2010

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Recommended Citation
Rieveley, Kathryn Diane, "Mutual ornamentation, sex-specific behaviour, and multifunctional traits in Neotropical royal flycatchers (Onychorhynchus coronatus)" (2010). *Electronic Theses and Dissertations*. 8249.
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Mutual ornamentation, sex-specific behaviour, and multifunctional traits in Neotropical royal flycatchers (*Onychorhynchus coronatus*)

by

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A Thesis
Submitted to the Faculty of Graduate Studies
through Biological Sciences
in Partial Fulfillment of the Requirements for
the Degree of Master of Science at the
University of Windsor

Windsor, Ontario, Canada

2010

Library and Archives Canada

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Ottawa ON K1A 0N4
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Direction du Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 978-0-494-70589-6
Our file Notre référence
ISBN: 978-0-494-70589-6

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I hereby declare that this thesis incorporates material that is result of joint research. Chapters 2 and 3 were co-authored with my advisor, Dr. Stéphanie Doucet, who supported my research financially, provided feedback on ideas, assisted with statistical analyses and field work, and imparted editorial suggestions during the writing process of both manuscripts. Chapter 2 is being prepared for submission to The Auk, and Chapter 3 was prepared as a manuscript for submission to Animal Behaviour.

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ABSTRACT

Sexual selection theory focuses largely on showy male traits and choosy females, with most studies drawing conclusions from sexually dimorphic species. Until recently, female ornamentation was relatively unexplored. I investigated sex-specific behaviour in the mutually ornamented Neotropical royal flycatcher (*Onychorhynchus coronatus*), where both males and females possess an elaborate concealable crest. From observations in the wild, I characterized vocal and visual displays and found that the crest is a multifunctional trait used in intersexual, intrasexual, and heterospecific contexts. Using a model presentation experiment, I discovered that females exhibited a stronger response than males to territory intrusion, that females were most aggressive towards female intruders, and that females frequently displayed their crests in heterospecific defense. In summary, males and females use their crests during courtship and competition, implicating sexual selection. However, persistent female nest defense behaviour suggests that elaborate female crests may be influenced by both natural and sexual selection.

ACKNOWLEDGEMENTS

I would like to thank my family and friends for their continued support throughout my schooling. To my mum for instilling in me the respect and fascination for all creatures, to my dad for motivating me to do my best, to my sister for always knowing what I need to hear, and to my brother for fostering my love of animals at a young age. I also thank my sister-in-law Danielle and new little niece Norah for always making me smile, and my in-laws for their unconditional love and support. I especially thank my husband Isaac for helping me reach my goals and always reminding of what's most important.

I would like to express my gratitude to my advisor Dr. Stéphanie Doucet. Her expertise and guidance ensured the success of my field seasons, and her attention to detail encouraged me to become a better writer and researcher. On a personal note, by welcoming me into her lab she exposed me to people and places that have changed my life. After a childhood spent watching Sir David Attenborough, I never imagined I would have the chance to explore tropical forests as I did during my field work, and for this experience I am most grateful.

I would also like to thank my committee members: Drs. Carlin Miller and Dan Mennill for their valuable suggestions to help improve my research. Dr. Mennill's knowledge and experience with tropical ecology was tremendously helpful in the field, and I thank Dan for all his support throughout my undergraduate and graduate programs. Additionally, I am most grateful for use of his royal flycatcher vocal recordings for Chapter 2 and sound equipment for playback methods in Chapter 3.

For logistical support in Costa Rica I thank the staff of Santa Rosa National Park, with special thanks to Roger Blanco Seguro. For emotional (and sometimes medical) support I would like to thank my Costa Rica field mates: Stéphanie Doucet, Dan Mennill, Sarah Douglas, Julie Koloff, and Anneka Osmun. Especially to my roommate Sarita, thanks for putting up with my nightly journal routine and all the memories.

To the past and present Doucet lab members, thanks for all your help proof-reading, providing feedback on presentations, and making lab time enjoyable. To Jessica Cuthbert, Allison Mistakidis, Celia Chui, Karen Cogliati, Daniel Hanley, Melissa Abdellah, Kara-Anne Ward, Pierre-Paul Bitton, Fabio Castelli, Michelle Bondy, Jillian Faraci, and Summer Ross. I am especially grateful to Jess and Celia for use of their 2006-2007 royal flycatcher field data.

I thank the following for financial support for my research and conference presentations: Animal Behaviour Society, the Government of Ontario, and the University of Windsor.

I would also like to thank a number of people at the University of Windsor. Thanks to Dr. Dennis Higgs for his support and encouragement throughout my undergraduate and graduate degrees, even though I don’t like fish. To Sara McNorton for hiring me as a graduate assistant in which I gained valuable teaching experience. And finally my thanks to the biology secretaries and library staff, especially at the interlibrary loan office, who I frequently sent searching for old scientific literature.

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CHAPTER 1

General Introduction

Multifunctional signals

Multifunctional signals are signals that function in more than one context, such as traits that are used during both mate choice and intrasexual aggression. Co-option is a term used to describe the mechanism that leads to the evolution of multifunctional traits, and has previously been referred to as 'trait borrowing' (Fisher 1954). Co-option offers an evolutionary efficient means of enhancing communication because the use of pre-existing traits in new contexts should occur much more rapidly than the evolution of a new trait, and a single trait with dual functions should be less costly to develop and maintain (McLennan 2008). A few hypotheses have been proposed to explain the evolutionary mechanism of trait co-option. Historically, multifunctional traits were thought to evolve primarily through the ritualization of displacement activities (Armstrong 1950, Huxley 1966). In general, displacement activities, such as preening out of context, are produced when an animal experiences conflicting drives. Over time, these displacement activities can be incorporated into displays within their secondary context and may gain functional significance (Armstrong 1950). More recently, male traits used in intrasexual competition that signal male quality are thought to be co-opted into courtship displays when females develop preferences for pre-existing male traits (Borgia 2006). Similarly, male eavesdropping on male-female interactions could lead to courtship traits becoming co-opted for use as signals during male-male competition (Morris et al. 2007).

Dual and multifunctional traits have been documented in a diversity of taxa, and are most commonly used in closely related contexts such as male-male competition and female mate choice. It is not difficult to imagine how a trait indicative of male quality used in male-male competition could also become important in revealing quality during female mate choice. Indeed, most examples of multifunctional traits are male traits that function in the context of sexual selection (see Berglund et al. 1996). Such dual-function male traits are widespread and occur across a range of signal modalities including visual (e.g., Morris et al. 2007), acoustic (e.g., Catchpole & Slater 1995), and chemical (e.g., Arakawa et al. 2008) signals.

Anti-predator signals as multifunctional traits

Of considerably greater complexity are multifunctional traits that function in seemingly divergent contexts such as defense against predation and sexual selection. The most intuitive examples of such traits involve sexually selected weaponry, such as antlers and horns that evolved for male combat but are also used during predator defense (Caro 2005). Sexual selection often leads to secondary sexual traits that are elaborate and conspicuous (Darwin 1871, Andersson 1994). However, it is a common assumption that conspicuous traits may increase an individual's risk of predation. Therefore, natural selection may present an opposing pressure that sets an upper limit on trait elaboration where the benefits no longer outweigh the costs (Darwin 1871, Butcher & Rohwer 1989). For traits that function in both sexual selection and predator defense, however, natural and sexual selection can work together to enhance signal conspicuousness. For example, bright colouration in *Dendrobates* poison frogs serves as warning colouration to deter predators by advertizing their toxicity (Daly & Myers 1967, Summers & Clough 2001). Interestingly, research has shown that this bright colouration is also maintained through mate choice in some species (e.g., Summers et al. 1999). Bright colouration facilitates predator learning and association with unpleasant taste or smells (e.g., Sillén-Tullberg 1985, Mallet 1987). Therefore, natural selection may favour conspicuous colouration to advertise toxicity to predators in *Dendrobates*, with additional selection pressure through mate choice.

Pursuit deterrence is a pre-emptive defense strategy whereby prey signal to approaching predators to notify them that they are aware of their presence (Woodland et al. 1980). Certain ambush-type predators rely on catching their prey off guard. Thus, when the prey signals to the predator that it has been detected, the predator benefits by perceiving this signal and aborting a costly pursuit that is unlikely to be successful (Woodland et al. 1980). The first described account of a pursuit deterrent signal is the 'tail flashing' that occurs in several ungulate species (Bildstein 1983). When a predator is noticed at a safe distance, individuals lift their tails to expose a conspicuous white rump, which notifies the predator that it has been detected and should abandon pursuit.

In turquoise-browed motmots (*Eumomota superciliosa*), both males and females possess unusual, racket-shaped tails where the central retrices are bare at the base and terminate into oval-shaped feathers. Recent research has shown that both sexes conspicuously swing their elaborate tail as a pursuit-deterrent display towards approaching predators (Murphy 2006). Additionally, tail morphology may be sexually selected in males as it is correlated with reproductive success (Murphy 2007). Therefore, the unique tail morphology of turquoise-browed motmots appears to be maintained by both natural and sexual selection in males, and natural selection in females.

Pursuit deterrent signals can also advertise signaller quality to further deter predators from costly pursuit (Caro 2005). In a sense, the prey is communicating 'I see you, and don't bother chasing me because I am in good condition and will escape.' Such traits can also be subject to co-option. For example, skylarks (*Alauda arvensis*) produce song for territory advertisement, and they also sing in flight while under predatory pursuit by merlins (*Falco columbarius*) (Cresswell 1994). Producing complex song while flying is presumed to be a costly behaviour, and individuals that sang a full territorial song while under attack were less likely to be chased or captured by predators (Cresswell 1994). A similar example occurs in *Anolis* lizards, where males and females perform a characteristic push-up display with corresponding throat patch (dewlap) extension. Both push-up (Leal 1999) and dewlap displays (Vanhooydonck et al. 2005) are produced in the presence of male and female conspecifics and also towards predators. Push-up displays signal endurance and condition (Leal 1999), and the dewlap can indicate body size, bite force, and jumping ability (Vanhooydonck et al. 2005). Therefore, with this single display an anole can reveal pertinent information about its individual quality to potential mates, rivals, and predators.

In summary, traits that function in both predator defense and sexual selection fall into three non-mutually exclusive categories: traits that function in sexual selection that are also 1) weapons that function in predator defense, 2) conspicuous traits that function as a) warning colouration or b) pursuit deterrents, and 3) quality indicators that signal relevant measures of condition to predators.

Last-resort predator defense mechanisms

The examples above reveal that prey have evolved a variety of traits for predator defense. The type of predator defense mechanism found in a given species will depend on several factors such as the extent of predation, predator-prey encounter rates, and also the types of predators prey face. When a predator is in final pursuit prey often employ last-resort defense mechanisms to increase their chances of escape or to threaten the predator (Caro 2005). Many species actively defend themselves against predators using their teeth, horns, claws, and various other weapons. However, several species have evolved more sophisticated last-resort defense mechanisms. Autotomy describes the shedding of particular body parts, which prey can resort to in response to predation. Autotomy functions as a deflection signal where the goal is to distract predator attention to some non-critical part of the prey to avoid fatal injury (Ruxton et al. 2004). The most commonly described example of autotomy occurs with lizard tails (Cooper et al. 2008). Several species of lizards shed their tail in efforts to distract predators and successfully escape (e.g., Vitt et al. 1977). Predators seize the tail while the lizard escapes and later re-grows a new tail. Similarly, many birds shed their rump feathers to escape predation (Møller et al. 2006).

Startle displays are another last-resort defense mechanism that functions to frighten or at least temporarily confuse an unsuspecting predator to allow prey time to escape (Edmunds 1974). Startle displays are reserved for close contact with a predator (Ruxton et al. 2004) and often involve an increase in apparent body size or the revelation of conspicuous concealed colouration (termed 'flash colouration', Cott 1940). The sudden appearance of colour or pattern that was previously hidden introduces an alarming factor which can have a psychological effect on the receiver, and may cause the predator to retreat (Cott 1940, Coppinger 1969, Stevens 2005). Invertebrates face numerous predators and often produce startle displays that involve flash colouration (see Witz

1990). For example, experiments with peacock butterflies (*Inachis io*) have shown that the display of the eyespot pattern on the butterfly's wings significantly and consistently caused predatory blue tits (*Parus caeruleus*) to avoid eating this palatable prey species (Vallin et al. 2005). Many *Mantis* species produce elaborate startle displays that involve flash colouration with stereotyped posturing, wing extension, acoustic components, death feigning, or thrashes at the predator (Edmunds 1972). These displays have been shown to efficiently startle and intimidate monkey (Carpenter 1921) and bird (Maldonado 1970) predators.

In summary, during last-resort predator defense prey may use weapons for counter attack, employ distracting mechanisms to avoid fatal injury, or use startle displays involving threatening postures and/or exposing bright colouration to intimidate predators at close range. Through previous examples I have shown that traits can function in both sexual contexts and predator defense, which suggests that natural and sexual selection can work synergistically to promote trait elaboration. Last-resort defense strategies involving, for example, weaponry or concealed colouration may similarly operate in sexual contexts. As such, predator-prey dynamics represent a relatively unexplored but influential factor in the evolution of conspicuous ornaments.

Concealed colouration

Traits that remain perpetually displayed, such as body colouration, are subject to continual selection from multiple sources. For example, sexual selection may drive the evolution of conspicuous body colouration whereas predation may constrain it (see Götmark 1993). Hingston (1933) coined the term 'colour conflict' to describe the opposing forces of natural selection for cryptic colouration to minimize detection by predators, and sexual selection for conspicuous colouration to attract mates or repel rivals. Concealed colouration refers to patches of conspicuous colour that can be hidden from view and exposed at will, and therefore represents a dynamic signal free from the constraints of being perpetually displayed.

In a recent study, Stuart-Fox and Ord (2004) compared the degree of sexual dichromatism of agamid lizards in exposed versus concealed body parts and their respective influences from natural and sexual selection. They found that habitat type influenced dichromatism of exposed but not concealed areas, such that species in closed habitats had increased sexual dichromatism on exposed surfaces. In addition, they found indices of sexual selection to positively correlate with dichromatism of concealed but not exposed areas. Taken together, these findings suggest that exposed colouration is more susceptible to constraints from natural selection, whereas concealed colouration may be more influenced by sexual selection.

Butcher and Rohwer (1989) refer to concealed colouration as 'restricted signalling'; where hidden conspicuous colouration is only used in certain situations, and Hingston (1933) hypothesized that species use this primarily in sexual contexts. As previously mentioned, however, several studies emphasize a role for concealed colouration in startle displays. Moreover, additional research shows that concealed colouration can function in multiple contexts such as warning colouration (e.g., Schultz 2001), pursuit deterrence (e.g., Leal & Rodríguez-Robles 1995), intrasexual competition (e.g., Lappin et al. 2006), and courtship (e.g., Langkilde et al. 2003).

Concealed colours can also function in multiple contexts in birds, although this phenomenon has received little research attention. Most notably, red-winged blackbirds (*Agelaius phoeniceus*) possess conspicuous red epaulet feathers, which they expose during displays to females and to other males (Yasukawa et al. 2009). Additionally, sunbitterns (*Eurypyga helias*) have false eyespots on their wings which are normally concealed, but are conspicuously exposed during a frontal display that involves outstretching the wings and fanning the tail. Both sexes produce frontal displays in courtship and towards predators (Thomas & Strahl 1990), but these behaviours remain virtually unstudied. Similarly, rufous bush chats (*Cercotrichas galactotes*) display bright white tail patches bordered by black spots in a tail fanning display that occurs during courtship, conspecific aggression, and nest defense (Alvarez 2000). Furthermore, birds with more white in their tail experienced higher reproductive success and lower nest predation (Alvarez 2000), highlighting the importance of this concealed trait for both sexual selection and predator defense. Likewise, red-necked nightjars (*Caprimulgus ruficollis*) are cryptically coloured nocturnal birds, but they can reveal concealed conspicuous white plumage on their wings, tail, and throat during agonistic, anti-predator, and sexual displays (Aragonés et al. 1999). These studies show that concealed colouration in birds may function multiple contexts, including sexual displays and predator defense.

Crests in birds as dynamic signals

Many species of birds possess conspicuous crests that appear in a variety of forms with differing degrees of elaboration. For example, the northern cardinal (*Cardinalis*

cardinalis) has elongated erectile crest feathers coming to a point at the back of the head, and this red crest is similar in colour to the rest of the body. Another species, the common firecrest (*Regulus ignicapillus*), has a semi-concealed yellow-orange crest that normally appears as a thin flat stripe on the top of the head. These birds can erect their feathers to reveal a conspicuous crest. Ptiloerection describes the erection or ruffling of feathers, and birds will ptiloerect their feathers for thermoregulatory purposes (Hohtola et al. 1980), but also in a variety of social contexts (Morris 1952), including predator defense (Caro 2005). Birds can change the appearance of their crests through ptiloerection; therefore bird crests represent an additional example of a dynamic signal.

Crest erection is a very common behaviour in birds (see Armstrong 1965). Yet far too often, crest erection is overlooked and merely described as occurring when a bird is 'agitated' or 'excited,' which provides no information relating crest behaviour to specific signalling contexts. However, several studies anecdotally report that crest erection may occur in a variety of contexts including during courtship (e.g., great bowerbird, *Chlamydera nuchalis*, Marshall 1954), during agonistic battles (e.g., Steller's jay, *Cyanocitta stelleri*, Brown 1964), while singing (e.g., red-crown ant-tanager, *Habia rubica,* Willis 1960), or to signal submissive behaviour (e.g., fox sparrow, *Passerella iliaca*, Hailman 1977).

In a recent study, Hagelin (2001) examined the function of the erectable head plumes in Gambel's (*Callipepla gambelii*) and scaled quail (*C. squamata*). In the Gambel's quail, head plume length did not correlate with the outcome of male-male contests. However, she found that winners of contests more frequently erected their crests than losers, and losers flattened their crest more often than winners. Additionally, she found head plume length to positively correlate to the likelihood of winning a male contest in the scaled quail. Hagelin (2001) reasoned that dynamic ornamentation, such as bird crests, can be selected for conspecific communication because it can provide information regarding the current motivational state of the individual, and thus provide more relevant information than static signals of status. As such, birds' crests may play an important role in social communication.

In many families of birds, both sexes possess conspicuous crests (e.g., Podicipedidae, Alcidae, Corvidae, Tyrannidae; Jones & Hunter 1999); however, the function of crests in males and females is not well understood. In one study, Jones and Hunter (1999) found that crests in male and female crested auklets (*Aethia cristatella*) function in mutual mate choice and signal dominance in both sexes. Future work investigating the function of conspicuous crests would help us to understand their widespread occurrence in birds. Furthermore, the study of both male and female crests may enhance our understanding of the role of mutual ornamentation.

Mutual ornamentation

In many species with intense sexual selection, sexual dichromatism is the norm, where males exhibit showy ornaments and females are relatively cryptic (Andersson 1994). Past research has focused largely on dichromatic species and the function of male ornaments in sexual selection (Andersson 1994). However, females also possess ornaments in some species (Amundsen 2000a, Amundsen & Pärn 2006), and we are only just beginning to explore their functions. In mutually ornamented species, both males and females exhibit similar ornaments. Here, I use the term ornament to describe any conspicuous trait (sensu Amundsen 2000b). In comparison to males, female ornaments may be reduced (e.g., horns in many ungulates), similar (e.g., tail morphology in motmots), or even more elaborate (e.g., colouration in eclectus parrots, *Eclectus roratus*, Heinsohn et al. 2005). In many mutually ornamented species, females possess a reduced version of the shared ornament (Amundsen 2000b). This observation led Darwin (1871) to believe that female expression of shared ornaments was a consequence of the 'laws of inheritance.' Accordingly, Lande (1980) proposed the correlated response hypothesis, which stipulates that mutual ornamentation occurs due to genetic similarity between the sexes. As such, this hypothesis explains that ornaments are selected in males and appear as correlated by-products in females. Although some studies provide evidence for this hypothesis (e.g., Muma & Weatherhead 1989), recent research highlights that female ornamental traits may also be under direct selection (Amundsen 2000a, Amundsen & Pärn 2006). In cases where females exhibit a diminished version of the male trait, it is important to realize that a lack of selection upon the female trait explains its current form (Amundsen 2000a), even if it exists due to genetic similarity with the male. However, when females exhibit a trait that is as elaborate as the male's and is utilized in a similar manner, selection is likely at play (Amundsen & Pärn 2006). Although the correlated response hypothesis likely explains many female traits and may explain the initial development of mutual ornamentation, it contributed to a widespread belief that female ornaments were non-functional and may have lead to a general disregard for the study of female ornamentation.

Selection for female traits

A growing body of literature suggests that in some species, selection can favour the evolution or maintenance of elaborate female traits. Male mate choice, female competition, and defense of nest and young all likely shape female trait expression. Female colouration has been linked to measures of condition (e.g., Velando et al. 2001, Jawor et al. 2004, Siefferman & Hill 2005), and males of various species have been shown to select females based on their colouration (e.g., McLennan 1995, Hunt et al. 1999, Amundsen & Forsgren 2001). In addition to colouration, other examples of female ornamentation are evident in a variety of species (Amundsen 2000a), and males can choose females based on their ornaments (e.g., Rosenqvist 1990, Jones & Hunter 1993). Male choice for female traits is not confined to sex-role reversed species, as females from various mating systems also experience male mate choice (e.g., Chan et al. 2009).

West-Eberhard (1983) proposed that sexually monomorphic elaborate plumage, where both males and females are brightly coloured or ornamented, evolved in species where both sexes participate in intrasexual aggression. Females of some tropical hummingbirds (e.g., *Amazilia*) defend feeding territories year-round and have correspondingly conspicuous plumage, whereas temperate females who only seasonally participate in territorial behaviour exhibit dull plumage (Wolf 1969). Additionally, Murphy and colleagues (2009) found that breast colouration in female streak-backed orioles (*Icterus p. pustulatus*) functions as a status signal used in female-female competitive interactions. In a recent study by Watson and Simmons (2010), reproductive competition between female dung beetles (*Onthophagus sagittarius*) was found to influence the evolution of female horns, such that females with larger horns experienced higher reproductive success during times of intense breeding competition. These studies indicate that female traits may also be influenced by female competition over sexual or non-sexual resources.

Most studies of female ornamentation have focused on male mate choice, and researchers have only recently begun to explore the role of intrasexual female competition. The influence of predation on female ornaments is left relatively unexplored. Females are often the sole or primary parent providing care to offspring; therefore they may face stronger selection for traits that function in predator defense to protect offspring (Caro 2005). Oftentimes females adopt crypsis to reduce nest predation; however females may develop other defense mechanisms. For example, caribou are the only ungulate where both sexes have antlers. Longer periods mothering in this species suggests that female caribou may have evolved antlers to better defend offspring (Caro 2005). Similarly, in a large comparative analysis, Stankowich and Caro (2009) provide evidence to suggest that female bovids evolved horns for predator defense. The presence of horns in female bovid is correlated with open habitats in which visually guided predators are assumed to have increased detection of prey. Therefore species that live in open habitats may face increased predation, and female bovids in such habitats possess horns that may function in predator defense. Although these examples involve female weaponry, additional traits such as conspicuous colouration and behaviour can function in predator defense (see previous sections on anti-predator signals and predator defense mechanisms). Moreover, in many species females aggressively compete with heterospecifics over non-sexual resources such as food and nest sites. Therefore, our understanding of female traits may benefit from increased attention to the influence of predation and other relevant heterospecific interactions on the evolution of female ornamentation.

In summary, mounting evidence suggests that females may exhibit elaborate traits that do not arise simply from genetic correlation, but serve important functional roles. With continued research, we can better understand the different selection pressures faced by each sex. Mutually ornamented species provide valuable study systems for investigating sex-specific selection and the function of traits that are expressed in both males and females.

Study species: The royal flycatcher

My research explores the behavioural ecology of a mutually ornamented Neotropical bird, the royal flycatcher (*Onychorhynchus coronatus*). Royal flycatchers are medium-sized suboscine passerines that inhabit mature forests from southeast Mexico to Peru and Brazil (Howell & Webb 1995). Historically, there has been debate over the taxonomic classification of royal flycatchers. Most accounts place *Onychorhynchus* in the Tyrannidae (New World flycatchers), within which their particular placement and proposed closest relatives have varied (Ames 1971, Traylor 1977, Lanyon 1988, Fitzpatrick 2004). However, there is growing genetic support to place *Onychorhynchus* outside of Tyrannidae, and perhaps even basal to Pipridae (manakins) (Rheindt et al. 2008, Ohlson et al. 2008, Tello et al. 2009).

Royal flycatchers are facultatively socially polygynous; males pair with up to two females in the breeding season (Cuthbert 2008). During the breeding season, females build nests and provide all care for offspring (Skutch 1960). Females build long (up to

2m), pendulum-shaped nests above riverbeds on thin branches or vines (Skutch 1945), making them very difficult for predators to reach. Their nest is made of a variety of plant fibres; at first glance the structure does not resemble a nest, but rather tangled debris. Due to their cryptic appearance, royal flycatcher nests are believed to exhibit a form of protective adaptation to deter nest predation (Peck 1910, Berg 1995).

Females lay two eggs, which are an unusual rufous-brown colour with some dark brown speckling (Skutch 1945). In addition, nestlings exhibit bright ochre and brown barred plumage that differs from that of adults (Skutch 1960). Little is known about pair formation and mate choice in this species. Similarly, the nest site selection process is poorly understood, but remnants of previous nests are often located very near to active nests (Skutch 1960, pers. obs.).

Royal flycatchers exhibit morphology that is unique among flycatchers. Although many flycatchers have colourful crests, crest feathers are highly elaborated in royal flycatchers. Both sexes possess a large, fan-shaped, erectable crest that is most often concealed, which gives the birds a 'hammerhead' profile (Stiles & Skutch 1989). Adult male crests are red, female crests are yellow, and juvenile male crests are orange (Ridgely & Tudor 1994). In adults, crest feathers terminate in iridescent tips with small black dots (Howell & Webb 1995) (see Fig 2.1). The remainder of adult royal flycatcher plumage is dull olive-brown with the exception of a pale yellow rump and rufous tail (Skutch 1960). Additionally, royal flycatchers have unusually short legs, long flat bills, and the longest rictral bristles of any flycatcher (Traylor & Fitzpatrick 1982, Ridgely & Tudor 1994).

The majority of published information on royal flycatchers pertains to their elaborate crest. This is undoubtedly a consequence of the bizarre crest display they perform when being handled by a human. There have been many descriptions of this behaviour, all of which include crest erection, open gape, and side to side head swaying. The function of the royal flycatcher's crest has intrigued naturalists since it was first documented in 1862 (Lawrence 1862). However, the majority of studies have hypothesized crest functionality based on this human-elicited crest erection. Far fewer studies cite natural occurrences of crest erections, and this is because of the inherent difficulty of studying royal flycatchers in their natural habitat and the infrequency of the display itself. From a small amount of anecdotal evidence, crest erections have been witnessed in the wild during multiple contexts including courtship (Skutch 1960, Whittingham 1993, Cuthbert 2008), copulation (Chaves 2006), agonistic encounters, and preening (Skutch 1960).

The goal of my thesis is to explore the ecology, behaviour, and life history of royal flycatchers with a specific focus on the function of the elaborate crest display seen in both sexes. In Chapter 2, I analyze detailed naturalistic observations from three royal flycatcher breeding seasons. I provide sex-specific information on royal flycatcher behaviour, including formal descriptions of their vocalizations and displays, and discuss the function of male and female crests in detail. In Chapter 3, I provide results from a model presentation experiment conducted on a wild breeding population of royal flycatchers in order to study their response to conspecific and heterospecific models, and in particular the function of crest displays in both males and females.

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CHAPTER 2

The form and function of sex-specific vocal and visual displays in the mutually ornamented royal flycatcher (*Onychorhynchus coronatus*) *

* This chapter was the outcome of joint research with my advisor, Dr. Stéphanie Doucet

SYNOPSIS

Historically, female ornamentation was believed to be nonadaptive and thus received little research attention. However, recent studies suggest that females can possess functional ornaments that operate in contexts such as male mate choice and intrasexual competition. Mutually ornamented species, in which males and females share similar ornaments, provide an excellent study system to explore the function of conspicuous traits in both sexes. We studied a mutually ornamented Neotropical passerine, the royal flycatcher (*Onychorhynchus coronatus*), where both sexes possess an elaborate, concealable crest. We observed a wild population of royal flycatchers to characterize the visual and vocal displays of males and females, and to infer the function of these displays by assessing the context in which they are used and their variation across different breeding stages. We found that females produce a nest-associated '*keeyup*' call, males produce a song, and both sexes produce agonistic '*chatter*' vocalizations. Males perform a multimodal courtship display that involves male crest erection, and can elicit crest displays in females and may lead to copulation. We found both sexes produce crest displays in multiple contexts including intersexual, intrasexual, and heterospecific interactions. In particular, males erected their crests during courtship and copulation with females, when aggressively chasing intruder males on their territory, and when chasing heterospecifics on their territory or in close proximity. Females displayed towards males in response to courtship displays and during copulation, and also produced crest displays towards females in agonistic competition, and towards heterospecifics that approached the nest. Our findings have implications for the evolution of multifunctional ornamental traits that function in intersexual, intrasexual, and

heterospecific contexts. Additionally, our research provides insight into the evolution of mutual ornamentation in tropical species.

INTRODUCTION

Historically, female ornaments received little attention and were believed to be a nonadaptive consequence of genetic correlation between the sexes (Lande 1980). However, recent studies suggest that females can possess functional ornamental traits (Amundsen 2000, Amundsen & Pärn 2006, Clutton-Brock 2009). These findings reveal a large gap in our understanding of the evolution of female ornamentation. Mutually ornamented species, where males and females share similar ornaments, provide an ideal system within which to explore sex-specific selection on similar traits. Mutual ornamentation occurs in many different species and females most often posses a reduced version of the shared trait (Kraaijeveld et al. 2007). Females of many species, however, can be just as ornamented as males, and recent research has revealed that females can experience direct selection for elaborate traits from male mate choice (e.g., Griggio et al. 2005), female competition (e.g., Watson & Simmons 2010), and predator defense (e.g., Murphy 2006).

Several studies have shown that, over evolutionary time, changes in female colouration contribute more frequently to the evolution of dichromatism than changes in male colouration (Björkland 1991, Irwin 1994, Burns 1998, Hoffman et al. 2008). Moreover, many of these instances of evolution from dichromatism to monochromatism involve a gain in conspicuous colouration in females. In addition, instances of bright monochromatism, where both males and females are brightly coloured, occur most commonly in the tropics (Badyaev & Hill 2003). In the context of song, an acoustic ornament typically attributed solely to males, Price and colleagues (2009) found that within the blackbirds (family Icteridae), female song is the ancestral state in tropical species, and this trait has been lost in temperate zone species. These studies show that there is a bias in classifying showy traits, such as conspicuous colouration and song, as 'male traits', even though they also commonly evolve in females. By comparing the expression and function of a shared trait between males and females, we can better understand how selection differs between the sexes. Comparisons of temperate and tropical species may also provide insight into the higher prevalence of female ornamentation in the tropics.

Mutual ornamentation appears to be particularly common in tropical birds (Kraaijeveld et al. 2007). Indeed, there are numerous species where both males and females exhibit conspicuous plumage (e.g., warblers and orioles, Hamilton 1961; hummingbirds, Wolf 1969; parrots, Heinsohn et al. 2005), where both males and females sing (e.g., antbirds, Morton & Derrickson 1996; wrens, Mann et al. 2009), or both (e.g., New World blackbirds, Price et al. 2009). Such species also tend to exhibit elaborate mutual displays (Armstrong 1965, Amundsen & Pärn 2006), but are often poorly studied. Our objective in this study was to characterize the vocal and visual displays of mutually ornamented Neotropical royal flycatchers (*Onychorhynchus coronatus*), and to elucidate the function of these displays in males and females.

Royal flycatchers are suboscine passerines with a geographic range that extends from southeast Mexico to Peru and Brazil (Howell & Webb 1995). During the breeding season, males appear to defend territories and females build nests and care for offspring

(Skutch 1960). Royal flycatchers are facultatively socially polygynous; some males pair with up to two nesting females during the breeding season (Cuthbert 2008). Previous accounts have reported that they seldom vocalize (Ridgely & Tudor 1994), but one male and one female vocalization have been documented; females, and less often males, produce a two-syllable call (Skutch 1960, Wetmore 1972, Stiles & Skutch 1989), whereas males produce a vocalization often described as a song (Skutch 1960, Stiles & Skutch 1989, Howell & Webb 1995). Little is known about the function of either vocalization, and other vocal behaviours remain undescribed.

Royal flycatcher plumage is generally dull olive-brown above and slightly paler below, with a light yellow rump and rufous tail. The most striking feature of the royal flycatcher is its elaborate crest, which is normally concealed, giving the bird a 'hammerhead' profile (Stiles & Skutch 1989). Both sexes possess this ornate, fan-shaped crest, which is red in males, yellow in females, and orange in juvenile males (Ridgely & Tudor 1994). In both sexes, the feathers terminate with iridescent blue plumage marked with small black dots (Howell & Webb 1995) (Fig 2.1). Royal flycatchers erect their crests only infrequently and crest erections are therefore difficult to observe in the wild (Skutch 1960). Based on a handful of observations, male crest erections have been witnessed in the wild during courtship (Skutch 1960, Whittingham 1993), copulation (Chaves 2006), male-male agonistic encounters (Skutch 1960, Graves 1990), agonistic heterospecific encounters (Skutch 1960), and while preening (Skutch 1960). Female crest erections have been witnessed in response to male courtship (Skutch 1960), during copulation (Chaves 2006), and while preening (Skutch 1960). In addition, both males and females perform a characteristic display when being handled by humans. There have been many descriptions of this bizarre behavior, but all of them mention crest erection, an open gape, and side-to-side head swaying. This display has puzzled naturalists since at least the 19th century, and has lead researchers to hypothesize that the crest may function in defense against predation (Bangs & Barbour 1922, Dick & Mitchell 1979, Sick 1993). Graves (1990) suggests that the courtship and agonistic functions of natural crest erections receive the most support; however, this supposition is based on a small number of anecdotal observations.

In this study, we provide the first formal description of the visual and vocal displays of royal flycatchers. Through comprehensive field observations, we also explore the function of royal flycatcher acoustic and visual displays based on the context in which they are used and variation in the frequency of their use across multiple breeding stages.

METHODS

We observed a population of royal flycatchers in Sector Santa Rosa, Guanacaste Conservation Area, Costa Rica (10°40'N, 85°30'W). We studied this population over the course of three breeding seasons (2006, 2007, 2009), and our observations took place between April and July each year. We captured royal flycatchers using mist nets and banded each individual with a unique combination of coloured metal leg bands to facilitate individual identification (note that plastic bands should not be used in this species as they cause injurious irritation and swelling on the legs; S. Doucet, pers. obs.). Royal flycatchers build long, pendulous nests that hang above rivers and streams. These birds live in low population densities in long, linear territories along streams and riverbeds, necessitating a very large study site. Each year, we monitored 15-25 pairs over an area larger than 12 km^2.

We recorded information about visual and vocal displays during both focal observation sessions and opportunistic encounters. During focal observations, an observer sat in a concealed location about 20 m from a royal flycatcher nest site. This is an ideal location for focal observations since royal flycatchers spend much of their time near their nest during the breeding season. As such, royal flycatchers perform the vast majority of their visual and vocal displays in the vicinity of the nest site. Focal observations were conducted in 2006 and 2007 and lasted an average of 95 minutes, totalling approximately 223 hours of focal observation on 14 pairs in 2006 and 18 pairs in 2007. Observers recorded all vocalizations and behaviour in the field including the frequency and context of male and female vocalizations, male courtship displays, and male and female crest displays. We recorded focal observations across four breeding stages: nest building, incubation, chick-rearing, and post-depredation. Nest building begins in early to mid April and continues until the onset of the rainy season in mid May. Following nest building, incubation lasts for 21-22 days and chick-rearing lasts for 21-22 days (Skutch 1945). Post-depredation observations were conducted after nests were depredated, or in rare cases where one member of the pair disappeared, most likely due to depredation. In 2006, 2007, and 2009, we also conducted opportunistic observations where we noted the frequency and context of male courtship behaviour and male and female crest displays.

To document vocalization types, we collected focal recordings using a directional microphone (Sennheiser MHK-70) and a solid-state digital recorder (Marantz PMD-660).

Files were recorded as uncompressed 16-bit and 44 kHz WAV recordings. In addition, some recordings were obtained passively using automated recording devices consisting of an omni-directional microphone (Sennheiser ME-62) and a solid-state digital recorder (Marantz PMD-670) with files formatted as 16-bit and 22.1 kHz MP3 recordings (see Hill et al. 2006 for details for our automated recording devices).

All statistical analyses were conducted using JMP (Version 6. SAS Institute Inc., Cary, NC, 1989-2006). We evaluated how vocal and visual displays varied across the four breeding stages using Wilcoxon/Kruskal-Wallis (rank sum) tests.

RESULTS

Vocalizations

Keeyup

Female royal flycatchers produce a two-syllable call that can be phonetically described as '*keeyup*' (Fig 2.2a; name modified from Stiles & Skutch 1989). Females produce the *keeyup* call most frequently upon arrival and departure from the nest, although they may also produce the *keeyup* call while stationary in their territory. Females produce the highest rate of *keeyup* calls during nest building and chick-rearing stages of breeding (Fig 2.3a; Wilcoxon rank sums: $\chi^2_3 = 11.6$, $P = 0.009$). Males rarely produce a *keeyup* call, but it may be lower pitched than the female's (Skutch 1960). On a few occasions, we observed males giving repeated *keeyups* at dusk prior to the onset of the breeding season. This behaviour is difficult to monitor, however, as royal flycatchers cannot be reliably located until they begin associating with a nest site. Males very rarely produce *keeyup* calls during the breeding season, except that they occasionally produce a single *keeyup* call when they are released after banding.

Male song

Male royal flycatchers produce a vocalization that has previously been classified as a 'male song' (Fig 2.2b; Stiles & Skutch 1989, Howell & Webb 1995). Howell and Webb (1995) describe the male song as a "...descending slowing series of plaintive whistles, usually 5-8 following a shorter intro note, '*whi-peeu, peeu, peeu, peeu, peeu*'...", although our observations and spectrograms reveal that the first note is longer than the other notes, not shorter (Fig 2.2b). Males sing during flight or while stationary and they frequently respond to a whistled imitation of this song. They often sing near the nest, although they will sometimes sing at some distance from the nest, perhaps as an attempt to attract a secondary female. Males sometimes also sing a song when they first arrive near the nest site in the early morning, and the rate of male song is generally very low (Fig. 2.3b). Nevertheless, male song rate is highest during nest-building and after a nest depredation event (Fig. 2.3b; Wilcoxon rank sums: $\chi^2_3 = 13.2$, $P = 0.004$).

Chatter

Both male and female royal flycatchers produce a series of repetitive staccato calls we classify as the '*chatter*' call. The *chatter* call is usually produced by the pursuer during aggressive territorial chases, but is not present during all chases. Because territorial intrusions are relatively rare, we do not have sufficient data to assess how this vocalization changes with breeding stage.

Display behaviour

Crest erection

Based on our focal and opportunistic observations, crest erections are produced in multiple contexts by both sexes. Crest erections occur in both sexes during courtship and copulation and during agonistic encounters with conspecifics and heterospecifics. Royal flycatchers fan out their crests most frequently during preening, a presumably passive, non-signalling context.

Male crest erection

Males display their crests to females during a characteristic courtship display (described below). The rate of these intersexual male crest displays did not vary significantly with breeding stage (Wilcoxon rank sums: $\chi^2_3 = 2.51$, $P = 0.47$, nest building 0.21 ± 0.068, incubation 0.12 ± 0.068, chick rearing 0.079 ± 0.079, depredation 0.077 ± 0.097 displays per hour). Males also erect their crests during copulation (also noted by Chaves 2006), which can last several seconds.

Males erect their crest during agonistic encounters with other males. Territorial males chase intruding males with their crest raised while producing the *chatter* vocalization. Males also chase and direct crest erections at other bird species, such as a buff-throated saltator (*Saltator maximus*) (Skutch 1960) and dusky-capped flycatcher (*Myiarchus tuberculifer*). In one case, a dusky-capped flycatcher landed and perched very near to a male royal flycatcher, which elicited a crest erection in response. The rate of male crest erections towards heterospecifics did not vary across breeding stages

(Wilcoxon rank sums: $\chi^2_3 = 1.31$, $P = 0.73$, nest building 0.032 ± 0.014, incubation 0.012 ± 0.014, chick rearing 0.018 ±0.16, depredation 0.0 ± 0.02 displays per hour).

Female crest erection

Females often erect their crest in response to a male courtship display. The rate of intersexual female crest displays did not vary significantly with breeding stage (Wilcoxon rank sums: $\chi^2_3 = 3.82$, $P = 0.28$, nest building 0.028 ± 0.011, incubation 0.017 ± 0.011, chick rearing 0.0 ± 0.013, depredation 0.0 ±0.015 displays per hour), although as with males, the rate was highest during nest building. Additionally, females erect their crests during copulation, and the female may even turn her head to face the male with her crest erect during copulation.

Females erect their crests while chasing both conspecifics and heterospecifics, in particular, when other individuals get too close to her nest. Females sometimes chase their mate with their crest erect when he is in close proximity to the nest. Additionally, we witnessed interactions at a nest that involved female-female crest displays, which have not previously been described. Over the course of several days, the resident female was harassed by an intruder female who prevented the resident female from approaching her nest. The intruder female chased the resident and the two made frequent physical contact during flight. Throughout this complex interaction, we witnessed crest displays from both females and *keeyup* vocalizations by the resident female.

Females build long, elaborate, pendulum-shaped nests that consist of a variety of loosely woven materials. On several occasions, we witnessed other species attempting to steal material from a royal flycatcher's nest (e.g., yellow-olive flycatcher, *Tolmomyias* *sulphurescens*), which elicited crest erection and chase behaviour by the territorial female. Even if a heterospecific unintentionally approaches a nest too closely, the female is likely to erect her crest and chase the bird away. We witnessed one such event where a male rufous-and-white wren (*Thryothorus rufalbus*) inadvertently approached a nest while singing and the female promptly chased it away with her crest erected. Due to the rarity of these displays, we do not have seasonality data on agonistic female-male or female-female crest displays. The rate of female crest erections directed at heterospecifics did not vary with breeding stage (Wilcoxon rank sums: $\chi^2_3 = 2.67$, $P = 0.45$, nest building 0.012 ± 0.024, incubation 0.05 ± 0.024, chick rearing 0.0 ± 0.028, depredation 0.0 ± 0.34 displays per hour).

Male courtship display

Male royal flycatchers perform a characteristic courtship display that has received brief mention (Skutch 1960, Whittingham 1993), but has not been formally described. The courtship display can be variable in length, but usually lasts no more than 30 seconds. The display involves male crest erection and a unique vocalization we classify as the 'male display vocalization' (Fig 2.2c). The male erects his crest and produces the display vocalization. He does this while performing hovering-type flight that is unlike their typical flight pattern. The display is always directed at a female and usually begins some distance from the female, with the male flying in successively smaller concentric circles and often approaching the female from above. After this elaborate flight, the male typically perches very near to the female and may rest or continue to display with or without vocalization. During this part of the display, the male continues to erect his crest, quivers his wings while holding them low at the sides of the body, and occasionally fans his tail. The male often moves all around the female by hovering in front of her or perching nearby, seemingly in an attempt to continue facing her directly with his crest fanned out. On occasion, males simply produce this part of the courtship display without having performed the flight portion beforehand. Skutch (1960) provides a description of this behaviour:

"Alighting on a vine near the nest, he spread his scarlet diadem to the full and turned his head from side to side so rapidly that the feathers quivered. At the same time, he shook his half-opened wings, fanned out his yellowish tail, and uttered a rapid series of peculiar notes, somewhat like the usual piping call but sharper."

All copulations were preceded by this courtship display, although not all courtship displays lead to copulation. It is important to note that there is no head waving during the male's courtship display. What Skutch accurately describes is that the male sometimes briefly and quickly shakes his head from side to side during the stationary courtship display, but this is not the slow, deliberate head waving that occurs in the handheld display, as has been suggested (Graves 1990, Chaves 2006). The rate of male courtship display was not significantly related to breeding stage (Fig 2.3c; Wilcoxon rank sums: $\chi^2_3 = 2.15$, $P = 0.54$), although these displays tended to occur most often during early nest building, coinciding with the female's fertile period.

DISCUSSION

In this study, we characterize the vocalizations and visual displays of royal flycatchers and elucidate their function based on context-specificity and variation across different breeding stages. We describe and infer function of three vocalizations: a female call, a male song, and an aggressive vocalization used by both sexes. We also provide the first formal description of male courtship display behaviour in this species. Our observations suggest that the royal flycatcher's elaborate crest functions in multiple contexts in both males and females; extensively in courtship, but also in threat displays to both conspecific and heterospecific individuals. Taken together, our findings provide evidence for sex-specific use of a shared ornamental trait in a mutually ornamented species.

Vocalizations

Females frequently produce the *keeyup* call, whereas males produce it only rarely. Female royal flycatchers usually produce the *keeyup* call when approaching their nest, and *keeyup* rates increase significantly during nest building and chick rearing. The use of nest-associated vocalizations seems counterintuitive since vocalizations produced near the nest can presumably attract predators (McDonald & Greenberg 1991). On the other hand, nest-associated calls might also serve beneficial functions, including reducing male harassment, increasing male vigilance, decreasing intruder female settlement, advertising willingness to copulate, and distracting predators away from the nest (McDonald & Greenberg 1991). For example, through audio playback and simulated predation events, Yasukawa (1989) found that the nest-associated '*chit*' call of female red-winged blackbirds (*Agelaius phoeniceus*) most likely functions to maintain male vigilance over the nest. Female red-winged blackbirds call upon arrival and departure from their nest and most frequently during incubation (Yasukawa 1989). In contrast, female royal flycatchers call more frequently upon arrival than departure of their nest, and call rate is highest during nest-building and chick-rearing stages. Although some of the proposed benefits of nest-associated calls seem unlikely in royal flycatchers, maintaining male vigilance represents a possible function. Both red-winged blackbirds and royal flycatchers are facultatively polygynous, and the female royal flycatcher's *keeyup* call may similarly signal to the male that she or the nest is unprotected. Our observations support this hypothesis as males often respond to female *keeyup* calls by approaching the nest or remaining nearby; experimental playback could provide a valuable test of this hypothesis.

Male royal flycatchers sing rather infrequently compared to typical songbirds. For example, male song sparrows (*Melospiza melodia*) sing about 6 songs/min (Stoddard et al.1998), whereas royal flycatchers sing 1-3 songs/hour, depending on breeding stage. Nevertheless, male song rate is highest after nest depredation and also more frequent during early nest building. Higher rates of male song early during the breeding season may represent a form of mate attraction and courtship. Males will also continue to sing after mating, often at some distance from the active nest, which may represent the male's attempt to attract a secondary female. After nest depredation, pairs often re-nest and each additional breeding attempt is condensed into a shorter time frame. Therefore, males may sing at a higher rate after nest depredation to court the female and initiate another nesting attempt (Hall 2004, Topp & Mennill 2008). Additionally, if nest abandonment is caused by the disappearance of the female, possibly through depredation, male song rate may increase in efforts to attract another female. Previous studies have shown male song rate to increase after the loss of a mate (Albrecht & Oring 1995), and our findings suggest that male song functions in mate attraction in royal flycatchers.

Male song does not appear to function in territory defense, as males do not characteristically sing at the periphery of their territory, nor have we witnessed male counter-singing battles at territory boundaries. Additionally, intruder males do not elicit song from territorial males, but rather chasing behaviour accompanied by the chatter vocalization. Our observations therefore suggest that the male song primarily functions in mate attraction and courtship in royal flycatchers.

The *chatter* vocalization and chase behaviour are used in aggressive contexts throughout the breeding season by both sexes. Smith (1966) documented similar vocalizations among several *Tyrannus* flycatchers, which are closely related to royal flycatchers (e.g., Fitzpatrick 2004, Ohlson et al. 2008). In *Tyrannus* flycatchers, both males and females use a chatter-type vocalization during nest defense, territory defense, and self defense. Chatter-type vocalizations may thus be a common means of communicating aggression in tyrant flycatchers.

Display behaviour

Our observations reveal that the elaborate crest displayed by male and female royal flycatchers is a complex, multifunctional trait. Crest erections in males occur during intersexual, intrasexual, and heterospecific contexts. In intersexual contexts, males display their crests towards females during their characteristic courtship display, and during copulation. The male's multimodal courtship display involves crest erection, a distinctive vocalization, and often a conspicuous flight pattern. The highest rate of male display tends to coincide with the female's fertile period, and copulation can follow a male display. During intrasexual interactions, males chase intruder males while displaying their crest. Additionally, a male may chase and crest display towards heterospecifics on his territory or in close proximity. Previous work involving colourmetric variables of the crest and measures of individual condition showed that the male's crest may function as a quality indicator in this species (Cuthbert 2008). Therefore, males may use their crest display to signal quality to conspecifics during courtship and male-male competition. Such dual-function male traits have been previously documented in other taxa (Berglund et al. 1996). For example, combs in male red junglefowl (*Gallus gallus*) are quality indicators (Chappell et al. 1997), and females prefer males with larger combs (Ligon & Zwartjes 1995). Additionally, male comb size signals dominance and is reinforced through male-male competition (Parker & Ligon 2002). The male royal flycatcher's crest provides a further example of a male trait that functions in courtship and intrasexual aggression. However, males also display their crest towards heterospecifics. Our findings suggest that the crest functions as a quality indicator in conspecific communication and is used as a threatening display towards heterospecifics.

Previously documented anecdotal sightings of female royal flycatcher crest displays occurred during preening (Skutch 1960), upon handling by humans (Dick & Mitchell 1979, Graves 1990), during intersexual contexts in response to male courtship (Skutch 1960), and during copulation (Chaves 2006). Here, we provide evidence that females display their crest during intersexual, intrasexual, and heterospecific contexts. Our observations corroborate previous findings that females display to males in response to male courtship displays. Additionally, females display their crest during copulation, which is notably lengthy in this species and can involve the female turning her head and directing her crest at the male. Furthermore, a female will occasionally chase a male while displaying her crest, including her mate, when he approaches her nest. We also provide the first documentation of female-female crest displays in aggressive contexts. As with males, female crests may similarly function as a quality indicator, as crest reflectance is correlated with measures of maternal quality (Cuthbert 2008). Therefore, female crest displays may also signal quality to conspecifics in both courtship and intrasexual competition. Female ornaments signal quality during male mate choice in other species, including northern cardinals (*Cardinalis cardinalis*) (e.g., Jawor et al. 2004). Additionally, several studies report that female traits can signal dominance during intrasexual female competition (Johnson 1988, Jones & Hunter 1999, Murphy et al. 2009). Together with previous research, our findings suggest that females may possess dual-function ornaments with the potential to reveal information about female quality.

We observed several instances of females chasing and displaying their crest towards heterospecifics that were attempting to steal material from their nest, or simply approached the nest too closely. Females build the nest and are solely responsible for parental care; therefore, females are more invested in reproductive attempts than males which may explain heightened female nest defense behaviour. Additional studies show that females may experience selection to develop traits specifically used for defense (e.g., Randall & Matocq 1997, Stankowich & Caro 2009). Conversely, both sexes may share similar traits used in predator defense (Murphy 2006). Both sexes of the turquoise browed motmot (*Eumomota superciliosa*) possess unusual racket-shaped tails that males and females use in a conspicuous pursuit deterrent display towards approaching predators (Murphy 2006). Additionally, tail morphology appears to be sexually selected in males but not females (Murphy 2007). Murphy's work highlights the use of an ornament, rather than armament, in predator defense, and sex-specific functions of a shared trait. As with males, female royal flycatcher crests may signal quality to conspecifics during courtship and intrasexual female aggression. In addition, females appear to frequently use their crests during heterospecific nest defense; however, it is unlikely that either the male or female crest signals quality to heterospecifics.

The bizarre display produced by royal flycatchers when they are handled by humans has led several authors to hypothesize the crest may function in predator defense (Bangs & Barbour 1922, Dick & Mitchell 1979, Sick 1993). Our finding that both sexes aggressively display their crest towards other species provides partial support for this hypothesis. Another example of an ornamental trait used in heterospecific defense occurs in sunbitterns (*Eurypyga helias*). Male and female sunbitterns possess concealed conspicuous colouration on their wings that they display in a characteristic posture during courtship and nest defense (Thomas & Strahl 1990). The sunbittern display is similar to the royal flycatcher's crest display in form and function. Displays from both species involve concealed colouration and an apparent increase in body size. The revelation of previously concealed conspicuous colour can startle predators (Edmunds 1974). Additionally, bright contrasting colours like those of the royal flycatcher's crest (red/yellow, black, blue) often function in warning colouration (Cott 1947). Although speculative, these observations suggest that of royal flycatcher crest displays may indeed function to deter predation, especially as a last-resort defense mechanism. Further observations of natural or experimentally-simulated predation events on royal flycatchers could help to clarify the possible anti-predator function of this elaborate crest. More emphasis should also be placed on natural contexts that induce crest erection, as the handheld crest display could possibly be a nonadaptive consequence of stress due to capture (Wetmore 1972), although the long-lasting and deliberate nature of the display suggests otherwise.

Of 429 Tyrannidae, 81 species (19%) possess concealed conspicuous crown colouration, and 58% of those species are monochromatic for crown colour. Therefore, concealed conspicuous crowns appear in both sexes in a substantial number of tyrant flycatchers. The signalling context of this prominent trait has not been thoroughly examined, although anecdotal observations suggest that courtship and aggression are likely functions in other species as well.

In conclusion, we found that male and female royal flycatchers exhibit distinct vocalizations and visual displays. Females produce a nest-associated call, males produce a song and a courtship display, and both sexes use a characteristic vocalization during agonistic chases with conspecifics and heterospecifics. Male and female crests appear to be multifunctional signals used in intersexual, intrasexual, and heterospecific contexts. Previous work on mutually expressed ornamental traits has focused on the influence of mate choice in the evolution of mutual ornamentation (e.g., Jones & Hunter 1993, Griggio et al. 2005). However, additional contexts such as intrasexual female competition (Watson & Simmons 2010) and predator defense (Stankowich & Caro 2009) may also favour the evolution of elaborate female traits. Further work is required to understand the evolution of mutual ornamentation and elaborate female traits. Research on the influence of intrasexual competition and heterospecific defense on the evolution of female ornaments may be particularly promising, especially in tropical animals.

Acknowledgements

We are very grateful to J. Cuthbert and C. Chui for help with data collection and organization. We thank D. Mennill for access to sound recording equipment and for providing sound spectrograms. We thank R. Blanco and the staff at the Guanacaste Conservation Area for logistical support in Costa Rica. Members of the Doucet lab provided helpful comments on the manuscript. Funding to KR was provided by the Animal Behaviour Society and an Ontario Graduate Scholarship and to SMD by the Natural Sciences and Engineering Research Council of Canada.

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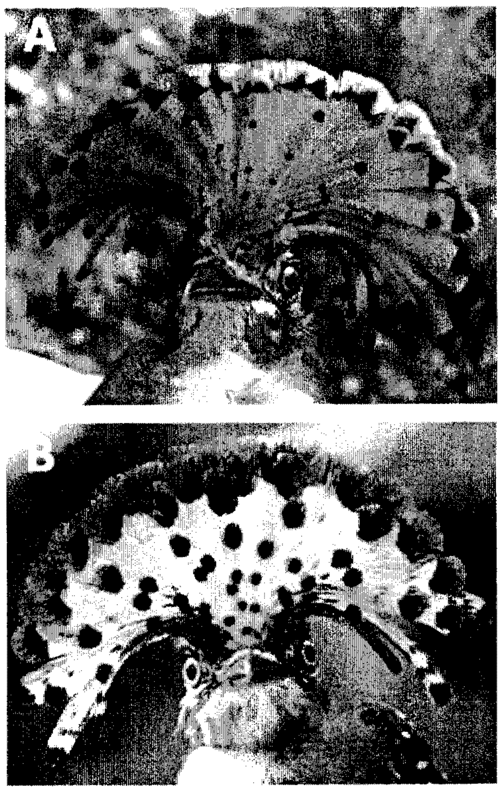

Fig 2.1 Expanded crests of male (a) and female (b) royal flycatchers.

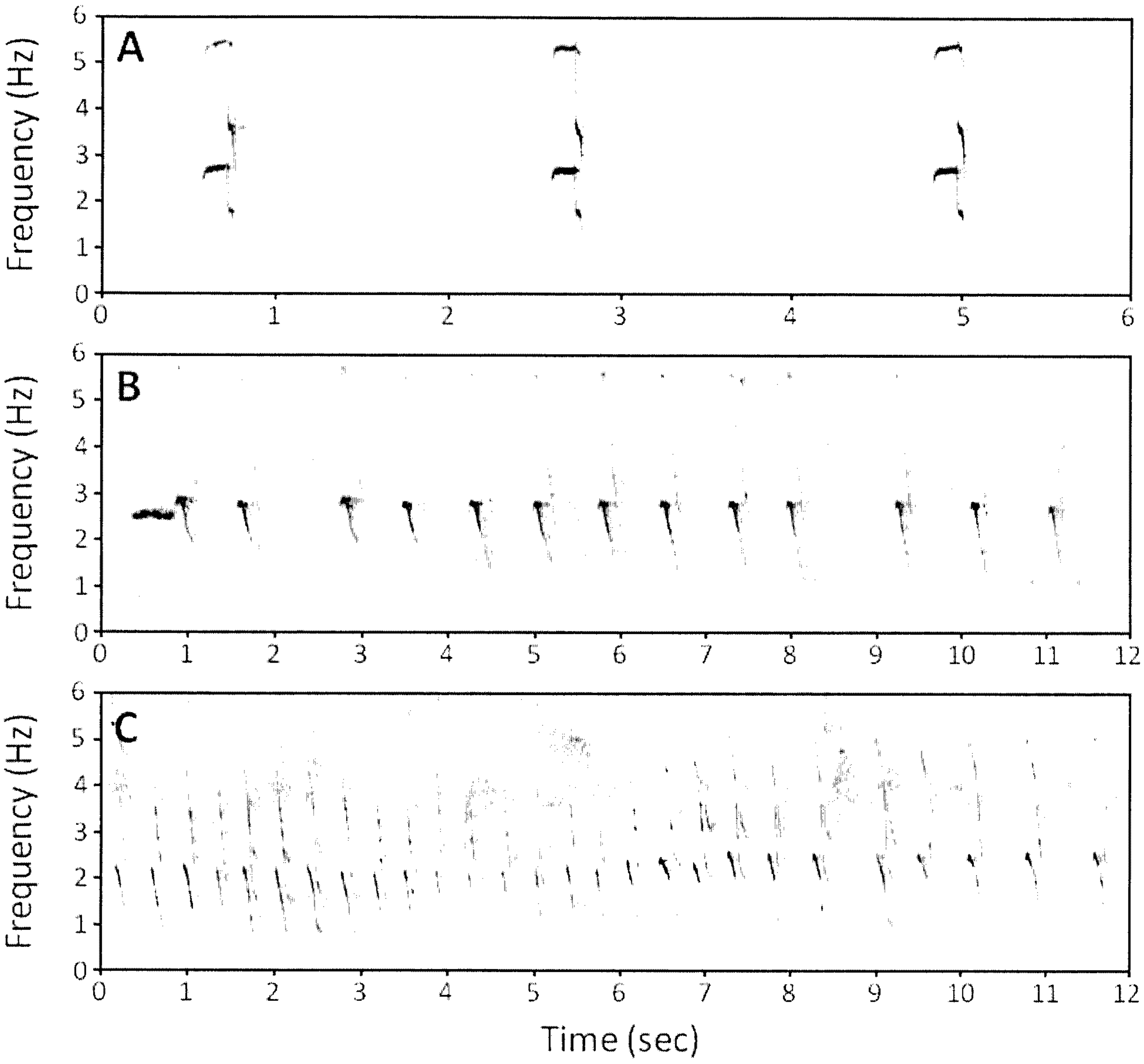

Fig 2.2 Spectrograms of three royal flycatcher vocalizations. Female *keeyup* (a), male song (b), and male display vocalization (c).

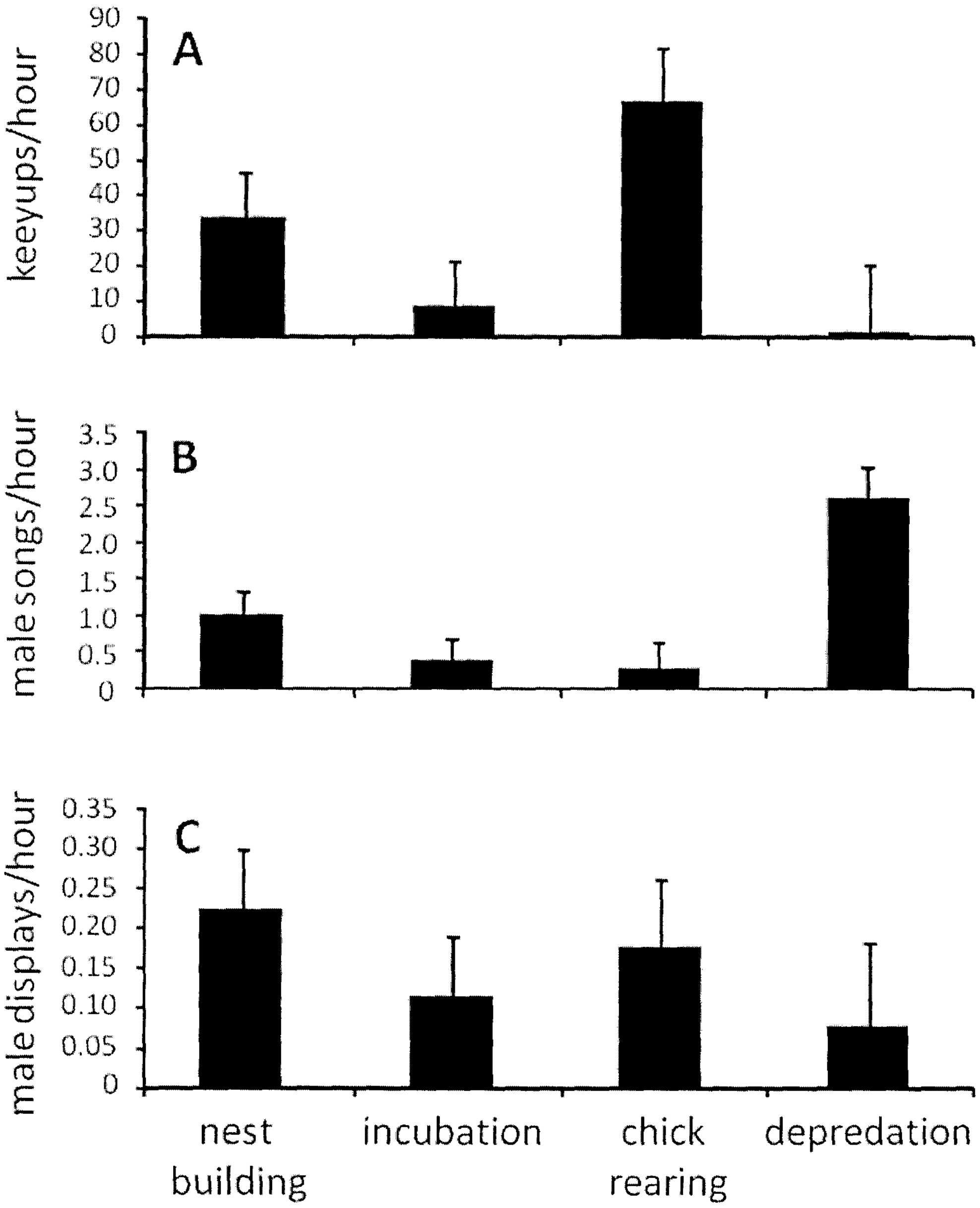

Fig 2.3: Variation in the rate of royal flycatcher display traits throughout the breeding season: female *keeyup* rate/hour (a), male song rate/hour (b), and male courtship display rate/hour (c).

CHAPTER 3

Behavioural responses of Neotropical royal flycatchers (*Onychorhynchus coronatus*) to conspecific and predator models: implications for the evolution of multifunctional traits and mutual ornamentation *

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* This chapter was the outcome of joint research with my advisor, Dr. Stéphanie Doucet

SYNOPSIS

Multifunctional traits represent an efficient method of animal communication because they allow individuals to communicate in multiple contexts using a single trait. Multifunctional traits are most commonly used in both intrasexual competition and female mate choice, but they may also function in more diverse contexts such as sexual selection and predator defense. Royal flycatchers (*Onychorhynchus coronatus*) are mutually ornamented Neotropical passerines where both males and females possess colourful, erectable crests. Little is known about their behaviour, including the function of their elaborate crest. Observational studies suggest that the crest may function in a variety of contexts including courtship, intraspecific aggression, and defense against predation. We conducted a model presentation experiment on wild royal flycatchers using conspecific and heterospecific models to induce courtship, territorial, and anti-predator behaviours. We found that females were more responsive to models than males and were most likely to approach, dive, and vocalize at the female royal flycatcher model. Although crest display rate did not vary across model type for either sex, both males and females used their crests most frequently during intersexual contexts. Additionally, females were more likely to display to heterospecifics during characteristic nest defense behaviour. Our findings corroborate previous studies and suggest that males use their crest primarily for courtship and during territory defense. In contrast, females use their crests in courtship, intrasexual female aggression, and heterospecific nest defense. Our study provides insight into the evolution of multifunctional traits and highlights the independent use of traits and sex-specific selection in mutually ornamented species.

INTRODUCTION

There is increasing evidence for the widespread existence of multifunctional display traits in animals. Multifunctional traits are single traits co-opted for use in multiple contexts, a process originally referred to as 'trait borrowing' (Fisher 1954). Multifunctional traits can occur at the molecular, morphological, and behavioural level (McLennan 2008), but relatively few studies have explored multifunctional display traits. Historically, multifunctional displays were thought to have evolved through the ritualization of displacement behaviours (Huxley 1966). A more recent hypothesis proposes that females may develop novel preferences for existing male traits used in male-male competition, causing them to be co-opted for use in courtship (Borgia 2006). Alternatively, male eavesdropping on male-female interactions could ultimately result in display traits used in both courtship and male-male communication (Morris et al. 2007). Although several hypotheses have been proposed to explain the evolution of multifunctional display traits, few studies have demonstrated the use of such traits, and most of these studies have focused on traits used only in sexual contexts.

The most commonly described multifunctional traits function in both male-male competition and female mate choice (Berglund et al. 1996). For example, in birds, male song often functions to both repel rivals and attract mates (Catchpole & Slater 2008). However, multifunctional traits are not confined to courtship and competition contexts. Fireflies, for example, use their bioluminescent signals in multiple contexts including intersexual communication (Lewis et al. 2004), species recognition (Moiseff & Copeland 2010), and predator defense (Underwood et al. 1997). Similarly, in *Dendrobates* poison frogs, bright colouration serves as a warning of toxicity to deter predators (Daly & Myers

1967, Summers & Clough 2001), but is also important in mate choice (Summers et al. 1999). In skylarks (*Alauda arvensis*), males sing for the purpose of conspecific territory defense, but also sing while under predatory attack which signals individual quality that deters predators (Cresswell 1994).

Multifunctional traits can also serve different functions in males and females. Murphy (2006) recently showed that both male and female turquoise-browed motmots (*Eumomota superciliosa*) use their unusual racket-shaped tail as a pursuit deterrent display towards approaching predators. In addition, tail morphology appears to be sexually selected in males, but not females (Murphy 2007). Similarly, horns present in both male and female bovids appear to serve different functions. Male horns are thought to have evolved for intrasexual combat over territories or mates (Clutton-Brock 1982), whereas female horns have likely evolved for use in predator defense (Stankowich & Caro 2009). Collectively, these studies imply that some multifunctional traits have evolved to function in both sexual selection and predator defense, and thereby highlight the possible influence of natural selection on conspicuous traits. These studies also show that males and females can experience independent selection for mutually expressed traits.

Although research on elaborate traits has focused largely on male ornaments, females can also be ornamented (Amundsen 2000). Selection for female traits is most evident in sex role reversed species and species wherein females possess a trait that is absent in males (Kraaijeveld et al. 2007). In many species, however, both males and females exhibit similar conspicuous traits - i.e. they are mutually ornamented. Previously, mutual ornamentation was explained through genetic correlation between the sexes, such that conspicuous traits were under selection in males and appeared as genetic by-products in females (Lande 1980). However, phylogenetic analyses have revealed that evolutionary transitions between sexual dichromatism and monochromatism have been numerous and have occurred in both directions (e.g., Price & Birch 1996, Wiens 2001), suggesting that ornamentation between the sexes is not always genetically constrained. Furthermore a variety of studies exploring the influence of both natural and sexual selection on female traits suggest that females can exhibit functional ornamentation. For example, female expression of a shared trait can be favoured or maintained through male mate choice (e.g., Jones & Hunter 1993, Griggio et al. 2005), intrasexual female competition (e.g., Johnson 1988, Murphy et al. 2009, Watson & Simmons 2010), and predation (e.g., Murphy 2006, Stankowich & Caro 2009). Such studies suggest that females can exhibit functional versions of 'male' traits. However, because males and females face different selection pressures, their traits may serve different functions.

There are numerous examples of mutual ornamentation among tropical birds, but most of these species are poorly studied (Kraaijeveld et al. 2007). Royal flycatchers (*Onychorhynchus coronatus*) are mutually ornamented Neotropical passerines distributed from Mexico to Brazil (Howell & Webb 1995). Although their plumage colouration is generally cryptic, both males and females possess elaborate, colourful crests that they can display or conceal at will. Until recently, little was known about this species, including the function of its remarkable crest. Royal flycatchers are typically found in low densities (Wetmore 1972), and erect their crests only infrequently, making it difficult for researchers to elucidate the function of this elaborate trait (Skutch 1960, Chapter 2). Nevertheless, the function of the royal flycatcher's crest has intrigued naturalists ever since Lawrence (1862) first documented the unusual way in which it is displayed when birds are handled by humans. During this display, both males and females erect their crest, open their bills, and sway their heads side to side while maintaining eye contact with the observer.

Multiple hypotheses have been proposed to explain the function of male and female crests including use in courtship (Skutch 1960, Graves 1990), male-male combat (Skutch 1960, Graves 1990), defense against predation (Bangs & Barbour 1922, Dick & Mitchell 1979, Sick 1993), and even aggressive mimicry of a flower to catch insect prey (Nutting 1882). These hypotheses were largely based on anecdotal observations since few crest displays had been observed in the wild. In a comprehensive observational study, we discovered that the crest is a multifunctional trait used by both sexes during courtship, conspecific aggression, and heterospecific aggression (Chapter 2).

In the current study, we conducted a model presentation experiments on wild, free-living royal flycatchers to induce courtship, agonistic, and anti-predator behaviours. We used stationary models with audio playback to simulate multiple signalling contexts including courtship (presentation of opposite sex conspecific model), agonistic (presentation of same-sex conspecific model), and threat of predation (presentation of predator models). Our objective was to experimentally test the behavioural response of male and female royal flycatchers in these different contexts to explore possible functions of their elaborate crests.

METHODS

We studied royal flycatchers in Sector Santa Rosa, Guanacaste Conservation Area, Costa Rica (10°40'N, 85°30'W). We conducted model presentation trials from the end of the dry season to the beginning of the rainy season between 30 April 2009 and 30 May 2009. This period corresponded to the start of the breeding season of royal flycatchers at this site and included the nest building and incubation stages of the royal flycatcher reproductive cycle. We used model presentation along with audio playback to investigate royal flycatcher behaviour in response to different contexts.

Models

We used five models in this experiment: male and female royal flycatcher, keel-billed toucan (*Ramphastos sulfuratus*), collared forest falcon (*Micrastur semitorquatus*), and white-tipped dove (*Leptotila verreauxi*). Royal flycatcher models were used to elicit intersexual and intrasexual behaviour in male and female subjects. We used two predator models, one nest predator (toucan) and one adult predator (falcon), to study anti-predator behaviour. Although little is known about royal flycatcher predators, the keel-billed toucan is a renowned nest predator in the tropics and toucans have been observed inspecting royal flycatcher nests (Skutch 1945). Collared forest falcons are predators with a range of prey items including many species of adult birds (Stiles & Skutch 1989). We used a white-tipped dove model as a nonthreatening heterospecific as they do not share common food resources with royal flycatchers and nest in different strata of the forest (Stiles & Skutch 1989). All three species are common at our study site. Our models differed in size because of the different sizes of the animals the models were designed to simulate. We attempted to control for this among heterospecific models by choosing large species for all three model types (head to tail model length dove: 27 cm, toucan: 41 cm, falcon: 51 cm).

Due to the field-based nature of our study, using rare museum skins of Neotropical species as models was not feasible. Similarly, creating taxidermic mounts of these birds from our field site raised ethical concerns. Therefore, we fabricated realistic models from a combination of plastic models, felt, and acrylic paint, and all models were similarly realistic. We created two royal flycatcher models from plastic martin mounts (Growers solution, TN, USA). We adjusted the size of these mounts to match royal flycatcher dimensions (head to tail length 17cm), painted them to mimic royal flycatcher plumage, and used felt for the beak and crest. We traced crest size and spot size from scaled photos of male and female crests. These removable crests were attached to the models with Velcro, and were alternated between the models in different trials so the same body was presented with different crests. We created a single keel-billed toucan model by stuffing a felt body, painting the bill to mimic natural colouration, and attaching black plastic eyes and blue plastic clips for feet. Similarly, we made a single collared forest falcon model from cotton batting and felt, painted the bill and ceres, added plastic eyes, and wooden tarsi. We created two white-tipped dove models from plastic dove mounts (Macks Prairie Wings, AR, USA). We adjusted the size of the models and painted them to mimic white-tipped dove colouration.

Audio Playback

We played species-specific vocalizations during each model presentation trial to enhance the realism of the simulation and to facilitate the royal flycatcher's ability to discriminate between model species (e.g., Kroodsma 1974, Ghalambor & Martin 2002). In addition, the use of vocalizations during stationary model presentation may help prevent habituation to models (Ghalambor & Martin 2000). We used a male song during male royal flycatcher model trials and the female royal flycatcher vocalization (the *keeyup* call) during female royal flycatcher model trials (see Chapter 2 for details). Similarly, we used the diagnostic vocalizations of the keel-billed toucan, white-tipped dove, and collared forest falcon during their respective trials. Output was standardized across all playback treatments, where the stimuli were played for 11 seconds followed by 49 seconds of silence, and this pattern was repeated three times for a total of three minutes of playback. Trials consisted of two sequences of three minutes of playback followed by 12 min of silence, for a total of 30 minutes. The speaker was placed below the model with efforts to camouflage it within foliage. For the first 11 trials, the playback apparatus consisted of a small loudspeaker (Sony, SRS-A37) connected via a 32 m cable to a playback device that contained the vocalizations (Apple, iPod). We then switched to a wireless remote-based system for ease of use in the field for the remaining 84 trials, which consisted of a camouflaged loudspeaker (Foxpro, Scorpion) connected wirelessly to a remote playback device (Foxpro, TX-200).

Trials

Model presentation trials took place between 05:30 and 11:00 CST. For all nests, we presented the male and female royal flycatcher models first, in alternate order at each nest, because we did not want to promote nest abandonment by presenting threatening predator models early during the nest-building period. We thereafter alternated the order of presentation of the dove, toucan, and falcon models and noted the order so that we could test for the possible influence of presentation order on focal pair response. Each pair was tested once for each model type, and a minimum of one day elapsed between consecutive model presentation trials at each nest (mean 76.5 ±10.2 hours). In total, we conducted male and female model trials at 23 nests, and due to nest losses by depredation (a common occurrence among many passerine species at our study site), we conducted toucan and dove model trials at 17 nests, and falcon model trials at 15 nests.

To ensure that the royal flycatchers would encounter the experimental models, we positioned them on natural foliage near active nests. Royal flycatchers build their long, pendulous nests above riverbeds (Skutch 1960). We placed models on the nearest possible branch to the nest that was thick enough to support the model, avoiding placing the model on the tree containing the nest. Model distance ranged between 1.8 and 6.2 m from the nest. However, we ensured that model location remained consistent at each nest for all five model types. We measured the distance from the model to the nest to test for a possible influence on the focal pair's behaviour.

We colour-banded most of the royal flycatchers in our population, facilitating identification of individuals and making the male and female easy to distinguish. For the few unbanded birds involved in this model presentation experiment (14 females and four males), males and females are readily distinguishable by experienced observers on the basis of appearance and behaviour. Once the model and speaker were set up, two observers sat a minimum of 20 m away, as concealed as possible by natural vegetation, and waited for a royal flycatcher to return to the nest site. If no birds appeared within one hour, the trial was aborted. We started playback only after sighting at least one individual within 20 m of the model (average 5.7 ± 0.76 min). Thus, vocalizations were not used to attract the birds from afar, but rather to direct their attention to models once they were already near the nest.

Two observers recorded male and female royal flycatcher behaviour continuously during trials, as this species is difficult to observe in the wild. Observers recorded male and female distance to model (to the nearest 0.5 m), closest approach to model (to the nearest 0.5 m), latency to closest approach (to the nearest minute), vocalizations (frequency and type), dives at model, crest displays, and incubation and courtship behaviour. We also video-recorded trials and later analyzed them to verify the accuracy of our field observations. We estimated distances in the field with the help of flagging tape markers and averaged the values when the two observers' records were more than 0.5 m apart. From these data, we determined a focal individual's proportion of the trial spent within 6 m of the model. We adjusted trial length when females incubated during trials by recording data only when the female was not incubating. We recorded vocalizations by counting the number of female *keeyup* calls and male songs per minute. We recorded dives when a focal bird flew directly at a model and approached it to within 0.5 m. We recorded a crest erection whenever the crest was erect and fully fanned out. We then categorized crest erections according to their context as 'intrasexual crest display' (display directed at a member of the same sex), 'intersexual crest display' (display directed at a member of opposite sex), 'heterospecific crest display' (display directed at another species), and 'model crest display' (display directed at a model). We determined nesting stage for each female in the field, and for those females that were incubating we noted whether or not they incubated during trials, the latency to incubation, and the duration of incubation. The main courtship behaviour we recorded was the male display, where males give a characteristic flight accompanied by a crest erection and a distinctive vocalization (Chapter 2).

Statistical analysis

All statistical analyses were conducted using JMP (Version 6. SAS Institute Inc., Cary, NC, 1989-2006). We omitted trials from analyses when the focal male or female was absent for the entire trial (four trials each). We were primarily interested in comparing subject behaviour to model type, but also tested for possible confounding effects of model order, model distance to nest, breeding stage, and individual identity. We used Wilcoxon/Kruskal-Wallis (rank sums) tests when there were no confounding effects, and included confounding variables as covariates in generalized linear regression analyses when they significantly predicted the behavioural response of male or female royal flycatchers. For regression analyses, we log-transformed response data to improve fit to normality. We also assessed the likelihood of females engaging in incubation during trials, and of males or females vocalizing during trials, using univariate Pearson's Chi-square tests or nominal logistic regression analyses when controlling for confounding variables.

RESULTS

Crest displays

We recorded all crest displays performed by male and female royal flycatchers during trials, which included displays to our models as well as displays to other birds. Crest display rate was not significantly related to model type for males (Fig 3.1a; Wilcoxon rank sums: $\chi^2_4 = 2.29$, $P = 0.68$) or females (Fig 3.1b; Wilcoxon rank sums: $\chi^2_4 = 5.39$, $P = 0.25$). However, we found significant variation in the context in which crest displays were produced most frequently for both males and females. Males displayed their crests more frequently to live females than to other males, heterospecifics, or experimental models (Fig 3.2; Wilcoxon rank sums: $\chi^2_3 = 24.8$, $P < 0.0001$). Females similarly displayed their crests most frequently to males, but also displayed their crests more frequently to heterospecifics than to other females or experimental models (Fig 3.2; Wilcoxon rank sums: $\chi^2_3 = 7.42$, $P= 0.06$).

Distance to models

Males did not approach models more closely in relation to model type (Fig 3.3a; Wilcoxon rank sums: $\chi^2_4 = 7.08$, $P = 0.13$). However, female closest approach was significantly influenced by model type, breeding stage, and individual (Fig 3.3b; whole model $F_{30, 59} = 5.53$, $r^2 = 0.74$, $P < 0.0001$, model type $F_{4, 89} = 7.14$, $P < 0.0001$, *breeding stage* $F_{2, 89} = 10.0$, $P = 0.0002$, *individual* $F_{24, 89} = 4.05$, $P < 0.0001$). Female closest approach was highest for the female model and was highest during the incubation stage. Latency to closest approach was not affected by model type for males or females (Wilcoxon rank sums: *males* $\chi^2_4 = 6.59$, $P = 0.16$, *females* $\chi^2_4 = 2.41$, $P = 0.66$).

The proportion of trials that males spent within 6 m of models was significantly affected by model type, with males spending more time within 6 m of male and female models (Fig 3.4a; Wilcoxon rank sums: $\chi^2_4 = 14.9$, $P = 0.005$). The proportion of trials that females spent within 6 m of models was only influenced by individual identity (Fig 3.4b; whole model: $F_{28, 48} = 2.30$, $r^2 = 0.57$, $P = 0.006$, *model type* $F_{4, 76} = 1.17$, $P = 0.34$, *individual* $F_{24, 76} = 2.61$, $P = 0.002$), however, females spent the greatest proportion of trials within 6 m to female models.

Dives at model

The rate at which males dove at models was not significantly influenced by model type (Fig 3.5a; Wilcoxon rank sums: $\chi^2_4 = 4.54$, $P = 0.34$). Females, which dove more frequently than males, dove at a higher rate during female model trials (Fig 3.5b; Wilcoxon rank sums: $\chi^2_4 = 10.5$, $P = 0.03$).

Vocalizations

Female *keeyup* rate was not significantly related to model type (Wilcoxon rank sums: $\chi^2_4 = 6.10$, $P = 0.19$). Because of variability between females to produce *keeyups*, we also assessed the likelihood that females would produce *keeyups* during different trial types. We found females were more likely to produce *keeyup* vocalizations during female model trials (whole model $\chi^2_{28} = 54.7$, $P = 0.002$, model type $P = 0.02$, *individual* $P = 0.004$). In contrast, neither the rate nor the likelihood of male song was significantly affected by model type (Wilcoxon rank sums: $\chi^2_4 = 2.72$, $P = 0.61$; Pearson chi-square: $\chi^2_{89} = 3.17$, $P = 0.53$).

Incubation

We observed female incubation behaviour during trials to determine whether the presence of different model types affected their likelihood of returning to the nest to incubate. Out of seven nests with females incubating, we found that females were most likely to incubate during female and male model trials and never incubated during falcon model trials (Pearson chi-square: $\chi^2_{40} = 23.9$, $P < 0.0001$).

Male courtship displays

We observed 14 male courtship displays, of which 35% occurred during female model trials, 29% during male model trials, 21% during dove model trials, and 14% during toucan model trials. No displays occurred during falcon model trials. Nevertheless, the rate of male courtship displays was not significantly related to model type (Wilcoxon rank sums: $\chi^2_4 = 4.12$, $P = 0.39$).

DISCUSSION

We sought to experimentally test the responses of royal flycatchers to conspecific and heterospecific models and to investigate the function of their elaborate crests. Our observations indicate that males and females seem to use their crests differently in different contexts. Our study revealed that crest displays were most frequently used during intersexual communication in both sexes, and that females also displayed their crest frequently during heterospecific nest defense. Our findings suggest that females play an active role in nest defense during the breeding season, and that males and females exhibit sex-specific use of their elaborate crests. Our model presentation experiment also revealed sex differences in territorial and aggressive behaviour in the royal flycatcher. Females responded more strongly to model presentation than males, and females exhibited the strongest response towards the female royal flycatcher model. These data present evidence for female-female aggression in this tropical species.

In tropical species, females often participate in territorial behaviour and may even respond more aggressively than males to intruders (e.g., Illes & Yunes-Jimenez 2009, Murphy et al. 2009). Additionally, work on tropical duetting species has shown that females can exhibit sex-specific aggression, reacting more strongly to same-sex intruders (Morton & Derrickson 1996, Seddon & Tobias 2006, Mennill & Vehrencamp 2008). In royal flycatchers, we found that females reacted more strongly than males to model presentation and, more specifically, that females approached female models more closely and dove and vocalized more frequently at the female royal flycatcher model. Female royal flycatchers build their elaborate nests without the help of males, and nest-building can take several days. Females are also solely responsible for parental care in this species (Skutch 1960). As such, females invest much more in breeding attempts than males, which may explain the heightened response from females we observed during simulated territory intrusions (see also Murphy et al. 2009).

The aggressive responses exhibited by females in response to models suggest that female royal flycatchers may compete for resources. Although previous work has focused largely on male-male competition, a growing number of studies reveal examples of intrasexual competition in females, and such female-female competition may be an important selective factor in the evolution of female ornaments (West-Eberhard 1983, Amundsen 2000, Amundsen & Pärn 2006), particularly among mutually ornamented tropical birds (Murphy et al. 2009). There are multiple potential causes of intrasexual female competition (reviewed in Slagsvold & Lifjeld 1994). In polygynous species, males must divide their time between multiple nests, and reduced male assistance may increase female competition (Slagsvold & Lifjeld 1994). Royal flycatchers are facultatively polygynous (Cuthbert 2008). Across three breeding seasons, polygyny occured on average at 10-11% of nests. Polygynous males occurred in two of 14 pairs in 2006, in one of 18 pairs in 2007, and in three of 23 pairs in 2009. Females may react aggressively to intruder females to prevent polygyny and its associated reduction in male investment (Slagsvold 1993), or to prevent nest usurpation (Dunn & Hannon 1991). Moreover, high levels of female competition in polygynous and polygynandrous mating systems have previously been associated with elaborate female traits such as female song (e.g., Langmore 1998) and conspicuous colouration (e.g., Heinsohn et al. 2005).

Our findings also suggest that female crest displays are an important component of intrasexual aggression. Certain females were particularly responsive during female model presentation trials and performed crest displays several times while diving at the female model. In addition, we have observed agonistic female-female crest displays in natural contexts (Chapter 2). At one particular nest, we observed the territorial female being repeatedly harassed and prevented from nest building by an intruding female over the course of several days. Both females flashed their crests frequently during the attacks. In a recent comparative study, Kraaijeveld (2003) found that mutual ornamentation was more common in cavity nesters than open nesters, supporting a role of female ornamentation in nest competition. Moreover, Sandell (1998) found that in polygynous

European starlings (*Sturnus vulgaris*), monogamous females were more aggressive than polygynous females toward intruder females. Individual variation in female aggressiveness may be similarly related to mating status in royal flycatchers, as the most aggressive females appeared to be nesting monogamously with the territorial male.

Females responded to predator models by reducing their activity level, which is a common anti-predator behaviour (Langerhans 2007). Females stayed the farthest away, and were least likely to dive or incubate during toucan and falcon model trials. Therefore, our predator models did not elicit active defense behaviour but rather increased cautionary behaviour in females. Female reaction to predator models follows predictions proposed by Ghalambor et al. (2001), who hypothesized that long-lived Southern Hemisphere species should be less involved in the defense of nests and young and more concerned with self defense than short-lived Northern Hemisphere species in efforts to increase lifetime reproductive success. However, females aggressively defend their nests from a number of non-predatory heterospecifics (Chapter 2) by chasing them, often with their crest erected. Additionally, a female performed a crest display towards the toucan model, our proxy to a nest predator. In general, female royal flycatchers did not exhibit active predator defense in response to our models, but our observations suggest they may use their crest aggressively toward heterospecifics in close proximity to their nest.

In general, males were less responsive to model presentation than females. None of the male behaviours we recorded were significantly related to model type, except for the proportion of the trial spent within 6 m of the model, which was highest during male and female model trials. Male royal flycatchers appear to compete for access to females, and they may also mate guard their partners to ensure paternity (see Birkhead & Møller

1992). We observed territorial males chasing intruder males with their crests erected, and territorial males becoming agitated when a male song was played on their territory. Males did not display any courtship behaviour towards the female model or active defense towards the predator models. However, males continued to produce courtship displays to their female partners, which involve a characteristic flight along with crest erection (Chapter 2), during all trials except for falcon model trials.

Our model presentation experiment allowed us to observe courtship, intrasexual, and defense behaviours in both male and female royal flycatchers. Males and females exhibited differential responses across model types, suggesting that they were able to distinguish between models. Although crest displays did not vary across model types in either sex, we found that males and females most often displayed their crests to each other, suggesting that their crest plays an important function in intersexual communication. Females also used their crests during heterospecific nest defense, a behaviour less often observed in males. Males appear to use their crests primarily during courtship and territorial contexts, suggesting that they are maintained by sexual selection. Females use their crests during courtship, intrasexual aggression, and nest defense; therefore, elaborate female crests may be strongly influenced by both natural and sexual selection. Recent research by Cuthbert (2008) suggests that royal flycatcher crests are quality indicators in both sexes. Thus, males and females may signal quality to mates and same sex rivals using their crest. However, the function of the crest in heterospecific contexts is less apparent.

Because of the ritualized crest displays that royal flycatchers produce when handled by humans, anti-predator defense has long been a hypothesized function of royal flycatcher crests (Bangs & Barbour 1922, Dick & Mitchell 1979, Sick 1993). Although our predator models did not elicit the head waving display that royal flycatchers produce in the hand, our observation that male and female royal flycatchers aggressively display their crests to other species provides some support for a defensive function of crest displays. Based on the method of display, which involves the rapid revelation of conspicuous colours and an apparent increase in body size, we hypothesize that the crest display may function as a last-resort predator defense mechanism (Edmunds 1974), and as such may only be elicited when the predator is very close, or physically touching a royal flycatcher. Therefore, our stationary predator models may not have provided a threatening enough stimulus for males and females to actively display their crests. The observation of predation attempts in the wild would help clarify the function of the crest in predator-prey interactions.

Genetic correlations between the sexes do not rule out selection for female traits. Recent work on mutually expressed weaponry suggests that sex-specific selection can differentially influence the evolution of horns in male and female sheep (Robinson & Kruuk 2007), bovids (Stankowich & Caro 2009), and beetles (Watson & Simmons 2010). These studies outline differences in male and female horn morphology and suggest that these differences in morphology provide clues about differences in function. For example, the broad horns in male feral Soay sheep (*Ovis aries*) function as weapons in male-male battles whereas the smaller, more pointed horns of females are optimized for intrasexual female competition (Robinson & Kruuk 2007). Male and female royal flycatchers use their crests to differing degrees in multiple contexts, and their crests differ in size and colour. These observations suggest that male and female crests may serve different functions (Amundsen & Pärn 2006). Future research exploring the degree of dimorphism in mutually expressed traits would help us to better understand the evolution of conspicuous traits in males and females.

In conclusion, our study provides a novel example of a mutually expressed multifunctional trait that may have function in intersexual, intrasexual, and heterospecific contexts. Many species possess multifunctional traits, and researchers are only just beginning to explore their complex evolution, particularly in non-sexual contexts. Our study system highlights the importance of taking a holistic approach to classifying signal function within a mutually ornamented species, as unconventional contexts such as female competition and predator defense, in addition to the classical modes of sexual selection, can differentially influence elaborate trait expression in males and females. Future work should investigate the evolution of multifunctional traits and the function of female traits in male mate choice, female competition, and defense against heterospecifics.

Acknowledgements

We thank D. Mennill for recording and preparing playback stimuli and providing all equipment required for playback. We thank R. Blanco and the staff at the Guanacaste Conservation Area for logistical support in Costa Rica. We are grateful for manuscript feedback by members of the Doucet lab. Funding to KR was provided by the Animal Behaviour Society and an Ontario Graduate Scholarship, and funding to SMD was provided by the Natural Sciences and Engineering Research Council of Canada.

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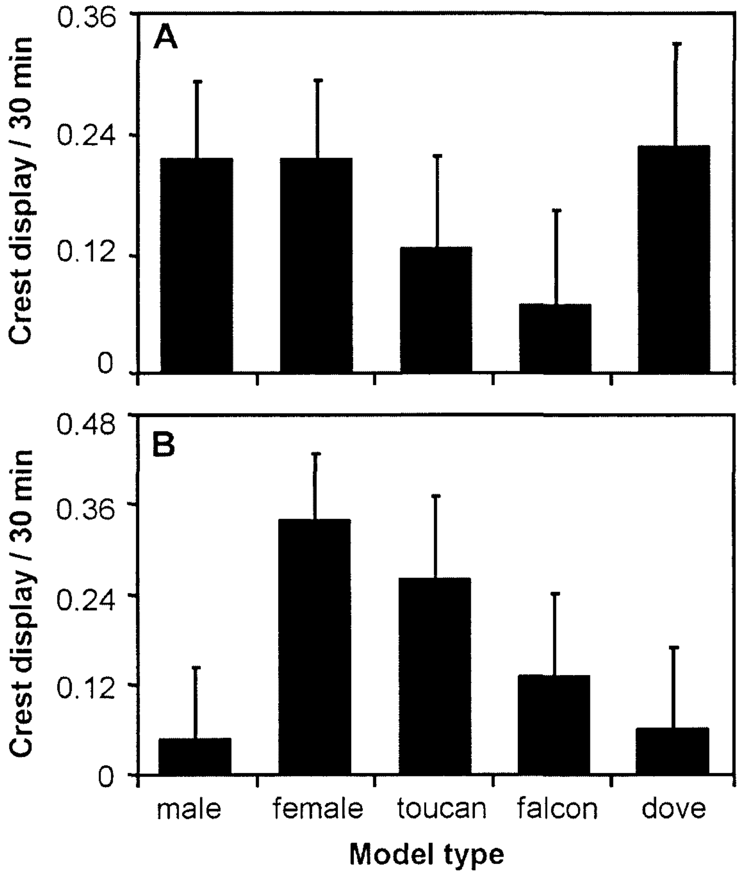

Fig 3.1 Rate of crest displays per 30 minutes during five different model trials by male (a) and female (b) royal flycatchers.

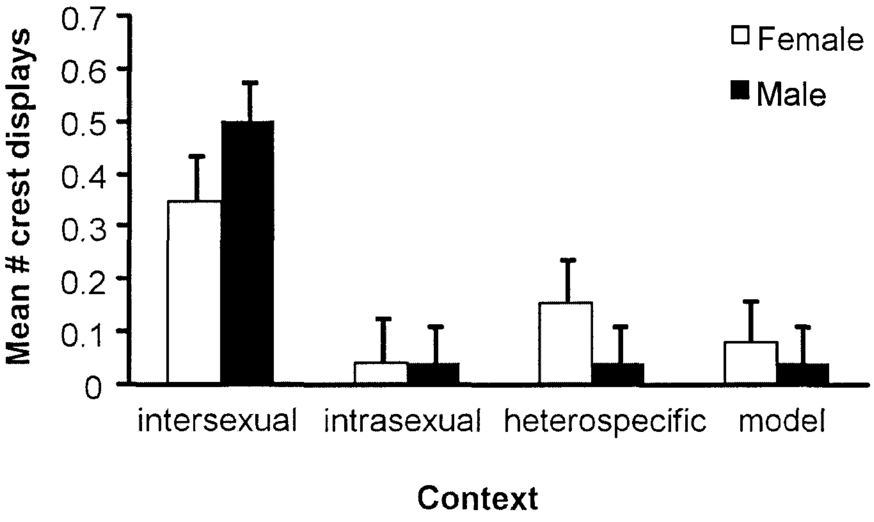

Fig 3.2 Mean number of crest displays by male (black bars) and female (open bars) royal flycatchers in four contexts: towards the opposite sex (intersexual), towards the same sex (intrasexual), towards another species (heterospecific), and towards a model (model).

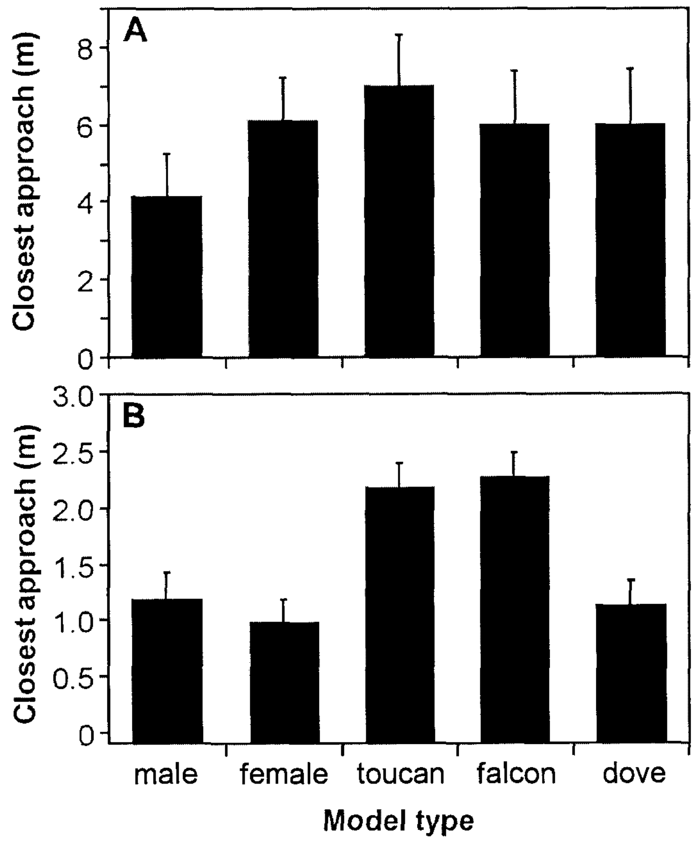

Fig 3.3 Closest approach (m) to five different model types by male (a) and female (b) royal flycatchers.

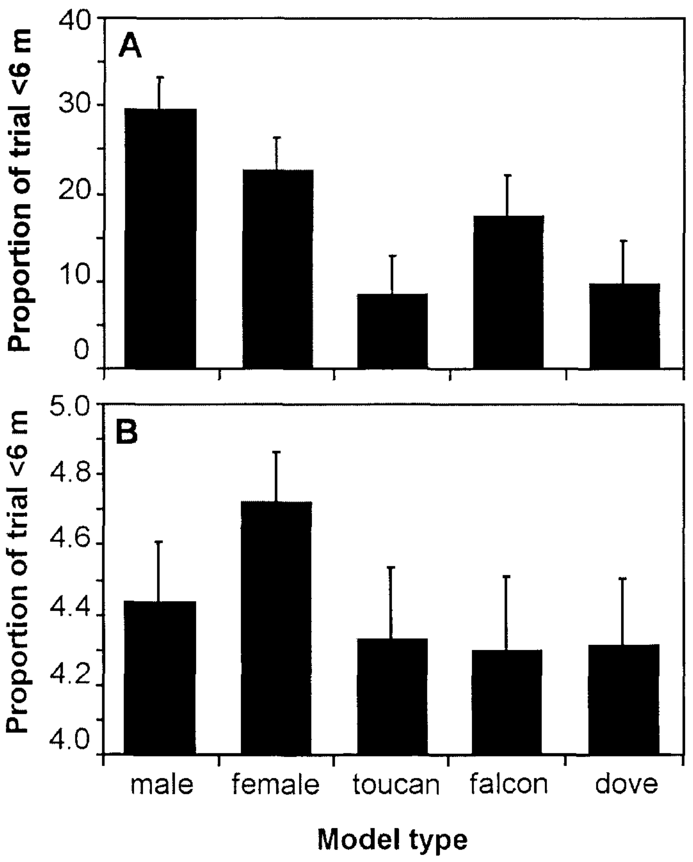

Fig 3.4 Proportion of trial spent 6 m or less from five different model types by male (a) and female (b) royal flycatchers. Raw data is presented for males and least squared means from generalized linear regression models for females.

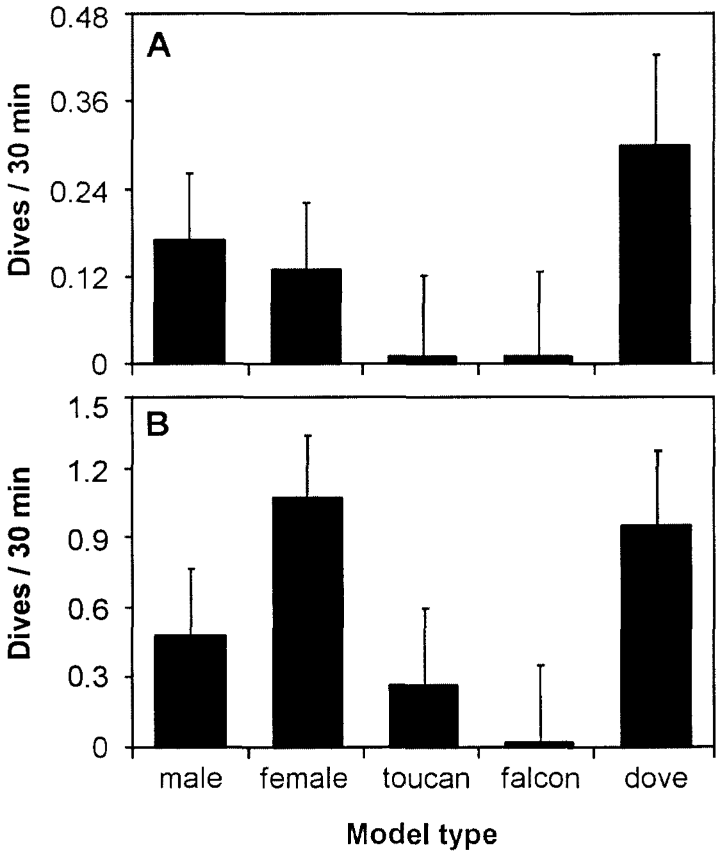

Fig 3.5 Rate of dives per 30 minutes at five different model types by male (a) and female (b) royal flycatchers.

CHAPTER 4

General discussion & conclusions

THESIS SUMMARY & DISCUSSION

Most studies of sexual selection have focused on dichromatic species with conspicuous males and cryptic females, and such studies may overlook the role of female ornamentation. As a result, it is common for researchers to assume opposing selection for ornamentation in the sexes; males are sexually selected to be bright and elaborate while females are naturally selected to be cryptic. However, females of many species exhibit some degree of ornamentation (e.g., Amundsen 2000). For example, 80% of passerines reside in the tropics (Skutchbury & Morton 2008), where monochromatism or mutual ornamentation is more often the norm (Badyaev & Hill 2003). An early hypothesis set forth by Darwin (1871), and thereafter modeled by Lande (1980), explained female ornamentation as a genetic by-product of selection on males, but recent studies suggest that this is not always the case. Phylogenetic reconstructions of plumage evolution suggest that genetic correlation between the sexes for plumage colouration is relatively lax in some groups, with numerous evolutionary transitions from sexual dichromatism to monochromatism and vice versa (Price & Birch 1996, Badyaev & Hill 2003). Moreover, Irwin (1994) found that in blackbirds, changes in dichromatism were attributed to changes in female conspicuousness rather than changes in male conspicuousness. Similarly, when exploring the evolution of 'bright' and 'dull' monochromatism, Peterson (1996) found that males were more likely to lose bright plumage whereas females were more likely to gain bright plumage. These studies indicate that females can also experience independent selection for conspicuous colouration. By studying mutual ornamentation, we can examine situations where opposing selection between the sexes is reduced and can explore the factors that may lead to independent selection for conspicuousness in both sexes.

The objective of my thesis was to investigate the function of mutual ornamentation in royal flycatchers. Through a combination of observational (Chapter 2) and experimental (Chapter 3) methods, I sought to characterize and test functionality of display traits in males and females. In Chapter 2, I characterized male and female vocalizations and display behaviours and elucidated their function based on variation in context and use throughout the breeding season. In particular, females produce a nest-associated '*keeyup*' call that may function to increase male vigilance at the nest. Males produce a song that seems to primarily function in mate attraction. And both sexes produce a '*chatter*' vocalization that occurs during agonistic chases with conspecifics and heterospecifics. Male courtship behaviour involves crest erection during a characteristic flight pattern along with a distinct vocalization. Our observations also suggest that the crest is a multifunctional trait in both sexes. Male crest displays were produced during courtship and copulation, agonistic male-male encounters, and also in agonistic encounters with heterospecifics. I provide novel observations of female crest displays and found that females display during courtship and copulation, agonistic female-female encounters, and towards heterospecifics during nest defense.

In Chapter 3, I conducted a model presentation experiment to explore courtship, territorial, and predator defense behaviour in male and female royal flycatchers by exposing them to conspecific and heterospecific models. Females exhibited a stronger response than males to models and the strongest response to the female royal flycatcher model. Our results suggest that females likely compete over sexual or non-sexual resources. Crest display rate did not vary across model types in either sex, although males and females were found to use their crest most frequently towards each other, suggesting that the crest plays an important role in courtship in both sexes. Additionally, a large proportion of female crest displays were performed to heterospecifics during nest defense behaviour.

Taken together, my two studies show that male and female royal flycatcher crests are used to differing degrees in several contexts and may diverge in function. Previous work found that several colourmetric variables of the royal flycatcher crest relate to measures of quality in both males and females (Cuthbert 2008). This result, taken with our observation that crest displays occur most frequently during intersexual communication, suggests that males and females may assess each other through observing each others' crests. Additionally, the observation that both sexes display their crests toward same-sex conspecifics suggests that this quality indicator may also be assessed by intrasexual competitors. Furthermore, because males and females display their crests towards heterospecifics, and potentially predators, their crest may also function as an 'intimidating' ornament. In summary, my research contributes to the understanding of multifunctional display traits and also suggests that there has been independent selection for elaborate female traits in a mutually ornamented tropical species. Although my research focuses on a rarely studied tropical bird, this work contributes to a growing body of research on the evolution of elaborate female traits and also highlights areas in need of further research.

FUTURE DIRECTIONS

Concealed colouration and multifunctional signals

A variety of species possess concealed colouration but because such traits are only exposed in particular contexts, this form of dynamic signalling has received little research attention. In terms of its use, the royal flycatcher's crest is not unique, as several recent studies have shown that concealed colouration is displayed in multiple contexts (Thomas & Strahl 1990, Aragonés et al. 1999, Alvarez 2000). Therefore, concealed colouration often functions as a multifunctional signal, but remains poorly studied despite the fact that it is a relatively common form of signalling.

Stuart-Fox & Ord's (2004) study on exposed and concealed colouration in agamid lizards provides evidence that the location of a signal on the body can influence the degree to which it is influenced by natural and sexual selection. Future work should explore differences in natural and sexual selection pressures on exposed versus concealed traits. Additionally, researchers should make efforts to investigate all potential functions of display traits to further our understanding of multifunctional traits, with the role of natural selection explored in as much depth as that of sexual selection. In particular, quality indicators (e.g., Cresswell 1994), morphological weapons (see Caro 2005), or conspicuous traits that function as pursuit deterrents (e.g., Murphy 2006, 2007) or in startle displays should be carefully examined as they have the potential to function in both sexual selection and predator defense.

Mutual ornamentation & selection for female traits

Mutual ornamentation has been described across a wide variety of species for a number of morphological traits such as horns (e.g., Stankowich & Caro 2009), colouration (e.g., Griggio et al. 2005), and specialized feathers (e.g., Kraaijeveld et al. 2005, Murphy 2006). When both males and females exhibit bright monochromatic colouration, they are often described as being mutually ornamented (Kraaijeveld et al. 2007). Previous studies have explored the evolution of dichromatism and monochromatism (e.g., Price & Birch 1996, Dunn et al. 2001), but due to a lack of distinction, little is known about the evolution of bright monochromatism (i.e., mutual ornamentation) versus dull monochromatism (Kraaijeveld et al. 2007, but see Peterson 1996). Additionally, because most cases of bright monochromatism occur in the tropics, less research attention has been focused on this pattern. However, conspicuous monochromatism is more common in species with monogamous mating systems (Badyaev & Hill 2003), and this pattern may be related to biparental care (see Amundsen & Pärn 2006). Therefore, mating system as well as male and female roles may influence the evolution of mutual ornamentation. As such, the most commonly explored aspect of mutual ornamentation involves studies on mutual mate choice (Kraaijeveld et al. 2007), and more specifically on male mate choice for female ornaments (e.g., Jones & Hunter 1993, Amundsen 2000, Amundsen & Forsgren 2001, Griggio et al. 2005). The degree of similarity between the sexes for a mutually expressed trait can be variable such that the trait can be exactly the same in the sexes, be equally elaborate but in different forms, or be more elaborate in one sex. However, these distinctions are not always clear or easy to establish. Future studies should categorize the degree of dimorphism in shared male and female ornaments and compare this with various life history traits such as mating system or habitat structure to provide insight into the evolution of mutual ornamentation.

As indicated above, there is geographic variation in dimorphism, where species with monochromatic bright males and females tend to reside in the tropics, and dichromatic species with drab females are more common in the temperate zone (see Badyaev & Hill 2003). Two decades ago, West-Eberhard (1983) suggested that 'social selection,' encompassing female competition over sexual or non-sexual resources, may select for conspicuous colouration in females, especially in tropical species. A recent study by Murphy and colleagues (2009) found support for this in the tropical streak-backed oriole (*Icterus pustulatus*), where female colouration functions as a status signal in female-female interactions. Murphy et al. (2009) further propose that elaborate female colouration and mutual ornamentation in the tropics may be the result of both sexes participating in year-round territoriality.

Recent studies suggest that female ornaments and armaments have evolved to function in female-female competition even in some non-tropical species (e.g., Heinsohn et al. 2005, LeBas 2006, Robinson & Kruuk 2007, Stankowich & Caro 2009, Watson & Simmons 2010). In addition, the degree of mutual ornamentation is positively correlated with divorce rate in birds (Kraaijeveld 2003). Higher levels of divorce imply increased levels of intrasexual competition in both sexes, and this may select for mutual ornamentation. Taken together, these studies show that female competition can play an important role in the evolution of mutual ornamentation. Future studies should examine the relationship between the level of female competition and degree of mutual ornamentation in a variety of mating systems in both tropical and temperate habitats.

Less research has explored the role of natural selection on mutual ornamentation, and more specifically on the expression of elaborate traits in females. However, a few recent studies provide evidence of mutually expressed traits that are sexually selected in the male and used for predator defense in the female (e.g., Murphy 2006, 2007; Stankowich & Caro 2009). These studies highlight that levels of natural and sexual selection can differ between the sexes and result in sex-specific selection for ornamentation. Indeed, females are regularly assumed to experience greater pressure from natural selection than males as they are often more involved in offspring care. As such, future studies should examine the role of natural selection on female ornamentation in particular, and its repercussions for the evolution of mutual ornamentation.

Across species, males and females can differ in their relative appearance and this simple observation has fostered countless studies on sexual selection. Mutually ornamented species allow us to examine differences between the sexes specifically by exploring their expression of a shared trait; however, most mutually ornamented species are found in the tropics and are consequently poorly studied (Kraaijeveld et al. 2007). Here, we provide evidence that male and female royal flycatchers use their elaborate crest in a variety of contexts, and likely experience different selection pressures. Indeed, the fact that male and female crests differ in colouration further supports this claim (Amundsen & Pärn 2006). Our study highlights the role of selection for female ornamentation, and contributes to our understanding of the behavioural ecology of tropical species. Future studies examining the degree of mutual ornamentation and such variables as mating system, mate preferences, intrasexual competition, and predator defense would be fruitful in our understanding of the different selection pressures affecting males and females and the evolution of mutual ornamentation.

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