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Coordinated display, social hierarchy, and the development of dancing ability in young long-tailed manakins, *Chiroxiphia linearis*

by

Katrina Lukianchuk

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2013

Coordinated display, social hierarchy, and the development of dancing ability in young long-tailed manakins, *Chiroxiphia linearis*

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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 2-4: I am the primary author, and share authorship with Dr. Stéphanie M. Doucet. Dr. Stéphanie M. Doucet contributed in the research design, data collection, and writing of these chapters, as well as providing logistical and monetary support for this project.

Chapter 5: I am the sole author.

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ABSTRACT

Although a considerable amount of research has been conducted on the development of bird song, the development of visual displays is still poorly understood. In this thesis, I investigate the coordinated courtship displays of male long-tailed manakins (*Chiroxiphia linearis*). By scoring complex behaviours from video recordings, I characterize the courtship display and dominance hierarchy in detail. I show that courtship is highly stereotyped and that the performance of specific subcomponents of the display can predict courtship success. I also provide evidence of an age-graded dominance hierarchy among young males. Finally, I show that courtship display differs significantly between older and younger males, and that certain display elements may develop over time. My research suggests that social interactions between males may be important in the maintenance of lek dynamics, and that social learning may play a role in the development of coordinated display in long-tailed manakins.

DEDICATION

I would like to dedicate my Master's thesis to my parents, Charlene and Gerald Lukianchuk, and to my baba, Ollie Lukianchuk. I can't thank you enough for providing me with constant support throughout both my undergraduate and graduate degrees. To my parents, I thank you for supporting me in all my interests, hobbies, educational pursuits, and for always encouraging me to try new things and to do what I love. Thank you for inspiring my interests in art and science, both consciously and subconsciously (who knew I'd be studying the science of dancing?). Thank you for always providing me with a welcoming home whenever I need it, and for your much appreciated calls and emails when I'm away. To my baba, I thank you for always supporting me and believing in me, and for spoiling me whenever I come home. Thank you for your phone calls and for always checking in on me wherever I am.

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CHAPTER 1

General Introduction

Cooperation and sexual selection

In some species, selective pressures have favoured the evolution of highly cooperative behaviour between individuals, and in certain cases it has become essential to survival (e.g., damaraland mole-rat; *Fukomys damarensis*, Young & Bennett 2010). Individuals of other species, however, may cooperate to increase mating success or gain access to other resources without requiring cooperation for survival (e.g., ruffs, *Philomachus pugnax*; Lank et al. 2002; huntsman spider, *Delena cancerides*; Yip & Rayor 2011). The evolution of cooperation between individuals of the same species has often been explained by invoking kin selection, whereby one individual gains indirect fitness benefits by helping a closely related family member increase its fitness (Hamilton 1964). In rare instances, unrelated individuals are known to cooperate for long periods of time without any obvious direct benefits to at least one member (McDonald & Potts 1994; McDonald 2009). Animals may exhibit cooperative behaviours for a variety of reasons, and the complexity of this cooperation can vary greatly depending on the species (Noe & Hammerstein 1994).

Although cooperation may be highly integrated into the life history of an animal, this does not exclude competition from occurring between cooperating individuals (Jandt & Dornhaus 2011). Cooperation occurs in social species, all of which conform to a social structure of some form or another (Maynard Smith & Price 1973). These social structures, or hierarchies, are made up of dominant and subordinate individuals whose ranks are determined through competition, or in some cases through other means such as age (Maynard Smith & Price 1973; McDonald 1989b; Suzuki et al. 1998). An individual's place within the dominance hierarchy, coupled with the type of mating system present, may be important in determining how cooperation functions within a group.

In many species, dramatic sexual dimorphism and elaborate courtship displays evolve as a result of strong sexual selection on males (Darwin 1859; Hoglund & Alatalo 1995). Sexual selection is strongest in polygynous species, where females devote their energy towards parental duties and become very choosy about their mates, while males compete with one another for access to mating opportunities (Trivers 1972; Emlen & Oring 1977). One specialized form of polygyny is the lek breeding system, in which males gather in lekking arenas or 'display areas' to perform courtship displays for females, allowing females to evaluate the quality of males and choose the best ones to mate with (Bradbury & Gibson 1983; Kirkpatrick & Ryan 1991). In this system, males do not provide any resources to either female or offspring, and contribute only gametes for reproduction (Höglund & Alatalo 1995).

The physical arrangement of leks varies between two types: classical and exploded (or dispersed). In classical leks, males are clustered into display areas that are closely packed, with the distance between leks being relatively far (Bradbury

1981; Bradbury & Gibson 1983). In exploded leks, display areas can be large, but are arranged relatively close to each other, and are generally visually (but not acoustically) isolated from one another (Bradbury 1981; Bradbury & Gibson 1983; Trainer & McDonald 1993).

Within a lekking arena, there is generally one dominant male amongst a number of subordinates that accrues most, if not all copulations with females (Bradbury 1981). This male often defends his position as the dominant male by chasing away other males or by simply performing the best undisturbed display (Borgia 1979; Bradbury & Gibson 1983).

Manakins (Pipridae)

Manakins (Pipridae) comprise approximately 50 species of suboscine passerine birds that range between Mexico and South America. Members of this group produce some of the most spectacular courtship displays and elaborate plumage traits in birds. Several species are known for producing mechanical snaps and elaborate visual signals through the use of modified feathers. Most species of manakins exhibit high levels of sexual dimorphism; females generally have dull olive plumage and males are often black with bright coloured patches (Snow 2004).

The Pipridae family contains an unusually high predominance of lek-breeding species (Emlen & Oring 1977; Prum 1994), in which one or more dominant males perform courtship displays for visiting females (Bradbury & Gibson 1983; Kirkpatrick & Ryan 1991). Coordinated display between top-ranking males is common to several species, and this is particularly evident in the genus *Chiroxiphia*, in which cooperative display may be essential to attract females and entice them to mate (Gilliard 1959; Foster 1981; McDonald 1989b, 2010; Prum 1990; Duval 2007a). Little is known about how cooperative display has evolved in manakins; the main objective of my thesis is to investigate how social interactions between males may influence a species with a complex dominance hierarchy and an elaborate dual courtship display, using long-tailed manakins (*Chiroxiphia linearis*) as a model study species.

Long-tailed manakins

Long-tailed manakins are small Neotropical suboscine birds distributed from Mexico to Costa Rica. They exhibit an exploded lek breeding system in which multiple males congregate in non-resource-based display areas to perform remarkably complex cooperative dance displays for females (McDonald 1989b). Display areas contain a horizontal vine relatively low to the ground that is used as a main dance perch for courtship displays (Slud 1957). These areas are 75-300m apart, and up to 13 individuals gather at each site and are thought to form age-graded dominance hierarchies, where the oldest males are dominant (Trainer & McDonald 1993; McDonald 1993b, 2007). At each display site, the top two males in the dominance hierarchy, known as the alpha and beta, form a long-term partnership to perform highly coordinated displays including both acoustic and visual components, which are used to attract and entice females for mating (McDonald 1989b). Dual display is both obligate and cooperative in the long-tailed manakin, unlike other manakin species in which coordinated courtship can be facultative (e.g. lance-tailed manakin, *C. lanceolata*; Duval 2007) and/or competitive (golden-winged manakin, *Masius chrysopterus*; Prum 1994). Although both males participate in the courtship display, females will only mate with alpha males (except in very rare cases; McDonald 1989a). Alpha and beta males are unrelated, and therefore beta males do not obtain indirect benefits due to kin selection (McDonald & Potts 1994). However, the beta male may eventually inherit the display area, becoming the next alpha male and finally attaining the long-awaited direct benefits from his partnership (McDonald & Potts 1994; McDonald 2010).

Male manakins undergo delayed plumage maturation whereby they exhibit distinct predefinitive plumage patterns each successive year after hatch until they attain their definitive adult plumage in their fifth year (McDonald 1989b; Doucet et al. 2007). This differs from other manakins that only experience a 1-2 year delay in plumage maturation (Snow & Lill 1974; Duval 2007a), but it also differs from other species that exhibit delayed plumage maturation in that each year the plumage is distinct from the last (McDonald 1989a). During their first year, male and female long-tailed manakins look alike, with an olive-green colour covering their entire bodies, much like most females and juveniles in other manakin species (Skutch 1949; Foster 1976). In their second year, males develop red crown feathers; in their third year they develop black feathers on their face and head, and during their final predefinitive stage they grow brilliant blue feathers on their mantle and develop most of their black body feathers (Doucet et al. 2007). Once males reach their fifth year they lose all traces of green feathers and are known as definitives – the final stage of their plumage maturation (Doucet et al. 2007; McDonald 2010). This unique trait allows for young males to be easily aged in the field.

Courtship display

Many species of manakins produce elaborate dance displays, and although some share similar elements, each species uses a different combination that results in a unique display for attracting and courting females (Prum 1990). In *C. linearis*, the main components of the dance display have been described (i.e. popcorn, butterfly, etc.), but a more detailed characterization of individual elements that make up these major components is lacking.

The alpha male first begins by singing ‘teamoo’ calls to attract his beta partner to the display area, a call generally given in the canopy above the display perch (McDonald 1989a; Trainer & McDonald 1993). Once the beta arrives, together they begin a series of simultaneous ‘toledo’ calls from the canopy to attract females to the area (Slud 1957; McDonald 1989a, 1989b). Once a female arrives near or on the display perch, the males descend to the dance perch and begin their elaborate courtship display which consists of a number of unique dance elements, as well as some accompanying vocalizations (McDonald 2010). The first component of the display has been described as a ‘backwards leapfrog’ display in which males hop over one another while hovering momentarily over the perch they use for the bulk of their performance (McDonald 1989a). They often alternate this component with a similar display called ‘popcorn hops’ in which they hop in place beside one another but do not leap over each other (McDonald 1989b). Both leapfrogs and hops are accompanied by a vocalization. Males transition to the next phase of the dance display when the alpha male gives a 'buzz-weent' vocalization at the peak of intensity during a bout of leapfrog hops, which is followed by the butterfly display (Slud 1957; Trainer & McDonald 1993; McDonald 2010). The butterfly display can be described as laboured flights to and from the main dance perch, which can be performed by both males as a dual performance, or as a solo display by the alpha male (Slud 1957; McDonald 1989a). However, many additional unique display components occur during this phase of the display and these elements, as well as several others exhibited during other phases of the display, require further examination.

Although the bulk of the courtship displays are performed by the alpha and beta pair associated with that display area, males visit display areas as early as their first breeding season to participate in coordinated dance displays with other males in the absence of females (Slud 1957; McDonald 1989a, 1989b). Males of all ages and dominance statuses continue to display throughout the day whether a female is present or not (McDonald 1989a), and it is during these practice sessions that younger males have the opportunity to display.

Dominance hierarchy

In many species, individuals use aggression to maintain their dominance status in a social hierarchy (Maynard Smith & Price 1973). Long-tailed manakins are thought to exhibit a dominance hierarchy in which the two most dominant males, the alpha and beta, perform all courtship displays for females (McDonald 1989a);

however, relatively little aggression is seen among individuals in this species (McDonald 1993b). In order to maintain this hierarchy, long-tailed manakins are thought to exhibit a linear age-graded dominance system, in which orderly queues are formed so that older males are dominant over younger males (McDonald 1989b, 1993b). By presenting taxidermic manakin models to males at display areas, McDonald (1993b) found that younger males exhibited more mobbing choruses towards the mounts than older males, and that these reactions were stronger towards mounts of older males. This suggests that intruders, particularly older males, pose more of a threat to a younger male's position in the queue than to an older male who is less vulnerable to losing his high rank (McDonald 2010).

McDonald's (1993b) study proposed that delayed plumage maturation in long-tailed manakin functions to signal the status of each individual by unambiguously marking males with their age. Females will often leave during a courtship display if males exhibit aggression towards one another, so it benefits younger males in the long run to accept their position in the queue and maintain the reputation of the lek (McDonald 1993b, 2010). Although the dominance hierarchy is thought to be age-graded, some males that reach definitive plumage never become an alpha or beta; therefore, there may be other factors influencing dominance besides an orderly queue (McDonald 2007). Young males that interact with more males at more display sites have a higher chance of rising socially later on in life than those with fewer interactions (McDonald 2007), suggesting that social interactions play an important role in the potential reproductive success of individuals.

It is well documented that a strict dominance hierarchy exists between the top two dominant males, the alpha and beta; only the alpha male performs certain components of the dance display and attains most, if not all copulations (McDonald 1993a). The alpha and beta are also clearly dominant to all other males as they alone can dance for females and exclude other males from the dance perch when a female is in the area. It is less clear, however, how strict the dominance hierarchy is among predefinitives, as younger males tend to associate with several display areas and may hold a different dominance status at each. Therefore, taking a closer look at dominance interactions between males of all age classes may help us to better understand how social factors influence the complex dominance hierarchy in this species.

Development of courtship skills

In many species, ritualized behaviours are innate; however, certain behaviours may have learned components to them as well (Mayr 1974; Freeberg 2004). Although considerable research has been conducted on the courtship displays of various animals, little is known about how males develop specific elements of their displays and become proficient enough in performing them to successfully acquire mates.

Recent studies have shown that social learning may play a key role in mating preferences and courtship displays (White 2004). Social transmission may involve imprinting by young animals on physical characteristics of their parents, and it has been shown through cross-fostering experiments that young birds adopt sexual preferences for morphological features exhibited by their adoptive parents (e.g. Zebra finches, *Taenopygia guttata*; Ten Cate 1984; Japanese quail, *Coturnix coturnix japonica*; Gallagher 1976; Freeberg 2000). Females can also alter their mate preferences based on the preferences of other females through mate-choice copying, which is seen in a number of polygynous and monogamous species (e.g. Trinidadian guppy, *Poecilia reticulata*; Amlacher & Dugatkin 2005; sage grouse, *Centrocerus urophasianus*; Gibson et al. 1991; zebra finches; Dugatkin 1992; Swaddle et al. 2005). Further studies on mate-choice copying have shown that female guppies prefer to copy mate choices of older females, which may suggest that young females seek information from older, more experienced females (Amlacher & Dugatkin 2005). Elements of courtship displays, such as birdsong, can also be influenced by social environment (Freeberg 2004). Red crossbill (*Loxia curvirostra*) males adopt the contact call variant displayed by foster parents even when it differs from the variant exhibited by their genetic parents (Sewall 2011), which suggests that elements of courtship displays can be socially transmitted in some species.

Social transmission of mating preferences and displays appear to occur more frequently in nature than was originally thought (Freeberg 2004); however, little is known about how unrelated individuals, particularly males, gain information about courtship displays from one another. Experimentally testing the effects of social learning can be difficult, but obtaining information about the development of quality displays may be an important step towards better understanding how individuals learn complex behaviours.

The courtship displays of the long-tailed manakin are unusually complex and although young males are permitted to congregate and occasionally participate at display areas, it is years before any particular individual can reach alpha status and have the opportunity to mate with females, and most never will (McDonald 2007). It is likely, then, that younger males develop their dance displays throughout their predefinitive years by observing and practicing with older males, and that it is not until they attain definitive plumage and dominant status that they are capable of attracting mates with their displays.

Thesis goals

The evolution of cooperation, dominance hierarchies, and unique mating systems may be intricately connected, though few animal models that combine these features have been studied thoroughly. Long-tailed manakins comprise an ideal study system that incorporates each of these features. My research will be the first to describe the courtship display of long-tailed manakins in detail, characterize individual variation in the display, and investigate whether this variation among males influences copulation success. In addition, I will examine dominance behaviours exhibited by males of all ages to provide evidence for a linear age-graded dominance hierarchy. Finally, I will compare the performance of unique dance elements between age classes to explore how the courtship display develops in young males. This research may help us gain more insight into how social interactions influence coordinated dual displays in this species, as well as other poorly studied tropical birds, and may enhance our understanding of the evolution of cooperation between unrelated individuals.

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CHAPTER 2

Cooperative courtship display in long-tailed manakins: predictors of courtship success revealed through full characterization of display

Introduction

Sexual selection has led to the evolution of a number of extreme cases of courtship among different species of animals, from exaggerated physical traits to elaborate displays (Darwin 1859). This is especially evident in polygynous species, in which strong sexual selection has emancipated males from parental duties and enhanced female choosiness (Trivers 1972; Emlen & Oring 1977). In lekking species, males gather at communal lekking arenas to perform courtship displays, where females evaluate these displays, as well as exaggerated physical characteristics of males, before choosing a mate (Bradbury & Gibson 1983; Kirkpatrick & Ryan 1991). Male mating success can vary throughout a population, and in lekking species there is a particularly high reproductive skew with only one or few males obtaining all mating opportunities (Kirkpatrick & Ryan 1991).

Manakins (family Pipridae) comprise 51 species of suboscine passerine birds distributed throughout Central and South America (Snow 2004; Mckay et al. 2010). Many species of manakins exhibit lek-breeding behaviours and are known for their elaborate courtship displays, but a great deal of variation exists among species (Prum 1990; Snow 2004). Within the genus *Chiroxiphia*, two or more males usually perform joint cooperative displays to attract females. In long-tailed manakins, *C.*

linearis, for example, two unrelated males coordinate their efforts to perform elaborate dual-male displays that include vocalizations, visual traits, and behaviours to attract and entice females to mate (Slud 1957; Foster 1977; McDonald 1989a, 1989b; McDonald & Potts 1994). Unlike other manakin species, the coordination of two males is obligate in this system to successfully attract females for copulations (Foster 1977). In addition, males undergo delayed plumage maturation whereby they develop a distinct 'predefinitive' plumage pattern for each of the first four years after hatch, finally attaining the 'definitive' adult plumage in their fifth year (Doucet et al. 2007). Up to 13 males are affiliated with each lekking arena, or 'display area', including the alpha and beta pair, several other subordinate definitive males, as well as a mixture of younger males in predefinitive plumage (Foster 1977; McDonald 1989b, 2007; Trainer et al. 2002). All males affiliated with a display area practice displaying in the absence of females; however, only the alpha and beta male perform the courtship display for females, and only alpha males copulate with females (McDonald 1989b).

The coordinated display of *C. linearis* consists of both acoustic and visual display elements. Pairs of alpha and beta males use duet 'toledo' vocalizations to attract females to their display area where they then perform a coordinated display that consists of two main components: the hopping display and the butterfly display. These displays are first performed jointly by the alpha and beta males, and eventually lead to a solo performance of the butterfly display by the alpha male. Previous research has shown that the mean output of toledos was correlated with female visitation, and that the length of the butterfly display was correlated with reproductive success (i.e. the number of displays that ended in copulation; McDonald 1989b; Ward 2012); however, many unique subcomponents of the display could influence this relationship. For example, butterfly-like flights are only one of the many unique display elements encompassed by the butterfly display, and therefore as the length of the butterfly display increases, so does the potential number of butterfly flights. By characterizing the full display in detail, we may be able to determine whether unique display elements can influence male mating success.

Although a considerable amount of research has been conducted on the breeding biology, behaviour, plumage, and vocalizations of long-tailed manakins (Foster 1976; McDonald 1989b; Trainer & McDonald 1993; Doucet et al. 2007), the individual elements of the courtship display have not yet been described in full detail. Here, we characterize and quantify 16 unique visual elements of the long-tailed manakin courtship display. To determine whether elements of the display follow a stereotypical pattern, we provide a generalized sequence of courtship behaviour using transitional probability matrices. We then examine how these manoeuvres vary across the population by investigating the relationship between performances of unique display elements and mating success.

Methods

We conducted our research in the Area de Conservacion Guanacaste, sector Santa Rosa, a UNESCO World Heritage Site in northwestern Costa Rica. Our long term study population is located in a small area of evergreen forest surrounded by tropical dry forest. With annual capture and banding efforts, over 750 manakins have been fitted with unique colour bands over the past nine years.

Long-tailed manakins are a Neotropical suboscine species with a distribution that ranges from Costa Rica to Mexico. Like many other manakins they exhibit sexual dichromatism, a frugivorous diet, a lack of male parental care, and a lek-based mating system (Foster 1976; McDonald 1989b). Unlike several other species within the Pipridae family, long-tailed manakins do not produce mechanical noises with their feathers. The four-year delay in plumage maturation in long-tailed manakins differs from most other manakin species that only experience a 1-2 year delay in plumage maturation (Snow and Lill 1974), and allows for easy identification of age in the field. Males use horizontal vines as display perches, and each display area contains one primary display perch and up to several additional practice perches.

From 2010-2012 we located and mapped the GPS coordinates of manakin display perches and assigned each of them to discrete display areas based on the associations of alpha males. Throughout the breeding seasons we set up video cameras within 5-15m of display perches and recorded behavioural data for approximately five hours starting at dawn. We targeted active display areas including both primary and practice display perches. We sampled active display areas a minimum of 3-5 times each per season for a total of 2500 hours of video footage. In addition, we conducted live observations in the field for two-hour segments at display areas and recorded over 100 hours of live observations using a hand-held voice recorder.

We identified and described 16 individually distinct components of the courtship display and scored videos for each of these behavioural elements as quantities, durations, or occurrences. We also scored videos for dominance behaviours, copulations, and vocalizations.

Statistical Analysis

We calculated the mean quantity or length of each display element per bout of dancing in JMP (10.0) and report means ± standard error. A bout refers to one continuous courtship display (i.e. no more than one minute between performed elements) including all elements of the display. A bout of hopping or butterfly display refers to only those segments of the display. We scored videos using JWatcher+video software (v1.0; Blumstein & Daniel 2007) to determine the stereotypical nature of the display. We created first order transitional probability matrices, based on 43 bouts of courtship display performed for females, to demonstrate the probability that one display element occurred after another. First, we created a transitional probability matrix that included repeated events, to illustrate the degree to which certain elements tended to repeat themselves within a display. Next, we recalculated the matrix so that repeated events were not incorporated and we could more accurately portray the progression from one element to the next. Using both of these matrices we created a schematic of the display to represent the sequence of elements as they most commonly occur (more than 10% of the time). To investigate the structure of the display at a higher order we created second order transitional probability matrices as well. These matrices illustrated the likelihood that given two specific elements occurred in a certain order, a third element followed.

Previous studies have revealed that the length of butterfly display is correlated with copulation success (McDonald 1989b; Ward 2012); however, we were interested in looking at individual elements within the display to determine which particular elements may be influencing courtship success. To determine which specific elements of the courtship display predict courtship success in long-tailed manakins, we used generalized linear mixed models in IBM SPSS Statistics (20.0). Our dataset was not normally distributed and could not be normalized by transformation, so we fitted our models with binomial distributions (logit-linked functions) and performed binary logistic regressions. Individually, we included each of 14 display elements as fixed factors to investigate whether the performance of one or more of these elements could predict a successful bout of courtship display. Several display elements were not quantified (scored for presence), or had small sample sizes, and were therefore omitted from these analyses. To account for repeated measures of individuals at the level of the lek, we classified the display area as a random factor. We performed these regressions for solo and dual-male displays separately and combined. We also performed Spearman's rank correlations on the display variables of interest to determine the level of intercorrelation between elements.

Results

Courtship display

We identified 16 unique visual elements performed by long-tailed manakins during courtship displays. All elements were performed to some extent in the presence of a female, though not all were necessary to elicit copulation. Manakins also produced 14 vocalizations, several of which were associated with specific elements the display.

The alpha male begins by singing ‘teamoo’ calls to attract his beta partner to the display area. This call is generally given in the canopy above the display perch. Once the beta arrives, the alpha and beta begin a series of simultaneous ‘toledo’ calls from the canopy to attract females to the area. When a female arrives, the males descend to the display perch and begin their elaborate courtship display which consists of at least 16 individual dance elements.

The visual components of the courtship display can be classified into two main categories based on the types of physical manoeuvres involved: the hopping display and the butterfly display, both of which have been previously described (McDonald 1989a). However, within these two categories are a number of individual subcomponents that we characterize here for the first time. Where possible, we use terminology that reflects any similarities to previously described manoeuvres exhibited during the courtship displays of other manakin species.

Hopping display

Stationary display – Two males perch roughly 10-15cm apart on the vine. To initiate the first part of the dual display, one male crouches down in a bowing position with his head lowered and his rump and tail in the air then proceeds to vibrate or ‘shiver’ his body. While in this position the male often appears to run in place, alternately lifting his feet. This display appears to occur in anticipation of the hopping display, similar to the stationary display in band-tailed manakins (*Pipra fasciicauda*) and the ‘wing shiver’ display in crimson-hooded manakins (*Pipra aureola*; Snow 1963; Robbins 1983). This display was common, but not always present before each bout of hopping.

Popcorn hop – After initiating with the stationary display, the same male leaps into the air above the perch and appears to hover there for several moments by rapidly flapping his wings. While in the air, the manakin hunches his back, lowers his head, and stretches his legs straight down, drawing attention to his bright blue, red, and orange body regions, respectively. He then descends to the perch in the same location where he began. As the first male lands, the second follows by hopping into the air in the same fashion as the first. The two males alternate this process. While the male on the perch waits for his partner to descend, he often performs the stationary display until it is his turn to jump. Similar display elements are exhibited in lance-tailed (‘up-and-down’; Duval 2007b) and orange-crested manakins, *Heterocercus aurantiivertex* (‘vertical dancing jumps’; Alonso 2000). The popcorn hop was previously described by Slud (1957) and later McDonald (1989a).

Leapfrog –Similar to popcorn hops, males alternate hopping into the air; however, instead of landing in the same place where he begins, the hopping male leaps backwards over his dance partner and take his place on the perch. Meanwhile, instead of exhibiting the stationary display, the male on the perch runs forward (towards the female) to take the place of the first male (Fig. 2.1a). The act appears as a backwards leapfrog dance and changes directions depending on which side of the perch the female is watching from. This type of display is common among other *Chiroxiphia* species (Gilliard 1959; Snow 1971; Foster 1977; Duval 2007a). Males frequently alternate between leapfrogs and popcorn hops within the same hopping display bout. On average, hopping bouts lasted for 36.6s ± 3.08 with a total of 35.6 ± 3.06 hops/leapfrogs per bout (7.6 ± 0.86 hops and 28.1 ± 2.89 leapfrogs).

While males participate in popcorn and leapfrog hops they emit calls that are synchronized with each hop. These calls have been described phonetically as 'nyanyownh' (Trainer & McDonald 1993). Males appear to switch between hops and leapfrogs depending on the location of a female (i.e. leapfrogs when female is on perch, hops when female is on nearby perch; per. obs.).

Buzz-weent – As the leapfrog display progresses and becomes more intense, males quicken their paces and reduce the heights of their hops, until the nyanyownh calls degenerate into a noisy series of buzzes. Eventually, the alpha male gives a sharp 'weent' call at the peak of his last hop and descends quickly in an arc down past the perch and swoops up to land on a nearby perch. The beta remains on the perch in a crouched position while the alpha completes this display. This call/manoeuvre is only exhibited by the dominant male of the pair, and is often absent during practice when younger males are displaying. After the alpha performs a buzz-weent, the beta either remains on the perch until the alpha begins the butterfly portion of the dual display, starts the butterfly dual display himself, or he leaves, allowing the alpha to begin his solo dance. Homologues to the buzz-weent display can also be seen in other *Chiroxiphia* manakins (Foster 1981; Duval 2007a).

Buzz-weents were common, with up to 6 per display, but were not always present at the end of hopping bouts.

Tucked wing-flick – Once the alpha performs a buzz-weent and lands on a nearby branch (either a horizontal or vertical branch) he begins to repeatedly flick his wings back behind his body without spreading them. He does this for several moments, an average of 5.9 ± 1.55 flicks, before beginning the butterfly display.

Butterfly display

All elements of the butterfly display occurred in both dual-male and solo performances. Butterfly displays varied between alpha and beta partnerships, and most (but not all) elements were performed to some degree at each display area. Males exhibited two types of elements during the butterfly display, including flight elements and landing postures. The average length of a dual-male butterfly display was 22.2s ± 1.73, and 190.3s ± 53.81 for a solo display.

Butterfly flight – Males make short, slow flights between the main display perch and other nearby perches with laboured wing flaps that resemble butterflies in flight. This is the iconic element for which the butterfly display was named and was previously described by Slud (1957) and McDonald (1989b). Butterfly flights are also seen in blue-crowned (*Lepidothrix coronata*) band-tailed, white-throated (*Corapipo gutturalis*), white-ruffed (*Corapipo leucorrhoa*) and white-crowned manakins (*Pipra pipra*; Snow 1960; Robbins 1983; Théry 1990; Rosselli et al. 2002; Castro-Astor et al. 2007; Durães 2009). Butterfly flights are the most common element in the butterfly display, with an average of 8.9 ± 0.72 flights per dual display and 34.5 ± 4.00 per solo display.

Dive – Dives are short flights between the main display perch and other nearby perches; each flight occurs very rapidly, with minimal wing flaps between take off and landing. They appear almost torpedo-like as males dart between perches. This display often alternates with butterfly flights. Occasionally males fly in an ‘s’-shaped flight pattern or a rapid upward arc towards the display perch (Fig. 2.1b). Straight rapid flights are also seen in the white-ruffed manakin (Rosselli et al. 2002), and flights with s-curved swoops are exhibited by crimson-hooded manakins and golden-headed manakins (*Pipra erythrocephala*; Prum 1990). Males exhibited an average of 1.87 ± 0.23 dives per dual display and 3.4 ± 0.60 dives per solo display.

Bounce – A male lands briefly on the perch and then immediately takes flight back in the direction from which he came, appearing to bounce off the perch (also seen in the lance-tailed manakin; Duval 2007b). Males performed an average of 0.1 ± 0.03 bounces per dual display and 1.5 ± 0.33 bounces per solo display.

Upright posture – A male lands on the perch after performing a flight element and proceeds to stretch his body, head, and bill upwards, before taking off again (Fig. 2.1b). This is similar to the upright postures seen in the red-headed manakin, *Pipra rubrocapilla*, and the round-tailed manakin, *Pipra chloromeros*, (Tello 2001; Castro-Astor et al. 2004). Males performed upright postures an average of 1.1 ± 0.15 times during dual male displays and 5.7 ± 0.91 times during solos.

Bill wipe – Males are often seen wiping their bills against the main display perch between butterfly flights and dives, in place of bounces, upright postures, or bows. It is unclear whether this is an important element of the courtship display, an excitatory response, or some other type of ritualized displacement behaviour (Tinbergen 1952; Scholes 2008). Males exhibited bill wipes an average of 1.2 ± 0.11 times in dual displays and 1.2 ± 0.20 times in solo displays.

About face – A male lands on a perch after a flight element, then quickly perform a 180° turn on the perch. This quick turn is either done in place, or results in the male landing approximately 10-15cm further down the length of the perch, almost as if he slides across the perch while switching directions. About faces are seen in other manakins including the golden-headed, lance-tailed ('quick-turn'), white-throated, white-crowned, and round-tailed manakins (Théry 1990; Tello 2001; Castro-Astor et al. 2004, 2007; Duval 2007a).

Lightning bolt – Between butterfly flights and dives, males occasionally fly to higher branches in the canopy to perform this display, in which they abruptly drop from the sky in a rapid vertical (or slightly diagonal) descent to land on the display perch directly below. Members of the genus *Corapipo* exhibit an 'above-the-canopy flight display', which incorporates a rapid plummet downwards from the canopy; however, it also includes a rapid upwards flight accompanied by a buzzy vocalization (Prum 1990), which not seen in long-tailed manakins. Males performed lightning bolts fairly infrequently, at an average of 0.1 ± 0.03 per dual butterfly display and 0.4 ± 0.11 per solo display (also observed by D.B. McDonald, pers. comm.).

Back-and-forth – During bouts of the butterfly display, one male often darts rapidly from side to side (approximately 10-15cm) on a horizontal (or more rarely, vertical) branch, seemingly using one wing at a time to propel him in the opposite direction (Fig. 2.1c). Males perform this display either individually or as a dual display (with two males facing each other on separate branches). This display is similar to the back-and-forth display of the lance-tailed manakin, the side-to-side display of the band-tailed manakin, and the side-to-side slide in both the red-headed manakin and the round-tailed manakin (Robbins 1983; Tello 2001; Castro-Astor et al. 2004; Duval 2007b). Males performed an average of 0.6 ± 0.21 back-and-forths per dual display and 2.4 ± 0.79 per solo display.

Angel flight – While on the perch, the male does a short, arcing, vertical flight and lands approximately 10-15cm further down the perch (or from another branch to the display perch), with his wing flaps exaggerated so the wings touch at each flap (Fig. 2.1d). Angel flights can also be performed from another branch towards the primary display perch. Usually the alpha male performs this display so that he positions himself directly next to the female prior to copulation. However, the alpha and beta occasionally perform this flight during the dual-male butterfly display, especially when multiple females are present or during practice dances in the absence of a female (pers. obs.). Males performed 0.04 ± 0.01 angel flights during dual-male butterfly displays and 0.5 ± 0.09 during solo displays.

Bows – After the alpha male performs an angel flight towards a female, he assumes an exaggerated bowing posture with his head lowered and his crest erected (Fig. 2.1d). Immediately after this display the alpha male makes a copulation attempt. On occasion males perform this display between flight elements during practice dances. Males displayed 0.02 ± 0.01 bows during dual male displays and 0.5 ± 0.07 during solos.

Copulation – A female observing the display often leaves the display area at any time throughout the courtship display, but if she remains for the entire display and is willing to copulate, she settles on the main display perch and allows the alpha male to mount her immediately following his angel flight and bow displays. After a short copulation, the male leaves the display area and the female generally remains on the perch for a few seconds up to a few minutes to preen. Copulations are not considered an element of the display, but rather the result of a successful display. Females generally copulated with males only once per display bout; however, 31% of display bouts that contained copulations included two copulation events. We were unable to determine whether multiple copulation events within a single display bout involved the same female.

Female display

Females are actively involved in the courtship display and exhibit several manoeuvres that appear to indicate excitement (Ward 2012).

Jump – Females often exhibit small jumps in place while observing courtship displays; jumps appear to increase with excitement.

Perch change – Females often observe the courtship display directly from the main display perch; however, they also fly to nearby branches and back, as if to observe the display from other angles.

Angel flight – On occasion, females fly between perches performing flights that appear to be identical to angel flights displayed by males. This usually occurs during an intense bout of the solo butterfly display, in which the female rapidly follows the alpha male from branch to branch. Female angel flights can also occur in place on the display perch.

Back-and-forth – This display is identical to the back-and-forth display performed by males, and is also exhibited by female lance-tailed manakins (Duval 2007).

Post-copulatory position – Immediately following copulation, females remain on the display perch and slowly stretch their legs so their bodies extended upwards for a few seconds.

Practice dancing

Predefinitive males tend to associate with several display areas and interact with many males before they gradually become associated with a primary display area (McDonald 2007). Males of all ages were often seen displaying in the absence of females, and there were several notable differences between practice displays and displays for females. Anywhere from one male up to five or six males practiced displaying simultaneously, with any combination of age groups participating.

Frenzied flutter – This display appears to be a pseudocopulation, in which males flutter on the display perch in the same fashion as if they had mounted a female, and is usually directly preceded by an angel flight and bow. Frenzied flutters are also seen in the blue-crowned manakin (*Lepidothrix coronata*), the red-headed manakin, the band-tailed manakin ('flutters'), the crimson-hooded manakin, the round-tailed manakin, the golden-headed manakin, and the white-crowned manakin (Robbins 1983; Prum 1990; Tello 2001; Castro-Astor et al. 2004, 2007; Durães 2009). This display is generally performed when a male is practicing a solo display, or shortly after female leaves the display area without mating (Tello 2001; Castro-Astor et al. 2004; Durães 2009), and may be reminiscent of displacement behaviour common to other species after being thwarted during courtship (Tinbergen 1952; Moynihan 1955).

Dual back-and-forth – In the absence of females, males occasionally face each other on parallel branches and perform this display as a dual-male display. They then take turns performing angel flights and bows towards each other, as if alternately imitating females.

Sequence and stereotypy of courtship display

All display elements but one (frenzied flutter) had a high probability of directly preceding at least one other element (>10% of the time); however, though no elements were completely independent of all others, some elements had only very low probabilities of directly following other elements (<10% of the time; see Fig. 2.2). Butterfly flights had high probabilities of both preceding and following the most display elements, with ten elements (including other butterfly flights) frequently preceding butterfly flights. Dives only had high probability of following other dives, and angel flights and lightning bolts did not have high probabilities of following any other display elements. There was a 30% probability that copulations would follow bows; however, all copulations that occurred were preceded by bows.

Long-tailed manakin displays demonstrated a moderate level of structure at the second-order as well, whereby certain display elements were highly likely to occur given that two specific elements directly preceded them. For example, given that a male performed a butterfly flight followed by a bounce, there was a 94% chance that a butterfly flight would follow (Table 2.1). All copulations followed angel flight-bow combinations (29% probability). Although courtship displays were highly stereotypical and structured, there was still considerable variation among individual displays, particularly between successful and unsuccessful displays.

Variation in display and copulation success

We were interested in investigating which specific display elements predicted copulation success during a bout of courtship display. Table 2.2 shows the results for solo displays, dual displays, and solo and dual displays combined. For solo displays, upright postures, angel flights, and bows predicted copulations. During dual displays, upright postures and leapfrogs predicted copulations. When combining solo and dual displays together, butterfly flights, upright postures, angel flights, and bows all predicted successful courtship displays. Many elements of the display were highly correlated (Table 2.3).

Discussion

Our study provides the first detailed description of all visual elements comprising the complex, coordinated courtship display of long-tailed manakins. Our study also reveals that many elements of the display follow a variable but stereotypical sequence, and that particular elements of the display can predict copulation success.

Long-tailed manakins exhibited a number of visual display elements that were similar to those of other manakins species. Several elements performed by long-tailed manakins were common to the genus *Chiroxiphia*, including variants of hopping, leapfrogs, butterfly displays, and buzz-weents (Gilliard 1959; Snow 1971; Foster 1981; Prum 1990; Duval 2007a). Furthermore, variants of the bow display occur in both lance-tailed and blue-backed manakins, both of which also acted as pre-copulatory displays (Snow 1963b; Duval 2007a). However, a number of display elements performed by long-tailed manakins were also similar to those performed by other manakin genera, including stationary displays, dives, upright postures, about faces, back-and-forths, and frenzied flutters (Snow 1963a; Robbins 1983; Prum 1990; Théry 1990; Tello 2001; Rosselli et al. 2002; Castro-Astor et al. 2004, 2007; Durães 2009). A recent phylogenetic study on Pipridae divided manakin species into two main clades, and placed the genus *Chiroxiphia* within one monophyletic group alongside *Antilophia*, *Xenopipo*, *Illicura*, *Masius*, and *Corapipo* (Mckay et al. 2010). Dives and about faces were similar to displays exhibited by members of *Corapipo*, though no elements were shared exclusively by this genus (Théry 1990; Rosselli et al. 2002). Many display elements, including several of those shared by members of *Chiroxiphia*, had similarities with displays exhibited by members of *Pipra*, a genus included in the other monophyletic group of manakins, which also includes *Lepidothrix*, *Heterocercus*, *Manacus*, *Machaeopterus*, and *Dixiphia* (Mckay et al. 2010). This suggests that some of these subcomponents may be basal elements of display among manakins, or that variants of these displays have evolved multiple times throughout the family (Prum 1997). Several other characteristics in this group have been known to evolve multiple times, including cooperative display, plumage patterns, and lek-breeding (Hellmayr 1910; Prum 1990, 1994, 1997; Mckay et al. 2010). Finally, at least one display element may be unique to long-tailed manakins. We have found no other record of displays similar to angel flights; however, full descriptions of courtship displays are not yet available for all species of manakin. Many descriptive accounts of manakin displays are brief and do not include detailed illustrations; therefore, it is difficult to determine whether certain elements of display differ significantly between species.

We were interested in whether long-tailed manakin displays followed a stereotypical sequence. We found evidence that certain transitions between display elements were highly probable in both first and second order transitional probability matrices, suggesting that long-tailed manakin displays are highly structured and stereotypical. Transitions between some elements were particularly stereotypical (e.g. angel flights to bows), suggesting that females may prefer certain combinations of elements more than the individual elements alone. Stereotypy is a common phenomenon in courtship (Tinbergen 1952); however, studies that quantify the level stereotypy in displays are relatively rare. Previous research on the sequence of courtship display of the closely related lance-tailed manakin has revealed a highly structured display (Duval 2007a). For elements shared between lance-tailed and long-tailed manakins, many of the same highly stereotypical transitions were observed, including the progression from hopping display to a buzz-weent homologue to butterfly display, as well as the transition from bow displays to copulations (Duval 2007a). A study on zebra finches (*Taeniopygia guttata*) demonstrated that dance displays tended to be stereotypical at the level of individuals and closely related family members, but not across all males (Williams 2001). A number of other avian studies report detailed accounts of stereotypical courtship displays, including barbary doves (*Streptopelia ristoria*; Fusani et al. 1997), and Anna's hummingbirds (*Calypte anna*; Clark 2009). Like manakins, birds of paradise are known for their diverse and spectacular courtship displays (Scholes 2006). Several studies conducted on the behavioural patterns of birds of paradise have revealed high levels of structure and organization in the courtship displays of several *Parotia* species (Scholes 2006, 2007, 2008).

Studies that focus on overall ethological structure, rather than individual display elements alone, may reveal important behavioural patterns that females use to choose mates. One study modified the display areas of golden-collared manakins (*Manacus vitellinus*) in such a way that the final pre-copulatory display element could not be performed properly (Coccon & Barney 2012). Therefore, males were no longer able to perform successful courtship displays because the stereotypical sequence of courtship display was interrupted, which probably reduced the attractiveness of the display to females (Coccon & Barney 2012). This type of study demonstrates the importance of understanding the structure of the courtship display as a whole; however, it is also important to understand how variation among displays can drastically affect the quality and outcome of these displays. Although we found high levels of stereotypy and structure in the courtship displays of long-tailed manakins, there was substantial individual variation among courtship displays, and this variation may influence copulation success.

We were interested in investigating the variation in performance of display elements between successful and unsuccessful dance bouts to determine whether specific display elements could predict copulation success. First we looked at complete displays, including both solo and dual performances, and we found that butterfly flights, upright postures, angel flights, and bows all predicted copulation success. This implies that butterfly flights and upright postures may be particularly important in the display, whereas other elements (e.g. bill wipes, back-and-forths) may not be necessary to elicit copulations. Similarly, for solo displays we found that upright postures, angel flights, and bows predicted successful displays. In contrast to previous research conducted on the correlates of mating success in long-tailed manakins (McDonald 1989b; Ward 2012), we did not find length of butterfly or total length of display to predict copulation. However, butterfly flights were the most ubiquitous display element performed, followed by upright postures, and therefore they probably both contribute largely to the overall length of the display. Angel flights and bows are display elements that directly precede copulation (McDonald 2010), so it is not surprising that these elements predict copulation success, particularly in solo displays wherein they most commonly occur.

When investigating dual displays only, we found that upright postures once again predicted copulations. In addition, leapfrogs also predicted mating success, but angel flights and bows did not. This suggests that the dual display plays an important role in the success of the overall courtship display, further reinforcing the idea that cooperative courtship is obligate in long-tailed manakins (Foster 1977; McDonald 1993a; Trainer & McDonald 1993). Leapfrog-like display elements are common to all *Chiroxiphia* species (Gilliard 1959; Foster 1981; Duval 2007a), and the highly conserved nature of this display among congeners may further suggest their importance in the courtship display. Angel flights and bows always occur directly before copulation attempts, and since copulations are relatively uncommon during the dual portion of the display, angel flights and bows are also much less likely to occur during dual display.

It is important to note that many of the display elements were highly correlated, and therefore it is difficult to determine which element, or combination of elements, may be responsible for influencing the mating success of courting males. For example, angel flights and bows are highly correlated, as are upright postures and a number of flight elements including butterfly flights, dives, and lightning bolts. We demonstrated earlier that the display is highly stereotypical in nature, and those elements of the display that are highly correlated are often elements that directly precede or follow one another. Perhaps females are not only cueing in on individual subcomponents of the display, but also how stereotypically the displays are performed by males. For example, females may be interested in upright postures, but perhaps they show stronger responses to upright postures directly preceded (or followed) by butterfly flights or dives. Certain combinations of display elements appear to be required, as all copulations were preceded by angel flight-bow combinations. Although there is variation between pairs of displaying males, reinforcement from choosy females has likely shaped the evolution of stereotypical displays in this species.

High levels of individual variation between displaying males, and thus high variance in copulation success is common among lekking species (Bradbury 1981; Bradbury & Gibson 1983; Hoglund & Alatalo 1995). Although courtship display may be highly ritualized, females can detect minute differences in attractive components of displays (Bradbury & Gibson 1983), and therefore understanding how variation at the level of individual subcomponents, as well as the display as a whole, has important implications for understanding mate choice. In lekking species, all parental care is provided by females; therefore, females likely choose males based on the potential of gaining indirect fitness benefits for their offspring (Bradbury & Gibson 1983; Kodric-brown & Brown 1984; Kirkpatrick & Ryan 1991). In long-tailed manakins, the performance of display elements such as upright postures, angel flights, and bows may indicate superior genetic quality to females, which could be based on rate of display, stereotypy, energetic requirements, or coordination with other males. Further research on how females assess these particular display elements will help our understanding of the underlying mechanisms of mate choice in this species.

Our research provides the first detailed characterization of courtship display in long-tailed manakins, and has revealed at least one subcomponent that may be unique to this species. We also demonstrated that courtship display is highly stereotyped in this species. Nevertheless, variation in display among pairs of alpha and beta males results in the performance of certain display elements predicting mating success. This research may help our understanding of how mate choice influences the evolution of a highly complex and stereotyped courtship display.

Tables and figures

Table 2.1: Common second order transitions between elements of the long-tailed manakin courtship display, showing the probability a third element occurs given that two prior elements have been performed (all transitions with 0.70 probability or higher).

Element combination	**Probability**
About face – upright posture -> butterfly flight	0.94
Angel flight – bounce -> butterfly flight	0.96
Bill wipe – about face -> butterfly flight	0.90
Bill wipe – stationary display -> hopping display	0.88
Butterfly flight – angel flight -> bow	0.82
Butterfly flight – bounce -> butterfly flight	0.94
Butterfly flight – lightning bolt -> upright posture	0.94
Butterfly flight – stationary display -> hopping display	0.87
Butterfly flight – upright posture -> butterfly flight	0.82
Dive – upright posture -> butterfly flight	0.71
Lightning bolt – upright posture -> butterfly flight	0.80
Stationary display – butterfly flight -> butterfly flight	0.81
Upright posture – about face -> butterfly flight	0.85
Upright posture – bill wipe -> butterfly flight	0.74
Upright posture – stationary display -> hopping display	0.76

Table 2.2: Elements of the long-tailed manakin courtship display, as performed by definitive males for females, predicting mating success during bouts of solo display, dual display, and a combination of both. Double dashes indicate display elements not included in solo displays.

	Solo display	**Dual display**	**Combined display**
Display elements	**$F_{1,50}$**	**$F_{1,89}$**	**$F_{1,141}$**
Hop length (s)	--	2.18	0.11
Leapfrogs	--	4.19*	0.99
Popcorn hops	--	1.37	3.3
Butterfly length (s)	0.19	2.17	0.001
Butterfly flights	1.92	2.54	4.20*
Dives	0.31	0.01	0.10
Lightning bolts	0.90	0.12	1.11
Upright postures	5.86*	6.00*	8.80**
Back-and-forths	0.26	0.80	0.28
Bounces	0.02	0.07	0.29
Bill wipes	1.43	1.35	1.09
Angel flights	5.68*	0.84	7.81**
Bows	7.61**	30.7	10.04**
Total length (s)	--	0.79	0.08

Stars indicate significant P-values: (*) represents P-values less than 0.05; (**) represents P-values less than 0.01. Degrees of freedom for each column of analyses are shown in subscript after ‘F’.

Table 2.3: Pairwise Spearman's rank correlations of fourteen elements of long-tailed manakin courtship display.

Display elements	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**
Hop length (A)	1													
Leapfrogs (B)	0.92**	1												
Popcorn hops (C)	0.56**	0.31	1											
Butterfly length (D)	-0.21	0.02	-0.58**	1										
Butterfly flights (E)	-0.09	0.13	-0.38	0.87**	1									
Dives (F)	0.12	0.20	-0.24	0.67**	0.65**	1								
Lightning bolts (G)	0.11	0.33	-0.17	0.34	0.50*	0.23	1							
Upright postures (H)	-0.25	-0.08	-0.46*	0.84**	0.77**	0.72**	0.46*	1						
Back-and-forths (I)	0.46*	0.57**	0.23	0.31	0.48*	0.25	0.54*	0.25	1					
Bounces (J)	0.37	0.52*	0.05	0.44*	0.66**	0.40	0.61**	0.36	0.82**	1				
Bill wipes (K)	0.13	0.30	-0.16	0.15	0.03	0.12	0.37	0.30	0.31	0.03	1			
Angel flights (L)	0.36	0.55*	0.06	0.39	0.55*	0.35	0.44*	0.29	0.74**	0.77**	0.23	1		
Bows (M)	0.32	0.56**	-0.02	0.42	0.57**	0.32	0.50*	0.32	0.71**	0.74**	0.30	0.97**	1	
Total length (N)	0.55*	0.73**	-0.11	0.49*	0.46*	0.34	0.31	0.26	0.43	0.43	0.34	0.48*	0.50*	1

Stars indicate significant P-values: (*) represents P-values less than 0.05; (**) represents P-values less than 0.01.

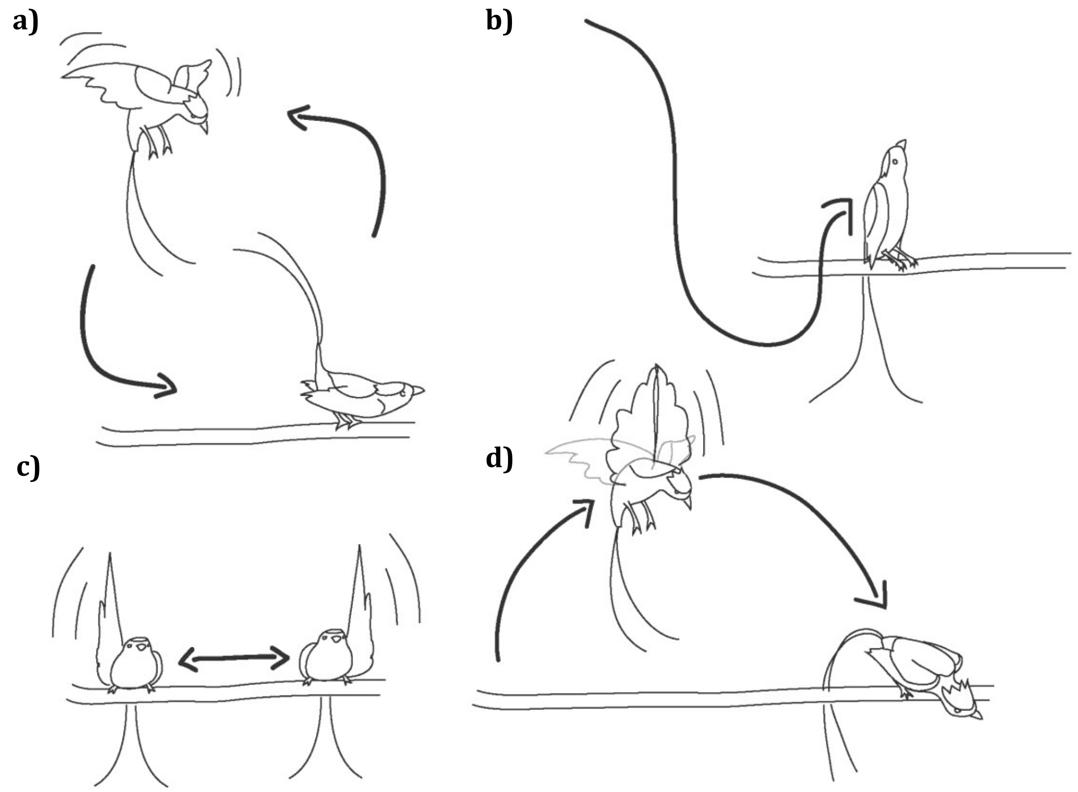

Figure 2.1: Elements of the long-tailed manakin courtship display: a) two males performing leapfrogs, b) male exhibiting an upright posture after performing a dive with an s-curved flight pattern, c) male exhibiting back-and-forth displays, d) male performing an angel flight and landing in a bow position. (Illustrations by K.C. Lukianchuk)

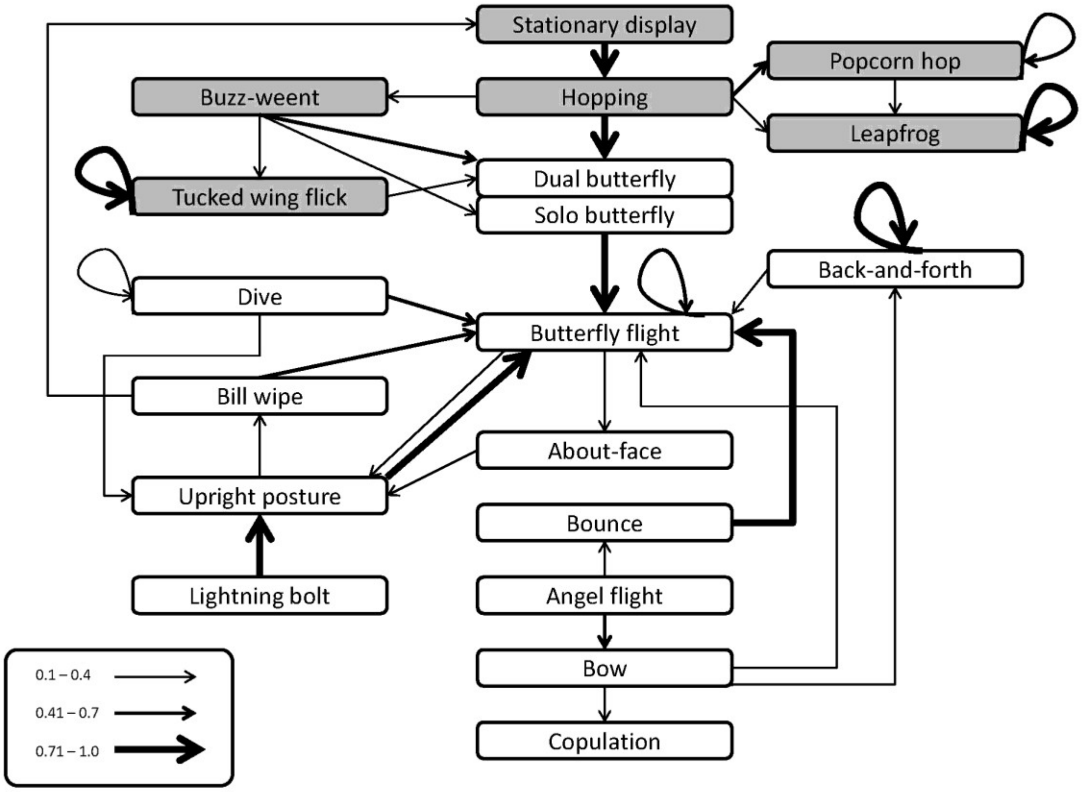

Figure 2.2: Schematic of individual display elements of long-tailed manakin courtship display during dances for females. Shaded boxes represent elements found within the hopping portion of the display; white boxes represent elements found within the butterfly portion of the display. Arrow thickness shows the probability that one display element follows another, based on the transitional probability matrix produced from 43 bouts of courtship display. Note that some elements are not preceded by other elements with high probabilities, as they occur more rarely during displays (e.g. lightning bolts, angel flights, etc.). Therefore, a direct sequence may not be drawn from the beginning of the display through to the end (copulation) using only probabilities above 0.1. However, when considering transition probabilities of less than 0.1, paths exist between butterfly flights and back-and-forths, and between back-and-forths and angel flights.

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CHAPTER 3

A young manakin knows his place: evidence for an age-graded dominance hierarchy among young long-tailed manakins

Introduction

In social species, dominance hierarchies are both common (McDonald & Shizuka 2012) and crucial in maintaining the organization and fitness of individuals within the group (Maynard Smith & Price 1973). In most cases, hierarchies are formed based on the outcome of aggressive interactions (Chase 1982), but the relative ranks of individuals in some species can be predicted by size (Andersson 1994; Beaugrand et al. 1996; Zucker & Murray 1996; Schuett 1997), testosterone (Rohwer & Rohwer 1978), previous encounter experiences (Chase 1982; Beaugrand et al. 1996; Daws et al. 2002; Francis 2010), bold behaviours (e.g. exploration rate; Verbeek et al. 1996), and even age (McDonald 1989a, 1989b; Bang & Gadagkar 2012). When dominance hierarchies are present, extreme aggression between competing males is relatively rare to reduce frequent injuries (Maynard Smith & Price 1973; Bang & Gadagkar 2012). Instead, ritualized displays, modified weapons, or status signalling mechanisms can resolve antagonistic interactions without physical violence and injury (Darwin 1859; Maynard Smith & Price 1973; Lyon & Montgomerie 1986; Maynard Smith et al. 1988; Andersson 1994). Status signalling mechanisms involve the use of variable characteristics, such as plumage, that act as honest signals to indicate quality or rank of individuals and reduce levels of intrasexual aggression (Rohwer 1977; Lyon & Montgomerie 1986; Moller 1987; Whitfield 1987; Maynard Smith et al. 1988; Senar & Camerino 1998; but see Rohwer & Ewald 1985). If males can establish a dominance hierarchy by evaluating physical characteristics, unnecessary fights can be avoided.

In lekking species, there are often very few high ranking individuals and many subordinates, resulting in steep dominance hierarchies (Beehler & Foster 1988; McDonald 1989a; Gibson 1996; Hogland et al. 1997). Males aggregate at leks to perform courtship displays for females, and only the highest ranking males gain mating opportunities (Bradbury 1981; Bradbury & Gibson 1983; Hoglund & Alatalo 1995). Long-tailed manakins exhibit an exploded lek breeding system (Foster 1977), in which unrelated males (McDonald 2009) gather at display areas to perform highly cooperative courtship displays. At each display area, one pair of top-ranking males (alpha and beta) form long-term partnerships and perform highly coordinated displays for females. Displays consist of two major components known as the 'hopping display' and the 'butterfly display' (McDonald 1989b). In the hopping display, males alternately perform vertical hops on the display perch, and during the butterfly display, they perform various flight elements and postures within the display area (McDonald 1989b; Chapter 2). Females visit and choose between display areas, but always copulate with the resident alpha (McDonald 1989b). Up to 13 males may be associated with each display area (McDonald & Potts 1994); however, younger males are often loosely affiliated with several neighbouring display areas (McDonald 2009). Although only alpha and beta males have the opportunity to display for females, males of all ages practice the display in the absence of females (McDonald 1989a). Males of this species undergo delayed plumage maturation, whereby young males take four years before achieving definitive adult plumage in their fifth year, with a unique plumage pattern for each of their predefinitive years (Foster 1987; McDonald 1989b; Doucet et al. 2007). Although delayed plumage maturation is relatively common among passerines (reviewed in: Hawkins et al. 2012), age-graded plumage categories are very unusual, and may facilitate the establishment of an age-graded dominance hierarchy in long-tailed manakins.

There is strong evidence for a dominance hierarchy among alpha and beta male long-tailed manakins, whereby alphas obtain copulations and perform dominance behaviours towards betas (Foster 1977; McDonald 1989a, 1993a, 1993b). Alphas and betas also routinely chase other definitive males and younger males away from display perches when females are present (McDonald 1989a, 1989b, 1993b; Trainer & McDonald 1993). In a model presentation experiment, alpha and beta reactions towards a mount in definitive plumage were much stronger than their reactions towards a mount in second-year plumage, suggesting that older males posed more of a threat (i.e. through stolen copulations or disruption of dominance hierarchy) than younger males (McDonald 1993b). This research provided some evidence that delayed plumage maturation in this species may serve as a status signalling mechanism (McDonald 1993b, 2010). However, it is unclear whether male long-tailed manakins of all ages exhibit dominance behaviours according to this strict orderly queue. Since higher levels of social connectivity in young males predict reproductive success later on in life (McDonald 2007), social interactions among young males may be particularly important.

The purpose of our study is to characterize the dominance hierarchy in long-tailed manakins and to determine whether a status signalling mechanism enforces a strict dominance hierarchy among males of all ages. Our aim is to evaluate whether older males exhibit aggressive behaviours more frequently than young males. If age indicates status, older males should direct aggressive behaviours towards younger males, and young males should rarely or never direct aggressive behaviours towards older males. In addition, if age indicates status, there should be less aggression between males from different age categories than males of the same age. Finally, we examined courtship displays to determine whether older males tended to initiate bouts of display more frequently than younger males, as older males are more likely to gain mating opportunities through display than younger males.

Methods

Long-tailed manakins (family Pipridae) are a Neotropical suboscine species that range from Mexico to Costa Rica. Delayed plumage in this species allows for the age of males to be easily identified in the field. We conducted our research in the Santa Rosa sector of the Area de Conservacion Guanacaste in northwestern Costa Rica. Tropical dry forest dominates this long-term study site and long-tailed manakins are abundant in patches of evergreen forest in this region. Through long-term banding efforts over the past nine years, over 750 manakins have been captured using mist-nets and banded with unique leg-band combinations. With the ability to recognize individuals in the field, we were able to locate discrete display areas based on the associations of alpha, beta, and subordinate males. However, many males remained un-banded; therefore, for the purposes of this study we classified males into age cohorts based on unique plumage patterns. Long-tailed manakin display areas contain a primary display perch as well as up to several additional display perches. Most courtship displays, for females or practice, are performed on the primary display perch; however, additional perches may be used frequently for practice displays or if a disturbance near the primary display perch has occurred.

We located 37 display areas and all active display perches within each area. We set up five video cameras 5-15m away from display perches each day for approximately five hours starting at dawn to collect video footage of courtship displays and dominance behaviours. We sampled each display area 2-5 times per season over the course of three years (April-Jun) in 2010-2012 for a total of 2500 hours. These observations were supplemented with over 100 hours of live observations performed in the field.

We scored videos for aggressive behaviours, elements of the courtship display, copulations, and vocalizations. When scoring for aggressive behaviours, we accounted for the number of males present, the age classes they belonged to, which male exhibited the behaviour, and towards which individual the behaviour was directed. Long-tailed manakins exhibit several types of aggressive behaviours that are common among other species, including chases and displacements (Rohwer 1977; Woolfenden & W 1977; Maynard Smith et al. 1988; Heindl 2002; Rosselli et al.

2002; Torney et al. 2011; Hernowo et al. 2011; Hawkins et al. 2012). In addition to these aggressive behaviours, we also scored videos for buzz-weent vocalizations and initiation of displays. We considered a chase to have occurred when a male actively chased and followed another male away from the display perch. Males often pursued the chase until the subordinate left the area. We considered a displacement to have occurred when a male flew towards another male and took his place on the display perch, causing the already perched subordinate male to move, but not necessarily leave the display area. Long-tailed manakins exhibit a behaviour (and an accompanying vocalization) called the buzz-weent, which is part of the courtship display but is also considered to be an aggressive behaviour, displayed only by dominant males towards subordinates (McDonald 2010). The buzz-weent occurs at the end of a hopping bout (Trainer & McDonald 1993). The subordinate male remains crouched on the perch while the dominant male performs a final leap into the air followed by a sharp arc down past the perch to land on a nearby branch. This behaviour is usually followed by the initiation of the butterfly display. Initiation of displays (both courtship and aggressive displays) by a particular male may also be an important indicator of status (Robbins 1983; Verbeek et al. 1996; Zucker & Murray 1996; Sih et al. 2009; Stukenborg et al. 2012). We considered initiation for either of the two main components of the courtship display (hopping and butterfly) to have occurred when one male performed the first hop or the first element of the butterfly display.

Statistical analysis

We used chi-squared tests to determine whether older males directed agonistic behaviours towards younger males more frequently than expected if interactions were directed equally in both directions. Interactions between all combinations of mixed-age males (i.e. a definitive and a predefinitive, or two predefinitives from different age classes) were scored as either ‘older’ or ‘younger’ when the behaviour was exhibited by the older or younger male, respectively. Therefore, all mixed-age pairs of males could be analyzed using one chi-squared test for each of the aggressive behaviours. We did not separate each dominance interaction down to the age level as sample sizes for each combination were too low. We also tested whether aggressive behaviours occurred more frequently between mixed-age pairs of males or equal-age pairs of males using chi-squared tests. Finally, we tested whether older males initiated dancing bouts more frequently than expected for both hopping and butterfly displays. Although we could not identify individuals, interactions between unique combinations of age groups occurred infrequently enough at each display site that that our observations can be considered independent from one another.

Results

When combining all mixed-age pairs of males involved in aggressive interactions, older males chased younger males significantly more than young males chased older males (older=73, younger=6; χ^2_1=56.82; P<0.001; Fig. 3.1a). Older males displaced younger males significantly more than young males displaced older males (older=79, younger=7; χ^2_1=60.28; P<0.001; Fig. 3.1b). When combining all possible male combinations (two or more males, whereby males were from at least two different age categories), older males exhibited buzz-weents towards younger males significantly more than young males exhibited buzz-weents towards older males (older=79, younger=4; χ^2_1=67.77; P<0.001). When only including buzz-weent behaviours exhibited by males in mixed-age pairs, older males still exhibited significantly more buzz-weents than young males (older=31, younger=1; χ^2_1=28.13; P<0.001; Fig. 3.1c).

When comparing aggressive interactions between mixed-age pairs of males and equal-age pairs of males, significantly more chases occurred between males of the same age than between males of mixed ages (equal-age=148, mixed-age=79; χ^2_1=20.97; P<0.001; Fig. 3.2a). Likewise, buzz-weents occurred significantly more times between equal-age males than between mixed-age males (equal-age=165, mixed-age=39; χ^2_1=77.82; P<0.001; Fig. 3.2c). However, significantly more displacements occurred between mixed-age males than between equal-age males (equal-age=60, mixed-age=86; χ^2_1=4.63; P=0.03; Fig. 3.2b).

Males often practiced hopping and butterfly displays with more than one display partner. In this case, when combining all combinations of mixed-age males, there were no significant differences between older and younger males initiating bouts of hopping (older=238, younger=276; χ^2_1=2.81, P=0.09) or bouts of butterfly displays (older=226, younger=241; χ^2_1=0.48; P=0.49). When only including displays between mixed-age pairs of males, there were no significant differences between older and younger males initiating bouts of hopping (older=128, younger=148;

χ^2_1=1.45; P=0.23; Fig. 3.3a) or bouts of butterfly displays (older=88, younger=87; χ^2_1=0.01; P=0.93; Fig. 3.3b).

Discussion

In this study, we provide the first evidence that age-graded dominance in the long-tailed manakin applies not only to alpha and beta individuals, but is consistent across all ages, and that status signalling is likely facilitated through differences in plumage stages. Specifically, we found that older males direct chases, displacements, and buzz-weents towards younger males across pairs of all age combinations, and that aggressive behaviours directed towards older males were extremely rare. This supports the prediction that males of all ages should be able to recognize the relative ages of males they interact with (presumably based on plumage pattern) to determine their place in the age-graded dominance hierarchy and perform dominance behaviours accordingly. We also found that aggressive behaviours were more common between males of similar age categories, where status signalling in plumage is likely less clear. We did not find any evidence that the initiation of courtship displays was an indicator of status during practice displays in this species.

Older males exhibited chases, displacements, and buzz-weents towards younger males significantly more often than young males exhibited these behaviours towards older males, suggesting that these behaviours serve as reinforcement mechanisms for the already established linear dominance hierarchy. McDonald (1989a) provided anecdotal evidence for this among top-ranking individuals, whereby alpha and beta males frequently displaced lower-ranking males that were participating in courtship displays. Foster (1981) also reported frequent displacements and chases among congeneric blue manakin males, *Chiroxiphia caudata*, whereby males often chased away males displaying for females and took over the solo phase of the display, indicating the chasers may be of higher status.

Dominance rankings between males from the same age categories may be less clear if males are not able to use plumage alone as a reliable status signalling mechanism (Maynard Smith et al. 1988; McDonald 1989a, 1993b). Although there is considerable variation in plumage within each age cohort (Doucet et al. 2007), it is unclear whether these differences are used for status signalling, individual recognition, or both; however, if age is the most important factor in determining dominance, then males within the same cohort are more likely to challenge each other often, especially when new individuals are involved. Furthermore, status between males of different age classes should be well established, reducing aggression between these males. Therefore, dominance interactions should occur more frequently between males from the same age category than between males from different age categories. This idea is supported by the frequency of chases between males from the same age category. The majority of chases that occurred between equal-aged males were between pairs of definitive males (142 chases of a total of 148); however predefinitives from the same age category did engage in aggressive behaviours as well. Definitive males displayed far more than younger males, so this may simply be a result of the overall quantity of time spent at display areas. However, chases appear to be much more aggressive than displacements, so it is intuitive that definitive males, who have much higher probabilities of obtaining mating opportunities than younger males, would be more aggressive towards intruding males of the same age (Maynard Smith et al. 1988). This has been demonstrated in other social species such as house sparrows (*Passer domesticus*), in which males have black bibs that differ in relation to social rank, and aggression is higher between males with similar sized patches (Moller 1987; Laucht & Dale 2012). On the other hand, male siskins (*Carduelis spinus*) avoid being in close proximity with other males who have larger bibs (Senar & Camerino 1998).

We found the opposite trend in the frequency of displacements, whereby males displaced males from different age categories significantly more than males from the same age category. Definitives exhibited the majority of displacements to either other definitives or to predefinitives (142 displacements of a total of 146), though predefinitives did exhibit aggressive behaviours to other predefinitives as well. If definitive males are expending more energy on highly aggressive behaviours like chases towards other definitives, it may not be necessary to expend as much energy towards fending off low-ranked predefinitives (Lyon & Montgomerie 1986; McDonald 1989a; Hawkins et al. 2012). Therefore, having a range of aggressive behaviours may be beneficial so that males can choose the most optimal dominance behaviour depending on the rank of their opponents, conserving energy and reducing the risk of injury. A broad range of aggressive behaviours is common among other species as well (Woolfenden & W 1977; Chase 1982; Lovari & Locati 1991; Jenssen et al. 2012; Baker et al. 2012), and although the reason for this remains unclear, it is possible those different behaviours may have varying levels of energetic expenditure required by the aggressor.

Significantly more buzz-weents occurred between males from the same age category than between males from different age categories. Once again, pairs of definitive males exhibited the highest quantity of buzz-weents between equal-aged pairs (158 buzz-weents of a total of 165). This is not surprising, as buzz-weents are not only used to exert dominance, but they are also used as a display element exhibited during the hopping phase of the courtship display. Therefore, it is likely that this element occurs much more frequently between definitives (and even more likely, between alpha and beta males) because they tend to display at a much higher rate than do younger males. In a study by Trainer & McDonald (1993) on the vocal repertoire of long-tailed manakins, buzz-weents were given only by dominant males, and only between an alpha and other males or between definitive males and predefinitives. In the closely related lance-tailed manakin, *Chiroxiphia lanceolata*, only alpha males performed the *eek* display (homologous to the buzz-weent display in long-tailed manakins) in the presence of females (Duval 2007b). Although in most cases we were unable to determine the initial ranks of males involved in buzz-weents, it is likely that the majority of interactions between two definitives involved an alpha male.

The use of display elements for dominance occurs in other manakin species as well, whereby males perform displays in the absence of females as a means of establishing dominance through competition (Tello 2001; Ryder et al. 2011). This may also be true for blue manakins, which, like long-tailed manakins, exhibit a dual hopping display that terminates with a buzzing component (Foster 1981). In black grouse (*Tetrao tetrix*), males perform a suite of display behaviours at lekking sites, however, only a small portion of these behaviours are actually performed in the presence of females, whereas the rest may be used to establish dominance hierarchies (Hogland et al. 1997). Buzz-weents are often present, but not necessary in the courtship display to elicit copulations from females (see Ch. 2). Perhaps long-tailed manakins use display elements such as the buzz-weent in addition to other dominance behaviours to easily enforce and maintain established dominance hierarchies in the absence of females.

In previous research conducted on long-tailed manakins, Foster (1977) observed that the alpha male tended to reinitiate displays after a disruption of the hopping bout, and that the third-ranked (gamma) male never reinitiated displays. Initiation of displays is an important indicator of dominance in other species as well (e.g. Florida scrub jays, *Alphelocoma coerulescens*; Woolfenden & W 1977; Apennine chamois, *Rupricapra spp.*; Lovari & Locati 1991; great tits, *Parus major*; Verbeek et al. 1996; pigs, *Sus domesticus*; Stukenborg et al. 2012). Therefore, we predicted that older males would initiate courtship displays more frequently than young males; however, we did not find any significant differences in initiation behaviour between older and younger males for either hopping or butterfly displays. Perhaps the initiation of display as an indicator of dominance is more important when females are present, which may explain why we were unable to detect a trend for practice displays. Practice display in has been documented in many other Pipridae species, and often these displays are reported to differ slightly from that of displays for females (Skutch 1949; Foster 1981; Robbins 1983; Théry 1990; Heindl 2002; Rosselli et al. 2002; Shorey 2002; Castro-Astor et al. 2004; Duval & Kempenaers 2008; Durães 2009).

A potential behaviour that we did not consider for the current study was whether males in the display area decided to participate when another male initiated a display. For example, if a predefinitive begins displaying, a definitive may be present but decide not to join the younger male. It is possible that the act of joining or declining an initiated display reveals certain relationships between males as well (Snow 1971). Furthermore, there are probably a number of submissive behaviours exhibited by subordinate male long-tailed manakins that may also help maintain the dominance hierarchy (e.g. chitter; Trainer & McDonald 1993; McDonald 1993b).

In conclusion, our research supports the presence of an age-graded dominance hierarchy among male long-tailed manakins, with older males exhibiting three of the tested dominance behaviours significantly more than younger males. It also provides support for delayed plumage maturation acting as a status signalling system, whereby more aggression is seen between males of the same age than between age classes. Finally, we found no evidence of older males initiating practice displays more frequently than younger males, suggesting that initiating these particular elements of the courtship display (i.e. hopping and butterfly displays) may not be important in establishing dominance hierarchies when females are absent from display areas. Although relatively few dominance interactions occurred between predefinitive age classes, older predefinitives did direct aggressive behaviours towards younger predefinitives. Differences in plumage patterns are likely enough to mitigate aggression between predefinitives, and in the long run young males may benefit from accepting their position in the hierarchy, as females tend to leave display areas when males exhibit aggression (McDonald 2010). Future studies may benefit from an entirely banded population so that ranks of individuals within age classes can be identified and monitored over the long term. Research on the variation in plumage within age classes may help elucidate whether males use these minor differences as status signals and/or individual recognition. This research contributes to our knowledge of intrasexual relationships in the highly cooperative long-tailed manakin, and may help us understand how complex hierarchical systems evolve.

Tables and figures

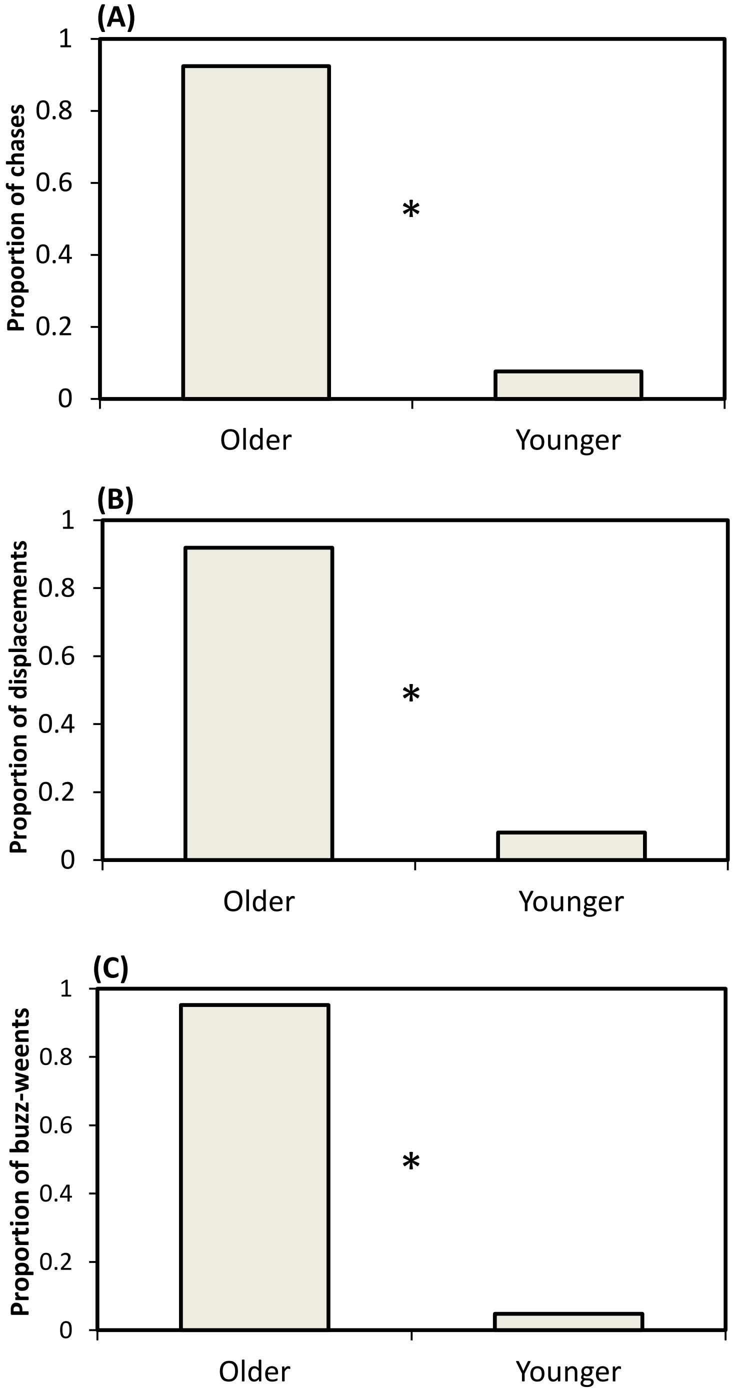

Figure 3.1. Proportion of aggressive behaviours performed by older versus younger long-tailed manakins during courtship displays, including, including (A) chases, (B) displacements, and (C) buzz-weent vocalizations. Stars between bars indicate a significant difference (P<0.05) between older and younger males.

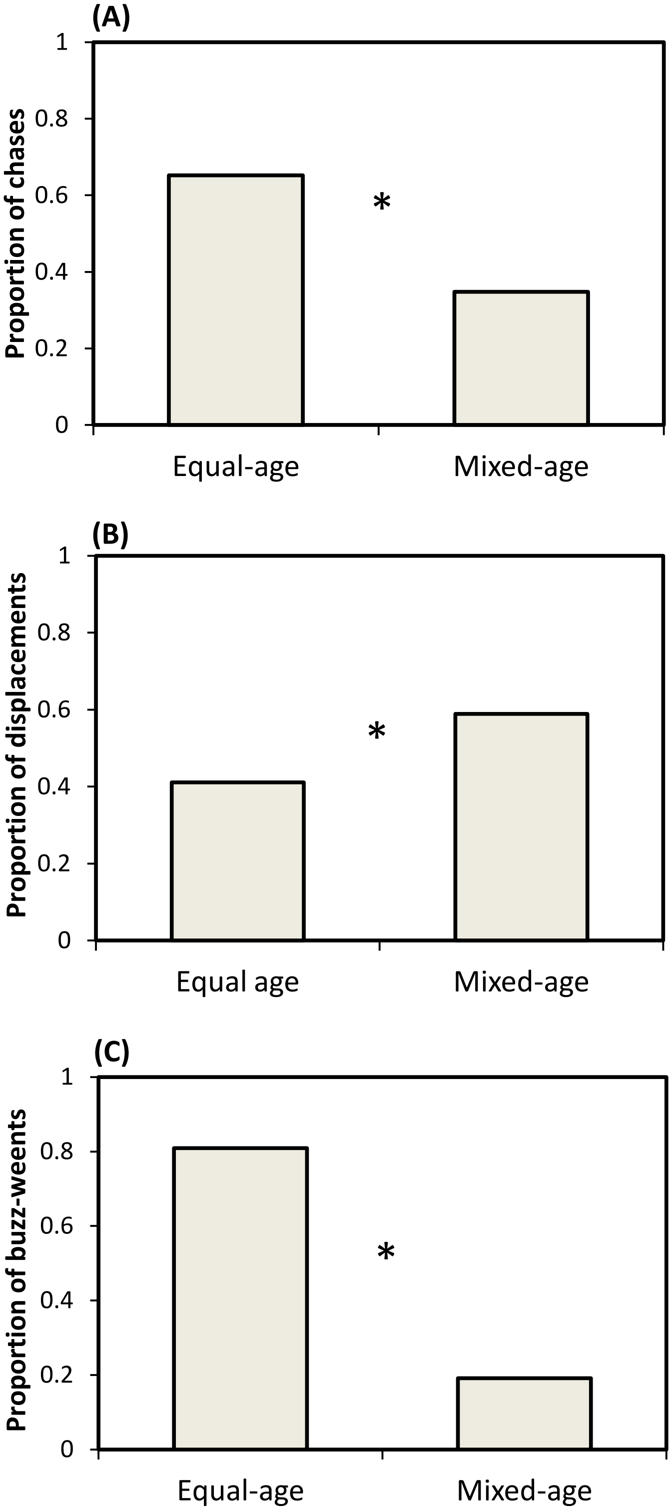

Figure 3.2. Proportion of aggressive behaviours performed by equal-age versus mixed-age pairs of long-tailed manakins during courtship displays, including (A) chases, (B) displacements, and (C) buzz-weent vocalizations. Stars between bars indicate a significant difference ($P<0.05$) between equal-age and mixed-age males.

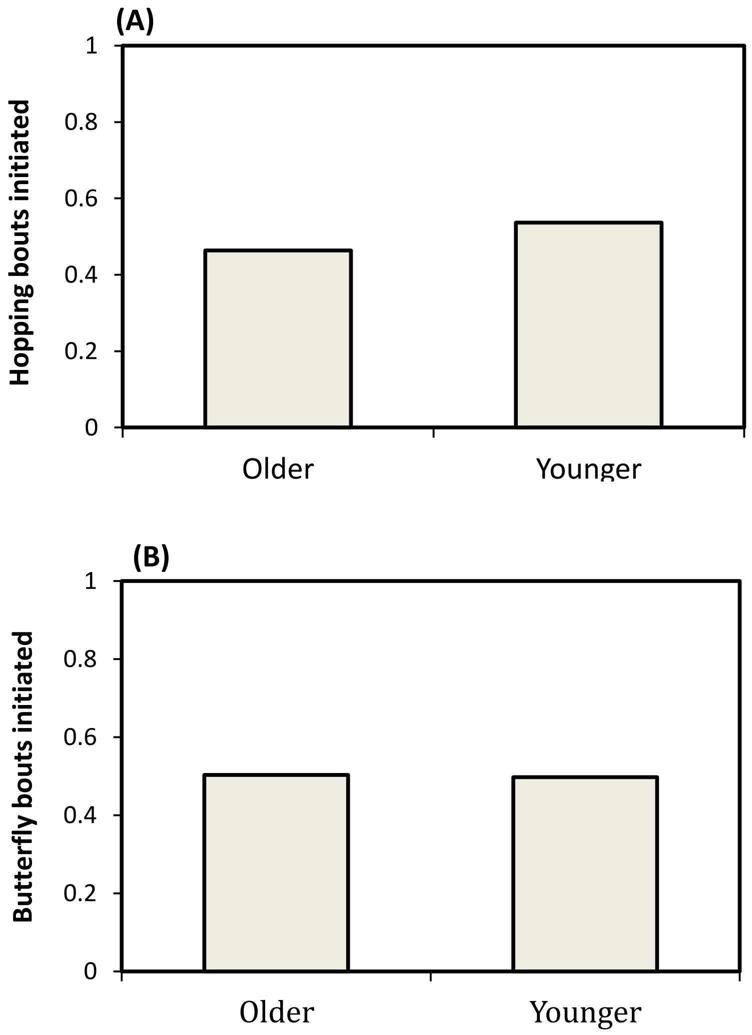

Figure 3.3. Proportion of initiation behaviours performed by older versus younger long-tailed manakins during courtship displays, including (A) initiating hopping bouts and (B) initiating butterfly bouts. Stars between bars indicate a significant difference between older and younger males.

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CHAPTER 4

So you think you can dance? Development of courtship display in young long-tailed manakins (*Chiroxiphia linearis*)

Introduction

The evolution of cooperation is often explained by the theory of kin selection, whereby individuals cooperate with close relatives to increase their inclusive fitness and gain indirect benefits (Hamilton 1964). In social species, cooperation is frequently used to gain direct benefits such as access to resources like food, territories, or mates (Sachs et al. 2004). On rare occasions, however, cooperation can exist between two unrelated individuals without any obvious direct benefits accrued by at least one of the individuals (McDonald & Potts 1994; McDonald 2009).

In animals that cooperate (e.g. ruffs, *Philomachus pugnax*, Hugie & Lank 1997; wild turkeys, *Meleagris gallopavo*, Krakauer 2005), the level of coordination between individuals may be important in determining whether their combined efforts are successful. Coordination often involves imitation, a form of social learning achieved by individuals observing and obtaining information from others that are demonstrating certain behaviours (Tomasello et al. 1987), and this may be particularly important for young individuals. Coordination alone does not necessarily indicate the presence of social learning in a species, but it can act as a precursor to such behaviour, and may often be a predictor of learning (Coussi-Korbel & Fragaszy 1995).

The use of learned behaviours is common in mate attraction and courtship displays, particularly song, and has been well studied in many bird species (reviewed in Freeberg 2000). Much of this research has focused on imprinting in young songbirds, in which cross-fostering experiments have provided evidence for the plasticity of song learning in a number of species (e.g. blue tits, *Cyanistes caeruleus*, and great tits, *Parus major*, Johannessen et al. 2006; red crossbills, *Loxia curvirostra*, Sewall 2011). Social interaction with conspecific males, whether it be influences from paternal or neighbouring males is therefore crucial in this process. Indigo buntings (*Passerina cyanea*), for example, learn songs from neighbouring males, but will not develop normal songs without social interaction with other males (Payne & Payne 1993). Furthermore, evidence suggests that learning from tutors during a critical period can influence song types in young males (Roper & Zann 2006; Wheelwright et al. 2008). In contrast to vocal mate attraction signals, however, the development of visual displays is poorly understood. In zebra finches (*Taeniopygia guttata*), visual elements of courtship displays were highly correlated between tutors and pupils in addition to vocal characteristics (Williams 2001), suggesting that social environment may also affect the acquisition of visual displays. Whether courtship displays are learned or innate, young males may not be proficient enough at performing them for some time, and social transmission may be an important part of the process.

In some species, strong sexual selection has led to extremely elaborate visual courtship displays (Darwin 1859). This is particularly evident in lek-breeding systems, in which males aggregate in small arenas to perform courtship displays for visiting females (Bradbury & Gibson 1983; Kirkpatrick & Ryan 1991). Long-tailed manakins (*Chiroxiphia linearis*) exhibit an exploded lek-breeding system, wherein up to 13 males are associated with discrete display areas where one male is dominant and accrues all mating opportunities (McDonald 1989a; McDonald & Potts 1994). Exploded leks differ from traditional leks in that display sites are relatively large and spaced close together, as opposed to densely packed and spaced further apart (Bradbury 1981; Bradbury & Gibson 1983; Trainer & McDonald 1993). The dominant male forms an alpha-beta team with the second highest ranking male in the display area to perform complex cooperative and coordinated courtship displays for females (Foster 1977; McDonald 1989b; McDonald & Potts 1994). Long-tailed manakin displays are composed of two major phases: the hopping display and the butterfly display (Slud 1957; Foster 1977; McDonald 1989b), which can be further broken down into 16 distinct and readily identifiable subcomponents (see Chapter 2 for full description). The hopping display consists of two males performing alternating side-by-side vertical hops or backwards leapfrog hops on the display perch; each hop is accompanied by a vocalization. The butterfly display, which is silent, is performed as both a dual performance (alpha and beta male both perform the display) and a solo performance (only alpha male displays) and consists of a number of different flight elements and landing postures, which may eventually lead to copulation.

Male long-tailed manakins undergo a four-year delay in plumage maturation before acquiring adult definitive plumage in their fifth year (Foster 1977; McDonald 1989a, 1993b; Doucet et al. 2007). They are a long-lived species, and it can take up to seven or more years before subordinate males have the opportunity to rise to beta status and perform courtship displays for females (McDonald 1989a). During this time, young (predefinitive) males display with other males (both young and old) in the absence of females. Little is known about the function of display in young males, as females tend to avoid display areas when young males are displaying and they never mate with predefinitives (McDonald 1989b). There is substantial variation in the displays performed for females across bouts of display (Chapter 2), and variation in display performance has been associated with copulation success (Chapter 2, McDonald 1989b, Ward 2012). It is therefore likely that females prefer certain subcomponents present in the display, and this may indicate that subordinate males are not performing them adequately enough to elicit a response from females. Young males may therefore be practicing the courtship display with multiple display partners to hone their display skills.

In this study, we aim to determine whether display quality appears to increase with age in long-tailed manakins. We defined 'high quality displays' as those performed by definitive pairs of males towards females that subsequently resulted in copulation. Thus, the closer a display is in similarity to displays of successful definitives, the higher the quality. We expect males displaying for females to have the highest quality displays, and that the quality of displays should decrease as the ages of male pairs decrease. When males practice with other males from different age classes, we expect the age of the partner to influence the display, wherein the quality of displays should increase with the addition of an older male to the pair. Our study will help us better understand the function of social interactions between males, and the development of complex courtship displays.

Methods

We studied a long-tailed manakin population located within a patch of evergreen forest in Sector Santa Rosa in Area de Conservacion Guanacaste, northwestern Costa Rica. Capture and banding efforts over the past nine years have yielded over 750 uniquely colour-banded individuals in the population. We identified discrete display areas according to the associations of certain alphas, betas, and other subordinate males. Most display areas had one primary display perch used by alpha and beta males to perform for both females and practice, while several other minor perches in the area were used primarily by subordinates for practice displays.

We selected 37 long-tailed manakin display areas and all active display perches in each of these areas for the purposes of this study. In 2010 through 2012 we placed five high definition video cameras at active display perches between 0500 and 1130 throughout the months of April-June to collect approximately 2500 hours of video footage of their courtship displays, vocalizations, and other behaviours at display areas. We used a rotating schedule to sample displays areas 3-5 times each, with approximately 1-2 weeks separating samples at the same display perch. Through live observations in the field, we confirmed that all components of courtship displays and copulations (except for toledo vocalizations; See ch. 2) occur on and around the display perch; therefore, we are confident that we captured all aspects of the visual display.

We scored videos manually using VLC (2.0.3) and Microsoft Excel (2007) to observe and record behaviours, respectively. We identified sixteen individual elements of the courtship display and quantified fifteen of them either quantitatively, for duration, or for occurrence. We recorded the perch area, perch, date, and time of each video, as well as the number of males and females present, any copulation that occurred, and the age of each individual, if discernible. Delayed plumage maturation in male long-tailed manakins allows for easy identification of age up to the fifth year when males acquire definitive plumage (McDonald 1993b; Doucet et al. 2007). Therefore, we classified males as predefinitives: second year (redcaps), third year (blackfaces), fourth year (bluebacks); and definitive males (fifth year and older).

Many elements of the courtship display were highly correlated, so we conducted an exploratory principal components analysis (PCA) with a quartimin (oblique) factor rotation using JMP (10.0) to examine how the variables (i.e. display elements) were grouped. Our variables were not normally distributed and could not be transformed; therefore, we used this analysis as a basis for grouping variables that were highly correlated in a biologically relevant manner, and chose one variable from each group as a proxy for that particular group to be used in further analyses. Proxies were chosen based on sample sizes. The first group of multi-correlated elements contained mean number of *back-and-forths*, *bows*, and *angel* *flights* (See chapter 2 for full description of display elements) per display bout. We referred to this group as the *pre-copulatory butterfly display*. The second group included the mean *length of butterfly display (solo and duo)*, and the *total length of display*. We called this group the *length of display*. The third group contained the mean number of *lightning bolts*, *bounces*, *upright postures*, and *bill wipes*. We called this group the *rare butterfly elements*. The fourth group of elements included the mean *length of hopping display* and number of *leapfrogs*. We called this group the *hopping display*. We included *butterfly flights* as a separate variable as it is the most ubiquitous element of the butterfly display and was correlated with several groups. Very rare behaviours (e.g. *frenzied flutters, tucked wing flicks*) that were not highly loaded onto any factors were not included in our analyses.

To test whether older pairs of equal-age males performed higher quality displays than younger pairs of equal-age males, we performed generalized linear mixed models. Given that our dance element variables were heavily skewed to the right and zero-inflated, our models were fitted using negative binomial distributions (log-link functions) using IBM SPSS Statistics (20.0). To account for repeated measures at each perch of each area, we included display area as a random factor. Our main independent predictor of interest, age class, was included as a fixed factor. To discriminate between successful and unsuccessful displays, we separated displays by definitive males into three categories: definitive practice display, definitive display for female (*unsuccessful*), and definitive display for female resulting in copulation (*successful*). Predefinitives took part in only practice displays and were divided based on age classes. We repeated this test to investigate any differences in the quality of display during solo performances by each age class. To understand whether the quality of the displays were different based on the presence of a male in definitive plumage, we compared pairs of males with one definitive and one of each predefinitive age classes (*definitive-predefinitive*). To determine whether the addition of one older predefinitive male would influence the overall quality of displays, we also compared pairs of mixed-age predefinitives with pairs of equal-age predefinitives (*predefinitive combination*). Age categories with very low sample sizes (<5) for any particular variable were excluded from analyses.

Results

Equal-age pairs

To determine whether older equal-age pairs of males performed higher-quality displays than younger equal-age pairs of males, we compared display quality across age classes and, for older males, whether the display was performed as a practice display, a display for females, or a display for females leading to copulation. There was significant variation in the performance of pre-copulatory butterfly displays between equal-age pairs of male long-tailed manakins (whole model: $F_{4,106}$=20.15; n=111; P<0.001; age: $F_{4,106}$=8.29; P<0.001), with pairs of practicing definitives and third year predefinitives performing significantly more pre-copulatory displays than all other pairs, including successful and unsuccessful definitives and pairs of second year males (Fig. 4.1a). There was also significant variation in the length of displays between equal-age pairs of males (whole model: $F_{4,838}$=11.61; n=843; P<0.001; age: $F_{4,838}$=37.62; P<0.001), with successful and unsuccessful definitive pairs displaying significantly longer than all practicing pairs, and practicing definitive pairs displaying the shortest displays ($P<0.05$). In contrast, there was no significant variation in performance of the group of rare butterfly elements across equal-age pairs (whole model: $F_{4,151}=0.92$; $n=156$; $P=0.457$). For hopping displays, there was significant variation between equal-age pairs of males (whole model: $F_{4,430}=6.29$; $n=435$; $P<0.001$; age: $F_{4,430}=13.33$; $P<0.001$), with successful and unsuccessful definitive pairs performing the longest hopping displays, followed by pairs of practicing definitives and third year males, and second year males with the shortest displays (Fig. 4.1b). Finally, for butterfly flights, there was significant variation in performance between equal-age pairs of males (whole model: $F_{4,337}=4.58$; $n=442$; $P=0.001$; age: $F_{4,337}=5.48$; $P<0.001$), with pairs of third year males performing more butterfly flights than all other pairs, and practicing definitives displaying more than unsuccessful definitive displays ($P<0.05$).

Solo displays

There was no significant variation in the performance of solo pre-copulatory displays across different age classes of male long-tailed manakins, including second year males, third year males, fourth year males, practicing definitives, and successful and unsuccessful definitives (whole model: $F_{4,65}=1.34$; $n=7$; $P=0.27$). In contrast, there was significant variation in the length of displays between age classes (whole model: $F_{4,721}=4.68$; $n=721$; $P=0.001$; age: $F_{4,721}=16.60$; $P<0.001$), with successful and unsuccessful definitives displaying longer than all practicing males, third year males with shorter displays than practicing definitives, and second year males intermediate between the two (Fig. 4.2a). For the group of rare butterfly elements, there was also significant variation in performance between age classes (whole model: $F_{4,203}$=4.29; n=208; P<0.001; age: $F_{4,203}$=13.75; P<0.001), with successful and unsuccessful definitives performing significantly more rare butterfly elements than all practicing males (Fig. 4.2b). Finally, there was significant variation in the performance of butterfly flights across age groups (whole model: $F_{4,411}$=6.22; n=416; P<0.001; age: $F_{4,411}$=21.77; P<0.001) with successful and unsuccessful definitives performing significantly more butterfly flights than all practicing males (P<0.01).

Definitive-predefinitive pairs

Among pairs of definitive-predefinitive males, there was no significant variation in the performance of displays between age groups for length of display (whole model: $F_{3,835}$=1.56; n=839; P=0.198) or hopping display ($F_{3,441}$=1.37; n=445; P=0.253). However, there was significant variation in the performance of butterfly flights between definitive-predefinitive pairs (whole model: $F_{3,348}$=4.92; n=352; P=0.002; age: $F_{3,348}$=2.08; P=0.103), with definitive-fourth year male pairs displaying significantly less than all other pairs (P<0.05), including definitive-second year, definitive-third year, and definitive-definitive practice. Pre-copulatory displays and rare butterfly elements were excluded from analyses due to low sample sizes for several age classes.

Predefinitive combination pairs

There was no significant variation in the performance among predefinitive combination pairs of males for pre-copulatory displays (whole model: $F_{3,27}$=0.92;

n=31; P=0.44; age: $F_{3,27}$=2.09; P=0.124); however, third year males did perform more pre-copulatory displays than second year males ($P<0.05$). There was no significant variation across predefinitive combination pairs in the length of displays (whole model: $F_{3,134}$=0.18; n=138; P=0.907), rare butterfly elements (whole model: $F_{3,46}$=0.71; n=50; P=0.550), hopping displays (whole model: $F_{3,60}$=0.51; n=64; P=0.676), or butterfly flights (whole model: $F_{3,79}$=2.55; n=83; P=0.062).

Discussion

Male long-tailed manakins differed in courtship display performance across age classes. In particular, definitive males performing displays for females (both successful and unsuccessful) outperformed younger males in several ways. Older males performed longer displays with more unique elements, while the youngest males performed the shortest displays. In some cases there was little variation in performance between predefinitive age classes; however, third year predefinitives outperformed younger predefinitives in several types of displays, suggesting males from this age class may have an advantage over younger males (e.g. experience, stamina, etc.). Although we found several differences in performance between equal-age classes, the addition of an older male to a pair did not greatly affect the performance of courtship displays. In this study, we provide evidence that the performance of some aspects of the courtship display improves with age in male long-tailed manakins. Our findings provide an important first step in understanding how complex displays develop in young males, and identify a possible role of social learning.

We were interested in determining whether pairs of male long-tailed manakins perform higher quality displays as they age. The length of display for both equal-age and solo displays was significantly longer for definitives displaying for females (successful and unsuccessful) than all other pairs of males during practice displays. This is intuitive, as the length of butterfly display has been shown in previous research to be an important correlate of mating success (McDonald 1989b; Ward 2012). These results support the hypothesis that older males perform higher quality displays, especially for a display component known to be important in mating success. Similarly, the hopping display was significantly longer for pairs of successful and unsuccessful definitives than for practicing males, with the youngest males (second year) exhibiting the shortest hopping display. This trend aligns with the results observed for total length of displays, suggesting that not only is the length of the butterfly display important to females, but that the hopping display contributes as well. The hopping display contains a number of manoeuvres that require precise coordination between males, as well as high levels of stamina to sustain the display. Previous research has shown that non-displaying definitives and predefinitives are often heavier than alpha males (McDonald 1993a), suggesting that high quality individuals may risk weight loss for a chance at copulating by displaying for longer periods of time. Alternatively, a lower weight may improve a male’s agility and ability to perform this complex display (Blomqvist et al. 1997; Székely et al. 2004). Therefore, it may be difficult to disentangle whether shorter displays are due to lack of experience, cost-benefit trade-offs (i.e. weight loss vs. copulation success), or physical constraints on young males.

Young males, or practicing definitives, may have little driving them to perform long displays in the absence of females, and are likely to practice many shorter displays. In brown-headed cowbirds (*Molothrus ater*), courtship displays and levels of social interaction between young males are influenced by female proximity (King et al. 2003). Additionally, the length of displays may be influenced by the availability of a partner or perch. Alpha and beta males tend to dominate primary display perches, which may give subordinates fewer chances to practice displays. Therefore, although it is highly likely younger males simply cannot perform displays as well as older males can, female motivation may also be an important factor that contributes to differences in displays among age classes.

We found that pairs of third year males and practicing definitives performed at similar levels during the pre-copulatory butterfly display, but had significantly higher rates of this display than pairs of second year males and definitives displaying for females. These results may seem contradictory; however, this analysis takes only dual display into account, and therefore we would expect to see fewer copulation attempts when a female is present during dual displays, as copulations generally occur during solo displays (Chapter 2). If successful definitive displays for females are considered ideal displays, then perhaps performing fewer elements from the pre-copulatory butterfly display is preferred by females during dual performances. One reason for this may be to reduce conflict between alpha and beta males (i.e. so beta males do not attempt copulations). In ruffs, females prefer male-male cooperation during courtship displays, however, this leads to higher risk of stolen copulations by satellite males (Hugie & Lank 1997). Perhaps male manakins attempt to reduce this risk by reserving pre-copulatory displays for solo performances. Avoiding pre-copulatory display during dual performances may also act to increase female excitation before attempting copulation. Recent research on long-tailed manakins has demonstrated that several female excitation behaviours exhibited during courtship display can predict copulation success (Ward 2012). Although pairs of definitives perform few pre-copulatory butterfly displays in the presence of females, high levels of practice by older males suggest that these displays are important and perhaps difficult to execute for younger males.

We found no significant differences between any age groups in the performance of rare butterfly elements by equal-age pairs, which suggests that the discrimination between the elements in this group and the pre-copulatory butterfly display group may be important. Since there are no differences between definitives displaying for females and young males practice displaying, the elements included in this group may be less important as cues to females for mate choice. It could be that these display elements simply contribute to the overall length of the display, though this seems unlikely, as the same effect could be achieved with only a single display element. In contrast, perhaps these elements do reveal certain characteristics of quality to females that may be determined through measurements other than rate, such as levels of coordination, energetic requirements, or performances of these elements in combination with other display elements (Chapter 2). Previous research has shown that alpha-beta partners slowly develop coordination in singing over a long period of time, and when definitives performed with young males, frequency matching increased with the age of the younger partner (Trainer et al. 2002). This increase in competency is likely to occur with aspects of the visual courtship display as well, where males develop coordination as they age and eventually reduce their number of display partners until they develop a stable partnership. It is important to note, however, that because alpha males have such high survivorship, only a very small percentage of males ever achieve alpha or beta status (McDonald 1989a). Therefore, even as they age, many males may continue to be loosely affiliated with several leks, reducing the likelihood that these individuals will develop their displays as well as those that eventually become alpha or beta males.

Butterfly flights were performed by pairs of third year males at a significantly higher rate than all other age categories, which taken together with their high rates of pre-copulatory butterfly displays and their short overall total length of displays, may indicate that this age group in particular favours practicing certain elements of the butterfly display. This could be for a number of reasons: the third year predefinitive stage may be a crucial age at which males become more socially active; they may finally have enough experience to develop some of the more difficult manoeuvres; or survival at this age may be considerably higher leading to more risky behaviours or simply higher numbers in the population than second year males.

We found no significant differences between any age groups for solo pre-copulatory butterfly displays. We might expect successful displays by definitives to differ significantly from displays by practicing males; however, a successful display is likely to only have one or few copulation attempts, therefore keeping the number of these displays at a minimum. Since the natural termination of a butterfly display ends in pre-copulatory displays, males may tend to terminate displays here during practice as well. In contrast, successful and unsuccessful definitives had significantly higher rates of solo rare butterfly elements than practicing males. This group of elements may be especially important during solo displays (Chapter 2), or they may simply be performed at higher rates due to the increased total length of display. Similarly, during solo displays, significantly more butterfly flights were performed by successful and unsuccessful definitives than all other practicing males. These results provide added support to our hypothesis that older males perform higher quality displays than younger males.

When predefinitives were paired with a definitive partner, we found that definitive-fourth year pairs performed significantly fewer butterfly flights than all other age groups. Since fourth year males are the oldest predefinitive age group, they may spend more time performing more complex display elements than younger predefinitives. In contrast, perhaps fourth year males are less tolerated by alpha and beta males, as they are more likely to be mistaken as definitives than any other predefinitive age class, therefore they may have fewer chances to display. In song sparrows, *Melospiza melodia*, adults tolerate juveniles during their first few seasons, which coincides with a crucial learning period, but become aggressive towards them in the spring (Templeton et al. 2012). Perhaps the extended delay in plumage maturation in long-tailed manakins provides younger males with more opportunities to interact with adults, which may be necessary to develop such a complex display.

We found no significant differences between predefinitive combination pairs for any of the displays, suggesting that the addition of an older male to an equal-age pair does not have a strong influence on the quality of the display. However, most display groups demonstrated at least a slight trend towards increasing display from youngest to oldest pairs. This pattern suggests that although in some cases we detected differences between equal-age pairs of predefinitives, that the addition of one older male to the pair may be too subtle a change to detect. Males likely exhibit high levels of individual variability in the time it takes to develop their displays, and this may be a distinguishing factor between males that will be successful and those that will not. Individual variability in the performance of complex courtship displays is seen in other manakins as well, including golden-collared manakins, *Manacus vitellinus* (Fusani et al. 2007). If variability in display performance is high within age classes, it may be difficult to detect differences between closely aged predefinitive males.

Overall, we provide some support for the development of certain aspects of the visual courtship display among predefinitive males. Our research shows that definitives displaying for females differ significantly from predefinitive displays in a number of elements of the display. This suggests that definitives (particularly alpha-beta teams) do have higher quality displays than younger males. We also found, however, that practicing definitive pairs often differed significantly than those displaying for females, which may suggest that the presence of females adds an element of motivation to displayers. In brown-headed cowbirds, the presence of females influenced the age at which males advanced through crucial stages of vocal development (Smith et al. 2000). Smith et al. (2002) also found that juveniles in contact with females sang less overall, likely due to increased feedback from females, reducing the need for practice. In other manakins species, practice displays have also been documented to differ from displays for females, wherein displays may be incomplete or males may exhibit slower manoeuvres (Crook 1963; Snow & Snow 1985; Castro-Astor et al. 2004). Therefore, feedback and motivation provided by females may be an important factor to consider in investigating the development of long-tailed manakin displays, particularly for subordinate definitives that are likely more proficient at displaying than predefinitives. Successful display areas tend to have not only higher levels of display for females, but also higher levels of practice displays (pers. observ.), which may suggest that display areas with high female visitation are preferable to practicing males as well.

We found more significant differences between predefinitive age classes during dual displays than during solo displays. This may imply that social interactions between young males are particularly important in this species. If social learning plays a role in the development of courtship displays in long-tailed manakins, we would expect that learning through observing, imitating, and practicing would occur most frequently during group displays. Research on brown-headed cowbirds demonstrated that juveniles who associated more with adult males had higher reproductive success (Smith et al. 2002). Conversely, White et al. (2002) found that adult males housed with juvenile males had higher reproductive success during mating tournaments than those housed without juveniles, suggesting that the presence of subordinates may affect the development of courtship skills in adults as well. Previous research on long-tailed manakins has shown that the level of social connectivity between males at a young age can predict their future reproductive success (McDonald 2007); therefore, the number of practice partners and social interactions a male has engaged in may be more important than the quality of any given individual display. Song potency and levels of stereotypy in brown-headed cowbirds were related to song practice, which may be influenced by opportunities available in the social environment (White et al. 1999). Therefore, comparing males based on social environment rather than age alone may be more fruitful to determine how individuals develop skills in courtship.

In conclusion, our study provides evidence that courtship displays performed by older males, particularly those in the presence of females, differ significantly from predefinitive practice displays, and that some aspects of the visual display develop as young males increase in age. In particular, older males tend to demonstrate more stamina for hopping displays and overall length of displays. Younger males also perform fewer pre-copulatory displays than older practicing males, which may suggest certain display components require more experience to perform. We did not find strong evidence that quality of displays increased with increasing age of display partner; however, social background may be a more important determinant of differences in quality than the age of a male's current display partner. This research provides a first step in understanding how coordinated courtship displays evolve in highly social species. Further research in this area should monitor individuals over the long term to determine factors other than age that might influence quality of displays, including social interactions, motivation from females, as well as possible physical and energetic constraints.

Tables and figures

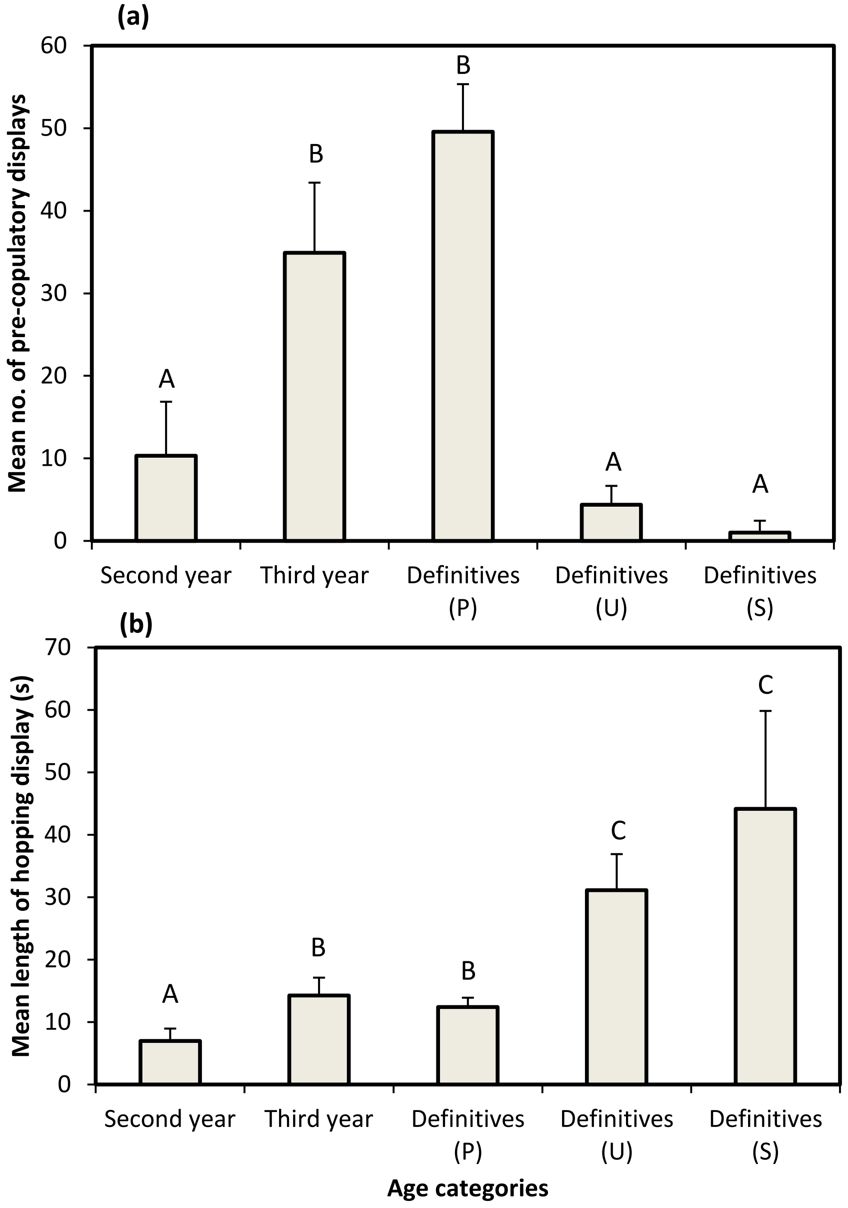

Figure 4.1: Differences in estimated means from GLMM between equal-age pairs of male long-tailed manakins in performance of: a) pre-copulatory butterfly displays (mean number of back and forths as a proxy variable), and b) hopping displays (mean length of hopping as a proxy variable). (P) represents practicing definitives, (U) represents unsuccessful displays by definitives for females, and (S) represents successful displays by definitives for females. Standard error shown by error bars. Significant differences between age categories distinguished by different letters above bars.

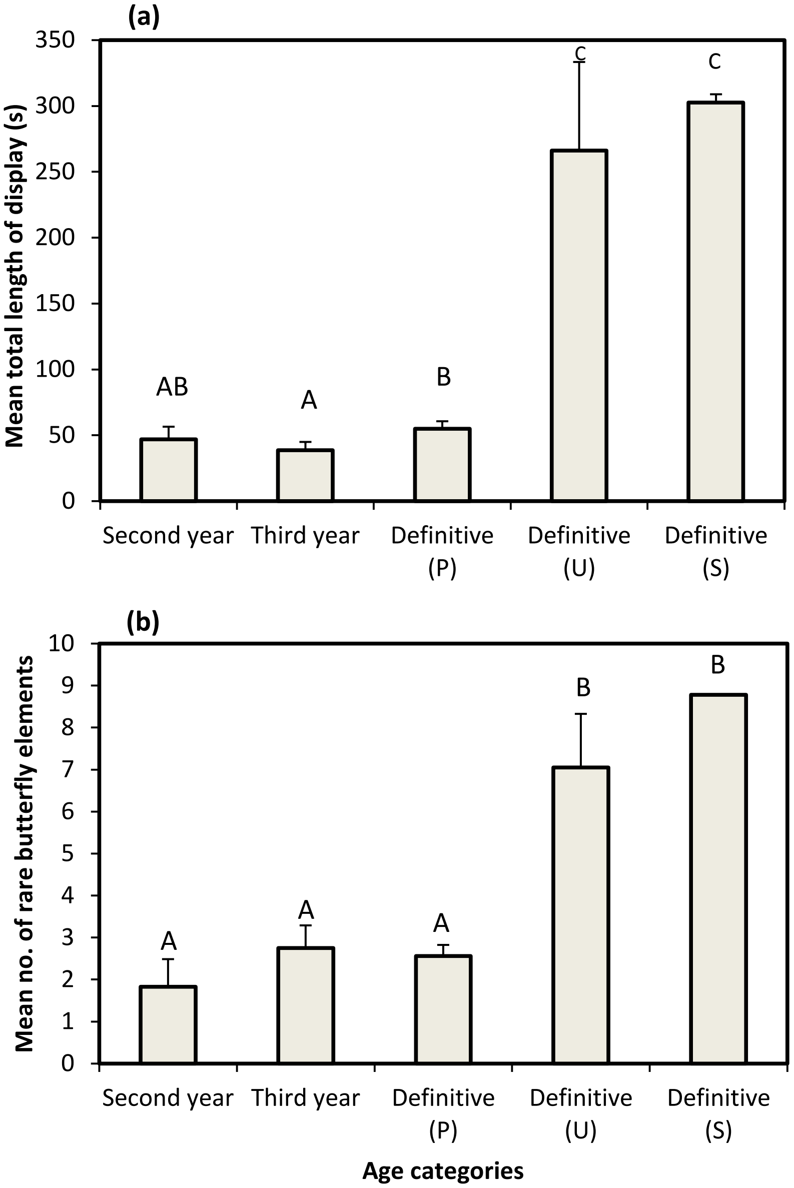

Figure 4.2: Differences in estimated means from GLMM between solo age classes of male long-tailed manakins in performance of: a) length of display (mean length of total display as a proxy variable), and b) rare butterfly elements (mean number of upright postures as a proxy variable). (P) represents practicing definitives, (U) represents unsuccessful displays by definitives for females, and (S) represents successful displays by definitives for females. Standard error shown by error bars. Significant differences between age categories distinguished by different letters above bars.

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CHAPTER 5

General discussion and conclusions

The development of courtship behaviour has been studied primarily in songbirds, and many studies have revealed the importance of social interactions during a critical song learning period (Payne & Payne 1993; Freeberg 2000, 2004; Roper & Zann 2006; Johannessen et al. 2006; Wheelwright et al. 2008; Sewall 2011). Little is known, however, about the development of complex visual displays, though some evidence suggests that social learning may play a role (Williams 2001). In species with complex mating systems, such as lekking species, the gathering of males in lekking arenas facilitates social interactions between males on a regular basis. To understand how complex mating systems evolve, studies that focus on how social dynamics influence complex behaviours are important. The purpose of my thesis was to investigate the dynamics between male long-tailed manakins (*Chiroxiphia linearis*) during both aggressive and cooperative behaviours that take place during courtship displays. My research will contribute to our understanding of how complex courtship displays are developed, and will help determine which factors may have influenced their evolution.

In chapter two I provided the first full characterization of the long-tailed manakin courtship display, further breaking down the two major components of the display previously described (McDonald 1989b) into 16 individual subcomponents. I was interested in not only providing a full account of courtship behaviour, but also determining the level of stereotypy of the display, and assessing which display elements may be particularly important for courtship success. Using video recordings, I quantified display elements during dance bouts performed by definitive males for females to investigate the sequence of courtship and identify elements that predict copulation success.

Many display elements exhibited by long-tailed manakins were common to all members of *Chiroxiphia*, including joint hopping displays, buzz-weent homologues, and butterfly flights (Gilliard 1959; Snow 1963b; Foster 1981; Prum 1990; Duval 2007a). Many display elements were also common to species in other manakin genera, including distantly related species such as members of *Pipra* (Snow 1963a; Robbins 1983; Prum 1990; Théry 1990; Tello 2001; Rosselli et al. 2002; Castro-Astor et al. 2004, 2007; Durães 2009; Mckay et al. 2010), suggesting either shared common ancestry, or display elements that have evolved multiple times within the manakin family (Prum 1997). I found no record of displays similar to angel flights for any other manakin species. Although many display elements were similar to those exhibited by other species, without detailed accounts including photographs, illustrations, or videos, it is difficult to determine which elements may be significantly different. Therefore, long-tailed manakins exhibit courtship displays with a unique combination of display elements, and appear to perform at least one display element that is unique from all other manakin species.

I also showed that long-tailed manakin displays are highly structured, such that many display elements are highly associated with others. Similar to lance-tailed manakins (*Chiroxiphia lanceolata*), long-tailed manakins progress from hopping displays to buzz-weents to butterfly displays (Duval 2007a); however, structure at a smaller level can be seen between individual display elements such as butterfly flights and upright postures, and angel flights and bows. Elements with high probabilities of preceding or following other elements were also often highly correlated. Females may prefer certain combinations of display elements, and mate choice has likely influenced the highly stereotyped nature of the display (Bradbury 1981; Bradbury & Gibson 1983).

Although the courtship display was highly organized and structured, dance bouts were variable between displaying males. I found that the performance of butterfly flights, upright postures, angel flights, and bows predicted successful courtship displays. Angel flights and bows were highly correlated and were performed immediately prior to copulation attempts, whereas upright postures were performed frequently throughout the butterfly display. Previous research found that the length of butterfly displays were correlated to mating success (McDonald 1989b; Ward 2012); however, the present study suggests that it may be the performance of certain elements within the butterfly display that females use as a basis of mate choice in long-tailed manakins.

Variation in behaviours other than courtship display can be responsible for influencing the success of males at lekking sites as well. In addition to courtship displays, successful black grouse (*Tetrao tetrix*) males exhibit stereotyped fighting behaviours in the presence of females, suggesting that females also rely on aggressive status-signalling cues to choose males (Hogland et al. 1997). A number of factors may be important in influencing mating success for lekking species, including not only display quality, but also dominance status and social interactions between conspecifics.

In chapter three, I investigated the dominance hierarchy among male long-tailed manakins. Males are thought to adhere to a strict age-graded dominance hierarchy in which older males are dominant to younger males, and previous studies have demonstrated that alpha and beta males are dominant to other males within their display site (Foster 1977; McDonald 1989a, 1993a, 1993b). However, little is known about dominance and social interactions between young males in predefinitive plumage. I aimed to characterize the dominance hierarchy among males from all age classes, and using video recordings, I scored the outcomes of five types of dominance behaviours as they occurred at the display area. I found that older males directed almost all chases, displacements, and buzz-weents towards younger males, and that younger males rarely directed these behaviours towards older males, suggesting that males do exhibit a linear age-graded dominance hierarchy in this species. This trend was consistent between young males in predefinitive plumage; however, dominance behaviours between predefinitives were relatively uncommon, and this is likely because predefinitive plumage stages act as a status-signalling mechanism, reducing the need for aggressive behaviours that would normally help determine status (Rohwer & Rohwer 1978; Lyon & Montgomerie 1986; Whitfield 1987; Hawkins et al. 2012). Females often leave the display area when males exhibit aggressive behaviours during the courtship display, so it may benefit younger males to reduce aggressive behaviours and maintain a good reputation at the display site, especially if females exhibit display site fidelity in future years (McDonald 1993b, 2010).

I also found that males from the same age category exhibited more dominance behaviours overall, suggesting that status-signalling is less clear between males with similar plumage. Furthermore, chases were exhibited more often by males in the same age category whereas displacements were exhibited by males in different age categories, which may suggest that long-tailed manakins use a range of aggressive behaviours that vary in intensity depending on the opponent. Chases generally include more active flight in order to chase and follow the opponent away from the display area, and these are likely a more costly behaviour than displacements, which were reserved for use against younger opponents. Therefore, it may benefit older males to exhibit dominance behaviours with lower energy requirements towards younger males if they pose less of a threat to their reproductive success (Lyon & Montgomerie 1986; McDonald 1989b; Hawkins et al. 2012).

I was able to provide support for an age-graded dominance hierarchy among long-tailed manakins, though dominance interactions were exhibited more commonly by definitive males, and most likely by alphas and betas. Females only mate with definitive males, and therefore higher levels of aggression between males with breeding potential may be expected. In a study on song sparrows (*Melospiza melodia*), adult males tolerated young males until they reached the breeding season in the following spring, during which they became aggressive towards them (Templeton et al. 2012), suggesting that aggression may not be necessary towards non-threatening, non-reproductive males. My research adds to a growing body of literature on plumage-mediated status-signalling mechanisms, and is the first to fully characterize the dominance hierarchy in long-tailed manakins.

In chapter four, I was interested in exploring courtship behaviours of young males. Although only alpha and beta males perform courtship displays for females (McDonald 1989b, 2010; Trainer & McDonald 1995), males of all ages practice this display in the absence of females. I scored video recordings for elements of courtship behaviour during both practice displays and displays for females to determine whether older males were more proficient at performing dance displays than younger males. I compared pairs of males from each age category for performance of display elements and found that displays performed by definitives for females were significantly different that displays performed by younger males. Displays performed by older males were longer and included more elements of the display, whereas the youngest males often performed the shortest, simplest displays. Previous studies have shown a correlation between the length of butterfly display and copulation success (McDonald 1989b; Ward 2012), and this trend is supported with the results in the present study. As shown in chapter two, both upright postures (part of the rare butterfly element group) and angel flights and bows (part of the pre-copulatory display) predicted courtship success. These results are also consistent with the results from chapter four, showing that successful pairs of definitives outperformed other males in these particular display elements.

I also found that blackfaces (intermediate predefinitives) outperformed other males in several categories, including butterfly flights and pre-copulatory displays. This trend might be explained in a number of ways, including increased social activity at this age, more practice experience, or simply higher survival than younger males. Social interactions with older males may be important for young males to help develop their courtship display. Juvenile brown-headed cowbirds showed higher reproductive success if they associated more with adult males (Smith et al. 2002), suggesting that social learning may facilitate courtship development. Previous research showed that higher levels of social connectivity in male long-tailed manakins predicted future copulation success (McDonald 2007). I did not find evidence that the presence of an older male in a pair of displaying males influenced the courtship display; however, if social learning is facilitated through multiple social interactions with different males, then it may be more beneficial to compare males with differing social backgrounds, as opposed to comparing performances between any particular individuals.

I provide evidence that older males perform courtship displays that are significantly different from displays performed by younger males, and that some elements of the display develop over time. It is important to note that even though only alpha and beta males perform displays for females, variation in display exists within this small subset of males as well. Copulations are attributed to only a small percentage of males within a population (McDonald 1993a), and therefore it may be important to consider non-alpha and beta definitives as a separate category when comparing display performance.

For my thesis I was interested the social dynamics of male long-tailed manakins. To understand these dynamics, I first had to explore the ways that males interact at display sites by characterizing the courtship display and dominance hierarchy exhibited by males. By studying intrasexual interactions, I was able to provide support for an age-graded dominance hierarchy among males, and that delayed plumage may facilitate status-signalling. By studying both intra- and intersexual interactions, I also demonstrated that males develop certain aspects of courtship displays over time, which suggests that the extra delay in plumage maturation may allow young males more time to interact with adults and other males to develop complex courtship displays, perhaps facilitated through social learning. Furthermore, I found that courtship is highly structured and organized, and that several characteristics of courtship display predict copulation success. This suggests that, ultimately, female choosiness has likely driven the evolution of cooperative courtship displays and male-male orderliness at display sites. Future research should aim to determine the social background of individuals, particularly young males, over the long term to better understand the factors influencing courtship development. My research enhances our understanding of the development of complex, cooperative courtship displays and the social dynamics of lekking species.

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