criteria necessary but they resulted in unequal sample sizes in the different playback categories.

In the actual playback session the playback speaker was set up 1.5 m above the ground and a stuffed male M. oleagineus specimen in an upright position was placed 30cm above it. A preliminary half hour observation period was then conducted. At the end of this half hour a two minute "before" observation period was begun followed by the two minute playback. During both the before period and the playback period male song rate, distance from the speaker, and behaviour was recorded onto tape. Distance was estimated to the metre each time the bird changed perches.

Statistical Analysis.

I compared males' behaviour during the 2 minutes of playback with their behaviour during the 2 minutes before playback. For song, I determined the proportion of the total amount of song sung during the experiment (i.e. song of before phase plus song of during phase) that was sung during the playback. If males showed no reaction and continued to sing as in the before phase, this proportion would be 50% on average. Proportions of less than and greater than 50% would occur if males decreased or increased song rates respectively. Proportions were arcsine transformed for analysis. I calculated the mean distance of focal males from the speaker in the

during playback phase and subtracted it from their mean distance in the before phase. In this instance a relative distance of 0 m represents no reaction on the part of males, and positive and negative scores represent movement towards or away from the speaker respectively.

Both parametric and non-parametric tests were used as appropriate. The sample size for solitary males, $n=5$, was set by the number of solitary males present on the study site during the experiment. Because of the low sample sizes in this category, I also used a randomization test with 10,000 iterations (Potvin and Roff 1993) when comparing stranger from outside playbacks for lekking and solitary males. Since in each case the results of the randomization test were qualitatively similar, and sometimes quantitatively identical to those obtained using parametric tests only the latter are presented.

RESULTS

During playbacks, males typically ceased singing and approached the speaker, apparently searching for the culprit. Sometimes males would approach the speaker only briefly, and then return to their territories. However, sometimes, and especially in response to a stranger's song played from outside the lek, they would vigorously search the area of the speaker and even attack the mounted specimen. Males did not visibly react to the control playback nor was any statistically significant effect detected during controls (control from outside, song: Mann-Whitney U-Test, $W=121$, $P=0.69$; control from outside, distance: MWU, $W=100$, $P>0.1$).

Lek Type and Male Responses.

Solitary males showed a greater decrease in song rate than did lek males in response to playback of stranger's song from outside the territory (t-test $t=2.81$, $df=17$, $P=0.049$, Figure 5.1). Lek and solitary males did not differ in their closest approach to the speaker (Mann-

Whitney U-Test, $T=45$, $P=0.66$), nor in their relative mean distance from the speaker during the playback ($t=0.835$, $df=17$, $P=0.41$, Figure 5.2). However, solitary males were more likely to attack the model than were lek males (lek males mean # of attacks/playback=0.071, solitary males=1.8, MWU $T=69$, $P=0.022$).

In this population, *M. oleagineus* shows three categories of male display dispersion: solitary males, exploded leks and classical leks. At exploded leks territories did not share common boundaries and only 2 males were ever present. There was no difference between the song rates of the top-ranked males at exploded leks and those of solitary males ($t=-1.55$, $df=1$, $P=0.261$, Figure 5.3). However, when top-ranked exploded lek and solitary males are combined and compared with lekking males, the combined exploded lek and solitary males show a greater decrease in song rate in response to the playback ($t=-4.4$, $df=7$, $P=0.003$, Figure 5.3).

Playbacks at Leks: Effects on Song.

Males decreased their song rates during all playbacks with the exception of neighbour's song played from that neighbour's territory (Figure 5.1). A two-way ANOVA of playback type x playback location was performed with proportion of song sung during the playback as the response variable. There was a significant effect of the type of playback, i.e. neighbour or stranger song ($F_{1,45}=6.012$, $P=0.018$; Figure 5.1). Neither playback location, i.e. outside the lek or from a neighbour's territory, nor the playback type*location interaction had significant effects (location: $F_{1,45}=1.266$, $P=0.266$; type*location: $F_{1,45}=0.538$, $P=0.467$). Post hoc tests revealed that the difference between playback types was due to males singing less during stranger playback from a neighbour's territory than during neighbour playback from that neighbour's territory ($F_{1,45}=4.59$, $P=0.038$; Figure 5.1).

Playbacks at Leks: the Effects on Distance from Speaker.

The effect of playbacks on relative mean distance from the speaker, i.e. mean distance prior to the playback minus mean distance during playback, is shown in Figure 5.2.

Two-way ANOVA with relative mean distance from the speaker as the response variable revealed significant effects of playback type ($F_{1,46}=26.695$ $P<0.001$), playback location ($F_{1,46}=7.948$, $P=0.007$) and type*location interaction ($F_{1,46}=13.598$, $P=0.001$). Because of the significant interaction effect some caution in interpreting the main effects is warranted. Post hoc tests show that males spent more time close to the speaker during playback of a stranger's song from outside the lek than during playback of the same song from a neighbour's territory ($F_{1,46}=23.015$, $P<0.001$). Males responded more strongly to stranger's song from outside the lek than they did to a neighbour's song from the same location ($F_{1,46}=2.774$, $P>0.001$). However, males did not differ in their response to stranger's and neighbour's song when these were played from the neighbour's territory ($F_{1,46}=1.052$, $P=0.311$).

DISCUSSION

Distinguishing between Neighbours and Strangers.

Playback of a stranger's song consistently elicited a stronger response than neighbour's song, irrespective of whether it was played to a solitary or lek male, or whether it was played from outside a lek or from a neighbours territory. Of the stranger's song playbacks, solitary males exhibited the strongest response (Figures 5.1 and 5.2). While solitary males did not differ from lek males in their mean distance from the speaker, or in their closest approach to the speaker during the playbacks, they did show a significantly greater decrease in the amount that they sang and appeared to search more intensely. The aggressive nature of the solitary males' response is underscored by the fact, that with one exception, only solitary males actually attacked and struck the model, or, in one case, a female blue-crowned manakin (*Pipra coronata*) unfortunate enough to be about the right size and colour and in the wrong place.

For lekking males, the reaction to a stranger's song varied according to where the song was played from. When the stranger's song was played back from a neighbour's territory, males did not approach the speaker as closely as when it was played from outside the lek. The

effect on song rate, however, was identical and resulted in a sharp decrease in song output during the playback (Figure 5.1). These results suggest that males always recognize a stranger as such, but also that they regard them as potentially threatening. It seems, however, that they attack strangers only when the stranger is outside the lek. Stranger's song emanating from a neighbour's territory is considered either as the neighbour's problem, or as a situation that, at least initially, need only be monitored. Though males are not loath to cross territory boundaries when females are present (Chapter 4), defence of a neighbour's territory probably has few benefits.

A criticism of the experimental design used in this study is that I have subjected a population of males to the playback of a single stranger male thereby limiting the generality of my conclusions (Kroodsma 1989). However, I believe my results can be generalized to all strangers for two reasons. First, all male *M. oleagineus* sing a simple song made up of the same three components (Snow and Snow 1979; Westcott and Smith 1994). This means that there is no variation in song repertoires and very little in song structure. Second, in a pilot study conducted in 1991, 10 lek and 8 solitary males were subjected to playbacks of the songs of two additional strangers. The mean response of these males to playback from outside the lek did not differ from those reported for the same experiment in 1992 (for lek males, song: t-test, $t=-0.436$, $df=23$, $P=0.667$; distance: $t=-0.703$, $df=23$, $P=0.49$; for solitary males, song: $t=0.97$, $df=12$, $P=0.35$; distance: MWU $T=1.623$ $P=0.239$).

The only response males made to the playback of a neighbour's song was to decrease singing when the playback came from outside the lek (Figures 5.1 and 5.2). In this instance males paused and then resumed singing. Since it is common for territorial males returning to their territories to commence singing a short distance from the territory, neighbour's song from outside the lek should not be a novel stimulus for most males. The slight decrease in song rates probably represents no more than a pause to confirm the identity of the singer.

These striking differences between the reactions of lek males to the playback of neighbour's and stranger's song are clear evidence that males can distinguish neighbours and strangers on the basis of song. Given that territory ownership is relatively stable within and even

across breeding seasons (Westcott and Smith 1994, Chapter 4), males have ample opportunity to learn the songs of their neighbours. In addition, since territorial defense is a significant component of a male's activity in both the breeding (Westcott 1992; Westcott and Smith 1994; Chapter 4), and non-breeding seasons (pers. obs.), it should pay a male to discriminate between singers that do and do not require a response. Interestingly, not only do males appear to determine the identity of the singer but they vary their response depending on where the playback comes from.

Individual recognition capabilities, based on song and other characteristics, have been demonstrated in a number of bird species (Weeden and Falls 1959; Falls 1969; Baker et al. 1981; Falls 1982). However, such abilities have not previously been demonstrated in lek-breeding birds. In several lek-breeding species there are indications of individual recognition. For example, females have been observed returning to, and sometimes re-mating with, particular individual males both within and between breeding seasons (e.g. Snow 1962, Lill 1974, Trail and Adams 1989, Gibson et al. 1992). While these observations suggest that females can identify individual males, it is not possible to rule out alternative explanations such as the territory history or location (Gibson 1992), or even whether a consistently high rank of the male in the pool of available males makes him a preferred mate. To my knowledge, this is the first experimental demonstration of song-based, individual recognition in a lek breeding species.

Male-Male Interactions and Lek Evolution.

In previous work on this species (Westcott 1992; Westcott and Smith 1994), territories were defined as the areas encompassed by a male's song posts; from which he would evict intruders and beyond which he did not pursue intruders. By performing playbacks from 10m outside these boundaries, I placed the speaker in locations from which males did not normally sing or evict intruders. Excursions by focal males outside their display territories boundaries to seek out and attack a simulated territorial male in these previously undefended areas can reasonably be interpreted as attempts to deter settlement adjacent to their display

territories. This conclusion is supported by observations of the defense of extra-territorial areas in the field. In two cases, one a solitary territory, the other at a lek (unpubl. data), this defense continued for a period of months. In both instances it was successful in preventing the repeated settlement attempts of several individuals in areas that were not otherwise used or defended by the resident male. In the case of the solitary male, this successful defense lasted for one full breeding season at least. Part way through the second breeding season a male finally managed to establish a new territory adjacent to this solitary male. Thus, males seem to be actively seeking to prevent other males from settling at a site and are capable of doing so for long periods.

The results of this study suggest that most current models for lek evolution are unlikely to provide much insight into lekking in *M. oleagineus*. The clear disinclination of males, particularly solitary males, to allow settlement adjacent to their territories indicates a preference for solitary display. This effectively rules out hypotheses that propose a benefit to males from display at large leks (predation reduction, Koivisto 1965; lek size as a sexually selected trait, Queller 1987; mate retention, Clutton-Brock et al. 1993; signal transmission/detectability enhancement, Otte 1974). Models that propose a benefit to females (Lack 1968; Bradbury 1981; Bradbury and Gibson 1986), however, cannot be ruled out on the basis of these data since it is possible that female preferences for leks conflict with the male preference for solitary display. Observations of female visitation and copulation patterns, however, have failed to identify a female preference for larger leks (Chapter 4).

An alternative model is the hotspot hypothesis (Bradbury 1981). In the simplest hotspot models, male settlement follows ideal free distribution rules, with males settling preferentially in the areas of highest female traffic in a manner such that each male encounters the average number of females. Under more complex versions of the model, however, males differ in their competitive abilities and individuals choose their lek on the basis of their quality relative to that of the other males present, i.e. settle according to ideal free rules with unequal competitors (Sutherland and Parker 1985; Parker and Sutherland 1986; Bradbury et al. 1986; Alatalo et al. 1992; Höglund et al. 1993). Unfortunately, both simple and complex models

assume that males can settle where they choose, an assumption that is precluded if established males can prevent settlement. Settlement models for this species, therefore, should be despotic (Bradbury et al. 1986), with highly competitive males not only obtaining a disproportionate share of the matings at a site, but also limiting the settlement options of other males at that same site.

Such a scenario is particularly appropriate if males are in fact defending not just the area of their territories but rather the whole hotspot itself. If this were the case, a solitary territorial male would be defending the "rights" to a display site where many females pass on a regular and predictable basis. All other things being equal, the cost to the original male of the settlement of a second male would be 50% of the copulations at the site. This represents a sharp decrease in the fortunes of any males' reproductive prospects (pers op.). As additional males settle at the site, the original male must share more and more of his access to females. However, as the cost per additional male decreases, so too might the aggressiveness of his response.

The data presented here fit this scenario nicely; males do defend extra-territorial areas and the response to playback does decrease from solitary to lek males. Neighbours also represent a cost in terms of increased intrusion rates. While intrusion rates remained constant across the range of lek sizes for the average male, they increased for the top ranked male at each lek (Chapter 4). The top-ranked male at the largest lek could expect an intrusion rate approximately double that of a solitary male. Perhaps more importantly, intrusion and interference at leks occurred during display to females, and sometimes resulted in the female leaving the territory. This did not occur at solitary display sites. Thus, losses in terms of both lost copulations to a new neighbour and of interference in display, are largest when the number of males goes from one to two. As this cost diminishes I predict a decrease in the level of aggression displayed by the original male towards additional settlers.

In summary, male-male interactions in M. oleagineus act to limit, rather than increase, lek size through direct interference by territorial males. The existence of a large pool of non-territorial males in this population is probably due to the high cost of territorial establishment in the face of interference by territorial males.

Figure 5.1:

Proportion of total amount of song that was sung during the playback, \pm S.E.. A score of 50% represents no change in song rate during the playback, less than 50% indicates a decrease. The numbers above the x axis represent sample sizes in each category. N>N - playback of neighbour's song from a neighbour's territory, N>O - playback of neighbour's song from outside the lek, S>N - playback of stranger's song from a neighbour's territory, S>O - playback of stranger's song from outside the lek. "Lek" and "solo" refer to playbacks performed to males at leks and solitary display territories respectively.

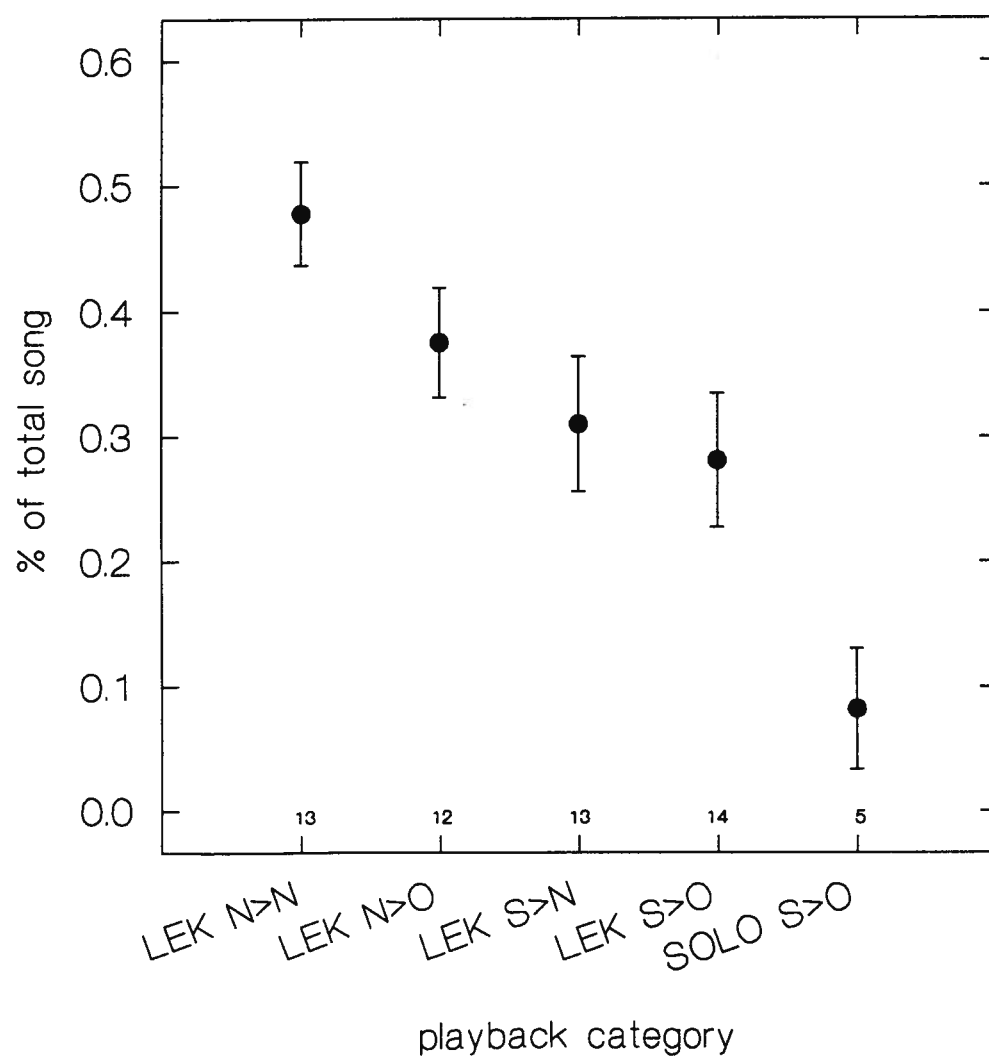


Figure 5.2:

Change in mean distance, \pm S.E., from the playback speaker in the two phases of the experiment.

A positive score indicates that males were y m closer to the speaker during the playback than prior to it. The numbers above the x axis represent sample sizes in each category. N>N - playback of neighbour's song from a neighbour's territory, N>O - playback of neighbour's song from outside the lek, S>N - playback of stranger's song from a neighbour's territory, S>O - playback of stranger's song from outside the lek. "Lek" and "solo" refer to playbacks performed to males at leks and solitary display territories respectively.

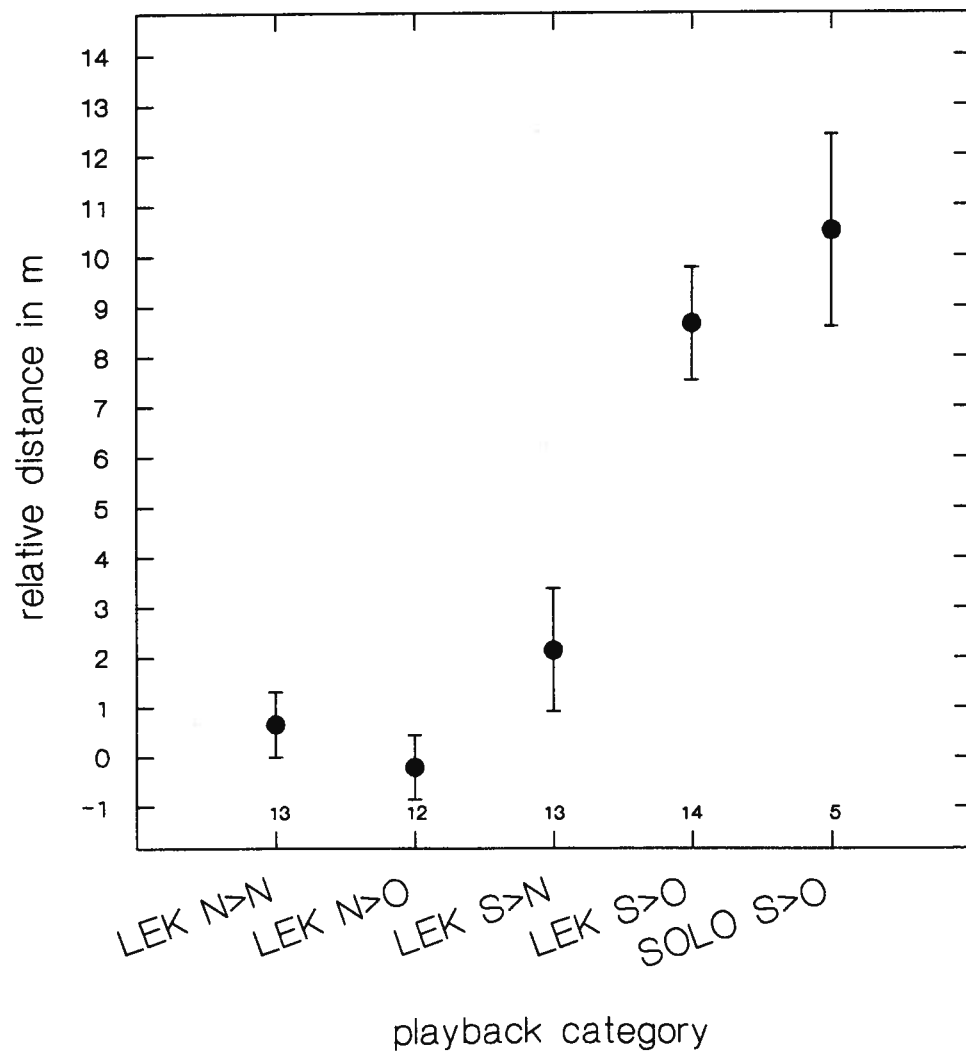
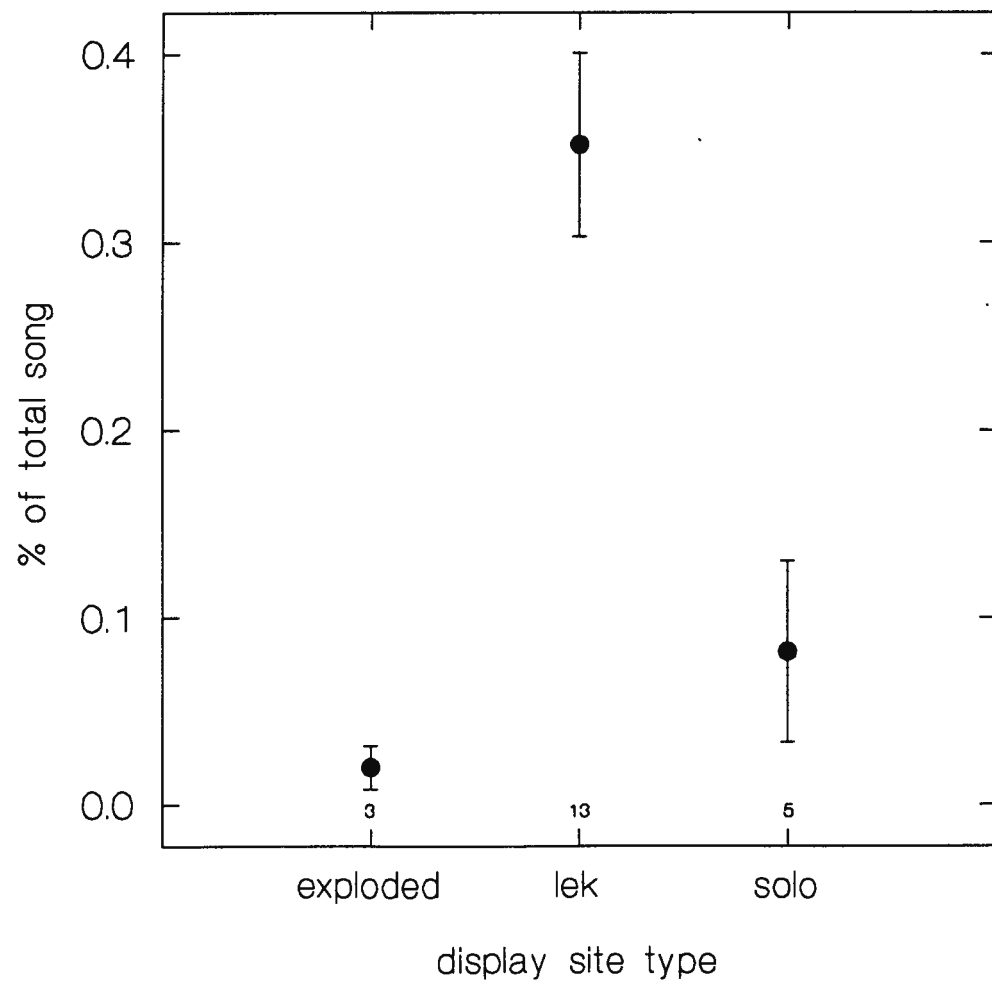


Figure 5.3:

Comparison of the proportion of song sung by males at the three categories of display site. The numbers above the x axis represent sample sizes in each category.



CHAPTER SIX.

CONCLUSION.

Community Level Patterns of Lekking.

Patterns in lekking within a community of lek-breeding species have only rarely been considered. When such comparison have been done, the purpose has always been to look for a correlation between the sizes of female home ranges and the degree of clustering in males across species (Bradbury et al. 1986; Théry 1992). At Sirena, not only are the leks of all lek-breeding, understory birds spatially aggregated, but they tend to occur close to environmental features that would channel the movements of birds through the habitat, e.g. saddles in ridge lines, the ends of ridgelines and the confluences of drainages. In addition, the sizes of the leks of frugivores tended to change in unison. These observations suggest that leks form as a response to the temporal and numerical distribution of females in space. The results are consistent with the predictions of the hotspot hypothesis (Bradbury et al. 1986) and suggest a role for hotspot mechanisms in determining both the location of leks and their sizes in lek-breeding tropical forest birds.

Female Movements and Distributions.

The results of my first chapter suggest that topographical features influence female movements and that leks are associated with some aspect of female distributions. The telemetry data presented in Chapter 2 confirm these suggestions. Not only do females tend to follow lines of least resistance when they travel between areas, but leks are strongly associated with areas of high female traffic. In contrast, leks are less strongly associated with sites with high female densities, and not associated with areas where females spend the most time. It appears that the problem males face is to maximize their exposure to as many females as possible when the exact locations of these females, and the times when they are sexually receptive, are uncertain. Males achieve this by settling at sites where females reliably pass when travelling through the habitat.

The observation that females use habitual travel routes suggests two avenues for future research. First, manipulation of these routes would allow an experimental test of the female traffic version of the hotspot hypothesis. Second, the effect of such structured movement patterns of seed dispersers on the distribution and recruitment patterns of the plants whose fruit they eat warrants consideration.

Is Lekking a Better Strategy?

Contrary to the expectations of several current hypotheses for lek evolution, i.e. the preference hypotheses and hotspot models with unequal competitors, display at larger leks is not associated with any apparent advantages in M. oleagineus. While female visitation rates increased with lek size, they did not do so on a per-capita basis as predicted by these hypotheses. Indeed, for males, rather than being advantageous, display at leks incurs the additional cost of interference during display. The patterns of the distribution of female visitation to leks and lek size failed to match the predictions of the hotshot hypothesis (Beehler and Foster 1988). However, the lack of a per capita increase in female visitation rates with lek size is consistent with the predictions of both the hotspot hypothesis (Bradbury et al. 1986) and the attractiveness version of the hotshot hypotheses (Höglund and Robertson 1990a). To determine whether one or both of the hypotheses are relevant to this system will require additional work; I have no idea what at the moment.

Despots and Lek Size.

The observation that a large proportion of males do not hold display territories (Westcott and Smith 1994) and that increased lek size is associated with increased costs, both suggest that established territorial males might be acting despotically, i.e. preventing the settlement of additional males at their lek. This was confirmed by the playback experiment. This experiment also demonstrated that males can distinguish neighbours from strangers on the basis of their songs.

The Evolution of Lekking in *Mionectes oleagineus*.

The picture that emerges from this study is that the major impetus for aggregation in *M. oleagineus* is provided by hotspot mechanisms. Males attempt to maximize their reproductive success by settling at sites where they will encounter the greatest number of receptive females. Because of the unpredictability in the locations of females and of the resources that they require over the 7-month breeding season, males cannot predict exactly where females will spend time or where the greatest female densities will be encountered. Males appear to overcome these uncertainties by settling at sites where female traffic is predictable, irrespective of the season and the exact locations between which females are travelling.

While hotspot mechanisms alone are sufficient to explain lek location and play a role in determining lek size (Chapter 2, 4, Westcott 1994), interactions between males, perhaps not surprisingly, are also involved in determining the number of males that settle at a site (Chapters 3 and 4). Clustering of other males around successful individuals, i.e. the attractiveness version of the hotshot hypothesis (Höglund and Robertson 1990a), is possibly part of this process. The net result is that, up to a threshold level of intruder pressure, territorial males limit the settlement by other males, thus keeping lek size below the level predicted by ideal free settlement. Beyond this limit, territorial males are forced to allow other males to settle adjacent to them. The manner in which territorial males attempt to prevent settlement in extra-territorial areas suggests they are defending the entire hotspot rather than just the area within their "usual" territory boundaries.

Several observations suggest that hotspots are involved in lekking in other taxa, particularly other tropical frugivores. First, my comparison of lek locations used members of three distinct families, the Tyrannidae, Pipridae and Trochilidae. All exhibited the same pattern of aggregation. Second, 'leks of leks' occur in other parts of the Neotropics and can involve members of at least one additional family, the Cotingidae (M. Théry, pers. comm.), as well as about 10 additional species not included in my analysis (M. Théry, pers. comm.; Westcott pers. obs.). Third, evidence for hotspot mechanisms has been found in at least two other studies of lekking tropical birds, the Pipridae (Théry 1992) and the Paradisaeidae (Pruett-Jones and Pruett-

Jones 1990).

I suggest that this convergence in lekking in tropical species is due to three factors: i) the extreme length of the breeding season, ii) the ephemeral nature of their food resources and the resulting lack of predictability in female distributions and, iii) low female reproductive synchrony. I predict that as the effect of these factors is diminished, so too will be the importance of hotspot mechanisms in lek evolution. Under such circumstances, e.g. grouse and shorebirds, the influence of other mechanisms, such as hotshots and female preferences for aggregated males, should predominate.

Lekking in an Evolutionary Time Frame.

The current mating systems paradigm postulates that mating systems are adaptive responses to current social and ecological conditions (Emlen and Oring 1977). Several recent studies have suggested that this paradigm is flawed and that phylogeny may override ecological influences in determining a species' mating system (Bjorklund 1991; Edwards and Naeem 1993; Rendall and DiFiori 1993; Prum 1994). This raises the question: to what extent can my results be applied to the evolution of lekking. I have considered lekking in an ecological time frame but the factors involved in an evolutionary time frame may be very different (Prum 1994). I believe, however, my results can be extended to an evolutionary time frame for two reasons. First, lekking in M. oleagineus is facultative within the population I studied (Westcott and Smith 1994; this study). The propensity to lek also varies geographically with leks being reported from some areas of Costa Rica (Sherry 1983; Westcott and Smith 1994) but not in others (Skutch 1960). Nor does M. oleagineus lek in Trinidad or Amazonia (Snow and Snow 1979; Willis et al. 1978). Second, as best as can be resolved from current phylogenies, M. oleagineus' closest sibling species lek, the Pipramorphas e.g. M. macconnelli, while its closest outgroup has solitary display, M. olivaceus (Caparella and Lanyon 1986; Sibley and Ahlquist 1986, 1991). These two factors suggest that lekking is apomorphic in M. oleagineus and that the factors responsible for its evolution are still operating on the species.

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