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Female mate-searching strategies and behavioural correlates of copulation success in lekking long-tailed manakins (*Chiroxiphia linearis*)

by

Kara-Anne A. Ward

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Declaration of Co-Authorship

I hereby declare that this thesis incorporates material that is result of joint research, as follows:

Chapter 1: I am the sole author.

Chapter 2: I am the primary author, and share authorship with Dr. Stéphanie M. Doucet, Dr. Daniel J. Mennill, and Dugan F. Maynard. Dr. Stéphanie M. Doucet contributed substantially in the writing of this chapter. This project would not have been possible without the monetary and logistical support, and guidance from my supervisor Dr. Stéphanie Doucet. Dr. Daniel Mennill and Dugan Maynard assisted in the field during data collection.

Chapter 3: I am the primary author, and share co-authorship with Dr. Stéphanie Doucet, Dr. Daniel Mennill, Dugan Maynard, Dr. John M. Burt, and Dr. Brian Otis. Dr. Stéphanie M. Doucet contributed substantially in the writing of this chapter. Dr. Stéphanie Doucet and Dr. Daniel Mennill were essential for the completion of this project. They provided funding for the project, guidance in the research design, assistance in data collection in the field, and assistance in data manipulation in the lab. Dugan Maynard assisted in data collection, and offered support in the field. Dr. John Burt and Dr. Brian Otis designed and produced the Encounternet technology that is central to the research. Dr. John Burt also provided assistance in the field deploying the technology.

Appendix A: Dr. Daniel Mennill is the primary author, and I share co-authorship with Dr. Stéphanie Doucet, Dugan Maynard, Dr. John Burt, and Dr. Brian Otis. This is the abstract of a technical paper that was designed to test the application of the Encounternet technology for use in Chapter 3. Dr. Daniel Mennill was the primary author. Dugan Maynard, Dr. Stéphanie Doucet, and I contributed to the field research, data manipulation in the lab, and editing the manuscript. Dr. John Burt and Dr. Brian Otis designed and produced the Encounternet technology, and provided technical support during its deployment as it was applied in this Appendix, as in Chapter 3.

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Abstract

Mate choice, a complex searching and decision-making process, is relatively understudied. I explore the process of mate choice in lekking long-tailed manakins (*Chiroxiphia linearis*) using video recordings to determine male quality, and a novel radiotracking system to monitor female search behaviour. I report how females may play an important role in the evolution of cooperative display through their choices and behaviours during courtship. I show that females are more likely to copulate at leks with higher attendance and display effort, and more cooperative dance manoeuvres. I also characterize the complex mate searching strategies employed by females. I show that females visit an average of 4.02±0.42 leks when assessing mates, and also revisit higher quality leks multiple times. Overall, my thesis provides insight into mate choice in long-tailed manakins, revealing that females make complex decisions that have important fitness consequences, and that females may also influence the courtship behaviours of males.

Dedication

I dedicate my Master's thesis to my parents, Leonard and Ruth Ward, and to my grandparents, William and Ruth Abbott, and Mary Ward. To my parents, I thank you for your continued support through my undergraduate degree for providing me with a loving home that was welcoming to my student lifestyle and study requirements (even when they were somewhat irrational). Thank you for the emotional support during my Master's degree; your phone calls and e-mails were key in helping to pull me out of my little world, and to remind what I was working towards. To my Abbott grandparents, thank you for continuously welcoming me into your home. The farm was a great way to get out from behind my computer and I couldn't have asked for a better place to spend the weekend. To Gram Ward, you are greatly missed, and I wish I could have shared this experience with you.

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Chapter 1: General Introduction

Sexual selection and mate choice

Natural selection is an evolutionary mechanism by which the frequency of traits changes within a population depending on the reproductive success of their bearers. For this to occur, these traits must have variation and heritability (Darwin 1859). Sexual selection occurs when competition over mates leads to variation in reproductive success among individuals (Darwin 1871). It is believed that this competition drives the development of traits used in combat as well as those used to attract the opposite sex, both of which may pose a survival cost (Darwin 1871; Fitzpatrick et al. 1995). Therefore, intrasexual competition and intersexual selection are both important mechanisms of sexual selection that influence the development of secondary sexual traits (Andersson 1982, 1994; Bateson 1983).

Mate choice, where an individual chooses their mate over at least one other individual (Halliday 1983), is a behaviour that can be found in both sexes; however, the intensity in each sex varies by mating system and by species. Within a species, it is thought that the choosiest sex is not constrained by the number of available potential mates and has the highest parental investment, while the other sex is restricted in the number of mating opportunities, has lower parental investment, and will therefore invest more in intrasexual competition and mate attraction (Trivers 1972; Emlen and Oring 1977; Halliday 1983; Clutton-Brock and Parker 1992). Under these conditions females tend to be the choosier sex. Females tend to perform most parental care, which requires a tremendous amount of energy, and can include but is not limited to nest construction, incubation, and offspring defence and feeding. Even when parental care is shared equally between the sexes, some behaviours, such as egg production, gestation, and lactation, can only be performed by the female, causing a skew in reproductive investment. In most promiscuous mating systems there is a male-biased skew in the number of sexually active individuals, where there are more males ready to mate than there are available females (male-biased operational sex ratio; Emlen and Oring 1977). Therefore, males tend to compete for access to females while females choose among those males. Conversely, in species where male parental investment is highest and females compete for access to mates, males tend to be the choosiest, which is most apparent in species with sex-role reversal (Petrie 1983; Gwynne 1991). In a few species that should favour female mate choice, both male and female mate choice occur simultaneously (e.g. Amundsen and Forsgren 2001; Bonduriansky 2001). This type of mating system is thought to evolve when there is high variation in female quality, the number of available females surpasses a male's mating capacity, and males incur high costs from male-male competition and mate attraction (Edward and Chapman 2011).

Female fitness can be influenced by mate choice decisions. Females can gain immediate or direct benefits from their mate, such as nuptial gifts, high quality nest locations, territories containing high quality food resources, and high quality parental care (Searcy 1979; Hoelzer 1989; Kokko et al. 2003). Similarly, females may also avoid the costs of mating with males infected by parasites and sexually transmitted diseases (Clayton 1991). Females can indirectly benefit from their choice of mate through male "good" genes that increase the viability and future fitness of offspring independently of the female's genes, and "compatible" genes that interact with the genes of the female to positively impact offspring fitness (Zahavi 1975; Searcy 1979; Mays and Hill 2004; Neff and Pitcher 2005).

Active female mate choice does not occur in all species; in some species, females are passively attracted to their mates. In species exhibiting passive choice, a female is attracted to, and mates with males producing the most conspicuous cues (Halliday 1983; Parker 1983). This is different from active female choice where a female actively assesses multiple males, and rejects some while accepting and mating with others (Maynard Smith 1991). Active female choice is a complex process that involves strategic sampling of potential mates, information gathering and processing to determine their quality, and calculated decisions to accept or reject those males as mates (e.g. Wittenberger 1983).

Female mate search strategies

Most mate choice studies focus on the outcome of the mate choice process: the preferred mates and their associated traits. Few studies focus on the steps that lead to female selection of a particular mate (Andersson 1994; Ryan et al. 2007). As a consequence, the rules that females use to make their mate choice decisions remain unclear (Ryan et al. 2007). Female search behaviours determine the likelihood of encountering high quality males. Therefore, alternative search strategies would be under selection because they have different fitness consequences (Wiegmann and Angeloni 2007).

Three primary models were developed to explain the information gathering and decision process of mate choice: the "fixed-threshold" decision model, the "sequential search" model (one-step decision, sequential-comparison), and the "fixed sample search" model (pooled comparison, best-of-*n*; Janetos 1980; Wittenberger 1983; Real 1990). Females that employ the "fixed-threshold" decision tactic sample prospective mates until the quality of an encountered male exceeds a certain threshold (Janetos 1980). Females that employ the "sequential search" tactic sample prospective mates until the quality of an encountered male exceeds either a previously-encountered male or the probable quality of a male encountered in the future (Janetos 1980; Wittenberger 1983; Real 1990). Females that employ the "fixed sample" search tactic sample a fixed number of males and mate with the one with the highest quality (Janetos 1980). These tactics are the basis for the two main female decision rules; in the "fixed-threshold" decision model females make a choice based on a fixed criterion of male quality, whereas in the “fixed sample” and “sequential search” tactics females make a choice based on a comparative evaluation criterion (Bateson and Healy 2005).

Based on the two decision rules, defining the process of gathering information on perspective mates has led to the development and further refinement of search strategy models. Initially, the “fixed sample” and “sequential search” models assumed that females have *no uncertainty* in the accuracy of information gathered about prospective mates. Therefore, these models assumed that females have accurate knowledge of the distribution of individual quality within the population, and upon first assessment gain perfect understanding of each male’s quality (Janetos 1980; Real 1990; Wiegmann et al. 1996). Recently, these models were refined by adding the assumption that females have *no control* over the accuracy of acquired information. Therefore, females either evaluate a subset of male attributes that accurately represent their contribution to female fitness (Wiegmann and Angeloni 2007), or females incorporate a degree of uncertainty as a component of their assessment (Phelps et al. 2006).

The “fixed sample” and “sequential search” strategies also assume that potential mates are encountered randomly. However, based on empirical data from studies on at least three bird species, females visit a non-random subset of males, a portion of which receive long strings of consecutive visits (Trail and Adams 1989; Dale et al. 1992; Uy et al. 2001). Luttbeg (1996, 2002) developed the “comparative Bayes” model to account for multiple non-random visits through the modification of both the decision rule and method of information gathering. In the “comparative Bayes” model, the decision rule is that after each encounter, females either use the information gathered to choose a mate or delay their decision to gather more information to reduce the uncertainty in their estimate of male qualities. Females *control* the accuracy of information by choosing the number of males to reassess and the number of times males are reassessed.

The most recent model, the “random-walk” model, includes both decision rules from the fixed and sequential models. It also adds the assumption that females control the *amount* of information they gather. In previous models, it is assumed that females gather perfect information about the quality of perspective males during initial sampling (but see Wiegmann and Angeloni 2007); however, this model assumes that information gathered is noisy, and requires multiple visits to gain a valid assessment. The “random-walk” model stipulates that females control the number of males sampled, and continue reassessing those males until the information gathered surpasses a threshold (Castellano and Cermelli 2011).

The “comparative Bayes” model was developed for systems in which potential mates can be regularly located in individual areas, and the “random-walk” model was developed for systems that facilitate the simultaneous comparison of multiple potential mates (Luttbeg 1996; Castellano and Cermelli 2011). Based on these criteria, the “comparative Bayes” and “random-walk” models should best describe lek mating systems.

Lek mating systems

Throughout the animal kingdom there are two main mating strategies: monogamy and polygamy. Monogamous individuals reproduce sexually with only one partner of the opposite sex, whereas polygamous individuals have multiple sexual partners of the opposite sex (Selander 1972). Within species, the type of mating system can be the same for both sexes, or can vary between the sexes, where one is polygamous and the other is monogamous. Systems where males mate with multiple females are termed polygynous and systems where females mate with multiple males are termed polyandrous (Alcock 2005). Polygamous systems tend to evolve when the mating availability of individuals of one sex is limiting. This skewed operational sex ratio leads to a high variation in mating success among individuals of the polygamous sex

(Trivers 1972). As such, the polygamous sex is subject to intense sexual selection, which results in highly developed ornaments and armaments, and various stereotyped behaviours for attracting and soliciting copulations (Emlen and Oring 1977; Darwin 1871).

Lekking is a widespread but uncommon polygamous system that has evolved independently in a wide variety of environmental contexts and a diversity of species including insects, fish, birds, amphibians, and placental mammals (Höglund and Alatalo 1995). Lek mating systems are characterized by adult males that gather in some degree of aggregation in display areas or arenas to attract and mate with females. The males spend a significant amount of time throughout the breeding season (and sometimes during the non-breeding season) on their lek territory, and will mate multiple times with multiple females each year if given the opportunity (Foster 1977b; Théry 1992; Höglund and Alatalo 1995). Male-male competition and convergent female choice is thought to cause the high mating skew characteristic of lek systems, with a few males acquiring most of the copulations (Bradbury and Gibson 1983; Pruett-Jones and Pruett-Jones 1990). Male display areas do not contain any defendable resources required by the females, such as food, water, nest sites, roosts, egg deposition or bathing sites (Höglund and Alatalo 1995). Because lekking males are unable to monopolize resources required to control females, females that visit the leks have relatively free choice of male, gain only sperm from successful interactions, and leave after copulation (Emlen and Oring 1977; Trail and Adams 1989; Reynolds and Gross 1990). Across species, females vary in the number of copulations and partners per mating bout and breeding season, and may mate with one male (once or multiple times), multiple males, or either (Petrie et al. 1992, Fiske and Kålås 1995).

Among mating systems, the way males are distributed in relation to one-another within their habitats, follows a continuum. This continuum is influenced by the range of variables that influence female choice, from an emphasis on the resources defended by the males, to an emphasis on the males themselves (Wittenberger 1978; Bradbury 1981). Resource-based monogamy is thought to be the most common type of avian mating system (Foster 1981). It is characterized by males being arranged in uniform fields throughout the habitat on contiguous territories. Males display independently to attract females, and female choice is based both on male genetic quality and the quality of the resources they defend (Bradbury 1981). Within lek mating systems, there are two main forms of male distribution: the classical or true lek and the exploded or quasi-lek (Bradbury 1981). Classical leks are composed of male display areas that are densely clustered so the males display in visual range of one another, and distinct leks are relatively highly separated. Conversely, exloded leks are composed of male display areas that are moderately separated from one-another so the males display in auditory, rather than visual contact. This form of lek is most apparent through mapping, where the seemingly solitarily displaying males are more clustered than would be expected from random placement (Emlen and Oring 1977).

Leks provide an ideal study system for investigations of female mate choice and female mate search strategies. In these systems, male-courting females are concentrated in small areas, copulations usually only occur at a few locations, females can easily be monitored as they move between males (Trail and Adams 1989), and there is a great potential for strong sexual selection (Wiley 1973; Lill 1976; McDonald 1989b).

Manakins (Pipridae)

Manakins (Pipridae) comprise a small family of neotropical understory suboscine birds with a high degree of sexual dimorphism. Males are mostly black with patches of conspicuous colouration, are usually larger than the females, and may have highly modified wing or tail feathers used as visual and/or mechanical noise signals. Females and immature individuals are a cryptic olive green colour (Snow 2004).

Lekking tends to be rare within families (Emlen and Oring 1977). In manakins, however, with approximately 45 lekking species, it is the rule (Prum 1994, Snow 2004). Across species, there is substantial variation in lekking behaviour and spatial organization. Exploded leks are thought to be primitive within Pipridae, which is contrary to Gilliard's original lek evolution hypothesis (Gilliard 1963; 1969). Exploded leks are also more common than classical leks in manakins, where 8 of the 13 genera (14 including the *Piprites*) and approximately half of the species are known to have an exploded-lek mating systems (Prum 1994; Snow 2004).

There are two main factors which are thought to pre-adapt species for polygyny with female choice in non-resource based systems: male emancipation from parental duties, and the inability of males to control females through female access to essential resources or to other males, a relatively long breeding season, and a highly skewed operational sex ratio (Lack 1968; Emlen and Oring 1977; Borgia 1979). Male manakins are thought to be emancipated from parental care for a combination of three factors: (1) they have open nests at a high risk of predation, so there is selection for cryptic nests with small clutch sizes and infrequent adult visitation; (2) clutch care requires low time and energy; and (3) food availability allows females to forage enough food for themselves and their offspring without male assistance (Höglund and Alatalo 1995). Manakins are all unspecialized frugivores, feeding mainly on small fruits that contain easily assimilated carbohydrates (Snow 1981). Thus, manakins must feed frequently to sustain their level of activity (Melo and Oliveira 2009). Their target fruits are found on heavily laden trees that are distributed patchily throughout the forest and that ripen out of synchrony through the breeding season. Therefore, it would be unnecessarily costly for the males to monopolize and control specific patches or resources (Emlen and Oring 1977; Beehler and

Pruett-Jones 1983). In summary, once emancipated from parental care and unable to control resources, it is thought that male manakins shifted to 100% self-advertisement, creating a lek mating system.

Some manakin species have evolved coordinated and cooperative displays. Two or more males may display interactively together, either as a form of competition between males competing for dominance (e.g., *Lepidothrix serena* in French Guiana; Théry 1990), or as a way to attract and excite females, which in some cases may be obligatory for copulations (*Chiroxiphia pareola, C. linearis*; Snow 1976, Foster 1977b). Cooperative displays that are used in mate attraction are thought to have evolved when the benefits to the subordinate male cooperating exceed the benefits of solo display and outweigh the cost of participation. Although there does not seem to be any indirect benefits through kin selection or reciprocity in many of the cooperative displaying manakin species, cooperative subordinate males gain direct delayed benefits through rare copulations, display area inheritance, and female site fidelity (McDonald and Potts 1994; Ryder et al. 2008, 2011).

Females may also benefit from cooperative display because it reduces the number of potential mates they assess and therefore the time cost of assessment. Within a cooperative group, the dominant male usually mates with the female, which is reinforced through both female choice and male-male competition, therefore reducing the pool of potential mates to between cooperative groups, as apposed to between all the males within the groups (Cox and Le Boeuf 1977; McDonald 1993; DuVal and Kempenaers 2008; DuVal and Goymann 2011). If cooperatively displaying males also have dominance hierarchies, then females can further reduce their pool of potential mates to the most dominant males. In addition, females selecting for males based on their coordinated displays have lower risk of injury than females assessing males engaged in aggressive interactions (Foster 1983).

Long-tailed manakins

Long-tailed manakins (*Chiroxiphia linearis*, Bonaparte 1838) are small, long-lived, neotropical passerines ranging from southern Mexico to northwestern Costa Rica along the tropical zone of the Pacific coast. Their typical habitats are humid or dry tropical forests with dense undergrowth (Snow 2004). As is typical for manakins, long-tailed manakins exhibit a high degree of sexual dimorphism; adult males have conspicuous red and blue patches on their crown and mantle, respectively, contrasting against their black body plumage; the females are a cryptic olive-green (Snow 2004, Figure 1). Male long-tailed manakins exhibit unusually long delayed plumage maturation where they progress through a series of transitional subadult plumages over four years before acquiring definitive colouration (Doucet et al. 2007).

Long-tailed manakins are primarily frugivores, although they are also opportunistic insectivores (Foster 1977a). Female long-tailed manakins are often seen in mixed flocks following army ant swarms, especially during the season of egg production (person. comm. Doucet and Mennill). Male manakins clean debris from on and around their display perches, low-hanging horizontal vines or branches on which males display for females (McDonald 1989b). These cleaning behaviours include breaking-up the tunnels of nasutiform termites (Isoptera, Termitidae; Marshall 2008) that run below some perches and opportunistically eating emerging individuals (person. observ.).

Mating system

Long-tailed manakins have a cooperative exploded-lek mating system, where pairs of males display for females at display areas and are within vocal range of each other. Each display area comprises of a group or lek of 3 to 13 males, within which there is an age-graded linear dominance hierarchy. The two dominant males, the alpha and beta, perform complex cooperative displays for visiting females. Typically, only alpha males copulate with females, and the females are effectively choosing between alpha males at neighbouring leks (McDonald 1989a, b). Males are usually at least 8 years old before they reach beta status, and 10-12 years old before they reach alpha status (McDonald 1989a). The 1-11 subordinate males of a lek practice their displays in the absence of females and move between neighbouring leks, forming social associations with numerous other males. These social connections impact future social status and reproductive success (McDonald 1989b, 2007). Copulations not performed by the alpha male are otherwise opportunistically performed by the beta male and occur when the alpha is either away from their display area, or otherwise distracted (either by the presence of multiple females, or aggressive displays towards other males in the display area; McDonald 1989a). There is extensive variation in copulation success between alpha males at different leks, with a small minority of males obtaining most of the copulations (McDonald 1989a). Each display area is characterized by 1 to 6 perches, where 1 to 2 primary perches are most frequently used by the alpha, beta, and visiting females. The younger subordinate males mostly use secondary perches for practice dancing and the establishment of social associations.

Displays and vocalizations

Male courtship follows a stereotype-coordinated sequence of displays that demonstrates an obligatory cooperation between alpha and beta males (McDonald 1989a, b ; Trainer and McDonald 1993). These displays begin with the alpha and beta singing a synchronous *toledo* duet in the subcanopy to attract females to the perch (described by Trainer and McDonald 1995). Once a female is either nearby or on the perch, males descend to the perch and perform an alternating sequence of vertical and leapfrog hops collectively dubbed “popcorn” that include an *nyanyownh* vocalization (Trainer and McDonald 1993; *miaow-raow*, Slud 1957). The males then perform laborious silent butterfly flights to and from nearby perches, travelling as far as 20m from the dance perch (McDonald 1989b). The male duo alternate between popcorn and butterfly dances in a seemingly ritualized pattern. Some popcorn dances consisting mainly of leapfrogs that escalate in intensity terminate in a *buzz-weent* vocalization given by the alpha male that is accompanied by a quick looping flight to a designated nearby perch where the male performs "tucked wing flicking" (Luckianchuck person. comm.). Following the *buzz-weent*, the beta male leaves the immediate area, either willingly or from the added motivation of a pursuant alpha male. The alpha then performs a solo butterfly dance that is usually much longer than the previous dual-male butterfly dances. An ordered pattern of dances occurs: long-distant butterfly flights are usually followed by quick perch changes near the dance perch, followed by a specialized vertical angel flight that lands the alpha beside the female with his head down and level with the dance perch, and his crown spread out. A copulation attempt, whether successful or not, usually follows this manoeuvre (Slud 1957; Foster 1977b; McDonald 1989b).

Male long-tailed manakins have a large vocal repertoire, most likely a result of the long-term relationship between cooperative males, which includes at least 13 distinct calls that are most frequently given during courtship displays to mediate cooperative intrasexual interactions and during noncourtship male-male interactions to express agonism and alarm (Trainer and McDonald 1993).

Females

Females are thought to begin breeding in their first year after hatching (Foster 1976; Lill 1976). Females provide sole parental care, performing all behaviours associated with nest building, incubation, brooding and feeding of the young (Foster 1976). Females are significantly heavier than all classes of males, whether or not they are carrying developing eggs (McDonald 1989b). Social interactions are less important, and thus less frequent in females than in males, both intra- and intersexually, apart from interactions with their offspring. It is probably for this reason that females have much less developed vocal repertoires; their most common vocalization a mobbing *wheeoo* call given in the presence of predators (Trainer and McDonald 1993).

Female long-tailed manakins do not have territories and exhibit free movement between food resources and leks within their large overlapping home ranges (up to 80 ha; McDonald 1989b). Females visit a subset of active leks based on male *toledo* output and the degree of frequency matching in duet *toledo* calls (McDonald 1989b; Trainer and McDonald 1995). Within the visited subset, females are more likely to copulate at leks with longer average butterfly displays. Age may influence mate searching strategies and mating preference in this species, as younger, but not older females visit the least successful leks, and mostly older females visit the most successful leks (McDonald 1989b).

Thesis goals

In the following chapters, I will explore the mating preference of female manakins through correlates of male mating success and outline the decisions made during the mate searching process, which will hopefully be a holistic representation of the mate choice process in long-tailed manakins. The purpose of Chapter 2 was to determine the influence of male-male interactions and female responsiveness on mating success in long-tailed manakins. To do this, I quantified the influence of female preference on male cooperative courtship display, examined the possible influence of females on the maintenance of orderly queues for status among leks, and investigated whether females provide accurate cues of their receptivity during displays. The purpose of Chapter 3 was to determine the mate searching strategies employed by female long-tailed manakins. To do this, I used the novel tracking system Encounternet to analyze the individual sequential visitation behaviour of females relative to lek quality.

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Figure 1.1. Adult male (a) and female (b) long-tailed manakins (*Chiroxiphia linearis*) from Costa Rica. The female is wearing a digital transmitter from the Encounternet system (antenna visible running above and parallel with the tail) employed in Chapter 3.

Chapter 2: The influence of male-male coordination, male-male aggression, and female responsiveness on mating success in a lekking bird

This chapter is the product of collaborative research, and is co-authored by S.M. Doucet, D.F. Maynard, and D.J. Mennill.

Chapter summary

Lek mating systems typically have a high skew in male mating success. Surprisingly, some lek mating systems have evolved cooperative male displays. Most studies recognize the importance of male intrasexual interactions on the evolution of male-male competition and cooperation; however, few have evaluated the influence of females on male intrasexual interactions. The purpose of our study was to investigate the influence of activity at the lek, male-male cooperation, male-male aggression, and female behaviour during courtship on mating success in a lekking tropical bird. We studied long-tailed manakins (*Chiroxiphia linearis*) a neotropical passerine with an exploded-lek mating system with obligate male-male cooperation during courtship. We used video recordings and behavioural observations in the field to quantify male and female behaviours at 38 leks. Female visitation and copulation rates were higher at leks with high male advertisement and attendance. Copulation rates were also higher at leks with higher proportions of butterfly displays and longer solo butterfly flights by alpha males. Dual-male dances were included in the displays preferred by females. Male-male aggression did not affect copulation success. Female activities during courtship displays predicted their likelihood of copulating, and female activities were also positively associated with male dance display length and aspects of dance that predicted copulation success. These results suggest that female preference for display may promote and maintain the evolution of cooperative display. Overall, our study presents support for the important influence of female preference on male intrasexual interactions.

Introduction

Lek mating systems are characterized by the aggregation of males at display areas for the purpose of attracting and mating with females (Höglund and Alatalo 1995). These display areas do not contain any defendable resources that could influence female mate choice decisions, and females can choose freely among males (Höglund and Alatalo 1995). Females leave leks after copulation to perform solitary parental care, while males remain to display for other females (Emlen and Oring 1977; Bradbury 1981; Höglund and Alatalo 1995). The combined influences of male-male competition and convergent female choice results in high mating skew (Wittenberger 1978; Bradbury and Gibson 1983; Pruett-Jones and Pruett-Jones 1990). Lekking is found in a diversity of taxa ranging from insects to mammals, and occurs in about 0.5% of avian species (Höglund and Sillén-Tullberg 1994). In birds, resource-based social monogamy is the rule, and lekking behaviour has evolved independently numerous times (Höglund and Sillén-Tullberg 1994). Leks provide a unique opportunity to explore influences of both aspects of sexual selection: male-male competition for positions of dominance and female mate choice within and between leks (Bradbury and Gibson 1983).

When there is strong intrasexual competition for mating opportunities, such as in lek mating systems, dominance hierarchies may form (Huntingford and Turner 1987; Aureli and de Waal 2000). Individuals reduce the time and energy spent in energetically costly aggressive interactions through an orderly ascension to the attainment of resources (Huntingford and Turner 1987; Kokko and Johnson 1999; Aureli and de Waal 2000), which is enforced through male intrasexual interactions (e.g. Foster 1981; McDonald 1993a; Magaña et al. 2011; Ryder et al. 2011). The formation and maintenance of dominance hierarchies can lead to ritualized, and sometimes coordinated, male-male interactions.

In some lek mating systems males display in coordination, where two or more males display simultaneously and interactively (Foster 1977; Prum 1994). Coordinated displays may result from a competition between males for positions of dominance, function as a cooperative unit in attracting females, or be a combination of the two (Prum 1994). Cooperative display among lek-mating animals is proposed to be a recently derived behaviour and is thought to have evolved either from coordinated aggressive interactions that became ritualized (Foster 1977), or from coordinated aspects of solitary display (Prum 1994). Cooperation among lekking males is puzzling, since reproductive skew, and therefore competition for access to copulations, is at its highest in lek mating systems (Mackenzie et al. 1995; Widemo and Owens 1995). As such, maintenance of cooperation is thought to occur when cooperatively displaying males are more successful than solitarily displaying males, and there is some benefit to all males involved in the cooperation (reviewed in Nowak 2006; Emlen 1978, 1993; Pizzari and Bonduriansky 2010). Dominant males usually obtain most if not all copulations, whereas cooperative subordinate males gain fitness benefits through rare copulation opportunities, territory inheritance, or increased inclusive fitness (Pizzari and Bonduriansky 2010).

In the few avian families where lek-based mating is common, cooperative courtship is limited to one or two species. For example, wild turkeys (*Meleagris gallopavo*, Phasianidae), ruffs (*Philomachus pugnax*, Scolopacidae), Goldie's bird of paradise (*Paradisaea decora*, Paradisaeidae), and black-and-gold cotingas (*Tijuca altra*, Cotingidae) all exhibit some form of cooperative display (Watts 1968; Watts and Stokes 1971; van Rhijn 1973; Snow and Goodwin 1974; LeCroy et al. 1980; Frith and Beehler 1998; Krakauer 2005; Frith and Frith 2009). Manakins (Pipridae) are an unusual family wherein lekking is common and five genera include species with coordinated displays that range from competitive to obligate cooperative (Prum 1994). Three of these genera (*Masius, Lepidothrix,* and *Machaeropterus*) have simple coordinated displays between transient male pairs that are thought to be mainly competitive (Prum and Johnson 1987; Théry 1990; Bostwick 2000). Within the *Pipra aureola* clade, the three species perform complex ritualized coordinated displays that influence reproductive success, but are not obligate for mate attraction and copulation (Snow 1963b; Robbins 1983, 1985; Prum 1985; Ryder et al. 2011). Within the genus *Chiroxiphia*, four of the five species are known to perform male vocal duets and cooperative courtship displays involving two or more males, which may or may not be obligate for copulations (Snow 1963c, 1971; Foster 1977, 1981, 1985; DuVal 2007). Long-tailed manakins (*Chiroxiphia linearis*), which are the focus of this study, represent an extreme example of cooperation. Their lek-based mating system is characterized by an obligate complex cooperative display performed by pairs of males that form long-term partnerships (Foster 1977; McDonald 1989b).

Long-tailed manakins are small, long-lived neotropical passerines with a cooperative exploded-lek mating system (Slud 1957; Foster 1977; McDonald 1989b; Prum 1994), where display areas are dispersed so that males are within vocal but not visual range of one another (Gilliard 1963). Each display area is used by a group or lek of 3-13 males that exhibit an age-graded linear dominance hierarchy, where the two most dominant males, the alpha and beta, perform vocal duets to attract females and perform a complex cooperative courtship display for visiting females (Slud 1957; Foster 1977; McDonald 1989a). The courtship display involves three main components: popcorn jumps, dual-male butterfly flights, and solo butterfly flights. Popcorn jumps are performed in an alternating rhythm between the alpha and beta male and comprise a combination of vertical hops and backwards leapfrog jumps. Dual-male butterfly flights are performed by both the alpha and beta male, and comprise laboured flights and rapid dives to and from perches around the main dance perch. Bouts of popcorn and butterfly flights alternate until a final high-energy bout of popcorn jumps terminates in a *buzz-weent* vocalization by the alpha male, signalling the commencement of a solo butterfly flight by the alpha male that may or may not lead to a copulation attempt (McDonald 1989b). Females are free to move between display areas and choose between displaying pairs of alpha and beta males, but they only mate with alpha males (McDonald 1989b). The alpha and beta males are not related, but beta males are thought to benefit by joining a dominance queue and acquiring delayed fitness benefits: they inherit the alpha position and the reputation of the lek, and develop appropriate courtship displays through their apprenticeship with alpha males (McDonald and Potts 1994).

Female choice may play an important role enforcing both dominance hierarchies and the cooperation between dominant and subordinate males within leks in cooperatively displaying species (Foster 1981; McDonald 1989a, 1993b). Females may influence the orderly queuing of male dominance hierarchies within leks through mate choice between leks based on levels of male disruptive behaviours (Lill 1974; Borgia 1979; Foster 1981, 1983; McDonald 1989a, b; 1993b; Théry 1992; Hovi et al. 1995). For example, in the blue manakin (*C. caudata*), females leave leks without copulating after repeated disruptions of courtship displays (Foster 1981). Similarly, in cooperative systems, aggressive and disruptive behaviours within cooperative units may influence female choice, enforcing the stable cooperation (Foster 1983). For example, alpha males displaying for females in *C. lanceolota* have lower androgen levels than alpha males not displaying for females, and testosterone levels are often correlated with social disruption, suggesting that females may discriminate against social conflict (DuVal and Goymann 2011). In addition, females may prefer cooperative displays because they may be more challenging to produce synchronously, such as female preference for frequency-matched male-male duets in long-tailed manakins (Trainer and McDonald 1995). Females may also prefer cooperative displays because they provide greater stimulation than solo displays, or because females prefer novel display components in cooperative displays not found in solo displays (Prum 1994).

Finally, females may indirectly prefer cooperative displays because high display rates are strong correlates of male reproductive success across lekking species (McDonald 1989a; Mackenzie et al. 1995; Fiske et al. 1998; Durães 2008), and cooperatively displaying species tend to have high display rates because of increased social stimulation of males within a cooperative group (Durães 2008; Ryder et al. 2011).

Although females are often portrayed as passive observers of elaborate male courtship displays, recent studies have shown that females of various species advertise their reproductive receptivity through visual, olfactory, and vocal cues (Sumner et al. 1994; Langmore et al. 1996; Semple and McComb 2000; Weiss et al. 2011). Males can use these cues to increase the likelihood of acquiring copulations, increase the likelihood that the copulations are successful, and reduce the costs of unsuccessful courtship displays (Preston et al. 2003; Mysterud et al. 2008). For example, young male brown-headed cowbirds (*Molothrus ater*) modify their songs to match female preferences based on visual cues provided by females (King and West 1983; West and King 1988). In satin bowerbirds (*Ptilonorhynchus violaceus*), males increase their courtship success by adjusting their display in accordance with female behaviours of receptivity (Patricelli et al. 2006). Thus, females may signal their preferences to displaying males, which in turn influences male reproductive success.

In this study, we performed a comprehensive analysis of male display behaviour, female behaviour during courtship, and copulation in long-tailed manakins. First, we assessed the relationship between male advertisement and lek attendance, and female visitation and copulation. Based on previous research (McDonald 1989b), we predicted that males with higher rates of advertisement and attendance would have high female visitation rates and copulation success. Second, we tested whether females prefer more coordinated male display. We predicted that if females prefer coordinated displays, there should be a positive correlation between female choice and coordinated components of male displays. Third, we examined the possible influence of females on the maintenance of orderly queues for status among leks. If females play an important role in the maintenance of orderly queuing within leks, we predicted that females would prefer to visit and copulate at leks with few male-male aggressive interactions. Finally, we investigated whether female behaviours during courtship signal their interest in male displays. If female behaviour during courtship provides information about their preference for displays, then females should increase their behaviours preceding copulation.

Methods

We studied long-tailed manakins from March to June in 2010 and 2011 within the Bosque Humedo in Sector Santa Rosa, Guanacaste Conservation Area, a UNESCO World Heritage Site in northwestern Costa Rica (10°40′N, 85°30′W). At this site, evergreen forests dominate the moist bottomlands, and tropical dry deciduous forests dominate the surrounding areas (Stiles and Skutch 1989). Long-tailed manakin lekking and nesting activity mainly occurs along the slopes and bottoms of valleys. The area displays marked seasonality, with a dry season from January through April, and a rainy season from May through December (Janzen 1988). Male long-tailed manakins display activity peaks from March through June, which coincides with the nesting season (Foster 1976, 1977b; McDonald 1989a, b, 1993b).

We began each field season by identifying pairs of alpha and beta males and the display areas they occupied. Within long-tailed manakins, each lek consists of a group of 3-13 males that form a linear dominance hierarchy, the most of dominant of whom are the alpha and beta male (McDonald 1989b). We identified individual leks by the presence of a unique alpha and beta male pair displaying for visiting females. We identified display areas as spatially distinct regions consisting of concentrated male lekking activity, usually encompassing one to four display perches. Display perches are low-hanging (~1.5m) horizontal vines or branches on which males display (McDonald 1989b). The display areas usually contained one or two primary dance perches where the dominant males displayed for females, and one or two secondary perches that were in close proximity to the primary perch and were mainly used for practicing subordinate males and rarely, if ever, had female visitations. We located and monitored 21 leks in 2010 and 39 leks in 2011 (19 leks were monitored in both years).

Once we identified leks, we captured long-tailed manakins using mist nets. We have captured and processed over 675 individuals since 2003. Due to the longevity of the species, some of the individuals we captured in 2004 were still present in the population during the 2010 and 2011 field seasons. We captured 88 individuals (40 females and 48 males) in 2010, and 109 individuals (59 females and 50 males) in 2011, many of which were previously unmarked. We fit all newly captured individuals with a uniquely numbered aluminium band and a unique combination of three plastic coloured leg bands for individual recognition during field observations.

We collected video data and conducted behavioural observations in the field to quantify activity at leks. We collected and analyzed 845.56 hours of video data over the 2010-2011 field seasons. In 2010 and 2011 from April to mid-June we recorded 236 videos (14.09 ± 0.91 hours per lek) between 0500 and 1100 (CST) (videos were 3.67 ± 0.07 hours long). In 2011, we supplemented video recordings with 2-hour behavioural observations in the field. Female visitation is highest in the morning (0630 to 0930) and decreases as the day progresses in our population (Maynard 2011). Therefore, our video recordings should adequately capture the period with the highest female visitation. From our video data, we quantified and timed male vocalizations, courtship display behaviours, aggressive interactions, and copulations, as well as female visitations and behaviour during courtship (details below). During behavioural observations in the field, we recorded the same activities as the videos with the exception of female behaviour during courtship. To better elucidate the factors contributing to the copulation success of the alpha-beta male pair of a lek, we analyzed the relationships for the final three objectives at two levels: between leks and between dance bouts.

Male advertisement

To identify whether male advertisement and lek attendance are associated with female visitation and copulation, we quantified seven variables previously found to influence female visitation in a different population (McDonald 1989b). *Toledo* calls are duets usually performed by a pair of alpha and beta males; they are the main advertisement call of long-tailed manakins (Trainer and McDonald 1993). We quantified *toledo* rate as the number of *toledo* calls per minute excluding time spent dancing for females, and *toledo* bout rate as the number of bouts of sequential *toledo* calls separated by at least 30 seconds of silence divided by the sampling period in minutes. *Teeamoo* calls are usually given by the alpha male to entice the beta male to join him in a bout of *toledo* duets (Trainer and McDonald 1993). Following previous work (McDonald 1989b), we also quantified the proportion of time spent practice dancing (dancing in the absence of a female), and the proportion of time with 1, 2, and ≥3 males dancing. Since our seven measures of male advertisement and lek attendance were highly correlated, we used a principal components analysis (PCA) with factor rotation to reduce these measures to two factors (those with Eigenvalues greater than 1.0), which together explained 75.80 % of the variation (Table 2.1A). PC1 explained variation in male advertisement and lek attendance and PC2 explained variation in practice dancing (Table 2.1A).

Male-male cooperative displays

We used five main variables to examine whether specific components of cooperative dual-male displays predict copulation success: the length of the dance bout, the proportion of a dance bout spent in butterfly flights versus popcorn dancing, the proportion of a popcorn dance spent engaged in more complex/coordinated leapfrogging versus hopping, the average length of solo butterfly flights, and the average length of dual-male butterfly flights that were sandwiched between popcorn dances. Since our five measures of male-male cooperative displays were highly correlated among leks, we used a PCA to reduce these measures to two rotated factors (those with Eigenvalues greater than 1.0), which together explained 77.06 % of the variation in cooperative display (Table 2.1B). PC1 explained variation in dual-male dancing, and PC2 explained variation in butterfly dancing (Table 2.1B). Since these same measures of cooperative dual-male display were highly correlated among dance bouts, we used a PCA to reduce these measures to two factors (those with Eigenvalues greater than 1.0), which together explained 74.16 % of the variation in cooperative display and loaded the same as in the previous analyses (Table 2.1C).

Male-male aggression

To examine whether male-male aggression influenced copulation success, we quantified three variables of male-male conflict that occur on or near the display perch during dances for females: chases, supplants, and *chitter* vocalizations. Supplants occur when one male flies towards a second perched male, causing the perched male to re-locate while the first male occupies the second male's former position (Hinde 1952; Dixon 1965). Chases occur when one male pursues another in flight, and is usually accompanied by the open beak of the pursuing male and/or *chitter* vocalizations (person. observ.) *Chitter* vocalizations are believed to signal submissiveness in an aggressive interaction between individuals (Trainer and McDonald 1993). Due to the low incidence of male-male aggressive behaviours, we combined all chases, supplants, and *chitters* into one measure of conflict. We calculated conflict rate as the total number of aggressive incidents divided by the sampling period.

Female courtship responsiveness

Female long-tailed manakins sometimes perform stereotyped behaviours on the display perch as male courtship displays proceed, and these behaviours have been proposed to signal female interest in copulation (McDonald 1989b). We quantified three measures of female responsiveness to male courtship behaviour: shuffles, jumps, and perch changes. Shuffles are rapid, low, side-to-side hops; jumps are vertical hops where females bring their wings straight up and above their backs; and perch changes are rapid flights to and from perches near the dance perch (McDonald 1989b). In the following analyses, we refer to this group of female behaviours as female courtship responsiveness. At the level of the lek, the three measures of female courtship responsiveness were poorly correlated (shuffle and jump rate: $r_s=0.67$, $P<0.0001$; other correlations: $r_s\leq0.20$, $P\geq0.26$) and could not be adequately summarized using PCA (explained only 52.83 % of variation in the data). We therefore used separate analyses for each measure of female courtship responsiveness. At the level of the dance bout, the PCA was also inadequate for summarizing the variation in the data because outliers greatly influenced the factor loadings. Therefore, we analyzed our three measures of female courtship responsiveness separately at the level of the dance bout.

Statistical analyses

We tested the influence of male-male coordinated and aggressive behaviours and female courtship responsiveness on copulation success, as well as the influence of male coordinated and aggressive behaviours on female courtship responsiveness at two levels: between unique alpha-beta male pairs at each lek (analyses across leks based on mean data at each lek), and between unique dance bouts (analyses across individual dance bouts). For analyses comparing between leks, we separated our tests by year. For analyses comparing between dance bouts, we used lek identity as a random effect in our models. We used standard transformations to normalize data where possible, and used non-parametric tests when data could not be normalized. We used Spearman's rank correlations to evaluate nonparametric linear regressions and normal logistic regressions to evaluate variables predicting copulation success between leks (JMP 9.0.2). We used generalized linear mixed models to evaluate copulation success (binary logistic response variable) between dance bouts (IBM SPSS Statistics version 20.0.0).

Results

In 2010, 3 of the 21 leks (14.3%) accounted for all recorded copulations. In 2011, 7 of the 39 leks (17.9%) accounted for all recorded copulations. Between leks, female visitation rate and copulation rate were positively correlated in both 2010 (r_s=0.56, n=21 P=0.008) and 2011 (r_s=0.48, n=39, P=0.002).

The influence of male advertisement and lek attendance on female visitation and copulation

We tested the relationship between male advertisement and lek attendance, summarized by two principal components, and female visitation and copulation rates. Between leks, there was a significant positive correlation between female visitation rate and the factor summarizing variation in male advertisement and lek attendance (PC1; Table 2.1A), both in 2010 (r_s=0.77, n=21, P<0.0001) and 2011 (r_s=0.74, n=39, P<0.0001). Similarly, the factor summarizing variation in male advertisement and lek attendance was positively correlated with copulation rate in 2010 (r_s=0.50, n=21, P=0.02) and in 2011 (r_s=0.49, n=39, P=0.002). There was no relationship between the factor summarizing variation in male practice dancing (PC2; Table 2.1A) and female visitation rate in 2010 (r_s=0.05, n=21, P=0.82) or in 2011 (r_s=0.09, n=39, P=0.57). Likewise, there was no relationship between the factor summarizing variation in male practice dancing and copulation rate in 2010 (r_s=0.001, n=21, P=0.99) or in 2011 (r_s=0.04, n=39, P=0.79).

The influence of male-male cooperative displays on copulation success

We tested the influence of male-male cooperative displays, summarized by two principal components, on copulation success. Across leks, the factor summarizing variation in butterfly dancing (PC1; Table 2.1B) positively predicted copulation success in 2011 (Whole model: χ^2=8.18, n=22, P=0.02; butterfly dancing: χ^2=4.56, n=22, P=0.03), and the marginally significant relationship had the same direction in 2010 (Whole model: χ^2=5.30, n=12, P=0.07; butterfly dancing: χ^2=5.11, n=12, P=0.02; Figure 2.1A). There was a marginally significant relationship for the factor summarizing variation in dual-male dancing (PC2; Table 2.1B) to positively predict copulation success in 2011 (Whole model: χ^2=8.18, n=22, P=0.02; dual-male dancing: χ^2=3.36, n=22, P=0.07); however, the factor summarizing variation in dual-male dancing did not predict copulation success in 2010 (Whole model: $\chi^2=5.30$, n=12, P=0.07; dual-male dancing: $\chi^2=0.0001$, n=12, P=0.99; Figure 2.1B).

Across dance bouts, the factor summarizing variation in butterfly dancing (PC2; Table 2.1C) positively predicted copulation success (Wald $\chi^2=6.53$, n=148, P=0.01). However, the factor summarizing variation in dual-male dancing (PC1; Table 2.1C) did not predict copulation success between dance bouts (Wald $\chi^2=0.31$, n=148, P=0.58).

The influence of male-male conflict on copulation success

We quantified aggressive interactions between the alpha and the beta male, or between the alpha or beta male and a subordinate male, during dances for females. At the level of the lek, conflict rate did not predict copulation success in 2010 ($\chi^2=1.61$, n=12, P=0.20) or in 2011 ($\chi^2=0.83$, n=22, P=0.36). At the level of the dance bout, conflict rate did not predict copulation success between dance bouts ($\chi^2=0.48$, n=148, P=0.49).

Male-male cooperative display, female behaviour during courtship, and copulation success

We tested the influence of female behaviour during courtship on copulation success. The female behaviours during courtship included jump rate, shuffle rate, and perch change rate. There was a marginally significant relationship for shuffle rate to positively predict copulation success in 2011 ($\chi^2=3.64$, n=22, P=0.06), but not in 2010 ($\chi^2=0.15$, n=12, P=0.70; Figure 2.2A). Perch change rate negatively predicted copulation success in 2010 ($\chi^2=6.95$, n=12, P=0.008), but not in 2011 ($\chi^2=0.18$, n=22, P=0.68; Figure 2.2B). Jump rate did not predict copulation success in 2010 ($\chi^2=0.27$, n=12, P=0.60) or in 2011 ($\chi^2=0.10$, n=22, P=0.75).

Shuffle rate and jump rate positively predicted copulation success between dance bouts (shuffle rate: Wald $\chi^2=23.64$, n=148, $P<0.0001$; jump rate: Wald $\chi^2=11.16$, n=148, P=0.001).

Perch change rate did not predict copulation success between dance bouts (Wald χ^2=0.039, n=148, P=0.84).

Although it is difficult to infer cause and effect from correlational tests, we were interested in whether males modified their displays in response to female behaviour during courtship. We found that between dance bouts, female jump rate and shuffle rate was positively associated with the factor summarizing variation in male butterfly dancing (jump rate: $F_{1,143}$=4.28, P=0.04; shuffle rate: $F_{1,142}$=24.13, P<0.0001; perch change rate: $F_{1,143}$=-0.32, P=0.75), and female jump rate was also positively associated with the factor summarizing variation in dual-male dancing (jump rate: $F_{1,142}$=6.31, P=0.01, perch change rate: $F_{1,134}$=2.73, P=0.10; shuffle rate: $F_{1,144}$=1.71, P=0.19). We also found that male courtship displays were longer when females had higher jump rates (jump rate: $F_{1,145}$=7.09, P=0.009; shuffle rate: $F_{1,146}$=1.15, P=0.29; perch change rate: $F_{1,138}$=1.90, P=0.17).

Discussion

In this study, we examined the influence of male advertisement and lek attendance, male-male cooperative display, and male-male aggression on copulation success in a lekking species with cooperative dual-male displays. We found that male advertisement and lek attendance strongly predicted female visitation rates and copulation rates. Likewise, we found that some components of male cooperative and solo displays (butterfly proportion and solo butterfly dance) predicted copulation success both between leks and between individual dance bouts. Our findings suggest that females choose among leks and among courtship displays, which may place additional selection pressures on the evolution of male-male cooperative displays. We found no evidence that male-male aggression at leks influenced copulation success, suggesting that the influence of females on male social organization might be driven by the benefits of cooperation rather than the costs of aggression. We also investigated whether female behaviours during courtship could signal their interest in mating with the displaying males, and found strong evidence that female behaviours predicted copulation success. In addition, we investigated whether males change their displays in response to female behaviours to increase their reproductive success, and found a positive association between dance duration and display quality, and female behaviours during courtship displays. Taken together, our findings suggest that females have an important influence on male-male interactions, and that despite their lack of conspicuous displays females in lek-mating species can play an active role in courtship.

Female long-tailed manakins preferentially visited and copulated with males exhibiting high advertisement rates and lek attendance. Lek attendance, display rate, and vocal output have been previously shown to influence male mating success in lek mating systems (Höglund and Alatalo 1995; Mackenzie et al. 1995; Fiske et al. 1998; Lanctot et al. 1998; Friedl and Klump 2005), including manakins (McDonald 1989b; Stein and Uy 2006; Durães 2008). It could be argued that females are passively attracted to longer and more frequent displays because these are more conspicuous (Parker 1983; Gibson 1996). However, females could also choose among males based on display rate if it honestly signals male quality. High levels of male advertisement and lek attendance are likely to be energetically costly; males that invest time in advertising trade off with self-maintenance activities such as foraging and grooming, and increase their risk of predation, suggesting that only males in good condition can effectively compete between leks (Vehrencamp et al. 1989; Andersson 1994a; Stoddard and Salazar 2011). In long-tailed manakins, for example, males with high advertisement rates produce up to 5000 *toledo* duets per day (Foster 1977). Moreover, several studies have shown that lekking males tend to lose weight or decrease in body condition over the breeding season (e.g. Vehrencamp et al. 1989; McDonald 1989a; Andersson 1994a), further attesting to the cost of male advertisement and display. Since males provide no resources to females in lekking species, the only direct benefit to be gained by females is avoidance of parasites or sexually transmitted diseases (Loehle 1997). As such, female choosiness is thought to evolve via selection for indirect fitness benefits (Bradbury and Gibson 1983; Kodric-Brown and Brown 1984; Sæther et al. 2005). Females could be choosing males with high display rates because display rate reveals some heritable aspect of male quality (Andersson 1994b; Kotiaho et al. 2001; Neff and Pitcher 2005). A non-mutually exclusive possibility is that females benefit from mating with males with high display rates because their sons will also produce these attractive displays (i.e., sexy sons; Weatherhead and Robertson 1979; Kokko et al. 2002). Although our measure of male advertisement and lek attendance included aspects that required both solo and dual-male participation, male advertisement is thought to be positively influenced by multiple male participation. For example, in the wire-tailed manakin (*Pipra filicauda*), display rates increase when males increase the percentage of their displays that are cooperative, which ultimately increases their relative reproductive success (Ryder 2008). In this and other species, it is thought that females base their choice of male on display quality or frequency, independent of whether the display is cooperative (McDonald 1989a; Mackenzie et al. 1995; Fiske et al. 1998; Durães 2008; Ryder et al. 2009, 2011). Thus males may cooperate to increase their attractiveness and mating opportunities, while females are still assessing honest signals of quality.

In mating systems with complex cooperative displays, one might expect females to show preference for specific components of the cooperative display. Our study provides mixed evidence of female preference for cooperative displays. Previous work has shown that female long-tailed manakins are attracted to more highly synchronized *toledo* duets (Trainer and McDonald 1995) and to courtship displays with longer dual-male butterfly flights (McDonald 1989b). In our study, however, our measure of butterfly dancing (solo butterfly length and butterfly proportion) was a better predictor of copulation success than dual-male dancing (dual-male butterfly length, leapfrog proportion, and bout length). Although both measures incorporate some component of cooperative display, it is interesting to note that solo and dual-male butterfly length loaded onto different axes, and that butterfly flights seemed more important than popcorns and leapfrogs. We have also observed females copulate after observing only a bout of solo butterfly display by the alpha male. While it is possible that these females had previously observed the complete dual-male sequence of displays, our observations suggest that within a bout, the solo butterfly display alone is sufficient to incite females to copulate. It has been argued that by preferring solo butterfly flights, females may be demonstrating a preference for stable dominance hierarchies, since during butterfly flights females are left unattended on the display perch and beta males have more opportunity and are more likely to attempt copulations (McDonald 1989b). Butterfly flights are also thought to be labour-intensive therefore energetically costly manoeuvre, which the alpha male must complete after having already performed all other components of the display, including mate attraction duets, popcorn and leapfrog jumps, and dual-male butterfly flights. Three other cooperatively displaying *Chiroxiphia* manakins (*C. caudata, C. pareola, C. lanceolata*) that have dual-male displays, sometimes have exclusively solo courtship displays that culminate in copulation (Snow 1963a; Foster 1981; McDonald 1989a; DuVal 2007), which suggests that preference for this type of display may be conserved among closely related species. Within manakins, many courtship manoeuvres are homologous (Prum 1990). There is little precedence for comparing the elements of display that support cooperation because there are so few species that employ cooperative display. Nonetheless, by evaluating behaviours and their relationship to female preference and reproductive success between related species, we can gain greater insight into their fitness consequences and evolution.

Male intrasexual competition and dominance are thought to shape the clustered male dispersion pattern characteristic of lek mating systems, and control female access to males (Beehler and Foster 1988). In classical leks, patterns of male-male aggression appear to have an important influence on female mate choice (Foster 1983; Beehler and Foster 1988). For example, in Guianan cock-of-the-rock (*Rupicola rupicola*) and golden-headed manakins (*Pipra erythrocephala*), females avoid the display territories of subordinate males, which are subject to frequent trespassing by neighbours and copulation disruptions, leading to increased reproductive success among dominant males (Lill 1976; Trail 1985; Trail and Koutnik 1986). In cooperative exploded-lek mating systems, most male intrasexual interactions occur in the absence of females and ultimately lead to the formation of stable dominance hierarchies (McDonald 1989a). We therefore expected to find a negative influence of male-male conflict on copulation success in long-tailed manakins (Borgia 1979). In a closely-related congener, the blue manakin (*C. caudata*), disruptions by other males appeared to reduce the likelihood that a display would lead to copulation, and females often left after disruption events (Foster 1981). Contrary to our expectations, however, male-male conflict did not affect reproductive success among leks, and females did not display an aversion to conflict during particular display bouts. Perhaps disruption levels in long-tailed manakins were too low to have an important influence on female mate choice (0.008 ± 0.05 conflicts/min). Alternatively, disruption levels may have been higher at higher quality leks. In 2011, there was a positive relationship between conflict rate and both butterfly dancing and dual-male dancing (whole model $F_{2,19}=4.33$ $P=0.03$; butterfly dancing: $t=2.04$, $p = 0.05$; dual-male dancing $t=2.07$, $P=0.05$). Possibly, higher quality leks that attract more females are more popular among affiliate males, leading to a higher number of attending males and a coincidentally higher number of disruptions (Fiske et al. 1998). Males higher up in the dominance hierarchy might also have greater motivation to test the dominance of the alpha and beta, since earlier ascension in status would be most beneficial at highly successful leks. In this situation, females may tolerate higher levels of disruption to mate with males that have more attractive displays, as also shown in blue manakins (Foster 1981). Further research is needed to understand the direct influence of females on male-male aggressive interactions.

In lek-mating species or other species with elaborate courtship displays, females are often portrayed as passive observers of male displays. As courtship display progresses in long-tailed manakins, females perform vertical jumps, side-to-side shuffles, and perch changes. We were interested in determining whether these behaviours might be associated with a female's likelihood of copulating with the displaying males. We found that female behaviour during courtship predicted copulation success among leks and between dance bouts. Our findings suggest that female behaviour during courtship can be interpreted as a measure of female courtship responsiveness. It is possible that these behaviours are simply a by-product of female excitement during courtship displays, but such behaviours could also serve as important signals to displaying males. Males invest considerable energy in attracting females, especially in lekking systems where male courtship displays and male-male competition exclusively determine their mating success (Höglund and Alatalo 1995). In these systems, it would be advantageous for males to invest more in courtship displays that were more likely to result in copulations. Males should not prolong courtship displays for females who are unresponsive because displays are energetically costly, increase predation risk, and may deter other receptive females (Balsby and Dabelsteen 2002). There is evidence that males invest more in receptive females than non-receptive females, because receptive females are more likely to accept copulations and those copulations are more likely to be successful (Preston et al. 2003; Mysterud et al. 2008). In long-tailed manakins, male displays were longer when females exhibited more jumping behaviour during courtship. Likewise, male guppies (*Poecilia reticulata*) increase their level of courtship and male-male competition when females showed receptive behaviour (Guevara-Fiore et al. 2010).

Female courtship responsiveness may also signal interest in specific elements of male courtship displays. Males often modify their courtship behaviour in response to female preference (King and West 1983; Balsby and Dabelsteen 2002; Patricelli et al. 2006;). In satin bowerbirds, for example, males modulate their display intensity in response to female behaviours to avoid startling females (Patricelli et al. 2006), and more successful males are better at modulating their displays in response to females (Patricelli et al. 2002). In long-tailed manakins, dual-male and butterfly dances increased in duration and quality when females exhibited more jumping and shuffle behaviour during courtship. However, it is impossible to determine whether males adjusted their courtship behaviour in response to females, or whether females became more excited by specific components of the male displays. Elucidating the relationship between female courtship responsiveness, male courtship behaviours, and female receptivity is often difficult and requires an experimental approach to better understand cause and effect. Studies modifying female courtship responsiveness using robotic females, playback, or artificially tutored individuals present a promising approach to future studies on this topic (King and West 1983; Balsby and Dabelsteen 2002; Patricelli et al. 2006).

In this study, we showed that high male advertisement and lek attendance predicted female visitation and copulation rates. Such high levels of male investment in display are likely costly and may honestly signal a component of male quality that can be assessed from a distance. By preferring males with high display rates, females may also be promoting male-male cooperation, because dual-male cooperative interactions tend to increase display rates. Females also appeared to prefer the butterfly flight component of displays, which may signal male quality during courtship displays, and strengthen dominance relationships within leks. Preference for solo butterfly displays is also found in closely related species. Therefore, assessing female preference for specific display components may lead to a better understanding the evolution of cooperative displays. Contrary to our expectations, there was no influence of male-male conflict on copulation success. However, conflict rates were higher during higher quality displays, which may be a product of increased activity and subordinate male attendance at higher quality leks. Female behaviours on the dance perch predicted their likelihood of copulating, and also predicted the quality of courtship displays. Therefore, males may be modifying their displays in response to female activities, although further studies are required to elucidate the cause and effect of these relationships. That females may signal their preference for displays with behaviours other than copulation remains understudied, but represents an important area for future research as it may shed some light on the evolution of courtship displays, especially if males recognize female signals and respond accordingly. Our findings suggest that the relationship between male interactions and female preference may have an important influence on the evolution of complex mating systems.

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Table 2.1. Summary of principal components analyses of male advertisement and display effort by lek (A), and male-male cooperative displays by lek (B) and by dance bout (C) in long-tailed manakins (*Chiroxiphia linearis*). All principal components used Maximum Likelihood factoring with a Varimax rotation to facilitate interpretation of the main factors.

Principal component and interpretation	Eigenvalues	Percent variance explained	Rotated factor loadings
A) Male advertisement and display effort by lek			
1 - Male advertisement	3.87	55.28	0.99 - *toledo* rate 0.73 - *teeamoo* rate 0.66 - *toledo* bout rate 0.54 - Time with 1 male dancing* 0.53 - Time with 2 males dancing*
2 - Male practice dancing	1.44	20.52	0.96 - Time practice dancing* 0.78 - Time with ≥3 males dancing*
B) Male-male cooperative displays by lek			
1 - Dual-male dancing	2.47	49.4	0.80 - dual-male butterfly length 0.77 - leapfrog proportion 0.73 - bout length
2 - Butterfly dancing	1.38	27.66	0.87 - solo butterfly length 0.65 - butterfly proportion
C) Male-male cooperative displays by dance bout			
1 – Dual-male dancing	2.04	40.85	0.77 - bout length 0.73 - dual-male butterfly length 0.69 - leapfrog proportion
2 - Butterfly dancing	1.67	33.31	0.86 - solo butterfly length 0.63 - butterfly proportion

* Proportion of the entire dance period

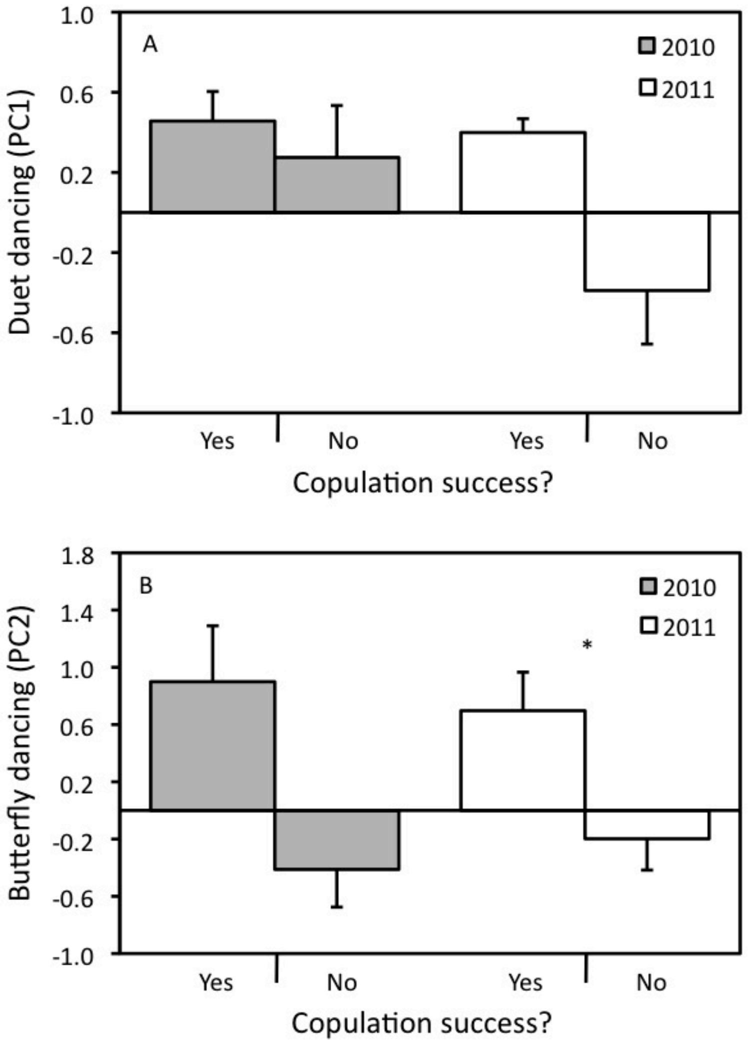

Figure 2.1. Measures of male-male cooperative display, (A) dual-male dancing and (B) butterfly dancing, in relation to copulation success in long-tailed manakins. Bars denote means, and error bars denote standard errors. Asterisks indicate significance at the 0.05 level.

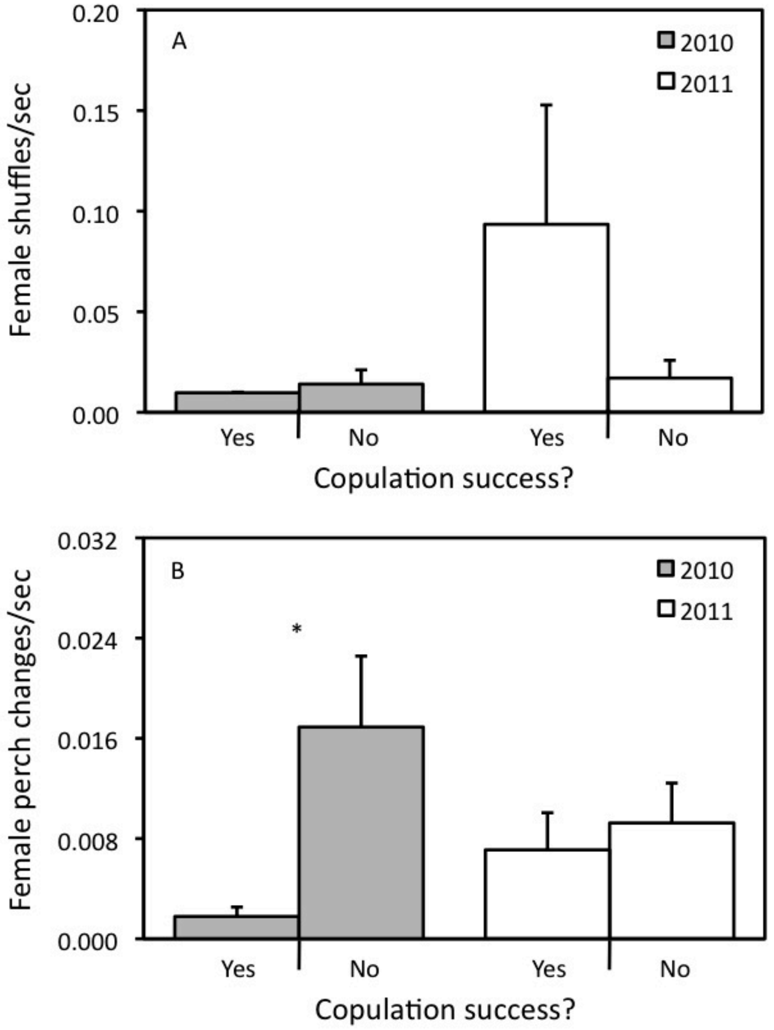

Figure 2.2. Female activity during courtship, measured as (A) shuffle rates (B) and perch change rates in relation to courtship success in long-tailed manakins. Bars denote means, and error bars denote standard errors. Asterisks indicate significance at the 0.05 level.

Chapter 3: Complex female mate searching strategies in Long-tailed Manakins (*Chiroxiphia linearis*) revealed by a novel tracking system

This chapter is the product of collaborative research, and is co-authored by S.M. Doucet, D.F. Maynard, D.J. Mennill, and J.M. Burt

Chapter Summary

Several theoretical mate search models have been developed to explain the strategies that females use to find a high quality mate. These search strategies include two main decision rules: the comparison tactic, where females compare the quality of males to that of others encountered in their search, and the threshold tactic, where females compare the quality of males to an internal standard of quality. The objective of our study was to determine the decision rules and mate choice strategies employed by female long-tailed manakins when choosing among potential mates. Long-tailed manakins have an exploded-lek mating system, where males perform complex cooperative displays for females, and females visit leks solely for the purpose of choosing a mate. We used a novel passive digital radiotracking system (Encounternet) to monitor female search sequences. We tracked the movements of 82 radiotagged females across 38 leks over a two-year period. Females visited multiple males, and visited multiple males more than once. These results are consistent with females employing a comparison decision rule, and a Bayesian updating system of a “comparative Bayes” or “random-walk” search strategy. Female visitation was positively associated with male advertisement and lek attendance, and revisits to leks was positively associated with the coordinated dancing behaviour of males, suggesting that females reduce the pool of potential males through rounds of comparison of difference male traits. Older females tended to revisit high quality males that were more similar in quality than younger females, suggesting that older females are more discriminating than younger females. Taken together our study suggests that females are able to identify high quality males based on elaborate multimodal courtship displays, using complex searching strategies.

Introduction

Mate choice is a complex process that involves searching, information gathering and processing, decision-making, and mating behaviour (Parker 1978; Janetos 1980; Real 1990; Bateson and Healy 2005). Since mate choice was first proposed as a mechanism of sexual selection (Darwin 1871), most observational and experimental studies have focused on the advantages of mate choice, such as the acquisition of resources and genetic benefits (Trivers 1972; Hamilton and Zuk 1982; Bateson 1983; Gwynne 1988; Andersson 1994; Kirkpatrick 1987). In recent decades, researchers have proposed that the benefits of mate choice could be influenced by the costs of the information-gathering and decision-making processes, such as time, energy, and risk of predation (Parker 1978, 1983; Janetos 1980; Real 1990; Reynolds and Gross 1990). This novel perspective spurred the development of theoretical models exploring how mate sampling strategies could be employed to minimize search costs, and to empirical testing of those models (Parker 1978, 1983; Janetos 1980; Real 1990; Widemo and Sæther 1999).

Several models have been proposed to explain female mate searching strategies. The "random mating" model stipulates that females will encounter males randomly, will not discriminate among males, and will mate with the first male encountered (Janetos 1980). The "best-of-*n*" model stipulates that females sample a fixed number of males or search for a fixed duration of time, and using complete recall, return to mate with the highest quality individual (Janetos 1980; dubbed "pooled comparison" by Wittenberger 1983; Real 1990). The "fixed-threshold" model stipulates that females have an internal standard for the quality of their desired mate, and will mate with the first male that meets or surpasses that standard (Janetos 1980; Wittenberger 1983). The "one-step decision" and the "sequential-comparison" models are modifications of the "fixed-threshold" model, with the addition of an adjustable threshold

(Janetos 1980, Real 1990). All of these models assume that females receive a perfect understanding of male quality during first visits to males (Janetos 1980; Wittenberger 1983; Real 1990). Counter to this assumption, Wittenberger (1983) proposed a priority decision-making system where different male characters are compared in each round of comparison (Wittenberger 1983). Recent empirical studies have shown that females repeatedly visit multiple males (e.g. Dale et al. 1992; Mazalov et al. 1996; Uy et al. 2001), suggesting that females may indeed make multiple visits to assess male quality. Two new models address this possibility. The "comparative Bayes" model, which is a modification of the "best-of-*n*" model, stipulates that during initial male assessments, females receive imperfect information about the quality of the males, and maintain an estimated quality level for the males visited. A select subset of the males are revisited and the information is used to update the males' estimated quality levels (Luttbeg 1996). The final and most recently proposed model, the "random-walk" model, is similar to the "comparative Bayes" model, but with the addition of a threshold. Females receive imperfect information about male quality with each visit, and revisit males until the accumulated quality surpasses a threshold (Castellano and Cermelli 2011).

Female mate searching models are based on two main decision rules. Females decide to accept or reject a potential mate based on a comparison of their quality to an internal standard of quality (threshold tactic), or to other males encountered in their search (comparison tactic) (Janetos 1980; Real 1990). These decision rules and their variants form the basis for all current mate choice strategy models (Brown 1981; Real 1990; Dombrovsky and Perrin 1994). Aside from these primary decision rules, females can choose to visit potential mates only once, or re-sample them. Identifying the decision rules employed by females of a particular species, and ultimately characterizing their search strategy, is often difficult. Researchers have proposed testable criteria to distinguish between these decision rules (examples in Table 3.1). However, even with these criteria, identifying search strategies remains challenging, particularly among wild animals because; females may exhibit cryptic behaviour, they may move over great distances, and they may make their decisions over long periods so that direct observations is difficult or impossible.

Most studies report intraspecific variation in female mate searching strategies (Bensch and Hasselquist 1992; Dale and Slagsvold 1996; Uy et al. 2001). Differential costs accrued by females may represent an important source of intraspecific variation in search strategy. For example, some females may be faced with competition from other females, poor body condition, or high parasite load (e.g. Dale et al. 1992, Höglund and Alatalo 1995; Cotton et al. 2006; Hedrick and Kortet 2012). Females experiencing these costs may reduce their time spent searching, the number of males they sample, and the quality of the males chosen (Smith-Trail 1980; Real 1990; Dale et al. 1992; López 1999). Previous mating experience represents another source of intraspecific variation in search strategy. Experience comes with age, and more experienced females may alter their strategy to reduce search costs. For example, older females may sample fewer males and show mate fidelity between years (McDonald 1989b; Rintamäki et al. 1995; Uy et al. 2001). Understanding variation in female mate searching strategies has important implications on both the mate choice process and its influence on the evolution of sexually selected male traits (Bakker and Pomiankowski 1995; Höglund and Alatalo 1995; Pomiankowski and Møller 1995; Jennions and Petrie 1997; Bakker et al. 1999).

Empirical studies of female mate choice strategies are often lab-based, allowing researchers to control most variables and thereby facilitate the assessment of a few key criteria to distinguish between different models (e.g. Downhower and Lank 1994; Moore and Moore 1994). For example, controlled chirp rates were presented to female field crickets (*Gryllus lineaticeps*) in specific sequences, which allowed the researchers to determine that they employ a threshold decision rule (Beckers and Wagner 2011). Yet lab-based studies have limitations. Research has shown that search costs influence female choosiness, thereby causing females to adopt whichever search strategy optimizes their fitness return (Real 1990; Reynolds and Gross 1990; e.g. Dale et al. 1992). The absence of costs in many lab-based studies may impact female search strategies (reviewed in Campbell et al. 2009). Lab-based studies may be further limited in their application to wild populations because; domesticated animals may not be representative of their wild counterparts, stressful environments may alter normal behaviours, and the lack of interaction between subject and stimuli in female mate choice studies often make it difficult to interpret motivation (Campbell et al. 2009). Some manipulative experiments have also been performed in the field. For example, researchers have manipulated the release of females into a wild breeding population, which is advantageous because individual females can be closely monitored as they are released one at a time (e.g. Dale et al. 1992; Forsgren 1997; Fagundes et al. 2007).

Some species are logistically challenging or impossible to study in a laboratory setting, particularly if they exhibit complex mate searching strategies, or if courtship behaviour is highly elaborate or requires environmental situations that cannot be mimicked in captivity. Although field studies are disadvantaged by uncontrollable external variables and confounding factors, they provide invaluable information on the mate choice process in wild animals (reviewed in Campbell et al. 2009). Observational studies of wild populations are uncommon, and often involve lekking species (e.g. Trail and Adams 1989; Reynolds and Gross 1990; Petrie et al. 1991; Gibson 1996; but see Reid and Stamps 1997; Fagundes et al. 2007; Lovari et al. 2008). In traditionally lekking species that mate in the open, females can be easily monitored as they move within and between leks (e.g. Gibson and Bachman 1992). Limitations of studying mate choice strategies of lekking species include the difficulty monitoring female movement within leks when males are tightly clustered or when males display in very densely vegetated environments, the time available to monitor leks for female activity, and potential confounding effects such as mate copying (Borgia 1979; Gibson and Höglund 1992; Höglund and Alatalo 1995).

So few studies on female mate searching strategies have been conducted on wild populations that it is difficult to identify the conditions that promote different mate searching strategies in different species (Uy et al. 2001; Kokko and Wong 2007). Nevertheless, it has been proposed that lek mating systems should promote the evolution of a typical, optimal female mate searching strategy (Wiley 1991). There is evidence that lekking species include some aspect of the comparison decision rule in their mate searching strategies (e.g. Trail and Adams 1989; Petrie et al. 1991; Rintamäki et al. 1995; Gibson 1996; Uy et al. 2001). Female mate searching strategies that contain some aspect of the comparison decision rule, such as the best-of-*n* model, the comparative Bayes model, and the random-walk model, are thought to be advantageous in lek mating systems because these systems tend to have low female mate searching costs, elaborate multimodal male courtship displays, and predictably located male display areas (Trail and Adams 1989; Bensch and Hasselquist 1992; Fiske and Kålås 1994; Rintamäki et al. 1995; Luttbeg 1996, 2002; Castellano and Cermelli 2011). Further research is required to better elucidate how mating systems influence female decision rules, and which factors promote variation among females in their mate searching behaviour.

Our study provides the first assessment of female mate searching strategies in long-tailed manakins (*Chiroxiphia linearis*). Long-tailed manakins have a cooperative exploded-lek mating system (Prum 1994), where groups of males cluster within a small display area, and are thought to form an age-graded linear dominance hierarchy through social interactions (Foster 1977; McDonald 1989b, 2007). Only the two most dominant males at each lek, the alpha and beta males, display for visiting females. Complex, cooperative courtship displays performed by the alpha and beta include male-male mate attraction duets and cooperative dances involving backward leapfrog flights and slow, laboured butterfly flights (Foster 1977; McDonald 1989b). Previous studies have shown that male advertisement and lek attendance predict female visitation rates and copulation rates, and that butterfly flights and leapfrog displays predict copulation success (McDonald 1989b; Chapter 2). In addition, female visitation and copulation rates are highly correlated, such that female visitation provides a good indicator of female choice (McDonald 1989b; Chapter 2).

Long-tailed manakins provide a compelling system for field studies of female mate searching strategies for a number of reasons: (1) alpha and beta male pairs display in the same location within and between breeding seasons (McDonald 1989a); (2) the quality of male pairs can be quantified using field observations and video and audio recordings (Chapter 2); (3) females choose their mates from among the dominant alpha males at leks that are spatially separated, thereby preventing the simultaneous assessment of neighbouring male courtship displays; (4) females are choosy, often leaving a display area after having watched entire courtship displays (McDonald 1989b); and (5) females have free choice and can leave at any time during male courtship displays, including after an attempted mounting (McDonald 1989b). Despite these advantages, mate-searching behaviour is poorly understood in this species because females are cryptic in appearance and behaviour, and their home ranges are so large that it is difficult to track the behaviour of individual females (McDonald 1989b; person. observ.). To overcome these challenges, we implemented a novel passive digital radiotracking system to monitor female mate searching strategies in long-tailed manakins (Mennill et al. 2012). Our objectives are to characterize the decision rules and ultimately the mate-searching strategies used by females, and to examine whether age, condition, or parasite load promote variation in female mate-searching strategies.

Methods

We studied a large population of long-tailed manakins in Sector Santa Rosa of the Guanacaste Conservation Area, a UNESCO World Heritage Site in northwestern Costa Rica (10°40′N, 85°30′W). In 2010 and 2011, we studied manakins from March to June, which coincides with peak male display activity and female nesting behaviour (Foster 1976, 1977; Janzen 1988; McDonald 1989a, b).

At the beginning of each field season, we identified pairs of alpha and beta males and the display areas they occupied. We classified leks as a unique alpha and beta male pair displaying for visiting females within a small spatially distinct display area (each separated by 95.74 ± 5.64 m), consisting of one to four display perches (all within 35.58 ± 3.63 m). Usually, the alpha and beta male use one or two primary display perches when they are dancing for visiting females, while practicing subordinate males use secondary perches. We located and monitored 21 leks in 2010 and 39 leks in 2011; 19 leks were monitored both years.

Once we located and identified leks, we captured individuals using mist nets. We captured 88 individuals (40 females and 48 males) in 2010, and 109 individuals (59 females and 50 males) in 2011, complementing the 480 individuals that we have banded between 2003 and 2009 in the course of our long-term studies. We gave all individuals a uniquely numbered aluminium band and a unique combination of three plastic coloured leg bands for identification in the field, and collected standard morphological measurements. To assess the influence of female age and condition on mate searching strategies, we aged females as either second year (SY) or after second year (ASY) based on mouth colour lining, feather wear, and feather colouration (see Doucet et al. 2007 for details). We quantified parasite load as the number of lice eggs around the eyes of individuals (Clayton and Walther 1997; Doucet and Montgomerie 2003). We used body weight as a measure of condition (there was no correlation between tarsus length and body weight; r_s=0.06, n=81, P=0.56).

To evaluate the influence of male quality on female mate searching strategies, we used measures of male advertisement and dance quality derived from a concurrent study (Chapter 2). In that study, we performed a principal component analysis of male advertisement and lek attendance recorded from field observations and videos, and found that the first principal component, representing male advertisement, was strongly positively correlated with female visitation and copulation in 2010 and 2011. We used this measure of "male advertisement" to estimate male quality such that females could evaluate it from a distance to decide whether they would visit a particular lek for courtship displays. Similarly, we performed a principal component analysis of dual male courtship displays, and found that the first and second principal components, representing dual-male dancing and butterfly dancing, respectively, also predicted copulation success. "Dual-male dancing" includes dance manoeuvres that require dual-male cooperation, and "butterfly dancing" includes both dual-male and solo dance manoeuvres. We used "dual-male dancing" and "butterfly dancing" as measures of male quality that females could only evaluate when observing male courtship displays on the dance perch, which they could use to decide whether to revisit males and eventually whether to copulate.

Tracking female lek visitation

To monitor female movements between leks, we used a novel tracking system (Encounternet), which consists of digital wireless transmitting tag devices fitted on females, and receivers placed at active display areas (Mennill et al. 2012). The receivers acquire the identification number and log the encounter time and signal strength value of tagged individuals whenever they come within range. Signal strength values decrease with increasing distance between the transmitter and receiver, and can therefore be used to estimate the distance between the transmitter and receiver (Mennill et al. 2012). To establish when tagged females were perched at a display perch, which they typically only do while observing a pair of alpha and beta males displaying (McDonald 2010), we performed a series of field tests of the Encounternet technology (see Mennill et al. 2012 for details; abstract provided in Appendix). Based on the criteria of the tests, when females were directly on a display perch we referred to these visits as "on-perch," and when females were in the general vicinity of a receiver we referred to these detections as "near-perch."

In 2010 and 2011, we outfitted a total of 82 females with Encounternet digital radiotransmitters. Females wore the transmitters on their lower back above their uropygial gland, held in place by a modified leg-loop harness of 1mm cotton-covered elastic beading cord (Rappole and Tipton 1991). The weight of the transmitters was within the 5% of total body weight recommended to minimize undue stress (Caccamise and Hedin 1985; Naef-Daenzer 1994). Females appeared to respond well to being fitted with the tags (Mennill et al. 2012). In total, we detected 70 of the 82 females that were tagged. Of those females, 50 were detected at least once with on-perch visits. We detected females for an average of 7.5 ± 0.8 days (range 1 - 24).

To monitor female visitation at leks, we placed receivers at primary perches at each lek included our study. In cases where we observed males dancing for females at more than one primary perch, we included a receiver at each perch. Our study population comprised a continuous assemblage of leks in evergreen habitat surrounded in most directions by drier habitat where manakins are less common. We monitored and, as needed, re-adjusted the internal clocks of the receivers at least every other day to ensure that the timing of the recorded encounters was accurate. In 2011, receivers logged their own time every ten minutes to ensure that their internal clocks were accurate. We programmed the receivers to turn on between 0430 and 1830 every day, and turn off during the night, to conserve battery life. Our Encounternet data contained obvious evidence of females sleeping near display perches (i.e. females recorded with a consistent detection rate for the last *ca*. 30 minutes of the recording day and the first *ca*. 30 minutes of the recording day). We therefore excluded detections where visit end times were later than or equal to 1825, and where start times were earlier than or equal to 0435.

Our study relies on the assumption that the female search sequences obtained using Encounternet data are representative of the female's mate searching activity. Our data include two main limitations. First, the length of time that we detected females visiting leks varied considerably between individuals, ranging from one to twenty-four days. Short sampling periods could result from females completing their search and leaving the detectable area to initiate nesting, from females leaving the area and visiting leks that we did not monitor, or from the batteries of the Encounternet tags expiring. Second, we cannot determine the portion of the sampling sequence that we measured relative to the entire searching period for each female. To evaluate whether the portion of the sampling sequence we monitored included the final portion of a given female's sampling sequence, we determined whether the female was detected with a near-perch visit after her final detected on-perch visit. Most on-perch visits (85%) occurred on sequential days, and we found that 22 of the 50 females had near-perch detections that continued at least one day after their final on-perch detections, and lasted an average of 2.77 ± 0.50 days (range 1 – 8). These data suggest that this subset of 22 females were likely to have completed their mate search sequence. We used this subset of 22 females to evaluate features of decision rules that focus on the end of the search period. All the female data were used to evaluate the other features of the decision rules, with the caveat that the totals may be an underestimation due to shortened battery life, incomplete assessment of the sampling period, or missed visits at leks that were not monitored. Nevertheless, we make the assumption that the majority of the females monitored with Encounternet made some or all of their mate choice decisions during the period we monitored them.

Statistical Analyses

To characterize female mate-searching strategies in long-tailed manakins, we analyzed the visitation sequences of females and compared them to the features of the two main decision rules that underlie the search strategy models (Table 3.1). The general descriptors of the visitation sequences are presented as means ± standard errors. To test for the influence of male quality on female search strategies, we used two-sample (paired) permutation randomization tests to compare groups of males visited by each female (Manly 1997). The sum of the observed difference between paired means, for example the sum of the difference of male quality between males that were visited multiple times, and males that were visited once for each female, was compared to the distribution of the sums of the expected difference between paired means when individuals were randomly assigned between groups. In each iteration, for each female, the number of males that were visited multiple times determined the number of male qualities randomly selected from the total group of males visited, then the difference in the mean quality of that random sample and the mean quality of the remaining males was calculated. Finally, the sum of the mean differences was calculated for all females. All randomization tests involved 10,000 iterations, to produce the distribution of the sums of the expected difference between paired means. We programmed all randomization tests using R (R Development Core Team 2011), and tests were considered significant at the 0.05 level. We used one-tailed tests for these paired comparisons since we had *a priori* predictions about the direction of the relationship based on theoretical models and empirical studies. All other tests were two-tailed. To investigate variation in female mate searching strategies, we explored the influence of female age, parasite load, and condition on female search effort. Female search effort was measured as three response variables: the number of males visited, the number of males visited multiple times, and the mean number of visits to each male. To test for associations between variables, we used Spearman correlations and least squares regressions. To test for the differences between independent and paired means we used Wilcoxon χ^2 and paired t-tests, respectively.

Results

Female decision rules

We evaluated female mate searching strategies in long-tailed manakins by comparing seven distinguishing features of the two main decision rules that apply to all mate searching strategy models: the threshold tactic and the comparison tactic (Table 3.1). Females that employ a threshold tactic end their search when they meet a male that surpasses a threshold in quality, whereas females that employ a comparison tactic sample a fixed number of males or sample for a fixed time period and return to mate with the highest quality individual. Females employing a comparison tactic should sample at least two males with an optimal number being five, whereas females employing a threshold tactic are not restricted by the number of males sampled but tend to sample fewer males (Table 3.1). Females visited an average of 4.02 ± 0.42 males, and 37 (74.0%) visited at least two males, which is more consistent with the comparison tactic.

However, 13 females (26.0%) only visited one male, which is more consistent with the threshold tactic.

Females employing the threshold tactic should exhibit a substantial amount of variation in the number of males they sample, whereas females employing a comparison tactic should exhibit less variation, since they should be sampling a similar number of males (Table 3.1). There was a substantial amount of variation between females in the number of males they visited (Figure 3.1A), which is more consistent with the threshold tactic.

Females employing a comparison tactic should revisit males, whereas females employing a threshold tactic should not (Table 3.1). In our study, 38 females (76.0%) revisited at least one male. Females revisited a few males on average (1.96 ± 0.25 males visited multiple times; Figure 3.1B), and revisited those males multiple times (2.33 ± 0.19 revisits; Figure 3.1C). Of the revisits, 69.7% were sequentially consecutive revisits to the same male. This pattern of male re-visitation is more consistent with the comparison tactic (Figure 3.1B).

Females employing a comparison tactic may visit a variable number of males between the penultimate and last time the final male is visited, whereas females employing a threshold tactic should not revisit males. To distinguish between these criteria, we restricted our assessment to the subset of 22 females showing evidence of having completed their mate searching (see Methods). There was variation in the number of males visited between the last two visits to the final male, with some females visiting up to 6 males (1.89 ± 0.59 males; Figure 3.1D), which is more consistent with the comparison tactic.

Females employing a threshold tactic should copulate on the first visit to the chosen male, whereas females employing a comparison tactic should not (Table 3.1). Although we did not know which male females mated with, for these analyses, we assumed that the final male visited was the one they chose as a mate. Of the subset of 22 females thought to have completed their mate sampling, eight (36.4%) visited only a single male; of the 14 females to visit multiple males, six (42.9%) visited the final male only once, which is more consistent with the threshold tactic.

Females employing a comparison tactic may initially sample only a subset of higher quality males, whereas females employing a threshold model should not choose a subset of males to sample based on quality. Of the males approached by each female within a detectable range of their dance perches (females were detected at 11.34 ± 1.13 leks), females visited only a subset for on-perch courtship displays (4.02 ± 0.42). Based on a measure of male advertisement that predicts copulation success devised in a concurrent study (Chapter 2), the quality of males receiving on-perch visits was higher than that of males that were only approached but not visited for courtship (paired comparison randomization test; n=49, P=0.05). These results are more consistent with the comparison tactic.

Females employing a comparison tactic should revisit males of higher quality, whereas females employing a threshold tactic should not re-visit males, or only re-visit males in random encounters. There was a trend for females to sample males multiple times later in their sequence of searching (paired comparison randomization test; n=30, P=0.06), which suggests that females mainly made single visits to males early in their search and then spent time revisiting males later in their search rather than visiting new males. In addition, males that were visited multiple times had a higher level of dual-male dancing, which is correlated with copulation success (Chapter 2), than males that were only visited once (paired comparison randomization test; n=9, P=0.04). However, females did not revisit males in relation to their degree of butterfly dancing (paired comparison randomization test; n=9, P=0.29). These date are more consistent with the comparison tactic.

The influence of female condition, parasite load, and age on mate searching behaviour

We investigated the influence of female age (SY, ASY), condition (weight), and ectoparasite load on female search effort. To account for the discrepancy in the number of leks that we monitored between years, we divided each measure of search effort by the number of hours that receivers were active in the field. Female age did not predict any measure of female search effort (Wilcoxon $\chi^2 \leq 1.09$, $P \geq 0.30$). Female weight and ectoparasite load did not predict any measure of female search effort ($F \leq 0.32$, $P \geq 0.25$).

Age may affect the decisions females make with respect to the quality of the males visited during their mate search. There was no difference in male advertisement rates between males visited by ASY (0.06 ± 0.11, n=38) and SY females (0.43 ± 0.29, n=12; Wilcoxon $\chi^2=1.04$, P=0.31). The *difference* in male advertisement between males that were visited on-perch and the males that were only visited near-perch did not differ between ASY (0.17 ± 0.10, n=38) and SY females (0.12 ± 0.19, n=12; Wilcoxon $\chi^2=0.0$, P=1.0).

Age may also affect the decisions females make with respect to the male quality of the males they re-visit during their mate search. Across both age classes of females combined, males that were visited multiple times had a higher dual-male dancing quality than the males that were visited only once (paired t-test: $t_{17}=3.66$, P=0.002). There was no difference in the dual-male dancing quality of the males that were revisited, between ASY and SY females (Wilcoxon $\chi^2=1.69$, n=19 ASY females and 7 SY females, P=0.19). However, the mean difference in dual-male dancing quality between males that were visited only once and males that were visited multiple times was greater in ASY females than SY females (Wilcoxon $\chi^2=5.05$, n=19 ASY females and 7 SY females, P=0.02; Figure 3.2), suggesting that older females revisit a higher quality subset of males than younger females. Conversely, across both age classes of females, there was no difference in the butterfly dancing quality of the males that were visited once and the males that were visited multiple times (t_{17}=0.62, P=0.55). Likewise, was no difference in the butterfly dancing quality of the males that were revisited, between ASY and SY females (Wilcoxon χ^2=0.24, n=19 ASY females and 7 SY females, P=0.62). Finally, the mean difference in the butterfly dancing quality between the males visited once and the males visited multiple times did not differ between ASY and SY females (Wilcoxon χ^2=0.0, P=1.0).

Discussion

Our study represents the first assessment of female mate searching strategies in long-tailed manakins, a species with a cooperative, exploded-lek mating system. We used a novel passive digital tracking system to characterize female visitation at leks and compared distinguishing criteria to assess female decision rules. Our findings provide evidence that females use a comparison search strategy with re-sampling. That is, females appear to compare multiple males, and evaluate male quality to make decisions about which males to revisit, and use revisits to improve their evaluation of male quality. Empirical studies of systems where females employ a complex comparison tactic with re-sampling are rare (reviewed by Luttbeg 1996 and Valone 2006). Our findings therefore help to validate the occurrence of non-random re-sampling and Bayesian updating in animals (Valone 2006), and our study can contribute to the development of empirically testable criteria to distinguish between similar re-sampling models such as the comparative Bayes and random-walk models. We found no evidence that female age, condition, or parasite load altered female decision rules. However, we found that variation among females in the quality of the males that they re-visited may be influenced by female age. Our findings provide some insight into the influence of female age on their mate choice decisions, and further explain how variation in female choice maintains variation in male sexually selected traits in systems with high mating skew (Borgia 1979; Jennions and Petrie 1997).

In our study, two thirds of females sampled multiple males, most females revisited males, and there was variation in the number of males visited between the last and second last visit to the final male. These observations suggest that females employ a comparison tactic decision rule when choosing males; females sample a pool of males and return to mate with the highest quality individual regardless of the order of their first encounter (Janetos 1980; Wittenberger 1983). Females were detected at several leks, but only made on-perch visits to a subset of those males with higher advertisement rates, a known indicator of male reproductive success (Chapter 2). Moreover, males that were revisited by females had higher levels of dual-male dancing, another index of copulation success, than males that were only visited once. These findings suggest that females use a priority system to reduce the pool of potential mates through rounds of comparisons of different male traits (Wittenberger 1983; Trail and Adams 1989; Draud et al. 2008). Finally, females repeatedly visited several males, and more than half of those revisits were sequential, which suggests that females are updating their perception of male quality, and are thus employing either a comparative Bayes or random-walk female search strategy model.

Theoretical models predict that the comparative Bayes search strategy results in the highest fitness outcome when modelled against the threshold and best-of-*n* tactic if assessment costs are low (Luttbeg 1996). In lekking species, males group to display for females, and males have the potential of mating with multiple females (Bradbury and Gibson 1983). In these species, search costs are low, if not negligible, and thus support the potential for a comparative Bayes search strategy (Pruett-Jones and Pruett-Jones 1990; Reynolds and Gross 1990; Petrie et al. 1991; Gibson and Bachman 1992; Uy et al. 2001). Female long-tailed manakins appear to have similarly low search costs. Females only assess males for a short period of time during their visits (3.62 ± 0.24 mins) and only visit a few males per day (1.61 ± 0.10 males), leaving plenty of time for self-maintenance and foraging. On the other hand, unlike in classical lek mating systems, females must cover large distances to visit multiple males, and if they use a comparative tactic, they cannot directly compare male quality and must use memory to compare between males. Moreover, females must remember the locations of males for revisits and to copulate. Finally, females experience greater adult mortality than males, which is most likely explained in part by higher predation risk by females (McDonald 1993). Despite these additional challenges faced by females in exploded-lek mating systems, our findings suggest that these costs are low enough, or the resulting benefits are high enough, to favour a comparative Bayes search strategy. Search costs play an important role in determining which search strategies offer the highest fitness outcome (Janetos 1980; Parker 1983; Wittenberger 1983; Real 1990; Luttbeg 1996). Therefore, identifying the search strategy and the associated search costs of a mating system are important for developing general patterns that govern the evolution of mate searching strategies.

Information updating through repeated visits, the core criterion of the comparative Bayes search model, would seem unnecessary if male quality is readily assessed. Therefore, repeated visits may indicate that females are assessing dynamic traits, such as behavioural displays (Sullivan 1994). In lek mating systems, genetic material is the unique paternal contribution to offspring fitness, and the potential benefits of choosing high quality males are thought to far outweigh the low costs of female search (Head et al. 2005; Alem and Greenfield 2010). However, many lek-based mating systems are also characterized by elaborate vocal and visual ornaments, as well as behavioural courtship displays that may be difficult to assess in a single visit. Male long-tailed manakins produce a very complex display that includes duet vocalizations, cooperative vocal leapfrog jumps, and long laborious silent butterfly flights. Males also have elaborate plumage colouration that includes a red crown, blue mantle, black body and two long central rectrices (Doucet et al. 2007). Females may also have difficulty assessing males during a single visit because courtship displays can be disrupted by intrasexual aggressive interactions among females or males, or by other species that are active near the dance perch (person. observ.). Given the complexity of the display and the potential for disruption, it is not surprising that females would need to visit males multiple times to properly asses their quality. Other species appear to use Bayesian updating to re-sample potential mates, such as in satin bowerbirds (*Ptilonorhynchus violaceus*) where male intrasexual interactions regularly influence the quality of the bower display which is used by females to assess males (Borgia 1985a, b). Similarly, female peacock wrasse (*Symphodus tinca*) use information about dynamic environmental conditions to make reproductive decisions, namely whether to spawn with nesting or nonnesting males (Luttbeg and Warner 1999). Bayesian updating is not only applicable to male assessment in mate choice, but food patch quality in foraging, as well. For example, red knots (*Calidris canutus*) employ Bayesian updating of the quality of patches with hidden prey during multiple visits (van Gils et al. 2003).

Although most studies exploring Bayesian updating assess either the mate search or the food search process, none, to our knowledge, compare the cognitive abilities of individuals as they apply to both. It has been proposed that in long-tailed manakins, the complex foraging skills required may have pre-adapted the females for complex mate searching abilities (Munk 2006; McDonald 2010). Manakins are frugivores with high food-intake rates, therefore, they are required to remember the location and timing of patchily distributed food resources, which may explain their well developed hippocampus (Munk 2006; McDonald 2010). McDonald (2010) and Munk (2006) argue that this spatial memory processing centre, which is larger in *Chiroxiphia* than in other manakin genera (Munk 2006; McDonald 2010), probably also facilitates female memory of male display locations and associated quality levels determined from complex cooperative male performance (Hampton and Shettleworth 1996). Our study partly supports this hypothesis since female long-tailed manakins employ a complex mate searching strategy with re-sampling. However, the foraging strategies of this species are still unknown. The link between cognition and memory, and foraging and mate searching strategies deserves more attention in future research.

In our study, most female sequence data support a Bayesian updating model, but thirty percent of our females only visited a single male, just under half of our subset of 22 females with final visit information visited the final male once, and there was variation in the number of males that females visited, supporting a threshold model. Similarly, in a study by Uy et al. (2001) most female satin bowerbirds supported a “comparative Bayes” search strategy, but a subset of females demonstrated behaviours supporting a threshold model. It was determined that older females were altering their search strategy and mating with males after single visits if they had mated with that male the previous year (Uy et al. 2001). The mating system of long-tailed manakins is amenable to similar female searching behaviours, because females are long-lived and males tend to display in the same locations between years (McDonald 1989b; 1993). However, our data were limited by our short sampling period relative to the long breeding season of long-tailed manakins, and by the unknown portion of the search sequence that we were sampling due to the unsynchronized breeding among females. Therefore, we do not know whether the features of the mate sequences supporting a threshold model were an artefact of the limits of the tracking system or a true representation of variation in female mate choice strategies. In a previous study, females tended to revisit and mate with the same male over multiple years, which suggests that there is potential in this system for older and more experienced females to change their search strategy to reduce search costs (McDonald 1989b; McDonald 2010). When the technology becomes available, future studies should follow the entire mate searching of female long-tailed manakins over multiple breeding season to determine whether there is variation in the search strategy used by females, and subsequently, what influences that variation. By further elucidating these relationships, we may gain better understanding about what causes variation among females in the decisions they make while searching for a mate, and whether long-term experience has an effect.

We compared female mate searching strategies between SY and ASY females in our study. We could not age older females beyond ASY status, and females in this age category likely ranged from two to several years old (McDonald 1993). However, all of the SY females in our study were experiencing their first attempt at mate searching and copulation. Theoretical models predict that female age might influence search strategy, and McDonald (1989b) proposed that the odd copulation obtained by a lower quality male might result from poor mate choices by inexperienced females. We found evidence in our data that there was a difference in search strategy between older and younger females. We also found no difference between older and younger females in the quality of the males that were initially sampled, or in the quality of the males visited multiple times. However, it may be difficult o compare the quality of visited or chosen males between females, because the distribution of male quality may differ depending on the pool of males that each female sampled (Dombrovsky and Perrin 1994; Bateson and Healy 2005). Moreover, our study design did not allow us to determine whether chosen males differed in quality between younger and older females, a pattern that has been found in other species (Dugatkin and Godin 1993; Gray 1999; Wilgers and Hebets 2012; reviewed by Höglund and Alatalo 1995). There was no difference in the search effort (the number of males visited, the number of times males visited, and the number of males visited multiple times) between younger and older females. There was, however, a greater difference in the dual-male dancing quality between the males visited once and the males visited multiple times in older females than younger females. These data suggest that older females may be better at discriminating male quality, allowing them to more easily select a subset pool of higher quality males to revisit. By contrast, younger females may have more difficulty discriminating based on quality and may choose to revisit some lower quality males as well as higher quality males. Although many studies compare the mate quality of older and younger females (e.g. Burley and Moran 1979; Prosser et al. 1997; Kodric-Brown and Nicoletto 2001), this study investigates the process and steps leading to the final mate choice and how it is affected by female age. Including the effects of female age on the mate searching process may help to further understand what causes variation among females in their mate choice decisions.

We investigated the influence of ectoparasite load and female condition on female search effort. There was no effect of body condition or parasite load on female search effort, which suggests that females do not change their search effort when they are in poor condition. There is conflicting evidence as to how condition should affect female mate searching. For example, in pied flycatchers (*Ficedula hypoleuca*), females in poor condition spent more time searching than females in good body condition, because females in good condition chose higher quality males, leaving fewer options for females in poor condition (Dale et al. 1992). Conversely, heavier female black grouse, *Tetrao tetrix* (of better condition), visited more males than lighter females, suggesting that better quality females have more energy to invest in male assessment (Rintamäki et al. 1995). Finally, similar to our study, female search effort in satin bowerbirds was not affected by body size or ectoparasite load (Uy et al. 2001). Similar to the satin bowerbirds mating system, long-tailed manakins seem to have low search costs. In species with low search costs, females may be less likely to alter their search effort in response to increases in individual costs, such as body condition and parasite load. Further research is required to better elucidate how and why female condition may influence female search effort, and whether individual female costs may be influenced by the search costs of a species as a whole.

Our study represents the first field test of a novel digital tracking technology that allows continuous remote monitoring of small mobile animals within a complex habitat. Despite the limitations of a short battery life, which is common in all radiotelemetry studies of small-bodied animals (Caccamise and Hedin 1985), we were able to gain insight into a complex mate searching process that would otherwise not have been possible in this species. The transmitters allowed us to continuously monitor cryptic females through dense habitats, for long periods of time, and without the potential disturbance of direct observation or tracking. Future studies should recognize the advantages of such a system for monitoring animal movements in wild populations and apply it to unanswered questions in behavioural ecology.

In this study, we determined that female long-tailed manakins employ a complex comparison decision tactic, and re-sample males to assess multiple aspects of male quality. We found no effect of female age or condition on female search effort; however, an increased parasite load among the females in one year coincided with a reduced number of re-visitations. These data suggest that females may not necessarily change their search strategy due to high costs, but rather reduce their search effort. We also found that older females may choose to re-visit a higher quality subset of males than younger females, providing evidence that older, more experienced females may be better at discriminating male quality. Our study relied on a novel technology that allowed us to monitor female movements between leks in an unprecedented way. Future studies should take advantage of these technologies to enhance our knowledge of behaviours that are otherwise difficult to monitor, such as complex mate searching strategies. Our findings contribute to a growing body of research on mate searching strategies, and our study provides one of the few empirical tests supporting Bayesian updating in a wild animal.

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Table 3.1. Criteria used in our study to distinguish between the two main decision rules of female mate searching strategies.

		Decision rule		
Feature		**Threshold tactic**	**Comparison tactic**	**References**
1	How many males do females sample?	Variable, may visit only one	At least 2, optimally 5 or 6	Janetos 1980; Real 1990
2	How much variation is there in the number of males sampled?	Variation between females	Little variation between females	Janetos 1980
3	Do females revisit males?	No	Yes	Janetos 1980
4	How many males do females visit between the penultimate and last time the final male is visited?	None	Variable	Wittenberger 1983; Real 1990; Janetos 1980
5	Do females copulate on the first visit to the chosen male?	Yes	No	Real 1990
6	Do females initially screen for suitable males?	No	Yes	Wittenberger 1983
7	Do females reduce the pool of males they sample over time based on quality?	No	Males revisited later in sequence Revisited > visited once	Wittenberger 1983

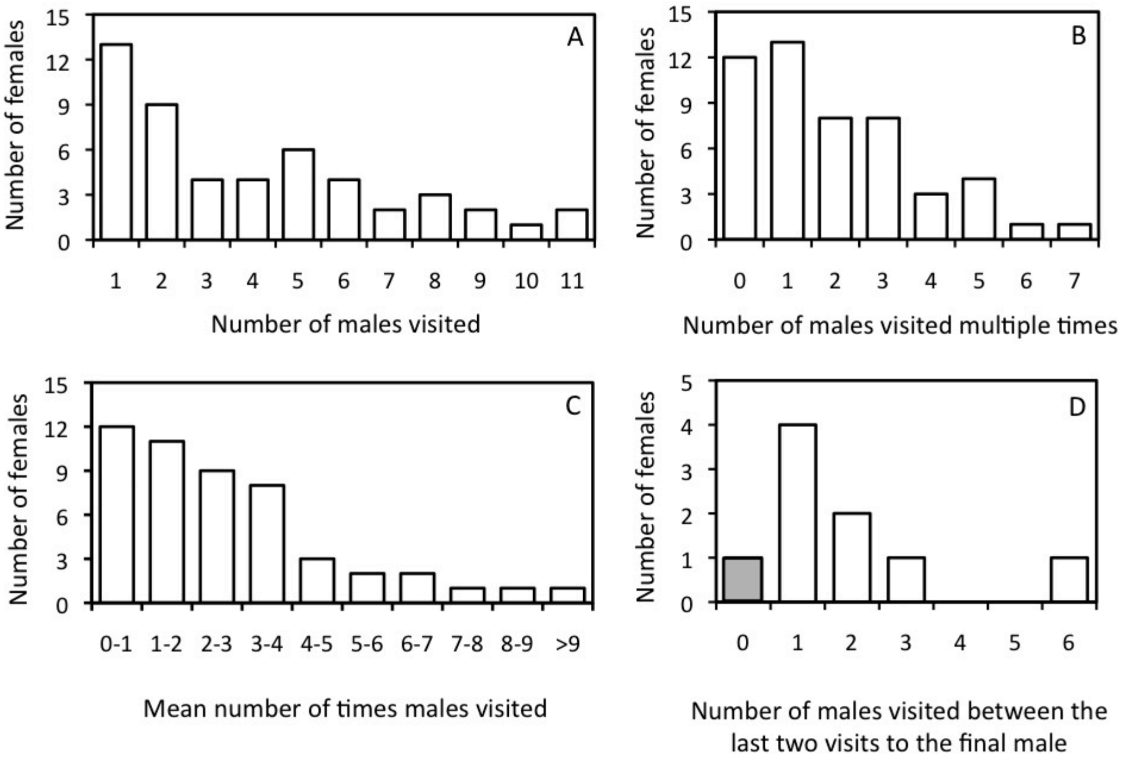

Figure 3.1. Female mate searching sequences monitored by a passive digital telemetry system in female long-tailed manakins. A – The number of males visited by each female (n=50). B – The number of males visited multiple times by each female (n=50). C – The mean number of times males are visited by each female (n=50). D – The number of males that are visited between the last two visits to the final male. Data include only females that had completed their search (see methods), had visited more than one male, and had visited the final male multiple times (n=9). Grey bar represents the single female that only revisited the final male on sequential final visits.

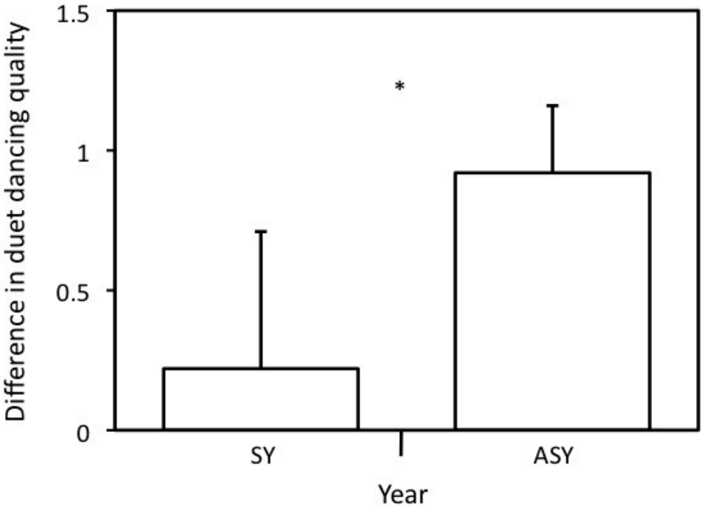

Figure 3.2. The mean difference in a composite measure of dual-male dancing quality (see methods) between males that were visited multiple times and males that were visited once in SY females (n=6) and ASY females (n=12). Asterisks depict significance at the 0.05 level, and error bars represent standard errors.

Chapter 4: General discussion and conclusions

General discussion and conclusions

In many mate choice studies, researchers either focus on the outcome of the mate choice process by studying correlates of male mating success (Bateson 1983), or they focus on the process leading to the female mate choice decisions by studying female mate searching strategies (Wittenberger 1983). However, to gain a thorough understanding of female mate choice as a whole, it is important to study the entire process. The purpose of my thesis was to study the entire female mate choice process in a lek breeding bird to further our understanding of how the costs and benefits of mate choice shape mate searching strategies. This evaluation was facilitated by the study of a lekking species because males display in the same locations within and between years and female visitation and courtship displays can be readily assessed. My research was also facilitated by the use of a novel tracking system to monitor females as they moved between potential mates. My thesis provides evidence of the importance of female mating behaviour in the evolution of complex cooperative courtship displays and lek mating systems.

In Chapter 2, I examined the effect of male advertisement and lek attendance, male-male cooperative displays, and male-male aggression on mating success in a population of long-tailed manakins (*Chiroxiphia linearis*) in Costa Rica during a two-year study. To quantify male and female behaviours at the lek, I used video recordings and in-person behavioural observations. My analyses revealed that females were visiting leks and copulating with males who showed high advertisement and lek attendance. Females also chose to copulate at leks with high quality components of male cooperative and solo displays. These results suggest that females are choosing between leks and courtship displays, which may place selection pressures on the evolution of dual-male cooperative displays (Foster 1977; Kruijt and Hogan 1967). Contrary to my expectations, female preference for male-male cooperative displays were not affected by male-male aggression, which suggests that female preference for high cooperative output were more important than the increased conflict that may be associated with higher quality leks. My results suggest which aspects of display females prefer; however, they do not necessarily explain why they were preferred. It is believed that male advertisement and the aspects of dual-male and solo display are costly, and therefore, may reflect the condition and genetic quality of the males (McDonald 1989). Future studies could experimentally alter the condition of males to determine whether it affects their display abilities. For example, in the houbara bustard (*Chlamydotis undulata undulata*), males were injected with a bacterium to artificially reduce their condition, which resulted in decreased courtship display and attractiveness (Chargé et al. 2010). Future studies should also examine the fitness benefits of mating according to display quality by monitoring offspring survival and fitness. For example, in the same study in the houbara bustards, it was also found that males in poor condition also have lower offspring viability (Chargé et al. 2010). This system also provides an opportunity to test the “sexy sons” hypothesis by tracking the progress of the offspring of the most successful males to see whether they also acquire a position of dominance (Weatherhead and Robertson 1979; Kokko et al. 2002). However, as males do not attain a beta position until at least 8 years of age (McDonald 1993), such a study would involve extensive long-term monitoring.

Female activity levels on the dance perch predicted the likelihood that females would copulate, which suggests that females signal their receptivity to male courtship displays. Sexual selection may favour female signals of receptivity and male response to those behaviours to reduce the costs of unsuccessful courtship displays (Balsby and Dabelsteen 2002). Male solo and cooperative displays increased in response to female activities, which suggests that males may be changing their displays in response to female interest. This may explain some of the variation in display behaviour of successful males. High quality males may not necessarily be the ones with the highest display output, but the ones that are better able to adjust their display in response to female preferences (Patricelli et al. 2002). Future studies should attempt to elucidate the cause and effect of female activity on the dance perch and male display output. This may be possible through the use of robotic females that could be attached to the dance perch and programmed to jump or shuffle at different rates to see whether it influences male display behaviours. A similar experiment in satin bowerbirds (*Ptilonorhynchus violaceus*) showed that males adjusted their display intensity in response to female startling behaviours (Patricelli et al. 2006). Overall, this chapter of my thesis provided insight into which aspects of male courtship display females are assessing, which qualities they prefer, and how their preference may shape the evolution of male-male cooperative display. My research also identified measures of male quality that females use to distinguish between leks, which can help us distinguish between different mate searching strategies employed by females.

In Chapter 3, I monitored the mate searching behaviours of 82 female long-tailed manakins. I used a novel tracking system to monitor female movement between leks of actively displaying males. To evaluate the influence of male quality on female search strategies, I used a measure of male advertisement that females could assess from a distance, and two measures of male courtship displays (dual-male and butterfly dancing) that females could assess only when observing male courtship displays on a dance perch; both measures were derived from the research conducted for Chapter 2. My study represents the first assessment of female mate searching behaviours in long-tailed manakins. This research would not have been possible without the use of a tracking system because females are very cryptic in behaviour and colouration, and span over such large home ranges that it is difficult to monitor the movements of individual females. My results reveal that females utilize a complex mate searching strategy that includes multiple rounds of comparisons of different male traits, which means that females may be using a form of Bayesian updating to assess the quality of complex male courtship displays (Wittenberger 1983; Luttbeg 1996). I found evidence that females assess male advertisement from a distance and assess male courtship displays on perch. Future studies should also assess the effect of male plumage colouration on female choice as another possible step in the mate choice process. The assessment of multiple characters through multiple rounds of comparison requires a good memory of male locations and their associated qualities. Female long-tailed manakins have a well-developed hippocampus that was initially attributed to their foraging behaviours, and which may explain how they are able to employ a complex mate searching strategy (Munk 2006; McDonald 2010). My study provides much needed empirical evidence that females may be capable of Bayesian updating, which may help to validate the application of theoretical models for use in animal behaviour (Valone 2006).

I also found variation among females in their search sequences and the search strategy they support; however, I cannot determine whether this represents true variation in female search strategies or whether it is a byproduct of the short sampling period of the tracking system. It is possible that older females visited fewer males, returning to mate with the same male as in previous years. Older females have been shown to alter their searching strategy in such a way in satin bowerbirds, another species with an exploded-lek mating system (Uy et al. 2001). McDonald (1989) observed that female long-tailed manakins did tend to return to mate with the same male within and between breeding seasons, suggesting that older females would benefit by altering their search strategy. However, whether females assessed other males before choosing the same male is not known. Since males maintain their dominance positions and display areas within and between years (McDonald 1989; McDonald and Potts 1994), there may not be a great enough benefit to re-sampling males between years. Alternatively, if lay date is important in improving offspring survival, then reducing the time spent mate searching may improve a female's ability to produce successful broods (e.g. Smith 1993). Clearly the benefits of reduced search costs may play an important role in altering female assessment as they gain experience. Future studies are required to better understand variation among females in their search sequences, and should monitor females for a longer period of time and over multiple years to better understand these results.

From the data I collected for Chapter 3, I gained important insight into the mate sampling process of female long-tailed manakins with the use of a novel tracking technology. However, to acquire all of the information needed to make a more thorough assessment of the mate sampling process, future studies would require tags with longer battery life, and a method of recording the location of copulations of tagged females. The tracking technology I utilized has already vastly improved since my initial field studies, and I anticipate that future studies employing this technology will reveal new important patterns within the field of behavioural ecology.

Comprehensive studies on the mate choice process are important for understanding female preferences, the evolution of male displays, and the evolution of mating systems. Many studies are restricted in their ability to evaluate this process because of the limited conclusions that can be drawn about wild populations from lab-based studies, or because of the challenges of monitoring the movements of wild animals. My research provides evidence for a means, using remote tracking technology, to successfully evaluate complex mate choice processes in wild populations. In so doing, my research provides important empirical support for theoretical models of female searching. My research also helps to explain the influence of female preference on the evolution of dual-male cooperative display and complex lek-mating systems.

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Appendix A: A novel digital telemetry system for tracking wild animals: a field test for studying mate choice in a lekking tropical bird

This appendix is an abstract of the product of collaborative research, and is co-authored by D.J. Mennill, S.M. Doucet, D.F. Maynard, B. Otis, and J.M. Burt.

Appendix citation

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Abstract

1. Radiotelemetry provides a tool for monitoring animals that are difficult to observe directly. Recent technical advances have given rise to new systems that present expanded opportunities for field research. We report the results of the first field test of Encounternet, a new digital radiotelemetry system comprising portable receiver stations and digital tags designed for long-term studies of the social behaviour and ecology of free-living animals.

2. We present results from a series of field tests designed to evaluate the utility of Encounternet for monitoring animals in a neotropical forest, with an emphasis on evaluating mate sampling behaviour in female Long-tailed Manakins. In this tropical species, females visit leks where males perform elaborate dances on horizontal perches. Females are highly cryptic in both plumage and activities, and therefore Encounternet might provide unique insights into female behaviour and ecology.

3. Our first two tests revealed that pulse strength and probability of detection decrease with the distance between tag and receiver, and that tags placed on a fixed perch near a receiver showed different patterns of reception than more distant tags. Our third test revealed that antenna angle had only a small influence on pulse strength.

4. Blind analysis of simulated bird movements confirmed that the Encounternet system provides reliable information on animal activity. Data from multiple receivers permitted

accurate reconstruction of simulated bird movements. Tag detections showed low levels of false negatives and false positives.

5. Female manakins responded well to carrying Encounternet tags attached by an elastic leg harness. Birds flew well upon release and were detected for 7.5±0.8 days after release. Recaptures and re-sightings of females were rare in our large study population, yet there were two occasions where we confirmed that the tag fell off within one year.

6. We conclude that Encounternet technology provides an effective tool for monitoring animal ecology and behaviour. We show that it is capable of providing accurate measures of distance and that it is a highly versatile system for studying the ecology and behaviour of free-living animals. We discuss the unique opportunities facilitated by this technology for future ecological and behavioural studies.

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