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FUNCTION AND EVOLUTION OF PLUMAGE TRAITS IN TROGONS (AVES TROGONIFORMES), AND THE IMPORTANCE OF PARAMETERIZATION IN VISUAL MODELS

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FUNCTION AND EVOLUTION OF PLUMAGE TRAITS IN TROGONS (AVES TROGONIFORMES), AND THE IMPORTANCE OF PARAMETERIZATION IN VISUAL MODELS

by

PIERRE-PAUL BITTON

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Windsor, Ontario, Canada

Function and evolution of plumage traits in Trogons (Aves Trogoniformes), and the importance of parameterization in visual models

by

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Declaration of Co-Authorship / Previous Publication

I. Co-Authorship Declaration

I declare that this thesis incorporates material that is the result of joint research, as follows: I am the sole author of the General Introduction, Chapter 1, and the General Discussion, Chapter 6. I am the principal author of the manuscripts that comprise the four data chapters: Chapters 2 through 5. All six data chapters are co-authored with my supervisor, Dr. Stéphanie M. Doucet. Chapter 4 was co-authored by collaborators Drs. Jeffrey DaCosta and John Klicka, and Chapter 5 was co-authored with Kevyn Janisse who also provided the spectral data for the analyses. For all four data chapters, I conceptualized the research projects and experimental designs, and I am primarily responsible for the experimental execution, data analysis, interpretation, and writing. Dr. Stéphanie Doucet contributed to experimental design, interpretation, and the editing of the manuscripts, as well as providing financial and logistical support. My others collaborators provided data, contributed to the analyses, data interpretation, and/or writing and editing of the manuscripts.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from my co-authors to include the above material in my thesis.

I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work.

Chapter 2 is published in Behavioral Ecology, and is formatted for that journal. Chapters 3, 4, and 5 have been formatted for future submission to Journal of Evolutionary Biology, Evolution, and American Naturalist, respectively.

II. Declaration of Previous Publication

This thesis includes one original paper that has been published in a peer reviewed journal, as follows:

Thesis Chapter	Publication title/full citation	Publication status
Chapter 2	A multifunctional visual display in elegant trogons targets conspecifics and heterospecifics	Published in Behavioral Ecology

Chapter 2 is a pre-copyedited, author-produced copy of an article published in Behavioral Ecology following peer review. The version of record "Bitton P-P., and S. M. Doucet. 2014. A multifunctional visual signal in the Elegant trogon *Trogon elegans* targets conspecifics and heterospecifics. Behavioral Ecology 25: 27-34." is available online at: http://beheco.oxfordjournals.org/content/25/1/27.short

I certify that the above material describes work completed during my registration as graduate student at the University of Windsor.

I declare that, to the best of my knowledge, my thesis does not infringe upon anyone's copyright nor violate any proprietary rights and that any ideas, techniques, quotations, or any other material from the work of other people included in my thesis, published or otherwise, are fully acknowledged in accordance with the standard referencing practices. Furthermore, to the extent that I have included copyrighted material that surpasses the bounds of fair dealing within the meaning of the Canada Copyright Act, I certify that I have obtained a written permission from the copyright owner(s) to include such material(s) in my thesis.

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Abstract

In this dissertation, I investigated the function and evolution of plumage-based visual signals in trogons (Trogoniformes), and assessed the influence of individual parameters in the receptor-noise model of colour discriminability. In Chapter 2, I investigated the function of tail raising in the elegant trogon. For this purpose, I used observational and experimental data collected in Costa Rica. Results demonstrated that tail raising in the elegant trogon is a multifunctional signal that targets both conspecifics and heterospecifics. Specifically, trogons used this behaviour during intra and intersexual interactions, and the experiment confirmed that tail raising is a pursuit-deterrent signal. In Chapter 3, I experimentally tested which plumage patches are used in species recognition in two species of trogons: the black-headed trogon, which is sympatric with a similar-looking congener, and the elegant trogon, which is not sympatric with a similar-looking congener. The results suggested that while both species use the back and belly colour as specie- recognition traits, the black-headed trogon but not the elegant trogon also assessed the tail banding pattern. In Chapter 4, I investigated the relationship between sympatry and plumage divergence in the genus *Trogon*. My results demonstrated that *Trogon* taxa diversified more rapidly, and that plumage trait divergence increased with sympatric overlap in South American but not Central American taxa. Together, my findings suggested that the rapid colonization of South America following the Great American Interchange resulted in reinforcement through character displacement or trait sorting. In Chapter 5, I investigated how dichromatism scores are influenced by individual parameters of the receptor-noise model of chromatic contrast threshold, using an avian-based tetrachromatic approach. I systematically tested parameter values for ambient light environment, photoreceptor sensitivities and densities, transmission properties of the ocular media and oil droplets, and compared the sensory experience of species for which the visual system has been fully characterized. My results demonstrated that oil droplet characteristics, photoreceptor densities, and the sensitivity of the SWS1 photoreceptor (ultraviolet sensitive or not) had the most influence on dichromatism scores. I encourage the complete characterization of visual systems when possible, and my results will inform researchers when making inferences about tetrachromatic visual models.

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Foreign Study Supplement from the Natural Sciences and Engineering Research Council of Canada, an Ontario Graduate Scholarship from the Province of Ontario, a Field Museum Visiting Scholar Award, an American Ornithological Union Research Award, and a Journal of Experimental Biology Travelling Fellowship. Financial support was also provided by my supervisor Stéphanie Doucet who received a Discovery Grant and Equipment Grant from the Natural Sciences and Engineering Research Council of Canada, a Canada Foundation for Innovation grant, an Early Researcher Award from the Government of Ontario, and from the University of Windsor.

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I would never have gotten where I am without the lifelong support of my parents and other important family members. My love for the natural world started at a very early age. My paternal grandmother Laurette Bitton would take me out to pick flowers and poke at minnows in the St-Lawrence river; my maternal grandfather Joffre Patenaude taught me about bees (but not the birds!). Throughout my childhood both my parents would take me out camping and encouraged outdoor play. I climbed Appalachian mountains with my dad Guy Bitton, and it was on a hike with my mom Marie-France Patenaude that I realized I wanted a career in biology. Their love and care have allowed me to chase my goals even if I chose the long and winding road. I thank Françoise Entrialgo who has always been there for us, and Carmine Romano who constantly radiates positive energy. I also thank Karen Ochs and Cameron Beck for accepting me in their family with open arms and spending time with us when we needed it most.

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Chapter 1

General Introduction

Animal Communication

The study of animal communication has greatly contributed to our understanding of natural and sexual selection (Bradbury and Vehrencamp 2011), the fundamental tenets of biology. This field of research is particularly rich because of the various modalities by which animals can convey information to one another. Indeed, animals can communicate by acoustic (Kroodsma and Miller 1982, Gerhardt and Huber 2002), visual (Hill and McGraw 2006a, Matthews and Matthews 2009), chemical (Bell and Cardé 1984, Vandenbergh 2012), electrical (Kramer 1990), and vibrational (Markl 1983, Lewis and Narins 1985, Hill 2008) means. Because of this diversity of signalling and sensory modalities, studies in animal communication cover a broad range of proximate and ultimate questions including physical, physiological, anatomical, and behavioural topics. Indeed, the study of animal communication is one of the most integrated fields in biology. From a sender's perceptive, investigations have focussed on how a signal is produced (e.g., Bennet-Clark 1970, Aroyan et al. 2000, Elemans et al. 2004), how it propagates (e.g., Naguib and Wiley 2001, Boncoraglio and Saino 2007), its cost (Olson and Owens 1998, Gil and Gahr 2002), how it is learned and/or developed (Beecher and Brenowitz 2005, Shawkey et al. 2014), and its physical and/or chemical attributes (Wyatt 2003, McGraw 2006a, b). Studies concerned with understanding the receiver's perspective have focused on sensory organs (Land and Nilsson 2012), the neuroscience of perception (Guilford and Dawkins 1991), cognition (Hunt 1996, Prior et al. 2008), and thresholds of detection (Vorobyev and Osorio 1998). The importance of signals in the interactions between senders and receivers has also generated much research. Major topics of interest include the reliability of signalling (Searcy and Nowicki 2005), the function and evolution of signals (Searcy and Nowicki 2005), and communication networks (McGregor 2005).

Function and evolution of plumage colouration in birds

Visual communication can take place through active signals (body movements) or passive signals (colour of plumage patch). In many circumstances, such as during ritualized courtship displays, behaviours are used to present and emphasize passive signals. Birds in particular have a long and rich history in studies of visual signals (Hill and McGraw 2006a, b). For example, Darwin (1871) discussed how plumage dichromatism was unlikely to have evolved through the process of natural selection, developing the hypothesis that sexual selection was probably responsible for differences between the sexes. Since then, bird models have been central in the development of several hypotheses formulated to explain the evolution of conspicuous secondary sexual ornaments, the maintenance of honest signals, and the benefits of mate choice. Bird examples have been used to advance Fisher's runaway selection (Fisher 1915, Andersson 1994) and sexy son hypotheses (Fisher 1930, Weatherhead and Robertson 1979), Zahavi's handicap model (Zahavi 1975, 1977), Hamilton and Zuk's hypothesis (Hamilton and Zuk 1982), the good genes hypothesis (Møller and Alatalo 1999, Griffith et al. 2002), and the compatible genes hypothesis (Kempenaers et al. 1999, Neff and Pitcher 2005, Akçay and Roughgarden 2007).

Visual communication can involve conspecifics or heterospecifics, but most visual signals have been studied in the context of intraspecific communication. In birds, for example, the colours of plumage patches and behaviours that display these patches have been thoroughly documented in intraand intersexual interactions (Hill and McGraw 2006a). In contrast, visual behaviours targeting heterospecifics are poorly documented. Stotting is one of a few well-studied examples. Several species of ungulates, especially gazelles, propel themselves high in the air with stiff legs in the presence of a potential predator. The pursuit-deterrent hypothesis, the currently favoured explanation for this behaviour (Caro 1986), states that such displays are honest signals of condition and convey unprofitability to predators. Behaviours with the same function have been observed in birds. For example, common moorhens (*Gallinula chloropus*) flash white under-tail coverts and turquoise-browed motmots (*Eumomota superciliosa*) wag their tails in the presence of potential predators (Alvarez 1993, Murphy 2006, 2007). Tail displays seem to be generally common in birds but whether they functions as conspecific signals or heterospecific signals has rarely been investigated.

The function of animal colours such as those found on the plumage of birds has often been studied in the context of mate choice, but rarely investigated for use in species recognition (Ord and Stamps 2009). This is surprising since closely related species often look similar, and there is evidence for character displacement of sexually selected visual traits (Sætre et al. 1997). Because the proper recognition of heterospecifics can prevent hybridization between incipient species (Price 2007), divergence in plumage traits could mediate pre-zygotic isolation through reinforcement. Therefore, evaluating which visual traits are used for species recognition can inform our understanding of interspecific communication and the ultimate mechanism of speciation. Furthermore, it is important to understand which conditions lead to differences in these traits. Evidence from pairs of closely related species has demonstrated that rapid sympatry can drive trait divergence (Martin et al. 2010), especially at intermediate levels of geographic overlap (Martin et al. 2015). However, the divergence of sexually selected colours has rarely been investigated in large groups of closely related species, which would be particularly informative to understand the evolution of visual signals. In all cases, to properly address questions that pertain to animal colouration, colours should be adequately quantified.

Quantification of colour

It has long been understood that animals do not all share the same visual sensory experience. Early experimental evidence demonstrated that while some animals perceive fewer colours than humans (Allen 1879), others could detect wavelengths outside the normal human range of vision, particularly in the ultraviolet (Kühn 1924). Nevertheless, the description of animal colours remained subjective to human perception until recently (Burtt 1986, Burkhardt 1989, Bennett et al. 1994). For example, feathers were described by matching their colour to that of a standard in the Munsell book of colours (Munsell Color Company 1976, Zuk and Decruyenaere 1994), or by calculating colour values based on the standard observer (Wyszecki and Stiles 1982, Burtt 1986, Andersson and Praguer 2006). Discussions regarding the pitfalls of relying on the subjective human visual experience to quantify colours (Burkhardt 1989, Bennett et al. 1994) prompted the widespread use of spectrophotometry as the most objective method to quantify the reflective properties of animal colours (Andersson and Prager 2006). Spectrophotometers collect spectral data across any range of wavelengths, which is particularly useful in the study of ultraviolet perception in animals such as birds (Bennett and Cuthill 1994).

Several methods can be used to extract quantitative information and compare colours from reflectance spectra; each one has advantages and disadvantages, and is applied in different contexts. From a descriptive approach, tristimulus variables have been developed to interpret spectral curves, of which measures of hue, saturation, and brightness are the most commonly used (Montgomerie 2006). Hue is generally defined as the wavelength which contributes the most to the total reflectance, saturation is a measure of a colour's purity, and brightness is a measure of the total amount of light reflected by a surface (Montgomerie 2006). Together, hue and saturation describe the chromatic component of a colour, whereas brightness describes the achromatic component. Because they describe physical properties of spectral curves, colour metrics are comparable across studies and intuitive measures. However, because they do not incorporate the ambient light or the receiver's psychophysiology, and therefore do not quantify the discriminability between colours, tristimulus scores have been criticised when used to infer how visual signals may be perceived (Delhey et al. 2014).

The comparison of several colours can be achieved by applying principal component analysis directly to multiple spectra (Endler 1990, Grill and Rush 2000), with the resulting components representing the wavelengths that contribute most to among-colour differences. This method has the benefit of simultaneously comparing several colours, but the multivariate assumptions of multivariate normality, sphericity, and independence of spectral measurements are often violated (Endler and Mielke 2005). Furthermore, the principal components are loaded differently for every data set, even from the same species, preventing direct comparison of results among studies. As a consequence, analysis of colours by principal component analysis is now uncommon.

To incorporate some element of psychophysiology in the measurement of colours, Endler (1990) proposed analyzing spectral curves using segment classification. This method incorporates the ambient light environment, and generates unitless colour coordinates by breaking down spectral data into equally-spaced regions, and comparing the relative stimulation of the short wavelength cone to the medium cone, and the long wavelength cone to the short wavelength cone. Segment classification is based on an opponency mechanism of colour vision (Wyszecki and Stiles 1982, Endler 1990), and as such, it is a receiver-independent classification scheme of colours, and captures common properties of many trichromatic vertebrate visual systems. This method has rarely been implemented (Endler and Théry 1996), perhaps because it may not properly capture the sensory experience of birds, which are tetrachromatic not trichromatic, and because a large number of spectral curves can generate the same colour coordinates (like the RGB colourspace, Wyszecki and Stiles 1982).

With the understanding that birds and other animals are tetrachromatic, Goldsmith (1990) proposed a tetrahedral colourspace model that could encompass all the colours perceived by birds. Further developed by Endler and Mielke (2005) and then by Stoddard and Prum (2008), colours are positioned in a three-dimensional space using coordinates representing the stimulation of the four cones, based on photoreceptor sensitivity functions. Several methods have been developed to compare the position in space of two or more points, their spread, volume, and the volume overlap of two or more clouds of colour points (Endler and Mielke 2005, Stoddard and Prum 2008, Maia et al. 2013). These methods of comparing colours have been very popular because they are likely a good approximation of the visual sensory experience of birds, require at a minimum only spectral and cone sensitivity data, but can also accommodate several other characteristics of the visual system that can influence the sensory experience.

To date, the most comprehensive model of animal vision is that proposed by Vorobyev and Osorio (1998). Their model, which uses receptor-noise as a determinant of colour thresholds, quantifies the chromatic contrast between two colours while considering the ambient light environment, the light transmission properties of the ocular media, the photoreceptor sensitivities and densities, the threshold sensitivity of the photoreceptors (Weber fraction), and in several taxa, the transmission properties of oil droplets found anteriorly to the photoreceptor (Vorobyev and Osorio 1998). Recently, methods have been developed to include photoreceptor density in calculations of colourspace distances (Pike 2012, Delhey et al. 2014), allowing the distances between points to be measured in just-noticeable-differences (Vorobyev and Osorio 1998). This popular model has been extensively used since it was initially proposed because it provides the best approximation of an animal's visual sensory experience and the units of measurements, just-noticeable-differences, are intuitive. However, the visual systems of very few animals have been completely characterized and researchers almost always have to make assumptions regarding one or many of the parameters listed above. The potential consequences of wrongful parameterization have been pointed out (Renoult et al. 2010), but the influence of individual parameters has never been systematically investigated.

Study group: the Trogons

The trogons and quetzals family (Trogonidae) comprise a pantropical group of approximately 40 species (Collar 2001), which arguably include some of the most beautiful birds in the world. Systematic classification of the group has been hampered by a highly conserved body plan throughout the order and a unique heterodactyl toe arrangement that is found in no other family of birds. An ancient lineage, their closest living relatives are considered to be the Coraciiformes (kingfishers, rollers, bee-eaters, Hackett et al. 2008), but they have been placed as sister clade to the Coliiformes (mousebirds) of Africa (Espinosa de los Monteros 2000). Their plumage is characterized by vibrant colours on most parts of their body. While the males of Neotropical and African species bear bright iridescent feathers on their upperparts and carotenoid based colours on their underparts, the Asian trogons seem largely coloured by carotenoids and melanins (Collar 2001). All species have a relatively long tail that displays barring patterns that vary across species. The phylogeny of trogons is well established at the genus level, but studies of the arrangements of clade groupings are equivocal (Hosner et al. 2010, Quinteros and Espinosa de los Monteros 2011). The two main phylogenetic hypotheses place either the African trogons (Hosner et al. 2010) or the New World trogons (Quintero and Espinosa de los Monteros 2011) as basal.

Trogons of the Neotropical genus *Trogon*, the focus of this dissertation, comprise of a group of 16 species for which 55 subspecies have been described (DaCosta and Klicka 2008, Forshaw 2009, Remsen et al. 2014). As with all other trogons, members of this genus have a highly conserved body plan and plumage patterns. Males bear iridescent feathers on their head, mantle, rump and upper-tail (ranging from deep purple to copper) and carotenoid-based colours on their belly and breast (red, orange, or yellow, Thomas et al. 2014). All species possess a long tail that ranges in barring pattern from all white to all black, and many have a white band separating the upper breast from the belly. The plumage colour of specific patches can vary considerably within species. For example, the rump of *T. rufus* varies from copper-green in the *sulphurous* subspecies to a purple-blue in the *rufus* subspecies. The genus *Trogon* is distributed from southern Arizona to southern Brazil, and is found across a broad range of habitats (Collar 2001, Forshaw 2009). Ancestral area reconstruction has demonstrated that the genus originated in Central America, and colonized South America through multiple migration events during and after the completion of the Isthmus of Panama (DaCosta and Klicka, 2008). Areas of tropical lowland can harbour many sympatric trogon species and/or subspecies. In general, trogons have been poorly studied. The natural history of very few species has been described in detail, and little is known about their biology and ecology.

Dissertation overview

In this dissertation, I investigate the signalling function and evolution of a tail raising behaviour in the elegant trogon (*Trogon elegans*) using observational data and a model presentation experiment. Also using a model experiment, I assess which plumage patches are used for species recognition by two species of trogons. To understand the evolution of plumage colouration at the genus level, I investigate the relationship between geographic overlap (sympatry) and plumage divergence across all subspecies of the genus *Trogon*. Finally, to clarify the potential consequences of parameterization error in receptor-noise models of avian vision, I systematically test the influence of individual parameters on the avian perception of sexual dichromatism for 70 species of Galliformes.

In chapter 2, I investigated the function of tail raising in the elegant trogon, a behaviour whereby the tail which normally rests vertically is rapidly lifted horizontally and slowly brought back down. The first goal of the project was to characterize the contexts in which elegant trogons perform tail raising displays. For this purpose, I conducted over 450 hours of behavioural observations of free living birds in Costa Rica. The second goal of the project was to determine the function of tail raising in the presence of heterospecifics. For this purpose, I presented elegant trogons with models of a potential predator, and models of a non-threatening control, to test the predictions of three competing hypotheses: the pursuit-deterrent hypothesis, the conspecific warning signal hypothesis, and the self-preservation hypothesis. This chapter was published in Behavioral Ecology.

In chapter 3, I experimentally tested whether the black-headed trogon (*Trogon melanocephalus*) and elegant trogons use plumage traits for species recognition and if so, which characteristics are used. I presented the two focal species with conspecific models, control models, and modified models that differed in the colour of the back or belly, or the pattern of banding on the tail. Furthermore, because the black-headed trogon is sympatric to the similar-looking violaceous trogon (*Trogon violaceus*) but the elegant trogon does not have a similar-looking sympatric congener in Costa Rica, I evaluated whether the presence of a similar-looking sympatric congener influenced which traits are used in species recognition.

In chapter 4, I investigated the influence of the colonization of *Trogon* into South America on plumage trait divergence and taxa diversification. The first objective was to compare diversification rates in Central and South American taxa by modelling continent-specific speciation and extinction rates. The second objective was to test whether character displacement and/or phenotype sorting were responsible for trait divergence. This was determined by collecting over 3500 spectral measurements of plumage characteristics from almost 150 museum specimens and testing whether the proportion of sympatric overlap explained plumage disparity among subspecies. The third objective evaluated whether the presence in sympatry of several species of trogons influenced the range of plumage colour values found in particular communities.

In chapter 5, I systematically evaluated the influence of individual parameters on the quantification of chromatic sexual dichromatic in tetrachromatic visual models. I used the receptor-noise model for colour discrimination developed by Vorobyev and Osorio (1998) to calculate the chromatic contrast (in just-noticeable-differences) of 15 colour patches for each of 70 species of Galliformes. I investigated the influence of light environments, photoreceptor sensitivities, oil droplet characteristics, ocular transmission, and photoreceptor densities on the total dichromatism scores, the dichromatism rank of species in relation to one another, and the dichromatism scores of individual patches. The main objective of the study was to determine the relative influence of each parameter and to guide researchers when implementing visual models for their study species.

Overall my dissertation uses a diversity of methods to understand visual communication in the genus *Trogon*, and the influence of proper parameterization in avian visual models. I incorporate observational and experimental field methods, as well as museum-based data collection, to provide insight into the function and evolution of plumage colouration in Trogons.

I also use modelling to understand how our assumptions regarding visual systems can influence our quantification of avian sensory experiences. My research contributes to the understanding of multifunctional visual signals, the use of visual traits in species recognition, the mechanisms that influence visual character diversification, and the importance of proper parameterization in avian visual models. Furthermore, this dissertation provides an important contribution to our knowledge of trogons, a tropical group of birds that is poorly studied. Together, my contributions should be of significant value to behavioural ecologists and evolutionary biologists alike, and should guide future research in visual ecology.

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Chapter 2

A multifunctional visual display in elegant trogons targets conspecifics and heterospecifics

Summary

Avian visual displays often target either conspecifics or heterospecifics, but few visual displays have been described where both conspecific and heterospecifics are the intended receivers. In this study combining observational and experimental approaches, we present evidence that a tail raising display performed by the elegant trogon (*Trogon elegans*) is used in multiple contexts and is directed at conspecifics and heterospecifics. We observed tail raising displays towards conspecifics in both inter- and intrasexual contexts, as well as towards heterospecifics. Displays performed towards heterospecifics were directed at humans, monkeys, or birds of prey, all of which could have been perceived as potential predators. We experimentally tested the possible functions of tail raising behavior in the presence of a predator by presenting elegant trogons with models of a natural predator and a non-threatening control. Tail raising displays were much more likely to occur when trogons were in the presence of a predator model (48% of trials) than a control model (6% of trials). The presence of conspecifics did not influence tail raising propensity (conspecifics present: 44% of trials, conspecifics absent: 50% of trials). Our results suggest that tail raising in trogons is a multifunctional visual display that may function as an inter- and intrasexual conspecific signal as well as a pursuit-deterrent signal directed at predators.

Introduction

Visual displays in animals can take many different forms, and are often directed at specific receivers. In the presence of other males during agonistic encounters, for example, cuttlefish display specific body patterns (Adamo and Hanlon 1996), hermit crabs wave enlarged chelipeds (Arnott and Elwood 2010), and many birds perform ritualized threat displays (Hurd and Enquist 2001). These displays can prevent the escalation of aggression between individuals and reduce the probability of harmful interactions. In the presence of females during mate attraction and courtship, male fireflies use bioluminescent flashes (Branham and Wenzel 2003, Lewis and Cratsley 2008), anoles bob their heads while presenting an extended colorful dewlap (Tokarz 1995), and many birds perform stereotyped dances (Gill 2007). In many species, the same displays can be used in both intra- and intersexual contexts. For example, male ruby-crowned kinglets (*Regulus calendula*) will raise their conspicuous red crest when confronting territorial intruders or when displaying to a female during courtship (Martens and Päckert 2006).

Not all visual displays are directed towards conspecifics; a number of behaviors appear to be targeted at heterospecifics. In birds for example, the turquoise-browed motmot (*Eumomotus superciliosa*) wags its tail from side to side in the presence of potential predators, a behavior identified as a pursuit-deterrent signal (Murphy 2006, 2007). This display warns potential predators that they have been detected and that a capture attempt would be unprofitable. The sunbittern (*Eurypyga helias*) also displays towards heterospecifics. It spreads out its wings, exposing large “eyespots”, to scare away predators or individuals of other species with which they compete for food resources (Frith 1978). The tail wagging in the turquoise-browed motmot and wing spreading of the sunbittern are used in the presence of heterospecifics, but do not seem to be used for signaling to conspecifics. In fact, relatively few visual displays have been adequately demonstrated to serve in both intraspecific and interspecific contexts, especially in birds (Table 2.1). One exception is the crest raising display of the royal flycatcher (*Onychorhynchus coronatus*). In this species, male and females raise their crests during courtship, aggressive intrasexual encounters, and when confronting heterospecifics near their nests (Rieveley 2010).

Elegant trogons (*Trogon elegans*), perform a conspicuous visual display whereby the tail is rapidly lifted above the horizontal and returned to its normal vertical position in a slow, controlled manner. When performing this display, birds can usually be heard producing a clucking sound (described in Taylor 1994). When positioned with their green back facing the observer, elegant trogons appear generally inconspicuous against the background vegetation; this display increases an individual's detectability because of the movement involved, and because it exposes the bright red belly and undertail coverts. This behavioral display has been mentioned twice in the literature. Cully (1986) was the first to note that elegant trogons produced this display in the presence of a live, tethered, great horned-owl (*Bubo virgianus*) near their nest, and Hall and Karubian (1996) described this behavior in the context of a mating display. The production of tail raising displays in the presence of heterospecifics and conspecifics raises questions regarding the general function of this display and the evolution of multifunctional displays in general. The first objective of our study was to characterize the contexts in which elegant trogons perform tail raising displays. For this purpose, we conducted behavioral observations of free living birds. The second objective of our study was to determine the function of tail raising in the presence of heterospecifics. For this purpose, we conducted an experiment testing the predictions of three competing hypotheses.

The conspecific warning signal hypothesis was developed in the kin selection framework (Maynard Smith 1965, Sherman 1977) and presumes that displays in the presence of a potential predator are directed at related individuals (kin). The display is designed to inform individuals that have not yet detected the predator of the potential threat. A specific prediction of this hypothesis is that birds should not display in the presence of a potential threat if conspecifics, specifically kin, are not in visual range of the individual producing the displays.

The self-preservation alarm signal hypothesis states that signals target conspecifics with the intent to trigger a reaction to deter or reduce the chance of a predator being successful by mobbing or confusing the predator (Sherman 1985). A specific prediction of this hypothesis is that on detecting a predator and after a display, conspecifics should approach the individual displaying (to form a larger and threatening group), mob the predator, or scurry in all directions to confuse the predator. The pursuit-deterrence hypothesis states that signals in the presence of predators target the potential predator, not conspecifics, and informs that predator it has been detected and an attempt at capture would be unprofitable (Woodland et al. 1980, Caro 2005). A specific prediction of this hypothesis is that individuals should display in the presence of potential predators regardless of the presence or absence of kin within visual range.

Methods

The elegant trogon is a member of the Trogoniformes and ranges from the southern United States to northern Costa Rica (Collar 2001; Forshaw 2009). The species is sexually dimorphic: males have bright iridescent green upperparts while females have coffee-brown upperparts. Females display white feathers on their breast and faded red feathers on their undertail coverts; males display brightly colored red feathers on their breast and undertail coverts. Immature males, which exhibit delayed plumage maturation, have patchy brown and red breast feathers (Kunzmann et al. 1998). They can be easily discriminated from mature males for more than one year after fledging. Differences between immature females and adult females are more subtle, but the two can be discriminated by tail feather wear: immature females leave the nest with well frayed feathers which are first molted at least a year after fledging (personal observation). Furthermore, immature females have a white tip on the tertials, which is lacking in older females (Pyle 1997). Both the male and female contribute to modifying nest cavities by taking turns to enlarge the opening. Males and females share responsibilities when incubating the eggs and feeding the nestlings (Kunzmann et al. 1998).

We conducted our research in Sector Santa Rosa, Guanacaste Conservation Area, Costa Rica (10˚ 40’N, 85˚ 30W). Our study site of nearly 9 km^2 is characterized by a mix of secondary dry deciduous forest, which has been in a regeneration state since the 1980’s, and older forest stands of evergreen tree species (Janzen 1988). Elegant trogon breeding density at this location is high; surveys during 2010 and 2011 estimated 20 to 30 breeding pairs per square kilometer across the entire study area.

Observation of natural tail raising occurrences

We recorded observations of trogons raising their tails during two 2 ½ -month periods: April 18 to June 28 2010, and April 30 to July 12 2011. Trogon observations were conducted in three different contexts: 1) opportunistically during trail surveys, 2) when following individuals located on a previous day to document their behaviors and find their nests, 3) during focal nest watches. We estimate that approximately 300 hours were dedicated to observing elegant trogons to quantify tail raising behaviors in 2010, and 150 hours in 2011. Nest initiation and the start of the breeding season in Santa Rosa is triggered by the arrival of the seasonal rains which usually start early to mid- May. Therefore, in both field seasons, we collected behavioral data both before and during the breeding season.

When tail raising behaviors were observed, we noted the sex and age (immature or adult) of the individual raising its tail and of any conspecifics in the area. Individuals were considered in the area when they could be seen or heard within visual range of the displaying individual. We noted the location of each observation to the nearest 5m by GPS and locations were geo-referenced on ArcGIS (ESRI 2013). We inferred the context of the display based on the interactions of the individuals and species present. The elegant trogons in our population are not banded; therefore, we could not determine the exact identity of individuals we observed displaying. However, based on local breeding density and time spent following individuals on foraging bouts, we estimated that territory size extend 100m from the nest site at most. Therefore, we considered any locations separated by more than 200m of each other to be observations of different individuals. On several occasions, we observed trogons raising their tails when we, the observers, were most likely the cause of the behavioral displays. This most often occurred when flushing an unsuspecting bird, immediately triggering a tail raising response. On other occasions we were certain that the displaying individuals were unaware of our presence because 1) we first heard the trogons displaying and crept-up to observe the displays without the birds ever looking in our direction, or 2) we observed the display when conducting nest watches under camouflaging textile from at least 20m away. None of the tail raising responses reported here were triggered on purpose by approaching birds or by making our presence obvious.

To avoid including the same individual in the same group context more than once in our analyses, we randomly selected a single observation in each year from those made in any given area (separated by at least 200m). While an individual from a specific location could have been included twice (from two different years) in our observations, the group context would always have been different.

Model presentation experiment

We conducted our experiment between May 1 and July 15 2011. To simulate the presence of a potential aerial predator, we fabricated models closely resembling the collared forest-falcon (*Micrastur semitorquatus*, Figure 2.1a, b). This species is known to consume trogons on occasions (L. Sandoval, personal communication) and regularly consumes birds of similar size (Thorstrom 2000). As a non-threatening avian control, we fabricated models closely resembling the squirrel cuckoo (*Piaya cayana*, Figure 2.1c, d). This species is an appropriate control to the collared forest-falcon for the following three reasons: 1) it is very similar in total length (forest-falcon 51-57 cm; cuckoo 45-50 cm), 2) it has a long narrow tail, 3) it often perches relatively upright. Therefore, the general silhouette of the squirrel cuckoo is similar to that of the collared forest-falcon. The squirrel cuckoo is not a parasitic species and its main diet is similar to that of trogons and does not include any birds (Payne 1997). Both the forest-falcon and cuckoo are common in Sector Santa Rosa.

Experimental designs that involve model presentation often rely on stuffed specimens (e.g. Götmark 1992, Götmark 1997). However, we elected to produce realistic looking models from craft materials rather than risk damaging valuable museum specimens, or collecting animals for the purpose of this experiment (Caro and Melville 2012). We constructed our collared forest-falcon model (Figure 2.1a) using peregrine falcon (*Falco pelegrinus*) polyresin decoys to which we glued two layers of commercially available black and white feathers in the color patterns found on the forest-falcon (Figure 2.1b). The first layer consisted of downy material, and produced a lofty, wind-sensitive layer. The second layer consisted of contour feathers that were positioned on the model to reflect the natural arrangement of feathers on live birds. The long tail was produced with commercially available black turkey (*Meleagris gallopavo*) feathers which were modified and arranged to match the shape and size of live forest-falcons. We constructed our squirrel cuckoo models (Figure 2.1c) using generic dove plastic decoys to which we glued two layers of custom-dyed feathers (Rit®) to match the patterns found in the live birds (Figure 2.1d). Two layers of feathers were applied to the decoys to give them a realistic feel and appearance. We produced two predator models and two control models.

Forty trial locations were selected from candidate sites at which individuals or groups of trogons had previously been observed and all trials were separated by at least 200m. The sites selected were forested (i.e. no trials in open areas), had relatively good visibility (15m in each direction), and did not include natural (e.g. river) or artificial (e.g. trail) features within 15m of the model which could have influenced the behavior of the birds near the model. For all trials, the model was positioned at the top of a 3m tall metal pole camouflaged with paint to resemble the background, near a realistic perch site. At the beginning of each session, the model was covered by camouflage textile tied to a clear fishing line. A loudspeaker was hidden at the base of the pole. The observer, also hidden under camouflage textile, was located at least 10m away from the model, sometimes up to 18m away. After setup, the observer waited 10 minutes under camouflage before starting the trials to avoid influencing the behavior of the trial subjects. Trogon subjects were drawn to the trial location using playback of an adult male call recorded the previous year (2010) outside of the area in which this experiment was conducted. Individual recognition based on call characteristics has not been demonstrated in this species. However, variation among individuals is distinguishable to the human ear, and using a call recorded outside the study area was meant to exclude the possibility that the call could be recognized as kin by any of the subject individuals. Playback of the trogon call was used for a maximum of 6 minutes to attract individuals. If an individual did not show up during that time period the trial was aborted.

Once a subject individual(s) arrived within visual range of the model (usually within 12m), the camouflage was removed by drawing the line and a second playback was concurrently initiated to replace the trogon calls. The playback consisted of a series of calls characteristics of the model species being displayed. The recordings were six minutes long and consisted of one minute of calls followed by one minute of silence, three times in a row. Trials always lasted six minutes even if the subject birds had left the area. Two versions of the recording were used for the predator model and two versions of the recording were used for the control model so that trial subjects were presented with one of four possible combination of model and playback.

For each successful trial, we recorded the following observations: 1) date, time, location (georeferencing coordinates) of the trial site, 2) composition of the trial subjects (number of individuals, sex and age), 3) perches used by the birds, 4) time at which perch changes occurred, 5) number of tail raising displays at each perch, 5) whether the model was attacked or harassed by the target individual or any other bird. A trial was considered successful if at least one bird remained within visual range of the model for at least two minutes. The actual distance between the perches used and the model were determined with a measuring tape (to the nearest 0.25m) and the perch heights were estimated (to the nearest 0.5m). Reported distances are the linear distance between the model and the perches. Conspecifics were considered to be in the area if they could be visually detected but also if they could be heard within 20m of the model's location.

Because we conducted both predator and control model trials at some but not all sites, and because group composition often changed between trials conducted at the same sites, we do not treat trials at the same location as paired trials. All analyses were conducted using the R programming language (R Development Core Team 2013).

Results

Observation of natural tail raising occurrences

We documented 22 tail raising events at 14 locations in 2010 and 18 tail raising events at 14 locations in 2011. Across both years, individuals directed their display towards heterospecifics in 24 cases: 18 towards humans and six towards other species (Table 2.2). All displays towards humans were observed during surveys, never when discreetly following birds or when conducting nest watches. These occurred before and during the nesting period; birds were usually flushed from or located near a trail and started displaying after detecting us (distance from observer = 14.5m ± 8.6m SD; max = 32m, min = 7m).

In 12 of the 40 observations, the individuals directed their display towards conspecifics, either in intraspecific or interspecific contexts (Table 2.2). Males displaying to other males lead to chases and/or displacements in three of the five interactions and we observed a nest-attending male chasing an intruding male after the paired female had raised her tail multiple times in the direction of the trespasser. In only four cases we were not able to determine the context of the display because we were unsure if the individual displaying had detected us.

After removing observations from locations where we witnessed a tail raising display on more than one occasion, 28 observations remained for analyses. We estimate that we observed 23 different individuals tail raising in 2010 and 15 in 2011. Tail raising was equally likely to be observed when either one, or two or more individuals were present (13 lone birds, 15 in groups; binomial test probability = 0.46, 95% CI = 0.27 – 0.66, p = 0.85). When observing groups, we detected multiple individuals displaying as often as we observed lone individuals displaying within a group (seven multiple individual displays, eight lone individual displays; binomial test probability = 0.53, 95% CI = 0.27 – 0.79, p = 1.00). In general, males were more likely than females to be observed displaying (25 males, 13 females; binomial test probability = 0.66, 95% CI = 0.49 – 0.80, p = 0.07), mainly because males were more likely to display towards conspecifics (11 males, 1 female; binomial probability = 0.92, 95% CI = 0.62 – 1.00, p = 0.006). In contrast, males were detected displaying to heterospecifics as often as females (14 males, 12 females; binomial test probability = 0.54, 95% CI = 0.33 – 0.73, p = 0.85).

Model presentation experiment

From 74 trial attempts, we attracted one or more elegant trogons close enough to initiate the experiment in 40 trials. We excluded data from one additional trial because a male started chasing another male towards the end of the trial, potentially confounding the reasons why tail raising may have occurred. Therefore, we included 39 trials from 25 different locations in our analyses, including 23 predator trials and 16 control trials. The average distance between arenas was 274m ± 36m SE (Max: 1100m; Min: 203m). In 24 of the trials we attracted only one bird to the area; 23 were males (three immature) and one was female. We attracted 2 individuals in 13 trials, and 3 individuals in 2 trials.

Because we did not have any influence over where the individuals landed in the arena, our initial analyses explored the possibility that initial conditions might have influenced the behavior of the trogons during the trials. The distance separating the initial perch of the test subject and the predator model (7.5m ± 0.44) was no different than the distance to the control model (8.1m ± 0.6 SE; t = 0.76, df = 29, p = 0.46). Furthermore, there was a clear indication that models were detected (subjects looking directly at the model) in the same proportion of trials (predator model: 16 of 23 trials, control model: 11 of 16 trials; Odds ratio = 0.96, 95% CI= 0.19 - 4.93, p = 1.00), and the experimental subjects were also startled by the exposure of the model in equal proportions (predator model: 7 of 23 trials, control model: 3 of 16 trials; Odds ratio = 1.87, 95% CI= 0.34 – 13.43, p = 0.48). Therefore, there was no significant difference in the initial trial conditions.

Tail raising displays were much more likely to occur when trogons were in the presence of a predator model (Figure 2.2a; Odds ratio = 12.9, 95% CI= 1.50 – 628.1, p = 0.01). However, the presence of conspecifics did not influence tail raising propensity (Figure 2.2b; Odds ratio = 0.80, 95% CI= 0.10 – 5.70, p = 1.00). Furthermore, when more than one trogon was present during predator model trials, we did not observe a single mobbing event.

The initial perch distance from the predator model influenced tail raising rate, which was best described by an exponential decay model, where tail raising rate was highest when the subject was near the predator model and decreased rapidly with increasing distance from the model (Figure 2.3; $F_{1,22} = 5.33$, p = 0.03). For birds that stayed within the arena for at least 4 minutes, tail raising rate decreased over time (Repeated measures t = 3.21, df = 8, p = 0.01).

Discussion

In this study, we document that tail raising in the elegant trogon is performed towards conspecifics both in intersexual and intrasexual interactions, and towards heterospecifics. Furthermore, the results from our experiment support the pursuit-deterrent function of tail raising in the presence of potential predators. These results imply that tail raising in this species is a visual communication behavior with multiple functions and inter- and intraspecific intended receivers. While such display behaviors have been documented in a few species of lizards, pursuit-deterrent visual signals that are also used in intraspecific communication have not previously been unequivocally demonstrated in birds or mammals (Table 2.1).

During natural observations, we documented individuals displaying towards conspecifics in five different contexts (Table 2.2), and these situations can be separated into two distinct probable functions: signals of dominance or aggression, and behaviors associated with courtship and mating rituals. During intraspecific male-male interactions, many tail raising displays resulted in one individual chasing another away. Therefore, it is probable that in certain situations tail raising signals dominance status and/or the intent to engage in aggressive behavior. Such pre-aggression signals are common in birds (Andersson 1980), are often stereotyped, and can prevent violent confrontations (Hurd and Enquist 2001). However, our conclusions are based on limited observations, and further documentation of this behavior in natural and experimental contexts is needed.

When we observed elegant trogons tail raising in the presence of a heterospecific, the target receiver was always a potential predator. Of the six species targeted by tail raising behavior, four were birds of prey that incorporate birds the size of trogons in their diets (de Silva et al. 1997, Panasci and Whitacre 2000, Schulze et al. 2000, Thorstrom 2000). Such birds of prey have been observed targeting trogons in Costa Rica, including a black-throated trogon (*Trogon rufus*) depredated by a collared forest-falcon (L Sandoval, personal communication). On one occasion, we observed elegant trogons displaying towards a Geoffroy's spider monkey (*Ateles geoffroyi*), a species that is not known to include birds or eggs in their diet (Henderson 2002). However, white-headed capuchin monkeys (*Cebus capucinus*) are common in Santa Rosa and are known to depredate adult birds, their eggs, and nestlings (Wainwright 2002). It is possible that elegant trogons have not developed the ability to distinguish between monkey species and display towards any monkey encountered. It also seems highly possible that the trogons would consider humans as potential predator, explaining why we were often the target of tail raising displays.

During our experimental trials, birds presented with predator models raised their tail regardless of the absence of conspecifics within visual range (prediction of the conspecific warning signal hypothesis), and this behavior never triggered a mobbing of the predator (prediction of the self-preservation alarm signal hypothesis). These results generally support the idea that tail raising in elegant trogons is a pursuit-deterrent signal. Caro (1995) argued that the exclusion of the conspecific warning signal and the self-preservation alarm signal hypotheses was not satisfactorily sufficient to claim a pursuit-deterrence function to behaviors; conclusive evidence of pursuit deterrent signals must include a demonstration that potential predators are deterred by the signal. However, he suggests that a reduction in rate of display once the predator retreats or is located further away as a reasonable argument (Caro 1994, 1995). In our experiment, we could not move the models once the trials had started but two behaviors support the idea that birds reduce their rates of display once the potential threat had been warned that it has been detected. First, the rate of signaling decreased significantly with increase in distance between the model and the first trogon perch. This suggests that indicating presence awareness to the predator is more pressing when the threat is nearby. Second, all birds that remained in the trial arena reduced the rate at which they displayed. This further suggests that once the trogons had been satisfied that the perceived threat had been reduced, the need for signaling their awareness of the predator was also reduced. While not directly demonstrating that predator behavior is implicitly affected by the display, the experimental results suggest that pursuit-deterrence is the most likely function of the behavior.

All situations in which the elegant trogon has been observed raising its tail are contexts where high levels of excitement could be expected, and this suggests the possibility that tail raising in trogons is not meant to signal specific information but is a by-product of agitation in general. However, if this were true, trogons would not perform this display when in the presence of a potential predator, especially one that has not yet detected them. In addition, since nest depredation rates in this species and in trogons in general is very high (Gonzales-Rojas et al. 2008, Steward and Pierce 2011), displaying at the nest during the excavation process could potentially draw the attention of nest predators and impose large costs to the individuals involved in the display. Therefore, we contend that a conspicuous behavior such as tail raising serves an adaptive function and is not the result of agitation.

Multifunctional signals are not uncommon in birds (e.g. Hoi and Griggio 2008) and other taxa (e.g. Morris et al. 2007). The multiple functions of bird songs, for example, are well documented in intersexual, intrasexual, and interspecific contexts (Catchpole and Slater 1995). However, visual signals with a similar diversity of contexts and functions seem to be either very uncommon or undescribed. As previously mentioned, only the crest raising display of the royal flycatcher has been described as a visual signal to multiple receiver types (Rieveley 2010), and the tail raising behavior in purple gallinule (*Gallinula chloropus*) and common moorhen (*Porphyrio porphyrio*) may target both inter-and intraspecifics (Table 2.1).

Our study demonstrates that elegant trogons perform their tail raising behavior in multiple contexts. This is a rare demonstration of a visual display targeting both conspecifics and heterospecifics, and our findings highlight an understudied topic in animal visual communication. Future studies should experimentally determine the exact functions of these displays and investigate how they evolved. This work also highlights the need for studies to successfully document the extent of multifunctional visual displays. Elegant trogons are not the only trogon species to perform tail-raising displays: we have also observed other trogon species perform tail raises when startled by humans. However, it is unknown whether or not these displays are also performed in intraspecific contexts. Furthermore, several members of other groups such as motmots (Snow 2001), and kingfishers (Woodall 2001) also raise or wag their tail in the presence of potential predators. A comparative analysis of such behaviors would provide a greater understanding of the evolutionary history of multifunctional visual displays in birds.

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Table 2.1 Summary of evidence for visual pursuit-deterrence behaviors in vertebrate animals. In birds and mammals, in contrast to lizards, there is no strong evidence that these visual signals are used in both inter- and intraspecific communication.

Species	Behavior	Type and strength of evidence for pursuit-deterrence function	Context of conspecific signaling
Birds			
Eumomota superciliosa[1,2]	Tail wag	Experimental Excluded other possible functions	No evidence[1,2]
Gallinula chloropus[3,4]	Tail raise	Observational & Experimental Conspecific signaling not excluded	Intra- and intersexual[28]
Motacilla alba[5]	Tail wagging	Observational Conspecific signaling not excluded	No evidence[5]
Porphyrio porphyrio[3,6]	Tail raise	Observational Conspecific signaling not excluded	Intra- and intersexual[29]
Sayornis nigricans[7]	Tail pump	Observational Conspecific signaling not excluded	No Evidence[30]
Lizards			
Anolis cristatellus[8,9]	Push-up Dewlapping	Experimental Excluded other possible functions	Intra- and intersexual[31]
Anolis sagrei[10]	Dewlapping	Observational Conspecific signaling not excluded	Intra- and intersexual[10]
Callisaurus draconoides[11,12,13,14,15,16]	Tail waving	Experimental Excluded other possible functions	Intra- and intersexual[32]
Carlia jarnoldae[17]	Tail display	Observational Conspecific signaling not excluded	Intra- and intersexual[17]
Cnemidophorus murinus[18]	Arm waving	Experimental	No evidence[33]

		Excluded other possible functions	
Cophosaurus texanus[19]	Tail raising	Experimental Excluded other possible functions	No evidence[19,32]
Holbrookia propinqua[19]	Tail raising	Experimental Excluded other possible functions	Intra- and Interspecific[32]
Gonatodes albogularis[20]	Tail wave	Experimental Conspecific signaling not excluded	No evidence[20]
Leiocephalus carinatus[21,22]	Tail curling	Observational Excludes other possible functions	Intra- and intersexual[21,22]
Oplurus cuvieri[23]	Push-up Dewlapping	Experimental Conspecific signaling not excluded	Intra- and Intersexual[34]
Podarcis muralis[24]	Foot shaking (Type 3)	Experimental Conspecific signaling not excluded	No evidence[24] (Type 1 and 2 signal conspecifics)
Mammals			
Alcelaphusb uselaphus[25]	Stotting Leaping	Experimental Conspecific signaling not excluded	No evidence[25]
Aepycerosm elampus[25]	Stotting Leaping	Experimental Conspecific signaling not excluded	No evidence[25]
Connochaetesta urinus[25]	Stotting Leaping	Experimental Conspecific signaling not excluded	No evidence[25]
Damaliscus korrigum[25]	Stotting Leaping	Experimental Conspecific signaling not excluded	No evidence[25]
Eudorcas thomsonii[25]	Stotting Leaping	Experimental Conspecific signaling not excluded	No evidence[25]

Gazella granti[25]	Stotting Leaping	Experimental Conspecific signaling not excluded	No evidence[25]
Odocoileus virginianus[26,27]	Tail raise	Experimental Conspecific signaling not excluded	No evidence[26,27]

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[1]Murphy 2006, [2]Murphy 2007, [3]Alvarez 1993, [4]Randler 2007, [5]Randler 2006, [6]Woodland et al. 1980, [7]Avellis 2011, [8]Leal and Robles 1997, [9]Leal 1999, [10]Vanhooydonck et al. 1999, [11]Cooper 2010a, [12]Cooper 2010b, [13]Cooper 2011a, [14]Cooper 2011b, [15]Eifler and Eifler 2010, [16]Hasson et al. 1989, [17]Langkildeet al. 2004, [18]Cooper et al. 2004, [19]Dial 1986, [20]Alonso et al. 2010, [21]Cooper 2001, [22]Cooper 2007, [23]Ito and Mori 2012, [24]Font et al. 2012, [25]Caro 1994, [26]Bildstein 1983, [27]Caro et al. 1995, [28]Bannor and Kaviat 2002, [29]West and Hesse 2002, [30]Wolf 1997, [31]Losos 2009, [32]Clark 1965, [33]Magnusson 1996, [34]Randriamahazo and Mori 1999

Table 2.2 Elegant trogons (*Trogon elegans*) were observed performing tail raising displays in various contexts

Receiver	**Context**	**Number of observations**
Intrasexual	Male-Male competition for female	1
	Male-Male competition for territory	5
Intersexual	Courtship display	1
	Nest building/preparation	4
	Territorial intrusion	1
Heterospecific	Spectacled owl (*Pulsatrix perspicillata*)	1
	Roadside hawk (*Buteo magnirostris*)	2
	Double-toothed kite (*Harpagus bidentatus*)	1
	Collared forest-falcon (*Micrastur semitorquatus*)	1
	Geoffroy's spider monkey (*Ateles geoffroyi*)	1
	Humans	18
Unknown		4
	Total	40

Figure 2. 1 Examples of the models (A and C) used during experimental trials and photographs of live specimens (B and D) for comparison. A and B collared forest-falcon (*Micrastur semitorquatus*; Mike Dazenbaker); C and D squirrel cuckoo (*Piyana cayana*; Fransisco Piedrahita).

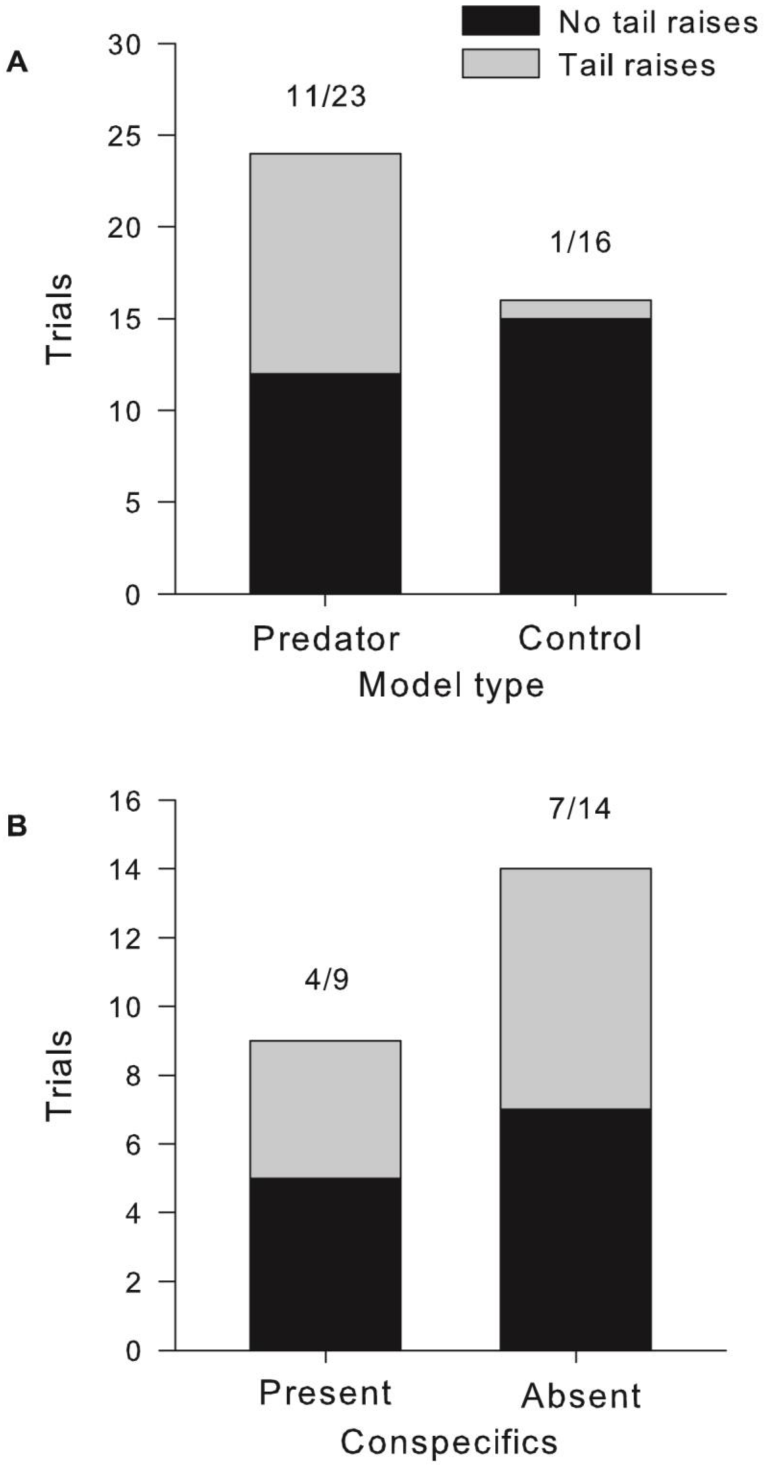

Figure 2. 2 A) Elegant trogons were more likely to raise their tail in the presence of a predator model than in the presence of a control model, but B) the presence or absence of conspecifics did not influence tail raising behavior of elegant trogons presented with a predator model. Numbers above bars indicate proportion of trials during which tail raising was observed.

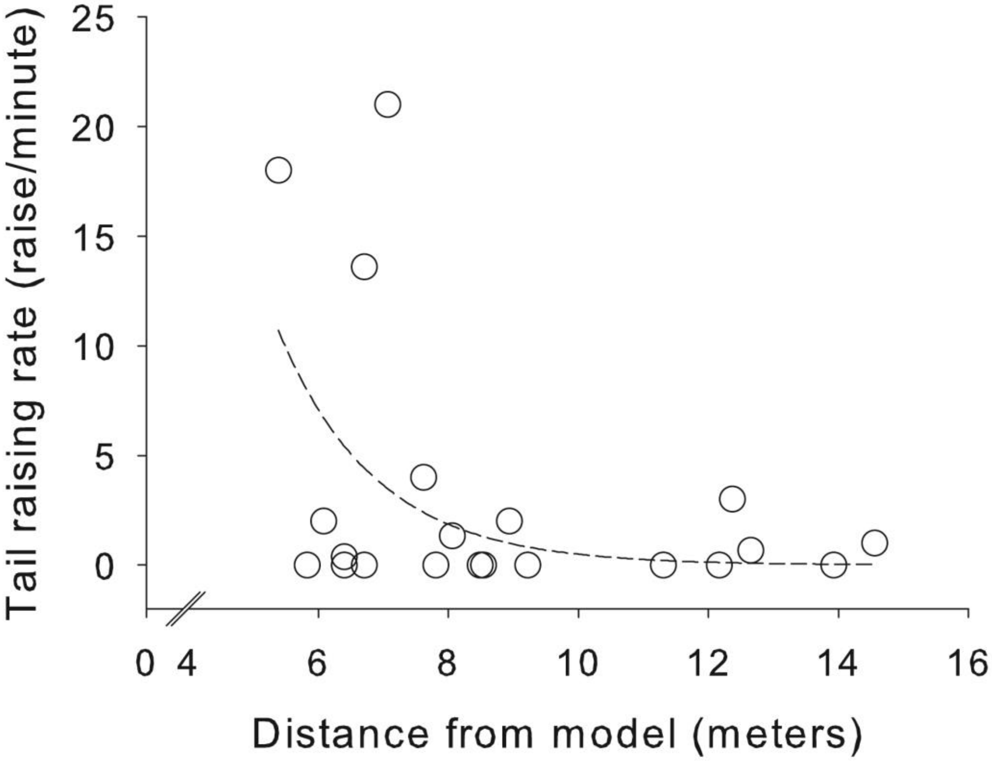

Figure 2. 3 The influence of first perch distance from a predator model on tail raising rate in the elegant trogon was best described by an exponential decay curve (dashed line).

Chapter 3

Sympatric black-headed and elegant trogons (Aves: Trogoniformes) focus on different plumage characteristics for species recognition

Summary

Divergence of sexually selected secondary characteristics is an important pre-zygotic isolation mechanism which promotes speciation. The ability of individuals to distinguish conspecifics from similar-looking congeners has important evolutionary consequences, yet few studies have determined which specific visual characteristics are used for species recognition, and if closely related species use the same characteristics. In particular, sympatry with similar congeners may influence which traits are important in species recognition. In this study, we experimentally tested which traits influenced species recognition in two species of trogons, only one of which was sympatric with a similar-looking congener. We presented elegant trogons and black-headed trogons with models that closely resembled conspecifics, and models that differed in either the colour of the belly, the colour of the upperparts, or the tail-barring pattern. Elegant trogons showed significantly more aggression towards the conspecific model and the tail model, suggesting that they could not distinguish between the two model types, or that these two models were equally threatening, and that belly colour and upperpart colour are more important for species recognition in this species. In contrast, the black-headed trogon approached all models very closely, except for the conspecific model. We interpret this counterintuitive behaviour as a reluctance to approach an unknown conspecific, suggesting that all three plumage traits are important for species recognition in this species. Because the elegant trogon is not sympatric with a similar congener, we argue that elegant trogons may lack the ability to discriminate fine-barring tail differences or may simply overlook this trait. In contrast, all three plumage traits appear to be important for species recognition in black-headed trogons. Our findings suggest that sympatry with the similar-looking violaceous trogon may have influenced species recognition in this species, favouring the use of all three plumage characteristics, including tail banding patterns, which differ between black-headed and violaceus

trogons. Our study is the first experimental evidence of specific plumage patches being used for species recognition in two sympatric congeners, and strongly suggests that the presence of a similar-looking congener can influence which traits are important in species recognition.

Introduction

The ability of individuals to discriminate between members of the same species and members of other closely-related species has important evolutionary consequences (Ord & Stamps, 2009). Most animals defend territories against conspecifics to prevent the takeover of important ecological resources such as foraging and nesting sites (Maher & Lott, 1995), which incurs large costs. These include expending energy during displays (e.g., Brandt, 2003), time lost to other activities such as foraging (e.g., Barnett & Briskie, 2011), and possibly sustaining injuries during physical contests (e.g., Lombardo, 1986). When similar-looking species coexist, species-specific characteristics are assumed to allow accurate species recognition and prevent unnecessary interactions with heterospecifics (Andersson, 1994; Bradbury & Vehrencamp, 2011). Mistakes in species recognition can also lead to potential cross-species mating, which often produces offspring with reduced viability (Martin & Martin, 2001). Thus, the evolution of species recognition traits is important in the context of male-male aggression and female mate choice.

Characteristics used to distinguish conspecifics from heterospecifics are varied, and span all sensory modalities. Across taxa, acoustic traits (e.g., de Kort & ten Kate, 2001; Teufel *et al.*, 2007; Rollo & Higgs, 2008), olfactory traits (McLennan & Ryan, 1999; Shine *et al.*, 2002; Rollmann *et al.*, 2003; Nunes *et al.,* 2008), and visual traits (Pearson & Rohwer, 2000; Couldridge & Alexander, 2002; Michaelidis *et al.*, 2006; Ord & Stamps, 2009) have all been implicated in species recognition. In a limited number of taxa, even electric discharges (Hopkins & Bass, 1981) and vibrations (Hill, 2008) are species-specific. In birds, the ability to discriminate between traits of closely-related species has usually been evaluated using vocal characteristics (Ord & Stamps, 2009). In *Streptopelia* doves for example, species respond more aggressively towards vocalizations of their own species, and the degree to which they respond to the calls of congeners reflects their phylogenetic relationship (de Kort & ten Cate, 2001; de Kort *et al.*, 2002, den Hartog *et al.*, 2007). While recent studies have shown that sympatry has an important influence on plumage divergence among closely related species (Martin *et al.*, 2015), the particular plumage colours or patterns used in species recognition have rarely been studied (reviewed in Ord & Stamps, 2009; Ord *et al.*, 2011), with some notable exceptions. For example, Montagu's harriers (*Circus pygargus*) and Hen harriers (*Circus cyaneus*), which are sympatric and only differ subtly in the colour of underparts and upperwing, are less aggressive towards taxidermied models of heterospecifics than conspecifics (García, 2003). Blackcaps (*Sylvia atricapilla*) can also discriminate between their own species and taxidermied models of Garden warblers (*Sylvia borin*), which differ in contour feather colour and the presence or absence, respectively, of a black crown (Matyjasiak, 2004). Furthermore, in an experiment involving taxidermied incipient *Monarcha* flycatchers, Uy *et al.* (2009) demonstrated increased aggressive responses with increased similarity in plumage. While the evidence so far suggest that overall plumage patterns alone are sufficient for species recognition, no study to date has demonstrated the extent to which plumage patches must differ for proper species recognition to occur, and whether closely-related species assess the same traits. Furthermore, no study has directly manipulated plumage traits in model presentation experiments to exclude the possibility that other cues such as bill shape and size, and body size could be used for species recognition. Because the divergence of secondary sexual characteristics is an important step in pre-mating isolation (Price, 2007), insight into how species recognize members of their own species is central to understanding the speciation process, particularly when closely-related species coexist in sympatry.

The avian genus *Trogon* comprises approximately 20 species with highly conserved plumage patterns (Collar, 2001; Forshaw, 2009). Up to six different species are sympatric in the lowlands of the Amazon suggesting that plumage traits may be important for species recognition. Males of all species possess a red or yellow belly (orange in one subspecies and one race) and display iridescent upperparts that range in colour from copper-green to purple-blue. Patterns on the ventral surface of the large and conspicuous tail vary from completely white to completely black, to banded with thin and/or thick white-on-black bands. As such, these three plumage characteristics (belly colour, upperpart colour, and tail barring pattern) are potential candidates for species recognition traits in males of this genus. In this study, we experimentally tested in two species of trogons 1) which plumage characteristics are used in species-recognition and 2) whether the presence of a similar-looking sympatric congener influences which traits are used in species recognition. We conducted our study on black-headed trogons (*Trogon melanocephalus*) and elegant trogons (*T. elegans*). At our study site in Costa Rica, the black-headed trogon is sympatric with the similar-looking violaceous trogon (*T. violaceus*); the elegant trogon coexists with both species but does not have a similar-looking sympatric congener in Costa Rica. We presented these two focal trogon species with conspecific models and modified models that differed in breast colour, upperpart colour, or tail barring pattern to assess which traits are important for species recognition in each species.

Methods

We conducted our experiment during the breeding season of all three trogon species, between May and July 2012, in the Guanacaste Conservation Area, Sector Santa Rosa, Costa Rica (10°

40’N, 85˚ 30’W). Our study site of nearly 10 km^2 is characterized by a mix of secondary dry deciduous forest, which has been in a regeneration state since the 1980’s, and older forest stands of evergreen tree species (Janzen, 1988).

The male elegant trogon displays green upperparts and a red belly (Figure 3.1). Its tail pattern is a series of thick white bars interspersed by equidistant thin white and black bars (Pyle, 1997); no other bird in our study area shares similar characteristics (Stiles & Skutch, 1989). The male black-headed trogon displays a yellow breast and belly, a black head, and blue-green to purple-blue upperparts. The ventral surface of its tail is solid white. The violaceous trogon is very similar to the black-headed trogon but its head is purple-blue, which often appears black from a distance. The tail banding pattern of the violaceous trogon is very similar to that of the elegant trogon. The black-headed and violaceous trogons are not known to hybridize (McCarthy, 2006) or compete for nest sites, but they can be seen in the same trees foraging for fruit or insects, especially caterpillars, which both species feed to their young (Forshaw, 2009). The males can easily be distinguished from the females by plumage in both black-headed and elegant trogons (see plates in Collar, 2001).

Models

To determine which plumage characteristics might be used as species recognition traits by the two focal trogon species, we presented individuals of each species with bird models that were as similar as possible to conspecifics, and models that were different from conspecifics in either tail banding pattern, upperpart colour, or belly colour. Experiments that involve model presentations often rely on taxidermied specimens (e.g., Götmark, 1992; Götmark, 1997; Uy *et al.*, 2009). However, we elected to produce realistic looking models from craft materials rather than risk damaging valuable museum specimens, or collecting animals for the purpose of this experiment (Caro & Melville, 2012). Moreover, we have shown previously that elegant trogons responded as expected to predator and control models (Bitton & Doucet, 2014). We produced models that were as similar as possible to elegant and black-headed trogons ('Conspecific' models), and models that differed from these only in the back colour ('Back' model). In addition, we produced interchangeable plastrons and tails which, when placed on the 'Conspecific' model, allowed us to produce models that differed only in belly colour ('Belly' model), or tail banding pattern ('Tail' model). As a control, we constructed models resembling the squirrel cuckoo (*Piaya cayana*, 'Control' model), a similar-sized species that does not prey on trogons and does not parasitize nests (Payne, 1997). This cuckoo is common in the study area and does not elicit aggressive responses from elegant trogons (Bitton & Doucet, 2014).

We used a plastic dove decoy similar in shape and size to the trogons as a base for all our models, and we glued feathers on top. We used a base layer of wind-sensitive downy feathers and covered these with pennaceous feathers to make the models realistic-looking (see Němec *et al.,* 2014 for details on the importance of life-like models). We used a similar technique to produce the belly plastrons using rigid fabric as a base. We placed Velcro® on the plastic dove models, and the plastrons and tails, to facilitate the interchange of the modifications. For each of the two experimental subject species (elegant and black-headed trogons), we produced three 'Conspecific' base models and three 'Back' base models. In addition, we produced five red and five yellow belly plastrons, as well as three elegant trogon type tails and three black-headed type tails for each of the two back colours (i.e., 12 tails in all). Therefore, by combining the bases (three), plastrons (five), and tails (three) we could generate 45 'different' models for each treatment (3 X 5 X 3). This allowed us to use a unique stimulus for each trial to avoid simple pseudoreplication (Kroodsma, 1989; Kroodsma *et al.*, 2001). We also produced three squirrel cuckoo control models.

To insure that the model feather colours matched those found on real trogons, we compared dyed feathers to real feathers using reflectance spectrometry and compared feather colours using an avian visual model. We first produced a library of coloured feathers by mixing commercially-available fabric dyes (Rit©). We objectively measured the reflective properties of the dyed feathers and those of real birds (three males of each species) obtained from museum specimens using an Ocean Optics USB 2000 spectrophotometer in conjunction with a PX-2 xenon light source (Ocean Optics, Dunedin, FL). For the dyed feathers and the red and yellow belly trogon feathers, we used a bifurcated probe fitted with a rubber stopper at the tip. The stopper kept the probe at 5mm from the feather surface and excluded the ambient light. To capture the iridescent nature of green and blue upper-back feathers of the trogons, we used two standard fibre-optic probes (instead of the bifurcated probe) in conjunction with a goniometer, which permits measurements of specular and diffuse iridescence (Meadows *et al.*, 2011). For each of three green and three blue feathers, we collected reflectance measurements at 10° increments between near normal incidence (85°) and 55°. This was done by concurrently moving both the light source arm and spectrophotometer arm of the goniometer to measure specular reflectance, and by moving the spectrophotometer arm alone to capture diffuse reflectance. Reflectance measurements were all relative to that of a diffuse pure white standard (WS-1; Ocean Optics). For each colour, we chose the dyed feathers that best matched the real feathers by selecting colours that were either included in or very near the 3-dimensional volume created by the colours of the real trogons in tetrahedral colourspace (Figure 3.2). In the visual model we used an ideal illuminant (pure white light) and the visual system of an average bird possessing a short wavelength cone that peaks in the ultraviolet, as found in another species of trogon (Ödeen & Håstad, 2013). We used these idealized parameters because trogons are found at different heights in the forest canopy and in a variety of habitats where light and background conditions change substantially. The avian visual model values were generated using the '`pavo`' package in R (Maia *et al.*, 2013; R Development Core Team, 2014).

Field experiment

For each focal species (elegant and black-headed trogon), we presented five types of models in an arbitrary order at each trial location: 1) a 'Conspecific' model with correct back colour, belly colour, and tail patterning, 2) a 'Belly' model with a different belly colour, 3) a 'Back' model with a different back colour, 4) a 'Tail' model with a different tail barring pattern ('Tail'), and 5) a 'Control' model of a squirrel cuckoo.

Trogon territory sizes at our study site are less than 100m in radius (Bitton & Doucet, 2014), as in other parts of their range (Corcuera & Butterfield, 1999). To prevent testing the same individuals more than once with the same treatment, we separated trial locations by at least 200m. We raised the models to 3m near a natural perching branch using a camouflaged-painted tripod below which a remotely-controlled loudspeaker was hidden. We hid the models under camouflaging textile, which could be removed using a clear fishing line. The observer was also under camouflage, at least 10m away from the model. After the initial setup was complete, the observer waited 10 minutes before beginning the trial to avoid potentially influencing the behaviour of the experimental subjects. We attracted trogons to the area using playback of an adult male species-specific territorial vocalization obtained in a previous year (2011). The playback vocalization was that of a single individual unfamiliar to the test subjects (recorded outside of the study area) and consisted of a loop of the same 1 minute vocalization bout. We broadcast playbacks a maximum of 10 minutes to attract a subject. Model presentation trials were either initiated as soon as a focal individual was in direct sight of the model feature of interest (i.e. subject had to be able to see the tail in 'Tail' model trials), or aborted if no bird approached close enough after 10 minutes of playback. The playback vocalization continued throughout the trial for two main purposes: to maintain the attention of the focal individual, and to simulate a territorial intrusion.

We initiated model presentation trials by removing the camouflaging textile from the model and trials always lasted 10 minutes in addition to the time needed to attract a model, regardless of whether or not the experimental subjects remained within view of the model. We recorded behavioural observations with a small hand-held recorder (Edirol R-09, Roland) and supplemented our data by taking measurements after the trial had ended. For each successful trial we took note of the distance between the observer and the model (in meters), the time before a bird was heard or sighted after initiating the playback (in seconds), the time between the start of the playback and the exposure of the model (in seconds), the perches used and at what time, and any kind of aggressive display. Elegant trogons, but not black-headed trogons, are known to perform tail raises as a signal of aggression in the presence of conspecifics (Bitton & Doucet, 2014). Therefore, aggressive displays included tail raises and flights at the model (displacement or attack attempts) for elegant trogon trials, but we only recorded flights at the model in black-headed trogon trials. After the end of a trial, we measured the horizontal distance between perches to the nearest 10 cm using a measuring tape and estimated the height of the perch by eye to the nearest 0.5 m. We calculated the linear distances between the model and the perches based on those measurements for use in the analyses. We used the amount of time before a bird was heard or visually located, and time to beginning of trial as measures of the focal subject's motivational state. Trials in which birds could be heard calling before the start of the playback were not included in analyses that included this time of first response as a factor. In addition to observations of tail raises and displacement attempts, we investigated the effects of model type on the distance of closest approach and the time at which birds reached this location (henceforth latency to closest approach).

We conducted successful trials of at least one model presentation at 49 different locations (average distance between location = 270m ± 8m SE; range: 200m – 420m). We initiated 427 trials, of which 200 were successful at attracting a trogon near enough to conduct a full trial. We conducted 99 trials with elegant trogons (Control: *n* = 19, Conspecific: *n* = 20, Tail: *n* = 20, Back: *n* = 20, Belly: *n* = 20) and 101 trials with black-headed trogons (Control: *n* = 20, Conspecific: *n* = 20, Tail: *n* = 20, Back: *n* = 20, Belly: *n* = 21). The average distance between the observer and the model was not different between model types for the elegant trogon trials (*P* = 0.99), the black-headed trogon trials (*P* = 0.70), or between trials conducted to each of the two species (*P* = 0.66). Moreover, the average distance between the model and the focal individual at the beginning of each trial was not different between model types for the elegant trogon trials (*P* = 0.43), for the black-headed trogon trials (*P* = 0.87), or between trials conducted to each of the two species (*P* = 0.58). There was no significant correlation between the time before a bird was heard or visually located, a measure of motivational state, and the distance of closest approach to the model in either elegant trogon trials (*n* = 91, Pearson's *r* = -0.04, *P* = 0.69), or black-headed trogon trials (*n* = 97, Pearson's *r* = -0.02, *P* = 0.82). Furthermore, there were no significant correlation between the distance of closet approach and the latency to closest approach for either elegant (*n* = 91, Pearson's *r* = -0.01, *P* = 0.91) or black-headed (*n* = 97, Pearson's *r* = -0.07, *P* =0.51) trogon trials.

Analyses

To determine the influence of model type on the distance to closest approach and latency to closest approach (both log transformed to normalize the data), we used two-way ANOVAs with model type, species, and the interaction between the terms as independent variables. To understand the influence of model type on the number of tail raise displays and displacement attempts, we first conducted a 1X5 Fisher's Exact test because the distribution of values did not meet the assumptions of standard contingency table analyses (see Results). This was followed by pairwise comparisons of model types using 1X2 Fisher's Exact tests. We present results ± SE.

Results

There was a significant effect of species (ANOVA, $F_{1,180} = 15.98$, $P < 0.001$) and species by model type interaction (ANOVA, $F_{4,180} = 8.49$, $P < 0.001$) on the distance of closest approach to the models. To understand the interaction term, we conducted a one-way ANOVA separately on each species. There was a significant difference in distance of closest approach between model types during black-headed trogon trials (ANOVA, $F_{4,93} = 6.00$, $P < 0.001$). *Post hoc* Dunnett's tests revealed that experimental subjects approached the 'Control' (Estimate = -0.47 ± 0.17, $t = -2.77$, $P = 0.024$), 'Back' (Estimate = -0.96 ± 0.17, $t = -5.79$, $P < 0.001$), 'Belly' (Estimate = -0.61 ± 0.17, $t = -3.64$, $P = 0.002$), and 'Tail' (Estimate = -0.61 ± 0.17, $t = -3.68$, $P = 0.001$) models more closely than the 'Conspecific' model (Figure 3.3). There was also a significant difference in distance of closest approach between model types during elegant trogon trials (ANOVA, $F_{4,87} = 4.78$, $P = 0.002$).). *Post hoc* Dunnett's tests revealed that experimental subjects approached the 'Conspecific' model more closely than the 'Control' (Estimate = 0.64 ± 0.22, $t = 2.93$, $P = 0.015$), 'Back' (Estimate = 0.58 ± 0.22, $t = 2.68$, $P = 0.03$), and 'Belly' model (Estimate = 0.88 ± 0.22, $t =$

3.99, $P < 0.001$), but not the 'Tail' model (Estimate = 0.28 ± 0.22, $t = 1.30$, $P = 0.50$, Figure 3.3). There were no effects of species (ANOVA, $F_{1,180} = 0.29$, $P = 0.59$), model type (ANOVA, $F_{4,180} = 0.50$, $P = 0.74$), or the interaction term (ANOVA, $F_{1,180} = 0.07$, P = 0.99) on latency to closest approach. Removing the interaction term did not improve the model (ANOVA, species: $F_{1,184} = 0.30$, $P = 0.59$; model type: $F_{4,184} = 0.51$, $P = 0.73$).

We detected aggressive displays in 19 elegant trogon trials, including 15 trials with at least one tail raising display. Tail raising displays were not equally distributed across all model types (Fisher's exact test; $P = 0.002$, Figure 3.4). The 'Control' model did not elicit any tail raises, the 'Belly' and 'Back' models each elicited tail displays in one trial, the 'Conspecific' model elicited displays in seven trials, and the 'Tail' model elicited tail raises in six trials. Pairwise Fisher's exact tests revealed that the 'Conspecific' and 'Tail' models elicited tail raises in significantly more trials than almost all other model types (Table 3.1). Flights towards the model were observed in four trials, all when presenting the 'Tail' model. Therefore, aggressive displays (tail raises plus flights towards models) were not equally distributed among all model types ($P < 0.001$), and were more common in trials with 'Conspecific' and 'Tail' models than for any other model presented (Table 3.1). We did not detect any aggressive displays in black-headed trogon trials.

Discussion

In this study, we used a model presentation experiment to investigate the plumage characteristics used for species recognition in two coexisting species of trogons: the black-headed trogon, which is sympatric with the similar-looking violaceus trogon, and the elegant trogon, which is not sympatric with a similar-looking congener. Elegant trogons were equally aggressive towards the similar-looking model and one with a modified tail, but did not behave aggressively towards the models with modified back or belly colours. Furthermore, elegant trogons approached the conspecific model closer than all but the modified tail model. These findings suggest that conspecific and modified tail models were both recognized as conspecifics, whereas the other models were not. In contrast, the black-headed trogon approached within very short distance all models except the conspecific model. Thus, black-headed trogons clearly distinguished between conspecific models and all other model types, but maintained their distance from this conspecific intruder. Although this behaviour may seem counterintuitive, reluctance to approach or even retreating from aggressive conspecific intruders has been shown in several song playback studies (e.g., Illes *et al.*, 2006; de Kort *et al.*, 2009). Our findings suggest that these two coexisting species of trogons use different cues for species recognition, and that their sensitivity to different traits may be influenced by the presence or absence of sympatry with a similar-looking congener.

Both elegant and black-headed trogons did not seem to consider models that differed in either the back or belly colour as members of their own species. These results are not unexpected considering that the differences between the 'Conspecific' and 'Back/Belly' models were large patches that differed in colouration. Much smaller differences in plumage traits have been shown to be sufficient for species (Matyjasiak, 2004) and individual recognition (Godard, 1991). However, elegant trogons were more aggressive towards 'Conspecific' and 'Tail' models than towards other model types, whereas black-headed trogons behaved differently towards 'Conspecific' models than with all other model types. Together, our results imply that elegant and black-headed trogons do not use exactly the same species-recognition characteristics and suggest that the presence of a similar-looking sympatric congener may influence the use of species-identity cues. Social learning and differential discrimination abilities at the population level could explain our results.

The ability to recognize conspecifics from heterospecifics has been demonstrated to result from social learning of songs (Catchpole & Slater, 2003) and plumage characteristics (Hansen & Slagsvold, 2003) in a large number of species. While song and plumage recognition is often acquired through imprinting in nestlings, evidence shows that regular interactions with heterospecifics that use similar resources lead to recognition of heterospecifics at later stages in life (e.g., Catchpole, 1978; Grether *et al*., 2009). This has been demonstrated in black redstarts (*Phoenicurus ochruros*, Gmelin), for example, where individuals are aggressive towards playbacks of the common redstart (*Phoenicurus phoenicurus*, Linnaeus) in areas of sympatry but not allopatry (Sedláček *et al.*, 2006). The black-headed trogons at our study site regularly come in contact with violaceous trogons, providing ample opportunities to learn the differences in tail barring patterns between conspecific and heterospecifics. In contrast, elegant trogons at our study site, which have bright red bellies, are only sympatric with yellow-bellied trogons and would not need to assess tail barring patterns to recognize conspecifics. The ability of black-headed trogons to recognize violaceous trogons may be local (i.e., population level); an experiment with black-headed trogons in an area where they are not sympatric with violaceus trogons could determine whether learning plays a role in heterospecific recognition in this study. Similarly, an experiment with elegant trogons in an area where they are sympatric with a similar-looking congener could yield important insights about the role of learning in species recognition.

Differences in species recognition between elegant and black-headed trogons could arise from each species focussing on particular traits, but could also possibly arise from differences in their discrimination ability. Indeed, the costs of incorrect species discrimination are expected to exert a strong selective pressure for accurate transmission on the part of the signaller, but also on the perceptive ability of the receiver (Tobias & Seddon, 2009). For example, playback experiments in closely-related Thamnophilidea antbirds with convergent songs demonstrated that females are able to distinguish between conspecific and heterospecifics, and recognize mates from strangers, even when songs are extremely stereotyped (Seddon & Tobias, 2010). This ability to discriminate among conspecifics is not present in males (Tobias & Seddon, 2009), demonstrating that even within species the perceptive abilities of the receiver can differ, and are potentially influenced by the differential cost of species misidentification within and among species. Females misidentifying heterospecific males would incur much larger costs, by producing potentially unfit hybrids, while males would only incur the costs associated with wasted time, misdirected aggression, and the risk of physical injury (Tobias & Seddon, 2009; Seddon & Tobias, 2010). In areas where similar-looking congeners occur, it is therefore possible that the perceptual abilities of individuals are fine-tuned to small differences in trait differences.

Several mechanisms, in different contexts, could promote the evolution of fine discriminating abilities. For example, sympatric closely-related species in which hybrid matings sometimes occur would be expected to recognize heterospecifics within the sympatric area, but not necessarily in the adjoining allopatric zones. The increased ability to recognize a heterospecific would evolve as part of a multifaceted reinforcement mechanism, favour assortative mating, and thus decrease the opportunity for hybridization (Coyne & Orr, 2004). Similarly, incipient species would be expected to have better heterospecific discriminating ability than fully established species, especially in cases where speciation is driven by slight changes in the ecological niche of the diverging populations (Price, 2007); failure to discriminate between diverging groups could lead to a collapse of the species pair through indiscriminate hybridization (e.g. Behm *et al.*, 2010). Finally, as in our study, we could expect species with sympatric similar-looking congeners to have better discriminating abilities than species without sympatric closely-related congeners, even in the absence of hybridization. Since the cost of misidentification would be relatively low in this context, we could expect the precision of species recognition to be weaker than in the situations explored above, and would not evolve as a mechanism of reinforcement following secondary contact but, rather, would evolve in the context of competitor recognition. Even in the absence of competition for resources, individuals can avoid the cost of aggressive interactions by recognizing non-competitive heterospecifics (Anderson & Grether, 2009; Anderson & Grether, 2010). Because divergence in traits can occur through agonistic character displacement (Grether *et al.*, 2009, Okamoto & Grether, 2013), perhaps interspecific interference competition could also lead to an increase in perceptual abilities that facilitate species recognition.

The elegant trogon subjects in our experiment showed the same level of aggression towards the ‘Conspecific’ model and the ‘Tail’ model. Even if the individuals had the capacity to discriminate between the different traits, it is still possible that they did not attend to the differences for two reasons. First, when species rely on several sources of information such as multiple coloured plumage patches, individuals may not notice small differences when initiating a response (Hankinson & Morris, 2003). However, the aggressive behaviours of elegant trogons towards the models always came after a relatively long period of visual assessment. In fact, the fastest display of aggression occurred after over a minute of close-range evaluation, sufficient time to evaluate the differences in characteristics between the model and conspecifics. The hypothesis that elegant trogons did not assess differences in tail-barring patterns because they do not notice small details should be tested by presenting a range of tail barring differences. Second, individuals would not react towards a modified signal if the response potentially incurred greater costs (such as reciprocal aggression) than not responding (Bradbury & Vehrencamp, 2011). We consider this explanation improbable in the context of our experiment because a large majority of the aggressive displays consisted of tail raises, which are low cost because they are not energetically demanding and, most importantly, do not risk injuring the individual. Therefore, our results suggest that elegant trogons simply dismissed small difference in tail-barring, or did not have the ability to distinguish between the ‘Conspecific’ model and the ‘Tail’ model.

Our study revealed that two coexisting trogons use different plumage traits for species recognition, and provides evidence that the presence of a similar-looking congener can influence the use of visual species recognition characteristics. The lack of ability to distinguish between two traits could result from simply ignoring those differences or inferior discrimination ability. Our findings also suggest that learning may play a role in species recognition, since both of our focal species are sympatric with similar-looking congeners in parts of their range but not others. Experiments conducted in different populations, with different sympatric species present, would help elucidate the exact mechanisms responsible for our results. Nonetheless, this study provides the first experimental evidence of species recognition based on a specific plumage patch in two sympatric congeners, and the first to demonstrate that the presence or absence of a similar-looking congener can influence which visual traits are used for species recognition. Because the evolution of divergent sexually selected traits and their assessment by conspecifics promote pre-mating isolation and speciation, our study demonstrates the importance of sympatry on these processes.

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Table 3.1 Elegant trogons performed more aggressive displays when presented with a 'Conspecific' and 'Tail' model than when presented with 'Control', 'Belly', and 'Back' models (see methods for model type definitions). Values presented are from Fisher's exact tests and significant tests are in bold. Displacements attempts were only observed during 'Tail' trials and did not influence the results of other trial results.

Aggressive display	Model comparison	Odds ratio	95% CI Odds ratio	P
Tail raises only	'Conspecific' vs 'Tail'	0.80	0.17 – 3.65	1.00
	'Control' vs 'Conspecific'	**0.00**	**0.00 – 0.59**	**0.008**
	'Control' vs 'Tail'	**0.00**	**0.00 – 0.76**	**0.02**
	'Control' vs 'Belly' or 'Back'	0.00	0.00 – 41.05	1.00
	'Conspecific' vs 'Belly' or 'Back'	**0.10**	**0.00 – 0.96**	**0.044**
	'Tail' vs 'Belly' or 'Back'	0.13	0.00 – 1.24	0.09
Tail raises + displacement attempts	'Conspecific' vs 'Tail'	0.55	0.12 – 2.27	0.52
	'Control' vs 'Tail'	**0.00**	**0.00 – 0.31**	**< 0.001**
	'Tail' vs 'Belly' or 'Back'	**0.06**	**0.00 – 0.50**	**0.003**

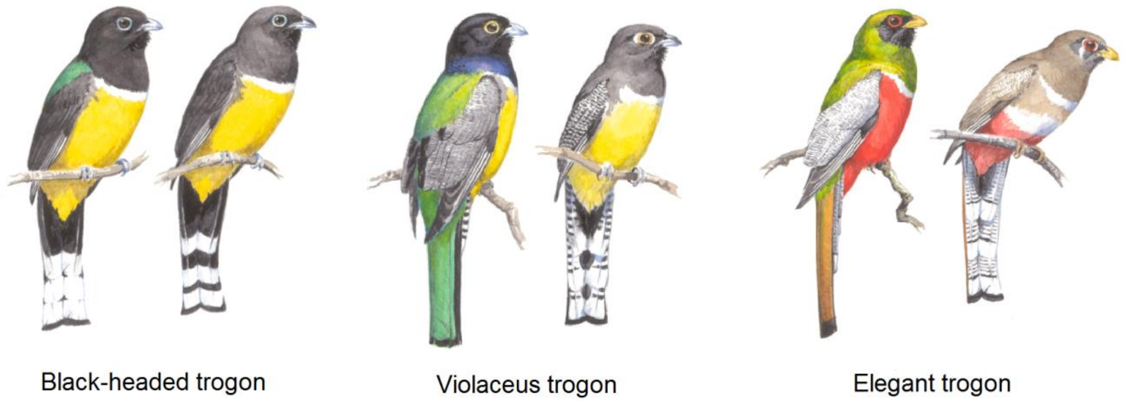

Figure 3. 1 Our experimental trials were conducted on the elegant trogon (*Trogon elegans*), which does not have a similar-looking congener in our study area, and the black-headed trogon (*T. melanocephalus*), which is sympatric with the violaceous trogon (*T. violaceus*). Painting credit: John Sill, with permission from owner.

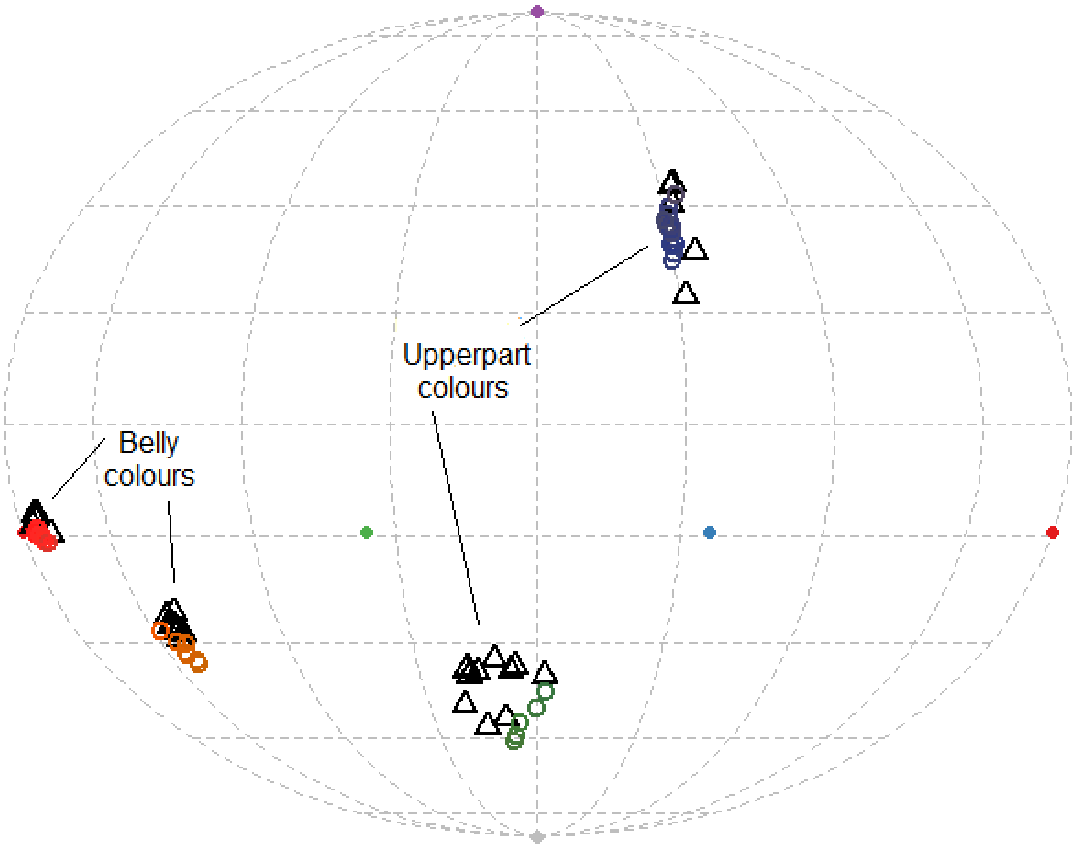

Figure 3. 2 The hue of the dyed feathers (coloured circles) on the models closely matched the hue of museum specimens (black triangles) in avian colourspace. Black-headed trogons have blue upperparts and yellow bellies, elegant trogons have green upperparts and red bellies. The Mollweide projection is a two-dimensional representation of the three-dimensional tetrahedral colourspace. Colours of the open circles are approximations of the perceived hues generated from the spectral data. U, S, M, and L mark the ultraviolet-, short-, medium- and long-wavelength sensitive photoreceptors, respectively, which are also marked with a solid circle symbol.

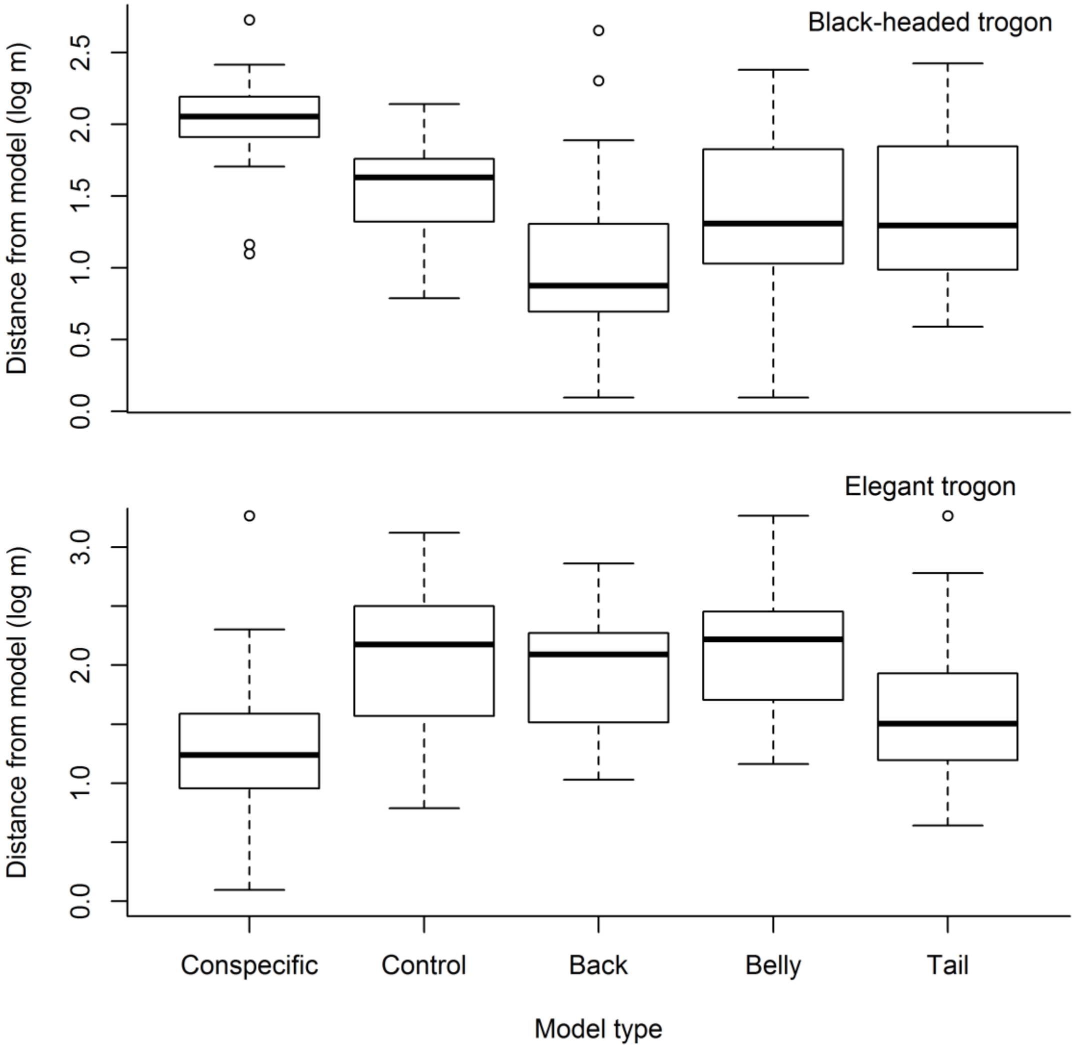

Figure 3. 3 Black-headed trogons approached 'Conspecific' models less than any other model type, and elegant trogons approached 'Conspecific' models more than all but the 'Tail' models (see Methods and Results for more details). Boxes show median (50th percentile) and interquartile range (25th to 75th percentile); whiskers indicate the 95% confidence intervals. Open circles are data points that fall outside the 95% confidence range.

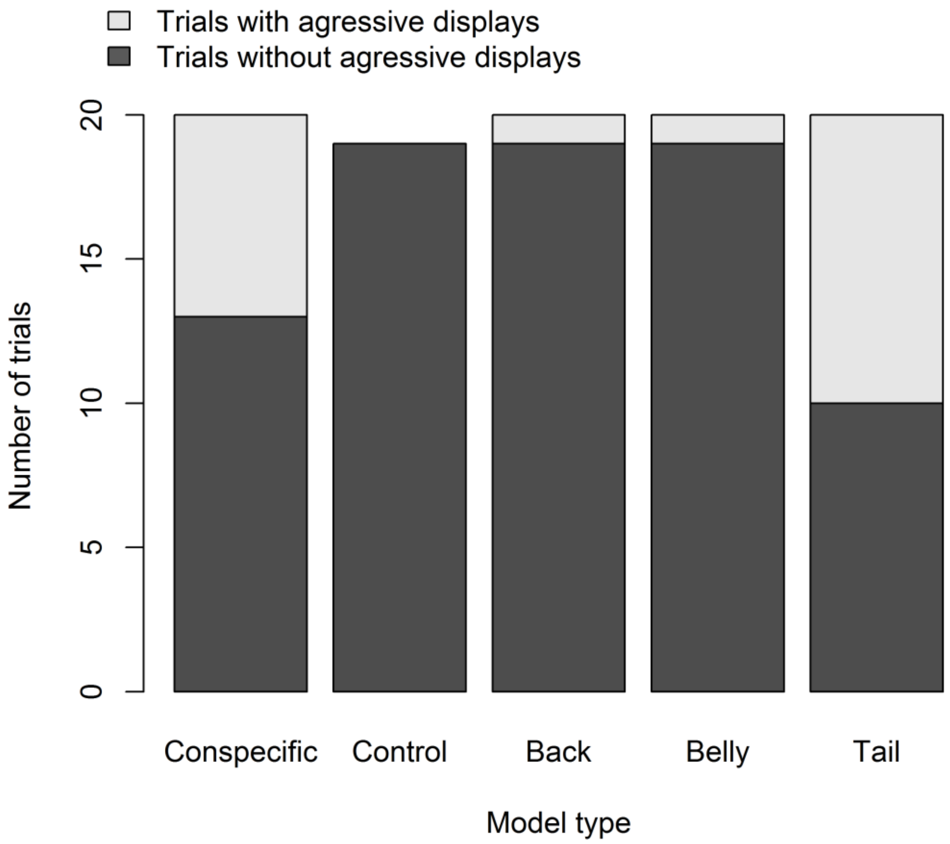

Figure 3. 4 Elegant trogons performed more tail raises when presented with models resembling conspecifics and models for which only the tail was modified, than when presented with other model types.

Chapter 4

Increased plumage divergence with sympatry in a rapid and recent diversification of the avian genus *Trogon*

Summary

The concept of character displacement can explain the diversification of phenotypes in closely related species. Applied to polymorphic species, this hypothesis has offered a framework to study reinforcement and speciation. The formation of the Panamanian land bridge between North and South America, followed by the Great American Interchange of biota, led to adaptive radiations in a number of avian taxa (e.g, oscines). This natural experiment has been instrumental in understanding patterns of biodiversity in the Western hemisphere, but the impact of the Great American Interchange on the diversification of sexually selected traits remains poorly explored. Using a combination of comparative methods, visual modelling of plumage coloration, and functional diversity measures, we show that taxa in the genus *Trogon*, which originated in Central America, diversified more recently and more rapidly in South America following the Great American Interchange. Concordantly, we show that sympatric extant taxa diverged more in plumage traits in South America than in Central America. Together, our results suggest that character displacement or linage sorting in an area of high diversification has shaped plumage patterns at the subspecies level across an entire continent. Our study is unique in demonstrating the impact of the Great American Interchange on the evolution of phenotypic characteristics in a widespread group of birds.

Introduction

Character displacement has been a powerful hypothesis to explain the divergence of morphological traits (ecological character displacement) and sexually selected traits (reproductive character displacement) between closely related species (Darwin 1859, Brown and Wilson 1956, Pfennig and Pfennig 2010, Stuart and Losos 2013). Invoked in classic models of speciation (Mayr 1963, Coyne and Orr 2004, Price 2008), character displacement is based on the premise that competitive interactions between incipient species that diverged in allopatry promote an increase in trait differences in the event of secondary contact. Competition for limited resources has been demonstrated to be a key mechanism in the rapid speciation of adaptive radiations (reviewed in Schluter 2000, Dayan and Simberloff 2005, and Stuart and Losos 2013), and the cost of inbreeding and production of low-fitness hybrids may have played an important role in promoting the evolution of reproductively isolated species (Serviendo and Noor 2003, Coyne and Orr 2004). In the initial postulation of character displacement, Darwin (1859) suggested that the most closely related forms should demonstrate the largest amount of competition, and thus character divergence would occur in the descendants of a single species. Indeed, ecological character displacement has been best demonstrated in recent adaptive radiations and species complexes (*Anolis* lizards: Losos et al. 1994, Losos et al. 1993; three-spine sticklebacks *Gasterosteus aculeatus*: Schluter and McPhail 1992; spadefoot toads of the genus *Spea*: Pfennig and Murphy 2000, Pfennig and Murphy 2002, Pfennig and Murphy 2003; Darwin's finches: Grant and Grant 2006). In contrast, evidence for character displacement of secondary sexual traits has been more commonly tested by comparing pairs or groups of related species (Brown and Wilson 1956, Sætre et al. 1997, Marshall and Cooley 2000, McNaught and Owen 2002, Martin et al. 2010, Anderson and Grether 2010). These studies, which test for greater phenotypic differences between species in sympatry than in allopatry, have demonstrated the importance of past sexual selection on diverging characters and reproductive isolation. Targeting incipient species, further studies of character divergence have investigated the source of intraspecific polymorphism (i.e. subspecies or race level differences) and have provided an understanding of the early stages of speciation (Goldberg and Lande 2006, Richards-Zawacki and Cummings 2010). Similarly, the evaluation of reproductive character displacement of a complete genus at the subspecies level could prove particularly informative for understanding the evolution of secondary sexual ornaments in closely related species, but few studies have taken this approach.

The rise of the Isthmus of Panama linking the North and South American continents around 3-3.5 million years ago (Mya) allowed the Great American Interchange of previously isolated biota (Stehli and Webb 1985). The mixing of these flora and fauna affected biotic assemblages, competitive interactions, and rates of extinction and speciation on both continents, and is thus an important contributor to the wealth of extant biodiversity in the Neotropics (e.g. Marshall 1988, Burns and Racicot 2009, Weir et al. 2009, Smith and Klicka 2010, Pinto-Sánchez et al. 2012, Leite et al. 2014). The range expansion of species to previously inaccessible areas and the associated exposure to novel habitat and resources likely allowed for the evolution of novel traits and ecotypes, further promoting diversification and potential speciation (Blackburn et al. 2013, Coyne and Orr 2004, Hollingsworth et al. 2013). While our understanding of the Great American Interchange impact on lineage diversification has greatly improved in recent years due to phylogenetic studies (e.g. Reaves and Bermingham 2006, Weir et al. 2009, Smith and Klicka 2010, Pinto-Sánchez et al. 2012), the ensuing consequences on trait evolution has rarely been investigated.

Trogons of the Neotropical genus *Trogon* comprise a group of 16 species for which 55 subspecies, including one to eight subspecies per species, which have been described using traditional taxonomic methods and confirmed using mitochondrial sequences (DaCosta and Klicka 2008, Forshaw 2009, Remsen et al. 2014). All species have a highly conserved body plan and similar plumage patterns that diverge in coloration. Males bear bright iridescent feathers on their upperparts (ranging from deep purple to copper) and carotenoid-based colors on their underparts (red, orange, or yellow). All species possess a relatively long tail of which the under part can be all white or black, or with conspicuous barring patterns. Many have a white band separating the upper breast from the belly. Among subspecies of the same species, the plumage color of specific patches can vary greatly. For example, the rump patch of *T. rufus* varies from copper-green in the *sulphurous* subspecies to a purple-blue in the nominate subspecies. In fact, almost all subspecies described are based on variation in the plumage of males (Forshaw 2009). Members of the genus *Trogon* range from southern Arizona to southern Brazil. Ancestral state reconstruction suggests that the genus originated in Central America, colonized South America through multiple migration events during and after the completion of the Isthmus of Panama, and subsequently diversified within South America (DaCosta and Klicka 2008). Currently, some areas harbour many sympatric trogon species and/or subspecies (e.g., five species in lowlands of Panama, up to six species in Amazonian forests), suggesting secondary contact among forms that diversified following the Great American Interchange. With its continuous distribution across the Neotropics, evolutionary history shaped by the Great American Interchange, and extant sympatry of recently evolved lineages, the genus *Trogon* provides an ideal system for understanding the evolution of plumage coloration at the subspecies level.

The first objective of this study was to compare diversification rates in Central and South American taxa of the genus *Trogon* by modeling continent-specific speciation and extinction rates in a phylogeographic context. Our second objective was to test whether character displacement is a possible mechanism of plumage evolution on each continent. To achieve this we tested whether the proportion of sympatric overlap explains measures of plumage disparity among subspecies. Our third objective was to determine whether the presence in sympatry of several *Trogon* taxa influenced the range of plumage color values. Indeed, the divergence in characteristics functionally adapted to the exploitation of limited resources is expected to lead to a greater range, and a reduction in overlap, of trait values (MacArthur and Levins 1967, Bulmer 1974), and the costs of hybridization between incipient species can be expected to promote the divergence of sexually selected ornaments. Because multiple traits or several morphological aspects of the same trait (e.g. width and depth of beaks) can concurrently change, measures of disparity in multidimensional morphospace are more informative than the individual characterization of traits (Gotelli and Graves 1996, Stubbs and Wilson 2004, Schamp et al. 2008). Similarly, the divergence in plumage color trait values of multiple sexually selected characteristics can be assessed by comparing their distribution in colorspace, a conceptual multidimensional space that encompasses all the colors that can be perceived by an animal considering its species-specific visual system (Endler and Mileke 2005). This analytical tool has been very useful for studying the evolution of plumage coloration in large groups of species (e.g. Stoddard and Prum 2008), but has yet to be used to evaluate color pattern differences in sympatric species.

Methods

We determined diversification rates of Central American and South American subspecies of the genus *Trogon* for which gene sequences were available on Genbank using binary state speciation and extinction models, and calculated time since speciation at each node from ancestral state reconstructions. To evaluate the influence of sympatry on plumage divergence, we compared plumage characteristics using a bird specific visual model, calculated the genetic distance, and quantified the proportion of geographic overlap between all pairwise trogon subspecies. To investigate the use of colorspace by geographically overlapping species, we collected plumage color data on all subspecies of the genus *Trogon* for which we could gain access to museum specimens and performed a series of randomization tests.

Phylogenetic analyses

We estimated the phylogenetic relationships among 41 *Trogon* taxa using DNA sequence data from the mitochondrial gene NADH dehydrogenase subunit 2 (ND2). A representative sequence for each taxon was retrieved from GenBank (Table S4.1), and a time-calibrated ultrametric phylogeny was estimated using BEAST v1.8 (Drummond et al. 2012). Two runs were completed with the GRT+I+Γ model of sequence evolution, a lognormal relaxed clock, a calibration rate of 3.41% divergence per million years (DaCosta and Klicka 2008), the birth-death with incomplete sampling tree model, 50 million generations, and sampling every 50,000 generations. Convergence between runs was evaluated using Tracer v1.5 (Rambaut and Drummond 2009). We conservatively removed the first 500 trees from each run as burn-in, and combined the remaining samples from each run to form a posterior distribution of 1000 trees. The maximum clade credibility tree from this posterior was used to evaluate the geography of ancestral nodes and compare speciation times in Central and South America. Following DaCosta and Klicka (2008) for repeatability, we traced the geographic history in Mesquite v2.75 (Maddison and Maddison 2005) using a parsimony model and four character states (Central America, Chocó, Andes, and *cis*-Andes). Character states for ambiguous nodes under a parsimony model were resolved using the most likely state under a maximum likelihood model, and the average age for

Central America and South America (Chocó+Andes+*cis*-Andes) nodes was compared using a *t*-test in R (R Core Team 2014).

Comparative analyses

We assessed the influence of the Great American Interchange on diversification patterns in *Trogon* using the binary state speciation and extinction (BiSSE) model (Maddison et al. 2007). On each of the 1000 trees in the posterior distribution derived from the BEAST analysis, we ran the model in R using the diversitree package (FitzJohn 2012). Extant taxa were coded as either Central America (CA: state 0) or South America (SA: state 1), and the sampling.f option was used to account for incomplete sampling (only 80% of all Central America and 71.4% of South American taxa were sampled, using taxonomy in Collar 2001). Since ancestral state reconstructions find that CA is the most parsimonious state of the root node (see Results; DaCosta and Klicka 2008), we also used the root.p option to constrain this node to a CA character state. Maximum likelihood (find.mle function) was used to estimate six parameters in the full BiSSE model: speciation in CA (lambda0) and SA (lambda1), extinction in CA (mu0) and SA (mu1), and state transitions (q01: CA to SA; q10: SA to CA). Speciation and extinction parameters were used to calculate net diversification (r) in each region (e.g., r0 = lambda0 - mu0). We also used the Akaike information criterion (AIC) to compare results from the full model to four constrained models: equal speciation (lambda0=lambda1), equal extinction (mu0=mu1), equal state transitions (q01=q10), and full constraint (lambda0=lambda1, mu0=mu1, and q01=q10).

Plumage characteristics and visual model

Members of the genus *Trogon* generally differ in seven plumage areas. The head, mantle, rump and dorsal part of the tail range in color from non-iridescent black to iridescent hues that vary from violet to copper. The belly is either red or yellow, except in the case of one subspecies (*T. surrucura aurantius*) and one race (*T. collaris puella aurantiiventris*), which display an intermediate orange. Some species display a clearly defined white breast band while others do not, and banding patterns on the ventral part of the tail varies greatly; some species bear completely white or black tails, most present alternating black and white bands of varying thickness.

We used spectrophotometry to objectively assess the colors displayed on the head, mantle, rump, dorsal part of the tail, and the belly of three different males per subspecies (accession numbers in Table S4.2; spectral data available in digital repository Dryad - http://datadryad.org/). We selected individuals from thoughout the subspecies range to best represent the within-subspecies variation even if among subspecies differences in plumage charateristics are much greater than within-subspecies differences (Forshaw 2009). Our apparatus consisted of a USB 4000 spectrophotometer (Ocean Optics, Dunedin, Florida) combined with a PS-2 Xenon pulsed light source, and connected to a bifurcated probe with a rubber stopper that maintained the light source 3mm above the feather surface and blocked external light (Andersson and Prager 2006). Therefore, all measurements were taken with the angle of reflectance at normal incidence (0°). We obtained five measurements from each plumage patch, changing the location of the measurement each time. We calculated spectral reflectance values in the visual range of birds (300nm to 700nm) relative to a pure white standard (Spectralon, Ocean Optics). We binned these values in 1nm wavelength intervals, and we aggregated the five repeated measurements by taking the mean at each wavelength.

Since birds possess four photoreceptors, the colors they perceive can be represented in a three-dimensional tetrahedron with the four cones at the apices (Goldsmith 1990, Endler and Mielke 2005, Stoddard and Prum 2008). For each individual plumage patch, we calculated the differences in color characteristics between all pairwise subspecies as the Euclidean distance in tetrahedral colorspace (Endler and Mielke 2005, Stoddard and Prum 2008). Even though Euclidean distances cannot be directly used to assess how differently two colors are perceived, they are highly correlated with perceptual distances (Pike 2012). In the tetrahedral colorspace model we assumed 1) general photoreceptor sensitivity values for species that possess an ultraviolet photoreceptor (based on *Trogon curucui*; Ödeen and Håstad 2013), and an ideal (wavelength independent) illuminant. Trogons are found in a variety of light environments, and using ideal illuminant values allows all colors to be compared objectively. We calculated the visual model values in R (R Core Team 2014) using the `pavo` package (Maia et al. 2013).

In addition to plumage color, we scored two prominent plumage patterns to further assess trait disparity among species. We qualified the breast band as either present (score of 1) or absent (score of 0), and the divergence score was calculated as the absolute difference between the two subspecies (i.e. only 0 and 1 possible). We also visually quantified the proportion of the tail covered by white with values ranging from 0% (black tail) to 100% (white tail), and the divergence score was calculated as the absolute difference between the two subspecies. To avoid giving specific plumage patches more weight in the overall distance score, we normalized the color Euclidean distances so that the maximum value for a specific plumage patch between two taxa was 1. The overall distance score was the sum of all seven plumage difference values (head, mantle, rump, dorsal tail, and belly color, plus chest band and ventral tail patterns) with a theoretical minimum of zero and maximum of seven.

Measurement of genetic distances and sympatry among subspecies

Because subspecies rarely overlap in geographic range, and because phenotypic similarity is often highly correlated with phylogeny (Webb et al. 2002, Losos 2008), we calculated uncorrected *p*-distances as a measure of genetic relatedness among taxa (Takahashi and Nei 2000, Nei and Kumar 2003) from all published ND2 sequences from GenBank (accessed Dec 2011). In total we obtained 145 sequences representing 43 out of 55 accepted subspecies (Forshaw 2009); all of the subspecies missing were from range-restricted taxa. We aligned sequences with ClustalW (Thompson et al. 1994) and we calculated distances between all pairwise subspecies using MEGA 5 (Tamura et al. 2011). We obtained range maps for all species from NatureServe's InfoNatura repository (http://www.natureserve.org/infonatura/), and subsequently partitioned them into subspecies-level range maps based on geographic range descriptions included in Johnsgard (2000), Collar (2001), and Forshaw (2009). The proportion of overlap between subspecies was calculated using Quantum GIS (Quantum GIS Development Team 2014) as a percentage of the smallest distribution (Barraclough and Volger 2000, Martin et al. 2010), such that a distribution completely covered by that of another species would yield a score of 1 (i.e. 100%). We also used QGIS to determine the latitude and longitude of the subspecies polygon centroid, which we used to classify subspecies as being located mostly in Central America or South America.

Statistical analyses

To test the hypothesis that geographic sympatry influences plumage dissimilarity between Trogon subspecies (i.e. character displacement), we compared generalized linear mixed models (GLMM) fit by restricted maximum likelihood. GLMMs were conducted in SPSS (IBM Corp 2013) including only pairwise comparisons of subspecies with some degree of sympatry (sympatry > 0), and included subspecies identity as the within-subject random factor. We compared a group of *a priori* candidate models with plumage dissimilarity as the dependent variable and, in various ecologically relevant combinations, sympatry, genetic distance, clade (categorical: brown-back/grey-backed, see DaCosta and Klicka 2008), location (categorical: Central America/South America), and latitude and longitude as independent factors (see Table S4.3 for full set of candidate models). In some models, we included the first-level interaction between clade and sympatry and/or between location and sympatry. The independent factors ‘sympatry’ and ‘genetic distance’ were kept in all models except for the intercept-only model. A global model included all the independent factors and the two first-level interactions. The models that best fit the data were selected using Akaike’s information criterion corrected for sample size (AICc; Akaike 1973, Hurvich and Tsai 1989, Burnham and Anderson 2002). We used the sample size corrected criterion because the ratio between sample size and number of parameters was smaller than 40 in a few models. The best fitting models where considered equally plausible when the AICc value differed by no more than 2.00 (ΔAICc < 2.00) compared with the model with the lowest value.

To understand which plumage characteristics contributed the most to the best fitting model, we performed *post-hoc* GLMMs using each of the seven plumage characteristics as the dependent variable. We kept the same independent factors as in the best-fit model. For crown color, mantle color, rump color, tail color, belly color, and proportion of white in the tail we used linear regression mixed models with a normal distribution and an identity link for the dependent variable; for the presence or absence of the white breast band we used a binary logistic regression model with a binary distribution and a logit link.

To further investigate the potential for character displacement in Trogon evolution, we identified two areas, one in Central America where five species overlap, and one in South America where six species overlap (see Figure 4.1 for provenance of museum specimens measured and subspecies assemblages). We evaluated the use of tetrahedral colorspace using two functional diversity measures (Mouchet et al. 2010). The first, functional attribute diversity (Walker et al. 1999), measures the sum of pairwise distances of all plumage patches between species found in a community. For colors, this represents the overall dissimilarity between species at the plumage-patch level as measured by the Euclidean distance between the points in tetrahedral colorspace. The second measure, sometimes known as functional richness (Cornwell et al. 2006), evaluates the overall volume used by the community of species as the smallest possible convex hull volume that includes all points in multidimensional morphospace. If competition occurs in colorspace, divergence in traits would be expected to lead to greater volume use. To determine whether the plumage characteristics of species found in large assemblages maximized pairwise distances within patch colors and/or used a larger than expected colorspace volume, we calculated the functional diversity measure values of the actual assemblages, and compared them to null distributions generated by calculating the diversity measure values for all possible assemblages of subspecies, including only species found in the specific areas. For example, the functional diversity attribute null distribution for the Panamanian lowland test included the 320 unique values generated by calculating the sum of pairwise distances of all plumage patches for each possible combination of subspecies of the five species that co-occur, without resampling at the species level (i.e. five species with 2, 2, 4, 4, and 5 subspecies respectively). We calculated the Euclidean distances and the convex hull volumes using the R package `pavo` (Maia et al. 2013). The values of the diversity measures from the actual assemblages were considered statistically different than expected by chance if they were greater or smaller than 97.5% of the null distribution values (two-tailed test with 0.05 significance level thresholds).

Results

The diversification of *Trogon* taxa has occurred much more recently in South America than in Central America. This was supported by our ancestral state reconstruction on the maximum clade credibility tree which revealed that the average node depth of Central American taxa (4.08 ± 0.77SE Mya) was statistically greater than the South American taxa (1.51 ± 0.23SE Mya; independent t-test: t = 2.79, df = 38, P = 0.008; Figure S4.1), indicating that South American *Trogon* species diversified more recently. Furthermore, the BiSSE analysis suggested that South American *Trogon* taxa diversified at faster rate than those of Central America. Although the fully constrained BiSSE model was the most likely model in most iterations (Table 4.1), the average ΔAIC of the equal speciation rate model was below 2.0 in more than half of the trees, and therefore equally plausible. In this model, South American taxa had lower distributions of extinction rates (95% value interval: Central America mu0 = 0.320 – 1.499, South America mu1 = 9.462E-8 – 0.578; Figure 4.2) which led to overall greater diversification rates in South American taxa (r1 = 0.583 – 1.58) compared to Central American taxa (r0 = -0.756 – 0.144; Figure 4.2). In this model, transitions of character states from Central America to South America (: q01 = 0.002 – 0.369) were similar to the opposite transition (q10 = 0.159 – 0.461; Figure 4.2).

When testing the influence of sympatry, genetic distance, clade, geographic location, and latitude/longitude on plumage dissimilarity, three of the candidate generalized linear mixed models were considered as equally plausible (ΔAICc ≤ 2.00, Table 4.2). The most parsimonious model included sympatry (GLMM, t = 2.02, df = 285.57, P = 0.45) and genetic distance (GLMM, t =8.00, df = 274.36, P < 0.001). The second most parsimonious model included sympatry (GLMM, *t* = 1.90, df = 284.02, *P* = 0.06), genetic distance (GLMM, *t* = 6.21, df = 270.05, *P* < 0.001), clade (GLMM, *t* = 2.16, df = 41.57, *P* = 0.04), and location (GLMM, *t* = 0.75, df = 39.65, *P* = 0.57). The more complex model included sympatry (GLMM, *t* = -1.12, df = 280.90, *P* = 0.26), genetic distance (GLMM, *t* = 6.37, df = 267.38, *P* < 0.001), clade (GLMM, *t* = -2.035, df = 40.14, *P* = 0.049; grey-backs plumage differences: 3.05 ± 0.15 out of a possible 7.00; brown-backs: 2.64 ± 0.14), location (GLMM, *t* = 1.96, df = 83.11, *P* = 0.05; Central America), and the interaction between location and sympatry (GLMM, *t* = -2.49, df = 281.65, *P* = 0.013; Central America). To investigate the nature of the location by sympatry interaction in this model, we separated the data based on whether the subspecies were located in Central America or South America and analysed the influence of sympatry, genetic distance, and clade on plumage differences (GLMM with subspecies as within species random factor). There was a strong positive relationship between sympatry and plumage differences in South American subspecies (GLMM, *t* = 2.98, df = 176.05, *P* = 0.003; after controlling for genetic distance, GLMM, *t* = 4.18, df = 174.29, *P* < 0.001; and clade, GLMM, *t* = -0.63, df = 29.31, *P* = 0.53; brown clade; Figure 4.3), but no effect of sympatry on plumage differences in Central American species (GLMM, *t* = -0.99, df = 101.03, *P* = 0.323; after controlling for genetic distance, GLMM, *t* = 4.83, df = 97.73, *P* < 0.001, and clade, GLMM, *t* = -2.41, df = 15.54, *P* = 0.03; brown clade; Figure 4.3). The *post-hoc* analyses of the effect of sympatry on differences in the seven plumage characteristics (dependent variables), including only South American subspecies, suggested that crown color (GLMM, *t* = 2.34, df = 177.71, *P* = 0.02), tail banding pattern (GLMM, *t* =2.28, df = 175.52, *P* = 0.02), and the presence or absence of the white chest band (logistic regression GLMM, *t* = 2.07, df = 144, *P* = 0.04) contributed the most to the observed pattern.

When investigating the use of colorspace in high diversity assemblages of *Trogons,* the permutation tests suggested that pairwise differences in plumage patch color were not greater than expected by chance in the Central American group (sum of pairwise distances of subspecies present in area of overlap: 7.08, possible permutations = 320, p = 0.55; Figure 4.4) or in the South American group (sum of pairwise distances of subspecies present in area of overlap: 11.39, possible permutation = 1920, p = 0.22; Figure 4.4). Furthermore, we found that colorspace volume was not greater than expected by chance in neither the Lowlands of Panama where five species coexist (actual volume = 0.0133, p = 0.69; Figure 4.5) nor in the Amazonian basin of South America where six species coexist (actual volume = 0.0089, p = 0.41; Figure 4.5).

Discussion

Within-species diversification of sexually selected phenotypic traits among allopatric populations, through selection or drift, is considered one of the first steps in the process of speciation (Coyne and Orr 2004). In the event of secondary contact, incipient species and differences in characters can collapse though gene flow (Behm et al. 2010), or further diverge through reinforcement and form distinct non-interbreeding species (e.g. Vallin et al. 2012). Our findings revealed that South American *Trogon* taxa diversified more recently and more rapidly than Central American taxa and that plumage divergence increased with the degree of sympatry in South American taxa, but not Central America taxa. These patterns provide evidence for greater and more rapid diversification rate of a clade of birds following the Great American Interchange, and further supports the influence of distribution range overlap on trait divergence and its potential role in rapid speciation.

The genus *Trogon* originated in Central America and colonized South America through multiple range expansion events (DaCosta and Klicka 2008). Ancestral area reconstruction previously presented (DaCosta and Klicka 2008) and our BiSSE models (Figure 4.2) confirm that *Trogon* colonization events from South America to Central America following the Great

American Interchange were not very common. Our analysis of ancestral area estimation also showed that Central American trogons diversified mainly before the Great American Interchange while the South American species diversified significantly more recently (average node age: 4.1 and 1.5 Mya, respectively; Figure S4.1 inset). Furthermore, the BiSSE results suggest much greater diversification rates in South American taxa; since the speciation rate was held equal in our models, this suggests that the greater net diversification rate in South America was driven by greater rates of extinction or fusion of lineages in Central American species. This could have occurred if the Central American habitat approached ecological niche saturation before the Great American Interchange, which would have limited the opportunity for allopatric diversification, thus limiting the opportunity for species accumulation (Price et al. 2014). In contrast, the novel habitat encountered on the new continent, as well as the rapid colonization of the relatively much larger landmass of South America would have allowed for greater opportunity for increased trait variability (Meyers and Bull 2002, Milá et al. 2007), either through drift or selection, and perhaps relatively longer periods of taxa isolation between secondary contacts. Greater phenotypic differences among incipient lineages would then have allowed for increased reproductive isolation through reinforcement rather than the fusion of undifferentiated lineages.

Our results suggest that the recent and rapid diversification of *Trogon* in South America was possible though the divergence of secondary sexual characteristics by means of character displacement or fusion of lineages. Plumage dissimilarity among subspecies was positively and significantly correlated with levels of sympatry across South America, evidence for reinforcement following secondary contact of partially differentiated lineages (Pfennig and Pfennig 2010, Martin et al. 2010). In contrast, we did not find any relationship between sympatry and color divergence in Central American species. In a study of several clades of birds, Martin et al. (2010) showed that rapid sympatry in high latitude birds, but not in the tropics, had led to greater color divergence. They argued that the that rapid and frequent secondary contacts would have been driven by frequent range changes due to variation in environmental conditions driven by the Milankovitch Oscillations, which have greater impact on the variability of the climate at higher latitudes (Jansson and Dynesius 2002). Our results suggest a similar mechanism (i.e. rapid and frequent secondary contacts), but implicate the Great American Interchange as the cause of recent and rapid diversification and resulting divergence in plumage characteristics in sympatry trogon taxa.

Traits that diverged under character displacement would be expected to have greater among-species variation than traits that were not under the same evolutionary pressure (Marchinko et al. 2004, Kirschel et al. 2009). In contrast, traits with discrete absence/presence character states would be expected to contribute relatively little to divergence in overall patterns. In South American trogons, differences in head color (continuous), tail banding pattern (continuous), and the presence or absence of a white breast band (discrete) exerted the most influence on overall plumage divergence of sympatric species. Among the five plumage patches that we quantitatively characterized using spectrophotometry, head color varied most (unpublished results), as would be predicted. However, the presence or absence of a breast band contributed to the overall plumage divergence. These results indicate that greater geographic overlap increases the probability that two species display opposite character states for this plumage patch; species with a white chest band are more often found with species without the white band. This situation is unlikely to result from *in situ* evolution of a novel phenotypic trait in areas of sympatry. Rather, it is more likely to occur through sorting of species with pre-existing variation acquired in allopatry, prior to secondary contact (Rice and Pfennig 2007). One implication of these findings is that a trait does not need to be highly variable to promote rapid diversification as long as it can contribute to reproductive isolation. Traits with such low variation may promote speciation in the early phases of reinforcement, but would potentially have much less influence on species recognition in areas of high congeneric diversity, because more than one species would display the trait.

While we found evidence for divergence of plumage characteristics across species of trogons in South America, we did not find any evidence for an increase in functional attribute diversity (sum of pair-wise plumage patch Euclidean distance) or any evidence for an increase in the use of colorspace volume in large assemblages of trogons. These findings suggest that trait divergence following secondary contact occurred within the existing colorspace occupied by trogons. Morphological and physiological constraints in feather color production may offer a possible explanation for the lack divergence in colorspace in areas of high trogon diversity. Natural and sexual selection can only act on available phenotypic variation (Darwin 1859), which may be proximately constrained by the form of the feature under selection (Wainwright 1988). The colors of these trogons are possibly under such constraint. In males, the upperparts range in color from copper-green to violet (Forshaw 2009), and are produced exclusively by hexagonally-packed hollow melanosomes found in the barbules of feathers (Durrer and Villiger 1966, Quitero and Espinosa de los Monteros 2011). While the theoretical range of colors that can be produced by these structures is relatively broad (Eliason et al. 2013), a large range of melanosome size is needed to produce a large range of colors. However, the range of melanosome size in trogons is quite limited (Quitero and Espinosa de los Monteros 2011) compared to the range of sizes found among other species (Eliason et al. 2013), suggesting a limit on the range of iridescent colors that can be produced in this group. Similarly, the breast/belly colors are limited to reds or yellows with little variation (Forshaw 2009). This is similar to the caciques (genera *Cacicus*, *Clypicterus* and *Ocyalus*; family Icteridae) where the rumps are exclusively colored red or yellow

(Kiere et al. 2009). Discrete color changes such as those observed in trogons and caciques are possible when one or very few pigment types are responsible for the feather colors, and can change from one state to the other with the modification of a single step in the metabolism of diet-derived carotenoids (Brush 1990; McGraw 2006). This mechanism of color production almost precludes the production of other colors since multiple pigments are needed to produce intermediate colors (McGraw 2006; Friedman et al. 2014). Therefore, the color of trogon breasts and bellies seem mainly limited to specific discrete character states. Furthermore, unlike many taxa in birds, trogons do not display any colors that are produced by combinations of mechanisms. Indeed, the gamut of colors possible in birds is greatly increased when carotenoids, melanins, and/or structural colors are combined (Stoddard and Prum 2011). Even though our results suggest that colorspace in *Trogon* may be constrained, differences between sympatric species found in large assemblages do not need to be maximized as long as species recognition is possible.

In this study, we found support for the role of plumage trait divergence in taxa diversification in a large group of closely-related Neotropical species using subspecies-level variation. Importantly, increased divergence in secondary sexual ornaments was associated with increased sympatry in South American but not Central American trogons. Our results suggested that this pattern was driven by faster diversification rates in South America following multiple colonisations by Central American taxa. The divergence in plumage traits between sympatric species likely occurred through character displacement in areas of secondary contact, and through the sorting of pre-existing discrete traits. These findings add support to the role of sexual selection in promoting species recognition through trait diversification, and are unique in demonstrating the impact of the Great American Interchange on the evolution of plumage characteristics in a broadly distributed group of birds.

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Table 4. 1 Summary statistics of 1000 binary state speciation and extinction (BiSSE) analyses comparing speciation, extinction, diversification, and state transition rates in South and Central American trogon subspecies. Results are for the 1000 posterior distribution trees obtained from a BEAST analysis. The 'Full' model allows for different rates in all parameters, the 'Constrained' model has equal rates in all three parameters.

Model	**Best (out of 1000)**	**Worst (out of 1000)**	**Average ΔAIC**	**≤ 2 ΔAIC (out of 1000)**
Full	0	887	3.46	94
Equal speciation rate	38	1	1.75	541
Equal mutation rate	2	99	2.34	102
Equal transition rate	6	12	2.09	348
Constrained	954	1	0.023	999

$\Delta AICc = AIC_i - AIC_{min}$

Table 4. 2 Summary of the top three best fitting generalized linear mixed models investigating the predictors of plumage color divergence among subspecies of the genus *Trogon*. All other candidate models were considered unlikely to be the best fitting (ΔAICc > 2.00). Models are presented in order of increasing ΔAICc.

Model	**AICc**	**ΔAICc**	**Evidence ratio**
Sympatry Genetic distance Location Clade	872.261	min	1.00
Sympatry Genetic distance	872.667	0.406	1.22
Sympatry Genetic distance Clade Location Location*Sympatry	873.552	1.291	1.91

ΔAICc = AICc_i - AICc_{min}

Evidence ratio = $\exp(1/2(\Delta_i))$

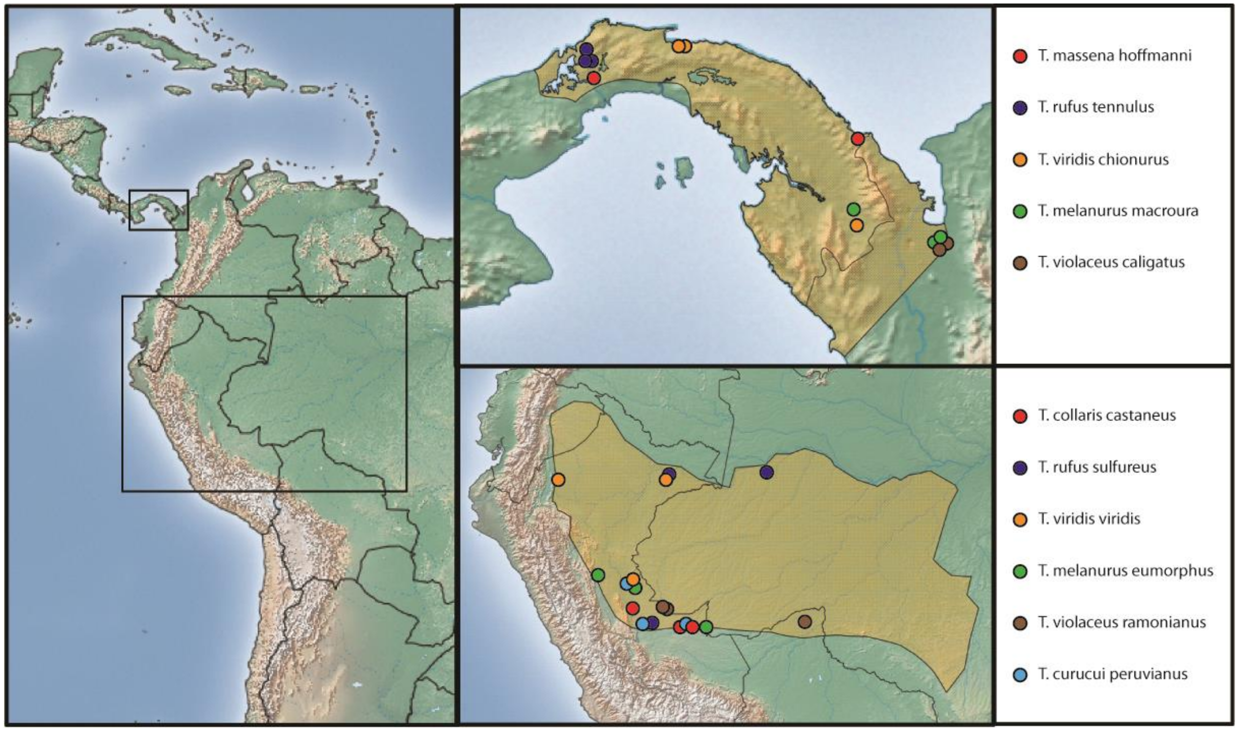

Figure 4. 1 Areas of high trogon diversity in Central America where five species coexist, and in South America where six species coexist (shaded in tan color). Colored circles indicate the approximate locations where the museum skins used for this study were collected, based on locality indicated on the specimen collection tag.

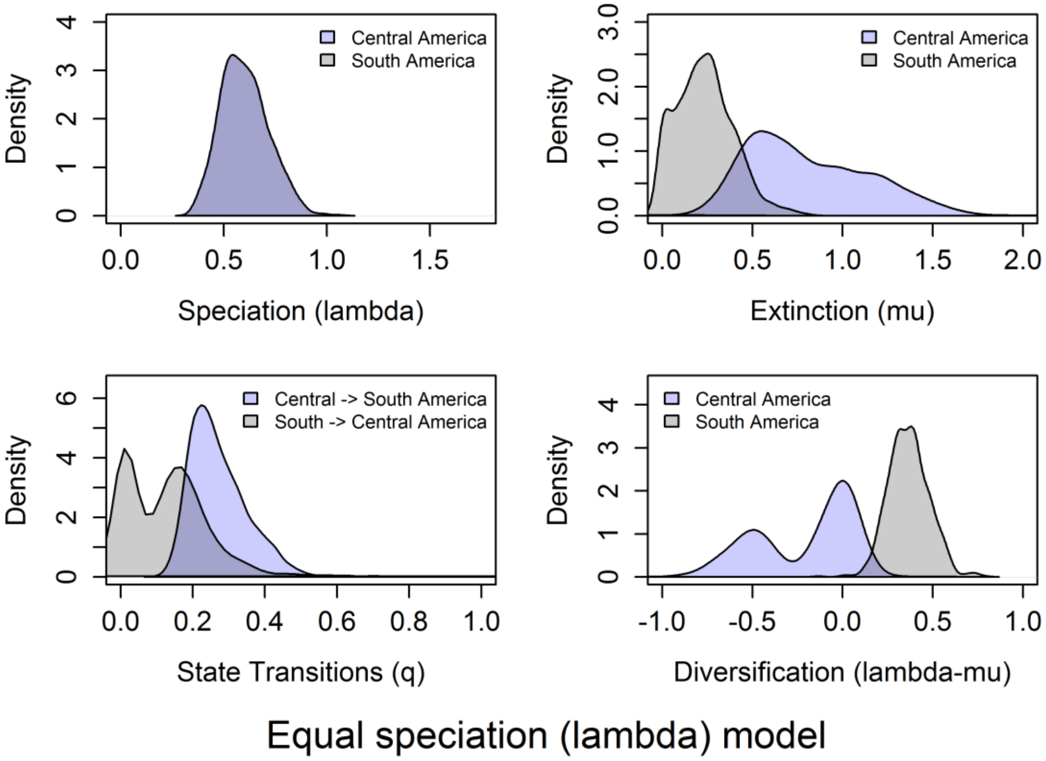

Figure 4. 2 Posterior probability density distributions of speciation (lambda), extinction (mu), transition (q) and diversification (r) rates of South (SA) and Central American (CA) trogon subspecies using a binary state speciation and extinction (BiSSE) model with constrained speciation rates. Results are from independent BiSSE runs on each of the 1000 posterior distribution trees obtained from a Bayesian phylogenetic analysis.

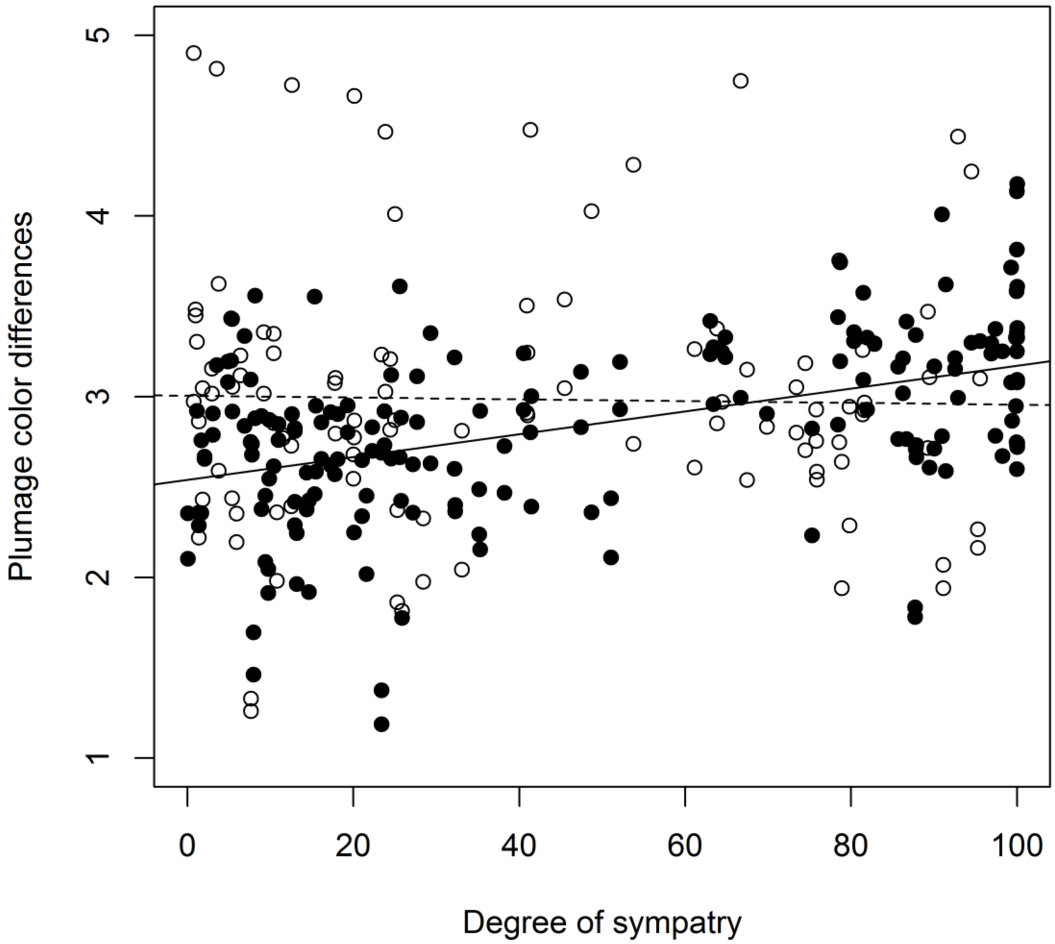

Figure 4. 3 Plumage characteristic differences among subspecies of *Trogon* are related to the degree of sympatry in South American (solid symbols, solid line) but not in Central America (hollow symbols, dashed line). Plumage difference scores (unitless) are predicted values from a generalized linear mixed model including uncorrected p-distances as a measure of genetic relatedness and phylogenetic clade (categorical: Brown-backed and Grey-backed) as fixed factors, and subspecies identity as random within-subject factor. Regression lines generated using least square regressions on the plumage difference values predicted from the generalized linear mixed model.

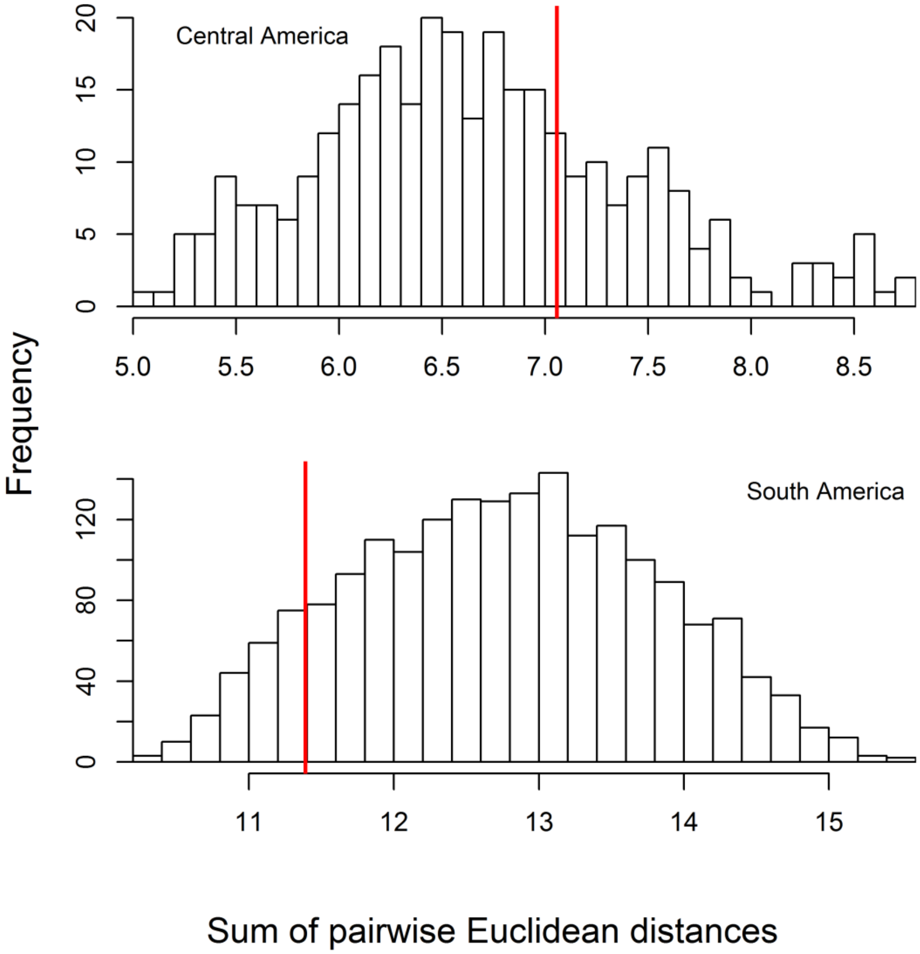

Figure 4. 4 The functional attribute diversity of colors in *Trogon*-rich areas (measured as the sum of pairwise color distances of all plumage patches between species found in a community) is not greater than expected by chance in Central America or South America. Red line highlights actual value from the observed subspecies and null distributions were generated using permutations (see methods for details).

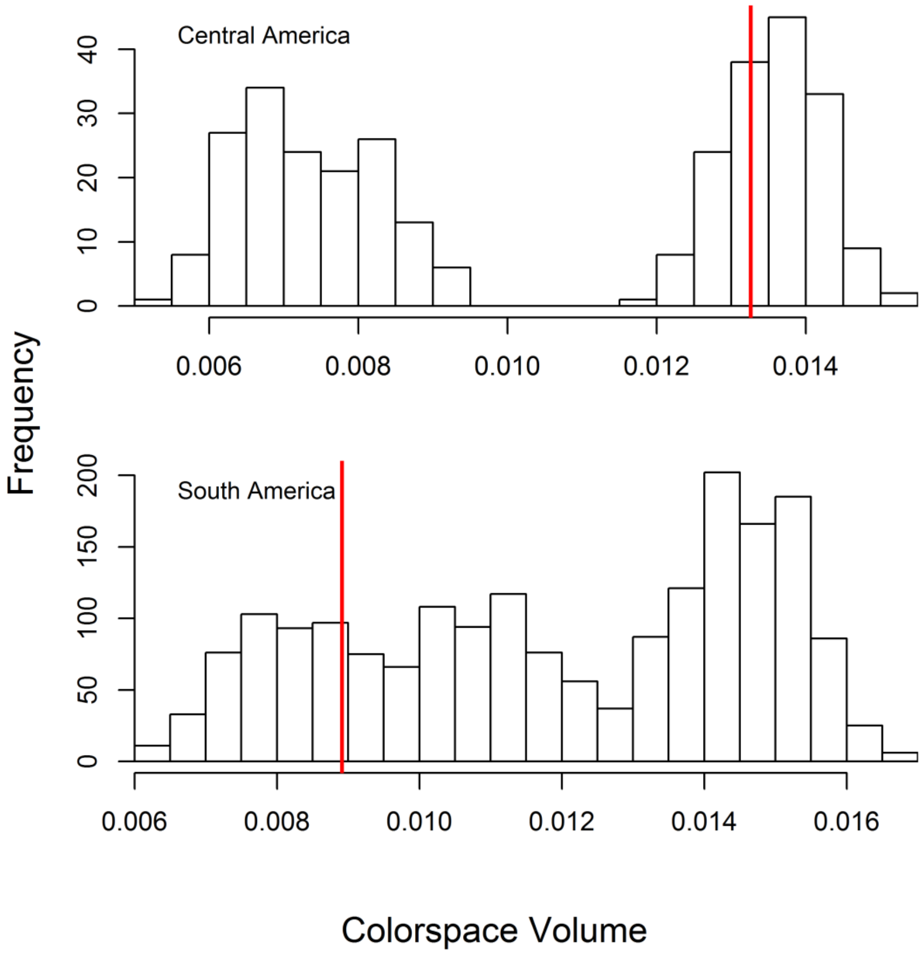

Figure 4. 5 The functional richness of colors in *Trogon*-rich areas (the smallest possible convex hull volume in colorspace used by the community) is not greater than expected by chance in Central America or South America. Red line highlights actual value from the observed subspecies and null distributions were generated using permutations (see methods for details).

Chapter 5

The importance of proper parameterization in tetrachromatic visual models when assessing sexual dichromatism

Summary

Perceptual models of animal vision have greatly contributed to our understanding of animal-animal and plant-animal communication. The receptor-noise model of color contrasts has been central to this research as it quantifies the difference between two colors for any given species of interest. However, if the properties of the visual system are unknown, assumptions regarding parameter values must be made, generally with unknown consequences. This study models the avian visual system to systematically investigate the influence of variation in light environment, photoreceptor sensitivities, photoreceptor densities, and light transmission properties of the ocular media and the oil droplets. We calculated the chromatic contrast of 15 plumage patches to quantify dichromatism in 70 species of Galliformes, a group of birds that display a wide range of sexual dimorphism. We found that the transmission properties of oil droplets, the photoreceptor densities, and the wavelength of maximum sensitivity of the SWS1 photoreceptor can increase dichromatism scores by 50% to 100%. In contrast, the light environment, transmission properties of the ocular media, and the peak sensitivities of the SWS2, MWS, and LWS cones had a smaller impact on the scores. Our findings demonstrate that improper parameterization of tetrachromatic visual models can have large effects on measures of dichromatism, potentially leading to erronus inferences. We urge more complete characterization of avian retinal properties and recommend that researchers determine through opsin sequencing whether their species of interest possess an ultraviolet or near-ultraviolet sensitive SWS1 photoreceptor.

Introduction

The study of animal visual systems has greatly enhanced our understanding of visual ecology and visual communication. Modeling the sensory experience of various taxa has permitted the study of animal-animal interactions such as mate choice among color morphs in butterflies (Limeri and Morehouse 2014), the evolutionary trade-off between predator driven crypsis and sexually selected conspicuousness in *Dendrobates* frogs (Willink *et al*. 2014), the influence of insect warning coloration on the predatory behavior of foraging birds (Cibulková *et al*. 2014), and the rejection of brood parasite eggs by host species (Croston and Hauber 2014, Spottiswoode and Stevens 2010). Furthermore, visual modeling of sensory experiences has been useful in studies of plant-animal interactions. These include, for example, the evolution of flower colors driven by pollinator visual systems (Muchhala *et al*. 2014), the evolution of seed color as a form of crypsis against foraging birds (Lev-Yadun and Ne'eman 2013), crypsis in plants to avoid predatory herbivores (Niu *et al*. 2014), the ability of birds to detect and select high-lipid fruits (Schaefer *et al*. 2014, Cazetta *et al.* 2009), and the comparative ability of dichromat and trichromat primates in discriminating fruit from leaves (Melin *et al*. 2014). Central to these studies is the concept of color discrimination thresholds limited by photoreceptor noise (Vorobyev and Osorio 1998, Vorobyev *et al*. 1998). This psychophysiological model of chromatic vision quantifies color perception in animals (Kelber *et al.* 2003, Osorio and Vorobyev 2005, Osorio and Vorobyev 2008), with the caveat that the properties of the visual system, which must be included in the model, are well understood.

Informative visual models must include the correct light environment, photoreceptor sensitivities, photoreceptor densities, transmission properties of the ocular media including the vitreous and aqueous humors, and for animals such as birds and turtles, the properties of the oil droplets which act as filters and micro-lenses (Hart and Vorobyev 2005, Stavenga and Wilts

2014). While molecular methods and microspectrophotometry are increasingly used to determine the physical properties of visual systems (e.g., Håstad *et al*. 2009, Lind *et al*. 2013), complete characterizations are available for relatively few species. Furthermore, groups of closely related species have rarely been compared (see Coyle *et al*. 2012 for an exception). To circumvent these lack of data, research using birds as models have relied on 'average' visual system information (calculations and data for ultraviolet sensitive and ultraviolet insensitive eye types presented in Endler and Mielke 2005), or used parameters from closely related species. Initial comparative analyses assumed a strong association between visual systems and phylogeny (Eaton 2005, Bridge *et al.* 2008, Renoult *et al.* 2010), but recent studies have shown that this is not always the case. Changes between ultraviolet sensitive (UV) and violet sensitive (VIS) eye types have occurred several times in some Orders (e.g., Passeriformes and Charadriiformes; Ödeen and Håstad 2013), and both UV and VIS eye types can be present within the same family (e.g., Maluridae: Ödeen *et al.* 2012). Furthermore, the very basic organizations of visual systems can differ among and within Orders. For example, a large majority of birds characterized to date possess four distinctive color-sensitive single cones (Short-wavelength-sensitive 1 – SWS1, Short-wavelength-sensitive 2 – SWS2, Medium-wavelength-sensitive – MWS, and Long-wavelength-sensitive – LWS, e.g., Hart 2001a, 2001b) but exceptions have been found. The tawny owl (*Strix aluco*), and possibly more nocturnal raptors, lacks the UV – VIS SWS1 pigment and is therefore trichromatic (Bowmaker and Martin 1978; Ödeen and Håstad 2003). In contrast, the bobolink (*Dolichonyx oryzivorus*; Passeriformes) possesses five distinct classes of single cones: four narrowly tuned photoreceptors and one broadband photoreceptor (Beason and Loew 2008). Clearly, not all birds share the same visual sensory experience.

The wrongful parameterization of visual models could potentially lead to erroneous conclusions for a variety of ecological questions. In a striking demonstration, Renoult *et al*.

(2010) showed that visual system parameter assumptions can sometimes produce questionable results. In a preceding paper, Avilés and Soler (2009) found a significant relationship between the gape coloration of nestlings and the visual characteristics of parents in altricial birds, and suggested that these findings implied adaptive communication between parents and offspring. Among other assumptions, Avilés and Soler (2009) assumed phylogenetic inertia of the ability of species to perceive UV wavelengths, and treated owls as tetrachromats. Renoult *et al*. (2010) concluded that the significant relationships previously reported by Avilés and Soler (2009) were not valid (but see reply: Avilés and Soler 2010), that phylogenetic inertia should not be assumed, and that simple assumptions of visual system models can lead to misleading conclusions.

The possible effects of differential visual model parameterization have been explored in diverse taxa. Studies have quantified the discriminability of objects between dicromats and trichromats (Perini *et al*. 2009, Cheney and Marshall 2009) and between trichromats and tetrachromats (Siddiqi *et al*. 2004, Håstad and Ödeen 2008). Others have tested the effect of different light environments (Avilés 2008, Holveck *et al*. 2010, Lind *et al*. 2013, Rick *et al*. 2012), photoreceptors sensitivities (Lind and Kelber 2009, Lind *et al*. 2013), photoreceptor densities (Ensminger and Fernández-Juricic 2014, Lind and Kelber 2009), oil droplet characteristics (Goldsmith and Butler 2003, Vorobyev 2003, Lind and Kelber 2009, Ronald *et al.* 2012), ocular media (Lind *et al*. 2013), and receptor signal-to-noise ratio (Lind and Kelber 2009). While these studies have been very informative when considered together, the use of different visual system starting points and non-standardized methods of presenting results have made it difficult to compare the relative effect of each parameter within a single context. In this study, we systematically test the effect of varying parameters on measures of sexual dichromatism among 70 species of Galliformes, a group characterized by extreme variation in sexual dimorphism.

The receptor-noise model for color discrimination is commonly used to evaluate sexual dichromatism within species, and to characterize color divergence among closely related or incipient species (e.g., Burns and Schultz 2012, Macías-Sánchez *et al.* 2013, Delhey and Peters 2008). These values of sexual dichromatism have been used to study the evolution of dichromatism (Price and Eaton 2014), the influence of sexual selection on dichromatism (Pérez i de Lanuza *et al*. 2013, Huang and Rabosky 2014), the relationship between dichromatism and conspicuousness (Doucet *et al.* 2007), and factors that may account for congeneric color diversity (Ödeen *et al*. 2012). In addition, sexual dichromatism has been used as a proxy for the intensity of sexual selection in comparative studies (Seddon *et al.* 2013, Huang and Rabovsky 2014). Although it has been demonstrated that human visual assessments produce different but similar approximations of dichromatism compared to tetrachromatic birds (Armenta *et al.* 2008, Håstad and Ödeen 2008, Seddon *et al.* 2010; Vorobyev *et al*. 1998), the effects of parameterization of bird visual models in assessments of dichromatism has never been systematically determined. In this study, we calculated the chromatic sexual dichromatism of 15 color patches for each of 70 species of Galliformes using the receptor-noise model developed by Vorobyev and Osorio (1998). For each patch, sexual dichromatism is calculated as the just-noticeable-difference (JND) in color between males and females. We evaluated the influence of light environments, photoreceptor sensitivities, oil droplet characteristics, ocular transmission, and photoreceptor densities on chromatic contrast values. The purpose of our study was to understand the relative effect of each model parameter on overall dichromatism values, and to guide researchers when making assumptions about visual systems in studies using visual models.

Materials and Methods

Spectral measurements

Species in the Order Galliformes exhibit a tremendous diversity in sexual dichromatism, ranging from completely monomorphic to highly dichromatic. Across the various species in this group, feather coloration is predominantly produced by melanin pigmentation or structural colors (Durrer 1977, Durrer and Villiger 1975), with some plumage patches colored by carotenoid pigments (Thomas *et al*. 2014). We selected 70 species, most of them broadly distributed across the Phasianidae (65 of 70 species), and measured 15 plumage patches on three males and three females of each species when available (list of species and specimen museum catalogue number in Table S5.1). We obtained spectral reflectance measurements using a USB 4000 spectrophotometer combined with a PX-2 Xenon light source (Ocean Optics, Dunedin, FL). We collected measurements using a bifurcated probe with a rubber stopper tip, which blocked out ambient light and maintained the probe at normal incidence and 3 mm above the feather surface. We measured each region five times, haphazardly relocating the probe each time, and used the average of the five measurements and three individuals in subsequent analyses (Dalrymple *et al*. 2015). The range of colors across the species measured covered ~40% of the gamut of bird colors obtained by Stoddard and Prum in a comprehensive survey of plumage coloration (Figure 5.1; Stoddard and Prum 2011).

General procedures

We tested the general influence of visual model parameterization on the total dichromatism score of each of the 70 species, and further examined the dichromatism scores most affected by the different parameters. For each plumage patch, we compared the spectral reflectance of the male color to that of the female color by calculating the chromatic contrast (the difference between the colors in JNDs). We calculated the total dichromatism score for each species as the sum of dichromatism scores across all patches. JND values smaller than 1 (i.e., non-discriminable) were given values of ‘0’ to avoid inflating the dichromatism scores based on non-detectable differences. Non-feathered facial patches were automatically scored as ‘0’ because skin colors quickly fade in museum specimens. This approach results in some scores being lower than if measurements had been taken from live birds, but these scores were not influenced by parameterization modeling.

We thoroughly surveyed the literature with ISI Web of Science (accessed Dec 1st 2014) for all bird studies reporting quantitatively assessed visual system parameters (e.g., using microspectrophotometry), but did not use predicted values based on gene expression (e.g., SWS1 peak sensitivity based on opsin amino acid substitution, Ödeen *et al*. 2009). We compiled the information available on avian photoreceptor sensitivities (Table S5.2), oil droplet characteristics (Table S5.3), transmission properties of ocular media (Table S5.3), and photoreceptor retinal densities (Table S5.4). We summarized these data separating UV from VIS eye type. We also extracted from the literature the most commonly used light environments (see below for more details).

We tested the influence of each visual model parameter by comparing dichromatism scores obtained from systematically changing the value of a single parameter. This was accomplished using the R package `pavo` functions (sensmodel, vismodel, and coldist; Maia *et al*. 2013, R Development Core Team 2014) modified to include the eye aperture used in Endler and Mielke (2005). Within-parameter effects were evaluated first by comparing each set of dichromatism scores against those obtained using the most commonly implemented visual models, the average VIS or UV eye type (Endler and Mielke 2005), followed by pairwise comparisons to find the parameter values that produced the most divergent scores. The effects of parameterization were assessed in two ways: 1) by calculating the Pearson's correlation coefficient between the total dichromatism scores, and 2) by comparing the ranks of the total dichromatism scores (as per Håstad and Ödeen 2008). We determined how many species maintained the same rank, the mean and standard deviation change in rank, and the maximum change in rank. The species most affected by the changes in parameterization, based on the absolute largest difference in total dichromatism score, and the species most affected based on change in rank, were selected for further analysis. For these species, we determined the number of patches (out of 15) considered non-distinguishable under each of the two visual models, the number of patches that changed by more than 1 JND, and the maximum dichromatism score change in a single patch (in JNDs and percentage).

Model parameterization

Average visual model – Our basis for comparisons were the two average visual models (UV and VIS eye type) presented by Endler and Mielke (2005). In addition to the parameter values detailed in Table S5, we used the relative photoreceptor densities of the Pekin Robin (*Leiothrix lutea;* SWS1:SWS2:MWS:LWS = 1:2:2:4) as used originally by Vorobyev and Osorio (1998) and Vorobyev *et al*. (1998), and set the signal-to-noise ratio at 0.10, generating a Weber fraction of 0.05 for the LWS photoreceptor (Maier 1992, Vorobyev *et al*. 1998, Olsson *et al*. 2015).

Light environment – We compared the influence of the six most commonly used environmental illuminants (Endler 1993, Cronin *et al*. 2014): 1) forest shade, 2) woodland shade, 3) blue sky, 4) daylight D65 standard (Schanda 2007), 5) woodland gaps, and 6) cloudy sky.

Photoreceptor sensitivities – The large majority of avian species possess four color-discriminating retinal visual pigments: two short-wavelength sensitive pigments SWS1 and SWS2, one medium-wavelength sensitive pigment MWS, and one long-wavelength sensitive pigment LWS. The spectral sensitivities of these pigments can be accurately estimated using a near-universal template (Govardovskii *et al.* 2000). The peak wavelength sensitivities of the four avian photoreceptors within species are not highly correlated (Hart and Vorobyev 2005), allowing for considerable variation in the individual sensitivity values within any given visual system. Therefore, we evaluated the influence of changes in single photoreceptor peak sensitivities, using the minimum and maximum reported for each photoreceptor type for each eye type (Table S5.6), and then compared visual models that expressed either all minimum or all maximum peak sensitivity values.

Oil droplets – Each photoreceptor type is paired with a specific oil droplet type which acts as a cut-off filter and microlens (Vorobyev *et al.* 1998, Hart and Vorobyev 2005, Stavenga and Wilts 2014). SWS1 photopigments are associated with non-filtering droplets (transparent – T type), SWS2 pigments with droplets clear in appearance (C type), MWS pigments with yellow droplets (Y type), and LWS pigments with red droplets (R types). The absorption profile of the oil droplets can be extrapolated if the wavelength at which the oil droplet transmittance equals 1/*e* (λ_o) and the absorptivity rate of decay (b) are known. In turn, these properties can be estimated from the cut-off wavelength (λ cut) and the gradient of line tangent to the absorbance spectrum (Bmid) at the wavelength at half-maximum absorbance (λ mid), the only values that are reported in some studies of oil droplet characteristics (formulae presented in Hart and Vorobyev 2005). Because there is no strong relationship between a visual pigment's peak sensitivity and the absorbance characteristics of its associated oil droplet type (Hart and Vorobyev 2005), we evaluated the influence of differences in extreme cut-off values within photopigment type first by changing single oil droplet parameters, and then by comparing visual systems with oil droplet values set with all maximums and all minimums, by eye type (Table S5.7). Extremes were selected based on λ cut, and actual values of either Bmid (if available from the literature) or Bmid calculated from λ mid (Table S5.3).

Ocular media – Similar to oil droplets, the ocular media of the vitreous and aqueous humors acts as a cut-off filter. Recent work has demonstrated that phylogeny and eye type can be used to estimate the approximate high-pass cut-off values of the ocular media in birds (Lind *et al*. 2013), but that variability within UV and VIS eye types, and in certain groups, is very high (e.g., waterbirds). The absorption curves of ocular media in birds are all very similar and can be well approximated (function in Endler and Mielke 2005) when the wavelength at 50% transmission (T50) is known. We evaluated the influence of varying the T50 value between 314nm and 344nm for UV type eyes (the range of values known to exist for this eye type, Table S5.3), and between 335nm and 395nm in VIS eye type (Table S5.3), using 10nm increments among models (Table S5.7).

Photoreceptor densities – The relative densities of photoreceptors vary within and among species, and even within individuals with some evidence for bilateral asymmetry in at least two species (European starling *Sturnus vulgaris* and Blue tit *Cyaniste caeruleus*, Hart *et al*. 1998, Hart 2001a). Furthermore, photoreceptor densities are more heavily influenced by the ecology of the species (diet, feeding behavior, habitat) rather than phylogeny (Hart 2001a). Therefore, patterns of receptor densities are difficult to predict. We tested the influence of this parameter by selecting nine different photoreceptor densities (not including the original 1:2:2:4; see table S5.8 for species and reasoning behind inclusion). So that the models would be comparable, we maintained the Weber fraction of the LWS photoreceptor at 0.05 in all cases by using a different signal-to-noise ratio for each model (Vorobyev and Osorio 1998).

Model visual systems – The physical properties of visual systems have been completely characterized in only eight species (see Results). These systems were compared to each other and to either the average UV or VIS system based on the peak wavelength sensitivity of their SWS1 photoreceptor. Because they are the most commonly used sets of parameter values, we also compared the dichromatism scores generated using the average UV and VIS eye type visual models. For all models we used a Weber fraction of 0.05 (the most commonly used) which was empirically determined for the LWS photoreceptor of *Leiothrix lutea* (Maier 1992), and confirmed through behavioral tests in domesticated chicken (*Gallus gallus*, Olssen *et al*. 2015).

Results

The total dichromatism scores across the 70 species were always highly correlated regardless of which visual system parameter was altered (summary in Table 5.1; details in Table S5.9 – S5.14). Pearson's coefficient (r) of the largest differences, within parameter, ranged from 0.9998 when contrasting the extreme T50 ocular media values for the UV eye type, to 0.9660 when contrasting the photoreceptor densities of the Black noddy (*Anous minutus*) to those of the Wedged-tailed shearwater (*Puffinus pacificus*) in a UV eye type (Table 5.1, Figure 5.2A). However, there was considerable variation in the number of species that maintained the same total dichromatism rank, the mean rank change, and the maximum rank change. For example, the extreme T50 ocular media values for the UV eye type had a relatively small effect on the overall ranks and rank changes (42 out of 70 with equal rank, an average rank change of 0.60, and maximum rank change of 4), but the differences in photoreceptor densities in the UV eye type had a large impact on the total dichromatism ranks (only 11 out of 70 with equal rank, an average rank change of 3.40, and maximum rank change of 13; Figure 5.2B). Comparisons of the dichromatism scores calculated with the commonly used average UV and average VIS eye sets of conditions displayed one of the largest difference in rank scores (Table 5.1, Figure 5.3). Overall, photoreceptor densities, oil droplet cut-off value for the VIS eye type (Figure 5.4), and the variation among model systems had the largest influence on the total dichromatism scores and rank differences. Variation in the transmission properties of the ocular media (within eye-type) and the photoreceptor sensitivities (within eye type) had less influence on the total dichromatism scores and on the ranks of species (Table 5.1).

Analyzing the scores of individual species most affected by changes in condition values, based on the largest differences in total dichromatism scores, we found that large changes in plumage patch chromatic contrast (in JND) can occur when manipulating single parameters (Table 5.2). The maximum changes in percentage JNDs ranged from 12.48% (0.71 JNDs) when comparing the extreme T50 ocular media values for the UV eye type, to ~98% (21.16 JNDs) when comparing photoreceptor densities in a UV eye type (Figure 5.2C). Values of oil droplet transmission properties (Figure 5.4C) and different model systems also had large effects on the chromatic contrast of some patches (Table 5. 2). The species most affected in their total dichromatism scores almost always had the same number of non-dichromatic patches under the two sets of conditions (Table 5.2), but the number of patches that changed by more than 1 JND varied much across parameters. For the T50 ocular media value in a UV eye, none of the patches changed by at least 1 JND. In contrast, 12 patches changed by more than 1 JND when comparing the photoreceptor densities of *A. minutus* and *P. pacificus* using the VIS eye type. Overall, individual patches were mostly influenced by condition changes in the photoreceptor densities and the variation among model systems. We also found large differences in patch dichromatism scores when comparing the average UV and average VIS eye type (Figure 5.3C). Variation in light environments, photoreceptor sensitivities, and ocular media values had relatively small but non-negligible effects on the dichromatism scores of some patches (Table 5.2).

When analyzing the scores of individual species most affected by changes in parameter values, based on the largest differences in total dichromatism ranks, we found that large differences in ranks were associated with changes in the number of distinguishable patches (number of patches with 0 JNDs) under the two conditions (Table 5.3). The parameter conditions that generated the largest changes in ranks also had large differences in the number of distinguishable patches under the different sets of parameters. For example, the extreme T50 ocular media values for the UV eye type differed by only a single patch that changed by more than 1 JND (4 patches with JND < 1 for T50 of 314 compared to 5 for T50 of 344). In contrast, comparison of the *A. minutus* (8 patches with JND < 1) and *P. pacificus* (1 patch with JND < 1) photoreceptor densities in a UV eye type generated 12 patches with changes in JND > 1 (Table 5.3). In contrast to species most affected when comparing total dichromatism scores, we did not find large changes in plumage patch chromatic contrast (in JND) when manipulating single parameters. Indeed, none of the patches differed by more than 4.5 JNDs across all parameter values. Differences in light environment, photoreceptor sensitivities, and ocular media values generally had the least consequential effects on dichromatism scores of individual patches in species with the greatest change in dichromatism ranks; changes in photoreceptor densities, and comparisons of model systems generated the largest effects (Table 5.3).

Discussion

Compared to fish and invertebrates, avian visual systems exhibit considerably less variation in physical and physiological properties (Cronin *et al*. 2014). Nevertheless, a number of studies suggest that variation in avian visual systems appears to be adaptive. Carotenoid-based signals are aligned with cone sensitivities across species of the Passerida clade of passerine birds (Bleiweiss 2014); the expression of opsin genes are associated with plumage dichromatism in New World warblers (Bloch 2015); the ocular media of UV eye types allow more UV light to reach the retina than the ocular media of VIS eye types (Lind *et al.* 2014); and the photoreceptor densities among species seem to be ecologically relevant (Hart 2001b). Other studies have failed to find alignment between the visual system and the behavior or ecology of species. Ultraviolet vision, for example, does not seem to have co-evolved with plumage coloration across most bird families (Lind and Kelber 2015, Coyle *et al.* 2012, but see Ödeen *et al.* 2012). Because there is relatively little variation in the properties of the visual system of birds, proper parameterization of visual models could be of paramount importance when investigating spectral tuning and the evolution of visual systems in birds. This also applies to studies of plumage dichomatism which have been used to investigate, among other topics, the influence of sexual selection on speciation (Seddon *et al.* 2013, Huang and Rabovsky 2014).

In this study we systematically compared the effects of changing single parameters in visual models on total dichromatism scores, and ranks of dichromatism scores, in 70 species of Galliformes. We found very high correlations between the total dichromatism scores regardless of the differences among the models, but found that the rank of species could be greatly affected. These results imply that even though parameterization has little effect on the general distribution of the total dichromatism scores, changes in visual system assumptions can have large effects on the relative position of the total dichromatism score of species in relation to one another. Furthermore, certain parameters had a large influence on the number of patches considered dichromatic (JND > 1), and the dichromatism scores of individual patches. Our findings suggest that the parameterization of avian visual systems should not be trivialized.

Light environment – Some of the earliest research aimed at assessing the importance of visual model parameters demonstrated that differences in light environments made Trinidadian guppies (*Poecilia reticulata*) more conspicuous in the presence of conspecifics than in the presence of heterospecific predators (Endler 1991). The importance of this parameter was further demonstrated in behavioral trials which showed that the absence of UV wavelengths reduced the foraging efficiency of three-spined sticklebacks (*Gasterosteus aculeatus*; Rick *et al.* 2012). In contrast, the light environment has almost no effect on the discriminability of vole urine against the vegetation background (~4% JNDs) suggesting little influence on the behavior of foraging raptors (Lind *et al.* 2013). The results from these studies, and others (e.g., Avilés 2008, Avilés *et al.* 2011, Holveck *et al*. 2010), indicate that the importance of the light environment in visual models is context dependent. In our study, differences in light environment had relatively small, but non-negligible, effects on the scores and ranks of total dichromatism in Galliformes. Some of the patches changed by more than 21% JNDs (> 3 JNDs), differences considerably larger than those modelled by Lind *et al*. (2013). Our largest observed differences included the D65 illuminant for both UV and VIS eye types (Table 5.3). This light environment is rich in blue (but not UV) wavelength and is likely to influence colors rich in red and UV wavelength such as those produced by some carotenoids (Goodwin 1980). Our light environment results should only be interpreted in the context of bright illumination since the receptor-noise model does not perform particularly well in dim light situation (Vorobyev and Osorio 1998).

Photoreceptor sensitivities – In a test of parameterization effects on models in foraging raptors, Lind *et al.* (2013) reported chromatic differences of ~16% ± 12% JNDs. These results were obtained by changing the SWS1 and SWS2 photoreceptor by 10nm towards short-wavelength sensitivity and the LWS by 10nm towards long-wavelength sensitivity. Our general results support these findings and demonstrate that differences greater than~40% JNDs are possible. These values were obtained by comparing all minimum-shifted and all maximum-shifted photoreceptor sensitivities (Table S5.3). However, changes in the sensitivity of single photoreceptors within eye type, even to the extreme known values across birds, had very little influence on dichromatism scores (Table S5.10). These results also support work presented by Lind and Kelber (2009), which found little influence of photoreceptor sensitivity in modelling chromatic differences between four colors (peak wavelength at 350, 450, 500, and 650 nm) against a green background. Overall, the parameterization of photoreceptor sensitivities should only have consequential influences on chromatic contrast calculations when all sensitivities are wrongfully shifted in the same direction (all towards short- or long-wavelengths) or when SWS and LWS photoreceptors are shifted in opposite directions. In contrast, changes in single photoreceptor sensitivities generally had limited effects on calculated JND scores.

Oil droplet cut-off value – Variation in the transmission cut-off values of oil droplets had similar but potentially slightly larger influence on dichromatism scores than variation in photoreceptor sensitivities. Our results demonstrate that differences greater than 75% (> 8 JNDs in this case) in single patch chromatic contrasts are possible. Lind and Kelber (2009) also demonstrated the importance of this parameter. In a behavioral experiment comparing the measured and predicted visual sensitivities in two species of galliformes, the match between visual models and behavioral results in tests of color discriminability improved tremendously by shifting the absorbance curves of oil droplets by 10nm in their models. Oil droplet properties of the avian eye should perhaps be given greater attention. Indeed, much variation has been found within species, both among individuals and between the sexes (Knott *et al.* 2012). Modelling of within-species differences suggest chromatic contrast differences as large as ~30% JNDs in some parts of the visual spectrum (Ronald *et al.* 2012), sufficient to influence the perspective of the receivers, and potentially affecting foraging and mate choice behaviors. Furthermore, recent experiments have revealed that dietary carotenoid content can influence the transmission properties of oil droplets in double cones, indicating condition-based within-species variation in visual properties and the potential of diet to influence color vision (Knott *et al.* 2010). To date, the influence of variation in oil droplet characteristics on color discrimination have only been modeled, never behaviorally tested.

Ocular media – The only other study to have explicitly modeled the influence of ocular media on chromatic contrasts found this parameter rather inconsequential (Lind and Kelber 2009). Our overall results (Table 5.1) agree with these findings but highlighted that this parameter is perhaps most important when modelling VIS eye types, not UV eye types (Table 5.3). Differences in this parameter will only influence the perception of UV-rich colors which are common in fruits and feathers that contain carotenoids (Goodwin 1980, McGraw 2006), vole-urine used by foraging raptors to assess prey density (Viitala *et al.* 1995, Lind *et al*. 2013), and some structural colors assessed during mate choice (e.g., Hunt *et al.* 1998, Andersson and Andersson 1998). Particular consideration to this parameter should be made when modeling color discrimination of these UV rich colors.

Photoreceptor densities – The photoreceptor density was the single most important parameter in our models both in terms of changes in total dichromatism ranks and chromatic contrast of individual patches (Table 5.1 and 5.3). Individual patches changed by as much as 20 JNDs (~95%), values almost identical to those presented by Lind and Kelber (2009), which demonstrates the importance of this visual system trait. Differences in photoreceptor densities are likely to have large consequences on among-species ability to discriminate between similar colors and, as for variation in oil droplets absorbance curves, within-species variation may be of consequence as well. For example, differences in densities among house sparrows (*Passer domesticus*) generated chromatic contrast differences of ~16% (>3 JNDs) when evaluating the perception of the white wing bars against the brown wing background coloration (Ensminger and Fernández-Juricic 2014). Even if these plumage patches likely differ more in the achromatic component of the signal, these chromatic differences may still have implications for mate choice and agonistic interactions. Because the characterization of complete visual systems requires specialized equipment and skills, and the sacrifice of animals, our knowledge of photoreceptor densities come from relatively few studies (see Hart 2001b for an exception a majority of species characterized to date). Future research on the physical properties of avian retinas should obtain as much information as possible, including counts of different photoreceptor types. These data have the potential to make large contributions to our understanding of the visual ecology of birds.

Model systems – Within eye types, there were relatively small differenced in total dichromatism scores among the model visual systems. However, our results suggest that one of the most influential parameters of visual models is whether a species possesses a UV or VIS eye type (Tables 5.1-5.3, Table S5.14). This is of particular importance since these are the two most commonly used sets of parameters in avian visual modelling. Because there was a strong belief in phylogenetic inertia in eye type (e.g., Eaton 2005, Bridge *et al.* 2008), studies have usually modeled a single eye type (exceptions include: Uy and Endler 2004, Gomez and Théry 2007, Langmore *et al.* 2009). However, as demonstrated by Renoult *et al.* (2010), using the wrong eye type can entirely alter the conclusions of a study. Fortunately, determination of a species' eye type does not require microspectrophotometry like many other physical characteristics of the retina. Even though not all SWS1opsin gene sequence variations have been compared to measured photopigment sensitivities, the peak absorbance of short-wavelength photoreceptor can usually be estimated (Ödeen and Håstad 2003, 2013). This method is relatively rapid, inexpensive, and could easily be implemented in any molecular laboratory (Ödeen and Håstad 2003).

Without doubt, sensory experiences are produced by the combined physical properties of sensory systems. However, our analyses only considered the effects of individual parameters, without comparing the potential compounding influence of variation in more than one visual model assumption. In certain instances, two or more parameters may cancel each other out (e.g., a short-wavelength shifted SWS1 value matched with a long-wavelength shifted ocular media value), but other combinations of wrongful parameters could dramatically alter calculated values. For example, a short-wavelength-shifted SWS1 photoreceptor sensitivity value matched with a photoreceptor density ratio that favours discriminability in the short wavelengths could mistakenly modify a UV-insensitive visual system to one that can detect small color differences in the UV range. It is also important to consider that animals do not perceive individual patches in isolation (Endler and Mielke 2005) and that the contrasts among several color patches may be evaluated differently than the sum of its parts, concepts that are currently being investigated (Cole and Endler 2015). In both of these scenarios, our results would provide a low-end estimate of the potential difference between the perceived and calculated chromatic difference.

Overall, our results suggest that if avian dichromatism scores are calculated by combining the chromatic contrast of several plumage patches and used in parametric analyses, individual parameters may have limited impact on subsequent analyses. However, if dichromatism scores are ranked (since they are often not normally distributed), or if individual patches are compared, a single parameter can have large influences on the position of a species in relation to another. To improve the reliability of avian visual models, information about photoreceptor densities and the sensitivity of the SWS1 photoreceptor should be investigated when possible. Because sequencing the SWS1 gene is cost effective, we recommend that researchers modeling avian visual systems determine, at least, whether their species of interest possess a UV or VIS eye type.

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Table 5. 1 Summary of the visual system comparisons that generated the largest differences, based on the lowest Pearson's r value, in the total dichromatism scores of 70 species of the Order Galliformes. Values reported describe how many species (out of 70) were assigned the same rank in the comparison (Equal rank), the average rank change (Rank change), the standard deviation of rank change (Rank SD), and the maximum rank change (Max change). See Methods and Results and Supplemental sections for more details.

Parameter	Eye type	Conditions	Pearson's r	Equal rank	Rank change	Rank SD	Max change
Light environment	UV	Sky vs D65	0.9986	28	1.17	1.56	10
	VIS	Ideal vs D65	0.9986	23	1.06	1.11	5
Photoreceptor λmax	UV	All Max vs All Min	0.9986	26	1.00	1.19	6
	VIS	All Max vs All Min	0.9966	25	1.17	1.45	8
Oil droplet cut-off value	UV	R Min vs All Max	0.9983	35	0.83	1.17	7
	VIS	R Max vs All Max	0.9880	10	2.69	2.39	12
Ocular media T50 values	UV	T314 vs T344	0.9998	42	0.60	0.92	4
	VIS	T335 vs T395	0.9976	20	1.20	1.15	5
Photoreceptor Densities	UV	*A. minutus vs P. pacificus*	0.9660	11	3.40	3.12	13
	VIS	*A. minutus vs P. pacificus*	0.9760	9	3.00	2.91	12
Model systems	-	Average UV vs Average VIS	0.9903	15	2.37	2.40	13
	-	*P. cristatus* vs *T. merula*	0.9847	12	3.17	2.85	14

Table 5. 2 Summary of the changes in dichromatism score of the species most affected by changes in the sensory exprience, based on the absolute largest difference in total dichromatism score among 70 species of Galliformes. Values reported describe the number of patches (out of 15) without any discernable dichromatism (just-noticeable-differences < 1) under the first set of conditions (Condition 1 – 0 JND) and under the second set of conditions (Condition 2 – 0 JND), the number of patches that changed by more than 1 JND when comparing the first and second set of conditions (>1 JND change), the maximum dichromatism value change for a single patch (Maximum change in JND) and its percentage change (Maximum change in percentage). See Methods and Results for more details.

Parameter	Eye type	Conditions	Condition 1 (0 JND)	Condition 2 (0 JND)	>1 JND change	Max change (JNDs)	Max change (%)
Light environment	UV	Sky vs D65	5	5	4	4.19	17.10
	VIS	Ideal vs D65	7	7	4	3.36	21.71
Photoreceptor λmax	UV	All Max vs All Min	0	0	4	3.28	17.98
	VIS	All Max vs All Min	0	0	6	4.40	44.38
Oil droplet cut-off value	UV	R Min vs All Max	0	0	9	4.73	28.53
	VIS	R Max vs All Max	0	0	8	8.40	76.45
Ocular media T50 values	UV	T314 vs T344	1	1	0	0.71	12.48
	VIS	T335 vs T395	7	7	4	4.82	31.60
Photoreceptor densities	UV	*A. minutus vs P. pacificus*	7	5	7	21.16	98.64
	VIS	*A. minutus vs P. pacificus*	0	0	12	9.68	45.71
Model systems	-	Average UV vs Average VIS	1	1	7	7.71	45.01
	-	*P. cristatus* vs *T. merula*	5	5	7	11.60	43.10

Table 5. 3 Summary of the changes in dichromatism score of the species most affected by changes in the sensory exprience, based on the largest difference in rank among 70 species of Galliformes. Values reported describe the number of patches (out of 15) without any discernable dichromatism (just-noticeable-differences < 1) under the first set of conditions (Condition 1 – 0 JND) and under the second set of conditions (Condition 2 – 0 JND), the number of patches that changed by more than 1 JND when comparing the first and second set of conditions (>1 JND change), the maximum dichromatism value change for a single patch (Maximum change in JND) and its percentage change (Maximum change in percentage). See Methods and Results for more details. NA values indicate that the score under one of the conditions is 0 JNDs.

Parameter	Eye type	Conditions	Condition 1 (0 JND)	Condition 2 (0 JND)	>1 JND change	Max change (JNDs)	Max change (%)
Light environment	UV	Sky vs D65	2	4	2	1.26	NA
	VIS	Ideal vs D65	10	10	2	1.37	NA
Photoreceptor λmax	UV	All Max vs All Min	7	8	2	1.30	35.66
	VIS	All Max vs All Min	7	3	4	1.32	NA
Oil droplet cut-off value	UV	R Min vs All Max	9	7	2	1.04	NA
	VIS	R Max vs All Max	9	2	13	2.18	127.45
Ocular media T50 values	UV	T314 vs T344	4	5	1	1.08	NA
	VIS	T335 vs T395	4	4	4	4.21	30.57
Photoreceptor densities	UV	*A. minutus vs P. pacificus*	8	1	12	3.88	77.66
	VIS	*A. minutus vs P. pacificus*	1	1	3	1.60	30.67
Model systems	-	Average UV vs Average VIS	2	10	12	2.20	128.04
	-	*P. cristatus* vs *T. merula*	8	0	12	3.02	171.3

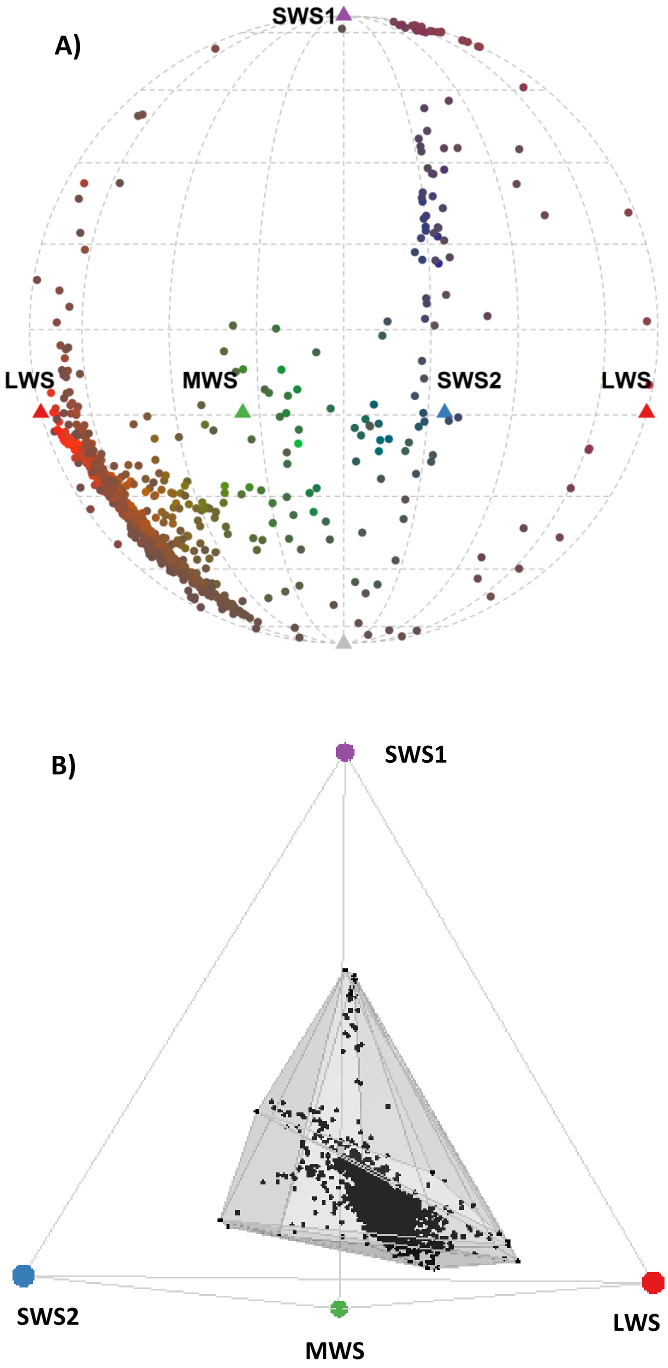

Figure 5. 1 A) Molleweide projection of the 2100 color patches used in this study when perceived by an average UV visual system under ideal illumination. The colors of the symbols are approximations of the colors of the patches based on a human visual system. B) Total volume, defined by the smallest convex polygon that contains all colors (shaded area), of tetrahedral colorspace occupied by the plumage patches compared in this study. SWS1, SWS2, MWS, and LWS refer to the ultraviolet-, short-, medium-, and long-wavelength photoreceptor, respectively.

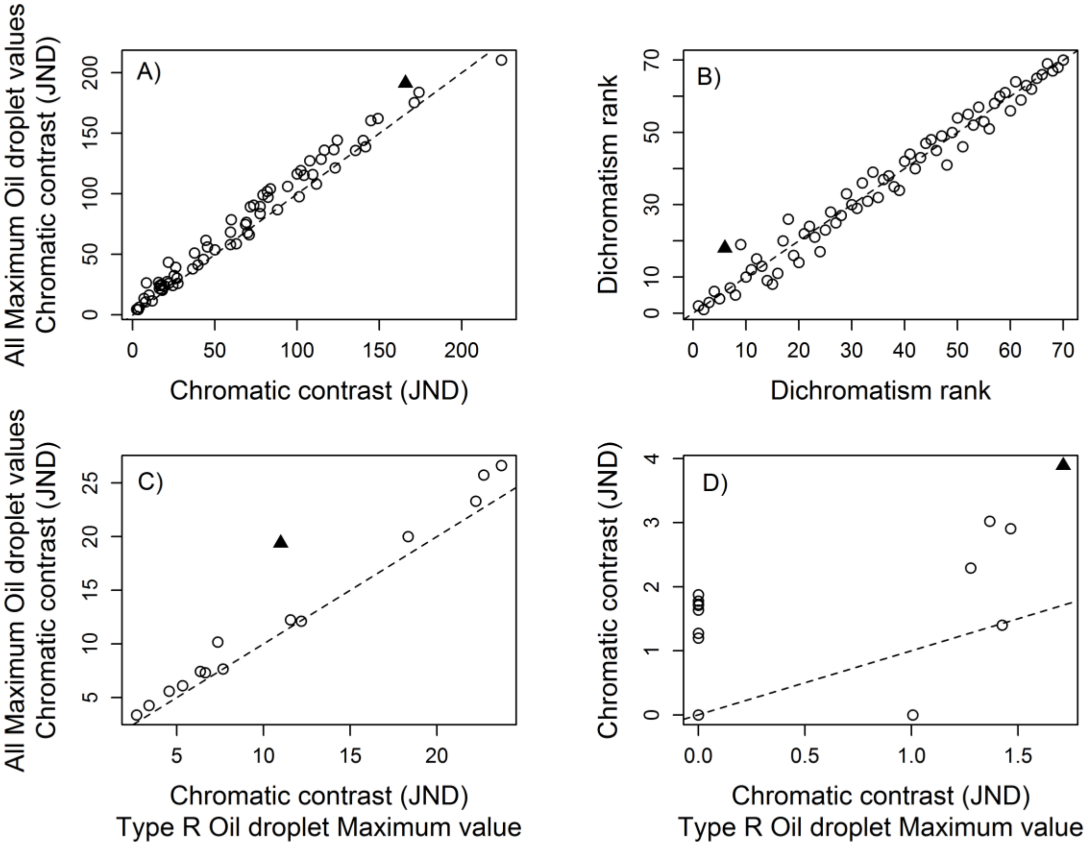

Figure 5. 2 Comparison of the A) total sexual dichromatism scores (in just-noticeable differences), and B) total dichromatism ranks of 70 species in the Order Galliformes contrasting two visual systems differing only in their oil droplet cut-off values. Scores were obtained by modifying the average visual system parameters (see Methods). Values on the x-axis were generated by modifying only the R-type oil droplet cut-off value (associated with the LWS photoreceptor) to the maximum value currently known to occur; values on the y-axis were generated by modifying the C-, Y-, and R-type oil dropet cut-off values (associated with the SWS2, MWS, and LWS photoreceptors, respectively) to the maximum values currently known to occur in birds. The dashed line represents the 1:1 reference line. The solid triangle symbol in A) identifies the species that experienced the greatest change in total dichromatism score, and the greatest change in rank in B). The sexual dichromatism score of each patch of the species highlighted in A), under the two sets of parameters, are presented in C). The sexual dichromatism score of each patch of the species highlighted in B), under the two sets of parameters, are presented in D). In C) and D), the solid triangle symbol identifies the patch that experienced the greatest change in dichromatism score.

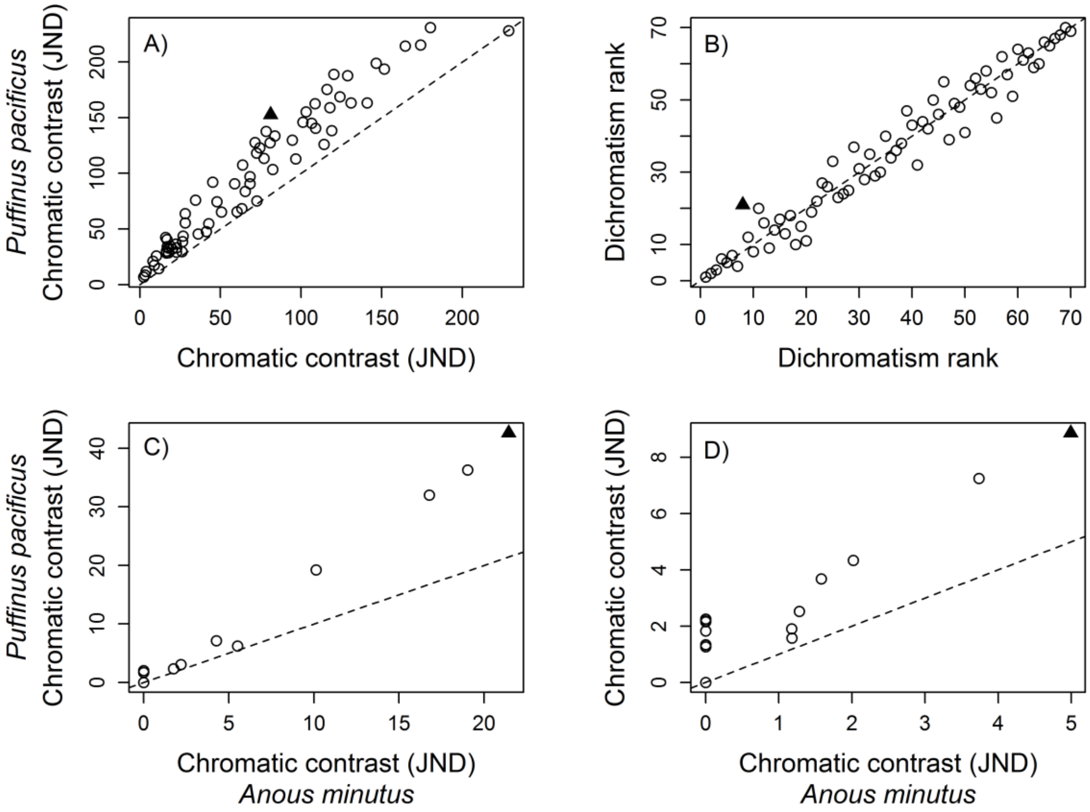

Figure 5. 3 Comparison of A) the total sexual dichromatism scores (in just-noticeable differences), and B) total dichromatism ranks of 70 species in the Order Galliformes contrasting UV eye type visual systems differing only in their photoreceptor densities. Values on the x-axis were generated using the parameters associated with the 'average UV eye-type' visual system but with the photoreceptor densities found in *Anous minutus*; values on the y-axis were generated with the 'average UV eye-type' visual system but with the photoreceptor densities found in *Puffinus pacificus* (see Methods). The dashed line represents the 1:1 reference line. The solid triangle symbol in A) identifies the species that experienced the greatest change in total dichromatism score, and the greatest change in rank in B). The sexual dichromatism score of each patch of the species highlighted in A), under the two sets of parameters, are presented in C). The sexual dichromatism score of each patch of the species highlighted in B), under the two sets of parameters, are presented in D). In C) and D), the solid triangle symbol identifies the patch that experienced the greatest change in dichromatism score.

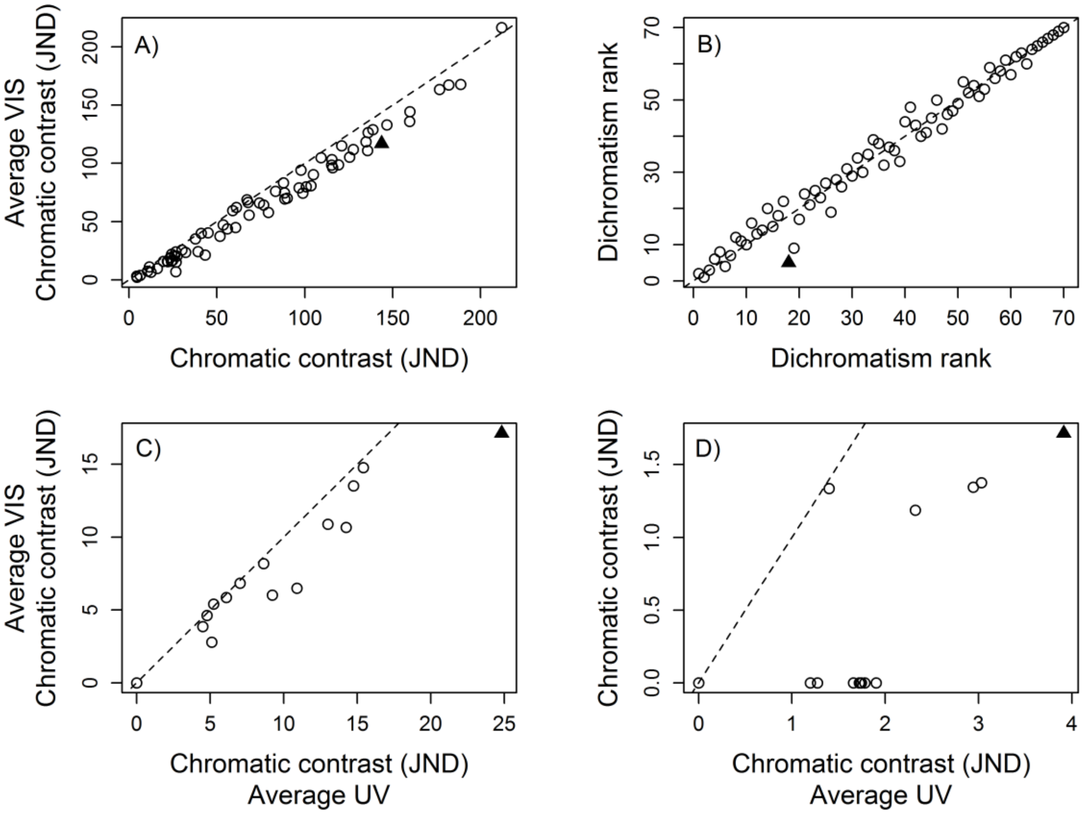

Figure 5. 4 Comparison of A) the total sexual dichromatism scores (in just-noticeable differences), and B) total dichromatism ranks of 70 species in the Order Galliformes contrasting the two most commonly used bird visual systems. Values on the x-axis were generated using the parameters associated with the 'average UV eye-type' visual system; values on the y-axis were generated with the 'average VIS eye-type' visual system (see Methods). The dashed line represents the 1:1 reference line. The solid triangle symbol in A) identifies the species that experienced the greatest change in total dichromatism score, and the greatest change in rank in B). The sexual dichromatism score of each patch of the species highlighted in A), under the two sets of parameters, are presented in C). The sexual dichromatism score of each patch of the species highlighted in B), under the two sets of parameters, are presented in D). In C) and D), the solid triangle symbol identifies the patch that experienced the greatest change in dichromatism score.

Chapter 6

General Discussion

Studies of visual communication continue to be central to our understanding of animal behaviour, evolution, and speciation. In this body of work, I provided the first experimental evidence for visual communication in trogons, an ancient group of pantropical birds. Specifically, I demonstrated in chapter 2 that tail raising in elegant trogons is a multifunctional display that targets, and likely conveys information to, conspecifics and heterospecifics. In chapter 3, I discovered that different plumage traits are used in species recognition in the elegant and black-headed trogon. Furthermore, I demonstrated that sympatry with a similar-looking congener may influence which visual traits are assessed for species recognition. My findings in chapter 4 imply that the colour of plumage patches in trogons evolved as a result of reinforcement following secondary contact, and identified the rapid colonization of South America following Great American Interchange as one of the driving forces of plumage trait diversification in this group. Finally, I presented in chapter 5 the first systematic study of the influence of visual model parameters on dichromatism scores using galliform birds. My results clearly demonstrate the importance of proper model parameterization, and emphasize the importance of the complete, rather than partial, characterization of visual systems. Overall, my findings make a significant contribution to our understanding of visual communication in birds.

Function of visual signals in Trogons

The functions of signals were originally studied in the framework of one sender one receiver (examples in Searcy and Nowicki 2005), but it was later demonstrated that certain signals can target several individuals and/or species (McGregor 2005). In some cases, the same signal can even be used in different context and convey different meanings (Mennill and Vehrencamp

2008). Multifunctional signals may not be uncommon but have received relatively little attention. Because understanding the function of a signal is the first step in determining how the signal evolved and how it contributes to the natural history of an animal, the study of multifunctional signals could be particularly revealing. Both male and female elegant trogons perform a conspicuous tail raising display whereby the tail, which is usually positioned vertically, is rapidly lifted horizontally and slowly returned to its original position. In Chapter 2 of my dissertation, I combined observational and experimental data to determine the functions of tail raising. I found that this behaviour is a multifunctional display that targets conspecifics and heterospecifics alike and is used by both male and females. Specifically, it is used during intra- and intersexual interactions such as courtship displays and aggressive territorial encounters, and is displayed towards potential predators as a pursuit-deterrent signal. Contrary to all previous studies in birds (Table 2.1), my experimental data excluded other potential functions of this display when performed in the presence of heterospecifics (e.g., it is not a conspecific warning signal). This study is therefore the first demonstration in birds of a visual signal that acts as both a pursuit-deterrent signal and an intraspecific signal.

Many questions remain about the functions of the tail raising behaviour when directed at conspecifics. If tail raising displays are pre-aggression behaviours, are they part of a stereotyped sequence of events leading to aggression (Hurd and Enquist 2001), and if so, when in the series of elements does it occur? Is it a useful predictor of aggression and/or an efficient mean by which aggressive interactions can be minimized (Baker et al. 2012)? Several of these questions would require extensive observational data as well as experiments, including perhaps the presentation of motorized models (Patricelli et al. 2006, Anderson et al. 2013).

Tail displays may be a common form of pursuit-deterrent signalling in birds. Tail raising has been observed in several but not all species of trogons (e.g., found in the collared trogon but not the black-headed trogon, pers. obs., Collar 2001) and several members of the Coraciiformes. For example, all motmots wag their tails (Snow 2001, Murphy 2006, 2007) and many kingfishers raise their tails and bob their heads (Woodall 2001). Tail raising, pumping, and wagging have been well documented in other avian Orders (studied examples presented in Table 2.1), but it is generally unknown how widespread the behaviour might be. Future studies should first develop a set of hypotheses with testable predictions that would guide investigations on the ecological conditions that may be necessary for the evolution of tail displays as pursuit-deterrent signals. Comparative analyses and ancestral state reconstructions would then inform us about when and why these behaviours have evolved (see Caro 1994 for a preliminary comparative study of stotting in ungulates). If the behaviours are also used for conspecific communication, as in the elegant trogon, it would be informative to determine whether the interspecific signalling displays have been co-opted from the intraspecific displays or vice-versa (Borgia and Coleman 2000).

Species recognition

Studies of avian traits involved in species recognition have rarely focussed on visual characteristics, with a majority of the literature focussing on acoustic communication (Ord & Stamps 2009). The few studies to have assessed the use of plumage characteristics as species recognition traits (e.g., Uy et al. 2009) failed to manipulate specific plumage patches, limiting inferences about the usefulness of specific traits in species recognition. Furthermore, the influence of sympatry with a similar-looking congener on the use of plumage traits in species recognition had never been investigated. In Chapter 3, I presented the results of a model presentation experiment that determined which plumage traits are used for species recognition in the elegant trogon which is not sympatric with a similar-looking congener, and the black-headed trogon which is sympatric with a similar-looking congener. I found evidence that the colour of the belly and of the back is used for species recognition by both species. I also found that the elegant trogon was as aggressive towards similar-looking models as towards models that differed only in the under-tail barring patterns. This suggests that this species does not pay attention to this particular trait when examining models that otherwise resemble conspecifics. In contrast, the black-headed trogon approached all model types equally, except for the conspecific model. An interpretation of this counterintuitive reaction is that black-headed trogons did not recognize the other model types as members of their own species, thus approaching the playback to find the source of the vocalization, but stayed further away from conspecific looking models to avoid potential confrontations with an unknown individual. These findings indicate that the black-headed trogon distinguished between the conspecific models and all other models, including those that differed only in the under-tail barring pattern. Overall, the research presented in Chapter 3 demonstrates that not all species, even closely related congeners, use the same visual characteristics for species recognition. My research further identifies the presence of a similar-looking sympatric congener as one of the possible ecological reasons for the differential use of species recognition traits among closely related species. It is uncertain if these differences in use of species recognition traits are learned at the population level or innate at the species/sub-species level. Because the ability of individuals to recognize conspecifics from similar-looking taxa has important evolutionary consequences, especially in incipient species (Price 2007), my research sheds light on a mechanism that may increase the ability of species to correctly identify members of their own species and avoid the costs associated with improper identification (Martin and Martin 2001). These findings should be of interest not only to behavioural ecologists, but also to evolutionary biologists interested in traits important to reinforcement through pre-zygotic isolation, character displacement, and speciation.

Because trogons have rarely been studied in the field, much work remains to be conducted to understand the functions of plumage colouration in this group. As it pertains to species recognition, other plumage patches such as the vermiculated scapular feather group, and non-feathered traits such as the colour of the eye ring, the bill, and the iris, could also be tested. Trait variation in some of these structures would be more subtle than the ones tested in my experiment and would provide complementary findings, especially regarding the discriminating ability of various species. Furthermore, my dissertation research and most similar studies (e.g., Matyjasiak 2004) have primarily investigated the plumage characteristics of males, not those of females. The genus *Trogon* is phylogenetically separated into two clades: one in which females bear brown upperparts, one in which females bear grey upperparts. Females also display either a pink or yellow wash on their bellies, and barring patterns on their tails and scapular feathers that differ from those of males. Since all brown-back females and all grey-back females are otherwise very similar among species, future studies could investigate whether any of these three characteristics are used for species recognition. Generally, more studies on visual traits used in species recognition are needed to understand the role of visual communication in pre-zygotic isolation (Ord and Stamps 2009). Field experiments involving incipient species with very small differences in traits would be best suited for determining the minimum difference between divergent characteristics necessary to be useful in species discrimination (Uy et al 2009, Seddon and Tobias 2010). At the other extreme, it is important to determine why certain species are highly polymorphic with different races interbreeding (Roulin 2004). An emphasis on whether species recognition traits are innately assessed or learned will also add value to future studies (Phelps et al. 2006). In addition, because plumage patches are used in species recognition in trogons, it is not unlikely that several colourful traits evolved by means of sexual selection. Indeed, in members of the genus *Trogon* males and females are highly dichromatic, and it is generally assumed that sexual selection would generate intersexual divergence in colour (Andersson 1994, Barraclough et al. 1995). However, it is yet to be demonstrated that the iridescent and carotenoid based plumage characteristics are selected by females, whether they are honest indicators of quality in any trogon. Future studies could evaluate the signalling value of the conspicuous coloration in male trogons, determine whether different patches indicate different aspect of individual quality or are integrated as a single signal (Hegyi et al. 2014), or preferred by females for other reasons (e.g., runaway selection, Andersson 1994).

Evolution of plumage in Trogons

The study of adaptive radiations has provided the most insight into the evolution of ecological and sexually traits and has been instrumental in our understanding of trait diversification and speciation (Coyne and Orr 2004, Price 2007). Many systems studied to date have involved island species (Losos et al. 1993, Losos et al. 1993, Grant and Grant 2006) with few continent-wide studies. The formation of the Panama land bridge connecting the North American and South American continents was followed by the Great American Interchange of biota and was responsible for several great diversifications of land birds (Burns and Racicot 2009, Smith and Klicka 2010). However, the consequence of the rapid colonization of South America on the evolution of ecologically and sexually selected traits had yet to be explored in birds. In Chapter 4 of my dissertation, I investigated the evolution of plumage colouration in the genus *Trogon*, a group of birds previously demonstrated to have originated in Central America prior to the Great American Interchange (DaCosta and Klicka 2008). Using spectral data obtained from museums, and genetic and distribution data obtained from public sources, I used comparative analyses to determine the impact of the colonization of *Trogon* into South America on plumage traits. My results demonstrated that diversification rates were more recent and more rapid in South American taxa than in Central American taxa. Furthermore, my findings indicate that the plumage traits of South American, but not Central American, trogons increase in colour divergence with increases in sympatry. Together, these results strongly suggest a role for reinforcement through pre-zygotic isolation of rapidly colonizing incipient taxa, resulting either from character displacement or trait sorting. In this chapter, I also tested the idea that the plumage traits of trogon communities comprising a large number of species would have diverged to maximize the distance in plumage traits among species, and maximize the use of colourspace. In contrast to my predictions, I did not find any evidence for trait divergence greater than expected by chance for assemblages of five and six species. These results suggest that trait divergence may not promote extreme diversification, as long as species recognition is possible. Nonetheless, functional diversity attribute metrics had never been applied to plumage colouration and may be useful tools in the study of other species complexes. Overall, the findings of this study will be of general interest to evolutionary biologist and biogeographers because it directly links the colonization of South America by a group of land birds following the Great American Interchange to rapid diversification of taxa and associated divergence in secondary sex traits.

The findings presented in Chapter 4 generate more questions than answers. It was recently demonstrated that intermediate levels of sympatry lead to greater patterns of colour divergence in birds (Martin et al. 2015). This pattern does not seem to be present in trogons (Figure 4.3) but was not explicitly tested in this research. Furthermore, to determine whether character displacement or lineage sorting was responsible for the divergence in plumage patterns observed in sympatric South American trogon taxa, it will be necessary to compare the plumage characteristics of species pairs both in sympatry and in allopatry (Brown and Wilson 1956, Pfennig and Pfennig 2010), preferably controlling for other similar-looking species present in the same geographic area (Martin et al. 2015). The trogons are an interesting group for studying character displacement in visual characteristics because they exhibit high degrees of sympatry, they all share similar visual traits, and evidence suggests that they also use fairly similar niches (Collar 2001, Forshaw 2009). Therefore, this group would be particularly useful for studying ecological character displacement and may provide valuable insight into the mechanisms responsible for adaptive radiation and speciation following the colonization of a land mass.

Parameters and visual models

The receptor-noise model as the determinant of colour contrast thresholds (Vorobyev and Osorio 1998) has been extremely popular in the study of animal-animal and animal-plant communication. It has offered an easily applicable quantification method to compare colours as perceived by any animal. However, it has been criticised for requiring knowledge of visual system properties available for very few species (Endler and Mielke 2005). For this reason, assumptions about visual model parameters are made, often without considering the implications of wrongful parameterization (Renoult et al. 2010). Results from my dissertation will guide investigators when incorporating visual modelling in their research. My study was the first to systematically compare individual parameters of the receptor-noise model (Vorobyev and Osorio 1998), and showed that the light transmission characteristics of oil droplets, the photoreceptor densities, and the wavelength of maximum sensitivity of the SWS1 photoreceptor can have serious consequences on calculated chromatic contrasts. In contrast, the light environment, the light transmission properties of the ocular media, and the wavelength of maximum sensitivities of the SWS2, MWS, and LWS photoreceptors have less influence on the quantification of the visual sensory experience of animals. While my analyses focussed mainly on the tetrachromatic visual system of birds, the results will also be useful in the study of other taxa. Indeed, certain species of fish, amphibians, reptiles, and insects are known to possess four or more photoreceptors that functionally act as tetrachromatic visual systems (Bowmaker 1998, Koshitaka et al. 2008).

While a valuable contribution to the understanding of visual models, my research focussed on the influence of single parameters, without considering interaction effects in improperly parameterized models. Future studies should determine the consequences of mistakes in two or more parameters, which could be conducted systematically using software programs such as `pavo` (Maia et al. 2013). My research also points to the need for more information on the properties of visual systems, especially in the context of comparative analyses. This would allow the production of more accurate visual models, and would allow comparative studies on aspects of the visual system other than photoreceptor sensitivities. Indeed, most multi-species studies in birds have investigated spectral tuning (match between the visual system and the visual environment) by looking at the wavelength of maximum absorption of photoreceptors (e.g., Bleiweiss 2014). Further knowledge of the oil droplet properties and photoreceptor densities would be particularly important for understanding which ecological pressures drive the evolution of avian visual systems and the potential influence on sensory drive (Endler 1992). At a minimum, my research will help researchers improve the reliability of their visual models and allow them to make better-informed inferences regarding the perceptual abilities of their species of interest.

Conclusion

My dissertation research generated interesting findings pertaining to the function and evolution of plumage colouration in trogons, and the influence of parameters in avian visual models. It provides the first experimental evidence of a multifunctional behavioural display in elegant trogons, the first experimental evidence of specific plumage patches being used for species recognition in two sympatric congeners, and the first demonstration of the influence of the Great American Interchange on divergence of secondary sexual traits in any land-based taxa. In addition, by demonstrating the relative influence of individual parameters in a psychophysiological model of animal vision, my dissertation can be used to guide researchers when making assumptions concerning the visual capabilities of their species of interest. My findings should be of general interest to ecologists, behavioural ecologists, and evolutionary biologists.

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APPENDICES

Formulae

Chromatic contrast for tetrachromatic visual system

The receptor noise model (Vorobyev and Osorio 1998) states that the colour stimulus of surface x is defined by the quantum catch of each photoreceptor class i:

$$Q_{i,x} = \int_{\lambda_{\min}}^{\lambda_{\max}} R_x(\lambda) S_i(\lambda) I(\lambda) d(\lambda)$$

where λ is wavelength, $R_x(\lambda)$ is the wavelength-specific reflectance spectrum of the object x, $S_i(\lambda)$ is the wavelength-specific spectral sensitivity of receptor i, and $I(\lambda)$ is the wavelength-specific spectrum of ambient light. Integration in this study was calculated over the visible spectrum of birds, from 300 to 700 nm.

The relationship between the quantum catch of two stimuli (a and b) for photoreceptor class i is:

$$\Delta f_i = \ln(Q_{i,a}) - \ln(Q_{i,b}) = \ln\left(\frac{Q_{i,a}}{Q_{i,b}}\right)$$

The standard deviation of the noise of a single photoreceptor cell is represented by v_i. The effect of this noise on colour perception decreases with increase in the proportion of photoreceptors of a given class, such that the overall noise for a given class of photoreceptors is:

$$e_i = v_i / \sqrt{\eta_i}$$

where η_i is the density of photoreceptors of type i relative to the UVS densities, and e_i is the noise of type i of the four photoreceptor classes. All relative photoreceptor densities are calculated in relation to the UVS cone density.

Incorporating the noise and the difference in quantum catch between two stimuli, the square of chromatic contrast (ΔS) of two stimuli in a tetrachromatic system is given by:

$$(\Delta S)^2 = ((e_1 e_2)^2(\Delta f_4 - \Delta f_3)^2 + (e_1 e_3)^2(\Delta f_4 - \Delta f_2)^2 + (e_1 e_4)^2(\Delta f_3 - \Delta f_2)^2 + (e_2 e_3)^2(\Delta f_4 - \Delta f_1)^2 + (e_2 e_4)^2(\Delta f_3 - \Delta f_1)^2 + (e_3 e_4)^2(\Delta f_2 - \Delta f_1)^2)/((e_1 e_2 e_3)^2 + (e_1 e_2 e_4)^2 + (e_1 e_3 e_4)^2 + (e_2 e_3 e_4)^2)$$

Chromatic contrast is in units of just noticeable difference (or JND), representing chromatic discriminability.

Ocular media

The absorbance curve ($T_e(\lambda)$)of the ocular media can be approximated using:

$$T_e(\lambda) = \ln(8.928 \times 10^{-13}\lambda^5 - 2.595 \times 10^{-9}\lambda^4 + 3.006 \times 10^{-6}\lambda^3 - 0.001736\lambda^2 + 0.5013\lambda - 55.56)$$

Formula optimized for λ T50 = 335.2; curves for other T50 are λ-axis shifted using λT50 – 335.2 (Endler and Mielke 2005).

Oil filter

The average visual systems defined by Endler and Mielke (2005) use λ_{o} (wavelength at which oil droplet transmittance is 1/e) and b (rate of decay) to calculate absorbance curves for C, Y, and R types. The R package `pavo` (Maia et al. 2013) uses λcut (cut-off wavelength) and Bmid (and the gradient of line tangent to the absorbance spectrum (Bmid) at the wavelength at half-maximum absorbance) because λcut is the most commonly reported value (e.g., Hart and Vorobyev 2005).

When λcut and Bmid were not provided, they were calculated using the following equations (from Hart and Vorobyev 2005):

$$\lambda cut = \lambda_o - \left(\frac{0.37}{Bmid}\right)$$

$$Bmid = \frac{b}{2.89}$$

For species for which b was not available we estimated Bmid:

$$Bmid = 0.5 \div (\lambda mid - \lambda cut)$$

Table S4. 1 Sample identification number and GenBank NADH dehydrogenase subunit 2 accession numbers of the 41 species/subspecies included in the phylogenetic estimation, diversification analyses, and ancestral state reconstruction. Museum letter code identity: ANSP – American Museum of Science Philadelphia, CNAV – Colección Nacional de Aves, Instituto de Biología, Universidad Nacional Autónoma de México, FMNH – Field Museum of Natural History, LSUMNH – Louisiana State University Museum of Natural History, MBM – Marjorie Barrick Museum, STRI – Smithsonian Tropical Research Institute, NMNH – National Museum of Natural History (Smithsonian), MZUSP – Museu de Zoologia da Universidade de São Paulo, ZMUC – Zoological Museum University of Copenhagen.

Species	Subspecies	Country	Museum	SampleID	GenBank
T. bairdii		Panama	STRI	TBA383	EU603767
T. citreolus	*citreolus*	Mexico	CNAV	P002919	EU603770
T. citreolus	*sumachristi*	Mexico	CNAV	PE25988	EU603771
T. clathratus		Panama	NMNH	B02029	EU603772
T. collaris	*castaneus*	Bolivia	LSUMNH	B22827	EU603775
T. collaris	*collaris*	Guyana	NMNH	B10636	EU603778
T. collaris	*extimus*	Panama	NMNH	B01545	EU603790
T. collaris	*heotimus*	Panama	LSUMNH	B2141	EU603789
T. collaris	*puella*	Mexico	FMNH	394271	EU603783
T. collaris	*virginalis*	Ecuador	ANSP	ANSP2032	EU603777
T. comptus		Ecuador	ANSP	ANSP2297	EU603792
T. curucui	*behni*	Paraguay	LSUMNH	B25715	EU603799
T. curucui	*peruvianus*	Peru	FMNH	433225	EU603801
T. elegans	*ambiguus*	Mexico	MBM	JK03280	EU603805
T. elegans	*elegans*	El Salvador	FMNH	434014	EU603803
T. massena	*hoffmani*	Panama	MBM	JK04273	EU603813
T. massena	*massena*	Honduras	MBM	JK01022	EU603809
T. melanocephalus		Honduras	MBM	JK01035	EU603818
T. melanurus	*eumorphus*	Brazil	FMNH	391999	EU603825
T. melanurus	*melanurus*	Guyana	ANSP	ANSP8244	EU603830
T. melanurus	*mesurus*	Ecuador	ANSP	ANSP4683	EU603829
T. mexicanus		Mexico	MBM	JK03279	EU603838
T. personatus	*assimilis*	Ecuador	ANSP	ANSP506	EU603852
T. personatus	*duidae*	Venezuela	LSUMNH	B7596	EU603859
T. personatus	*heliothrix*	Peru	FMNH	397889	EU603857
T. personatus	*personatus*	Colombia	ZMUC	134954	EU603849
T. personatus	*submontanus*	Bolivia	ZMUC	115519	EU603848
T. personatus	*temperatus*	Ecuador	ANSP	ANSP3791	EU603851

T. rufus	*chrysochoros*	Paraguay	ZMUC	115780	EU603871
T. rufus	*cupreicauda*	Ecuador	ANSP	ANSP2216	EU603862
T. rufus	*rufus*	Guyana	ANSP	ANSP8471	EU603863
T. rufus	*sulphureus*	Peru	LSUMNH	B27391	EU603872
T. rufus	*teneullus*	Panama	MBM	GMS975	EU603867
T. surrucura	*aurantiventrtris*	Brazil	MZUSP	X7	EU603875
T. surrucurra	*surrucura*	Argentina	NMNH	B05982	EU603873
T. violaceus	*concinnus*	Ecuador	ANSP	ANSP5154	EU603880
T. violaceus	*ramonianus*	Bolivia	LSUMNH	B18257	EU603877
T. violaceus	*sallei*	Honduras	MBM	GAV1688	EU603884
T. violaceus	*violaceus*	Guyana	ANSP	ANSP8664	EU603882
T. viridis	*chionurus*	Ecuador	ANSP	ANSP4659	EU603898
T. viridis	*viridis*	Guyana	NMNH	B11332	EU603902

Table S4. 2 Accession numbers for all museum skins from which plumage characteristics were measured. Letter code preceding numbers indicate the museum identity: ANSP – American Museum of Science Philadelphia, FMNH – Field Museum of Natural History, LSUMNH – Louisiana State University Museum of Natural History, NMNH – National Museum of Natural History (Smithsonian), UMMZ – University of Michigan Museum of Zoology.

Species	Accession numbers		
T. bairdii	FMNH72259	FMNH72257	FMNH72258
T. citreoleus citreoleus	FMNH119116	FMNH102577	FMNH12703
T. citreoleus sumachristi	UMMZ95656	UMMZ102334	UMMZ102336
T. clathratus	UMMZ132437	UMMZ132436	
T. collaris castaneus	FMNH310556	FMNH299112	FMNH397885
T. collaris collaris	FMNH91962	FMNH41631	UMMZ87794
T. collaris extimus	NMNH238035	NMNH238533	
T. collaris exoptatus	FMNH261142	FMNH261143	FMNH261147
T. collaris heotinus	NMNH484311		
T. collaris puella	UMMZ102328	UMMZ101971	UMMZ102326
T. collaris virginalis	FMNH278528	FMNH278529	FMNH372522
T. comptus	ANSP157260	ANSP180260	ANSP182335
T. curucui behni	UMMZ90785	UMMZ98112	UMMZ111382
T. curucui curucui	FMNH63529	FMNH63530	FMNH63532
T. curucui peruvianus	FMNH283679	FMNH310557	FMNH248627
T. elegans ambiguus	UMMZ87803	UMMZ21305	UMMZ85777
T. elegans elegans	FMNH434014	FMNH212774	FMNH212773
T. massena hoffmani	FMNH111560	FMNH6964	FMNH302808
T. massena massena	FMNH95212	FMNH95214	FMNH95217
T. melanocephalus	FMNH120984	FMNH41590	FMNH119529
T. melanurus eumorphus	FMNH283676	FMNH153708	FMNH262791
T. melanurus macroura	FMNH48988	FMNH190784	FMNH72251
T. melanurus melanurus	FMNH120074	FMNH295591	FMNH260239
T. melanurus mesurus	ANSP183900	ANSP183901	ANSP185287
T. mexicanus	FMNH343219	FMNH183358	FMNH93699
T. personatus assimilis	ANSP180261	ANSP180262	ANSP181038
T. personatus duidae	AMNH270848	FMNH318851	
T. personatus heliothrix	FMNH44271	FMNH44272	FMNH44273
T. personatus personatus	FMNH43354	FMNH99532	FMNH119402
T. personatus submontanus	UMMZ154015	UMMZ154016	
T. personatus temperatus	NMNH436155	NMNH436156	NMNH446363
T. rufus chrysochlorus	UMMZ100718	UMMZ111061	UMMZ101727
T. rufus cupreicauda	FMNH255536	FMNH262664	FMNH292789
T. rufus rufus	FMNH260247	FMNH260246	FMNH295595

T. rufus sulphureus	AMNH431982	FMNH248628	FMNH456560
T. rufus tenellus	FMNH73768	FMNH372524	FMNH372526
T. surrucura aurantius	AMNH242298	AMNH316669	AMNH317394
T. surrucura surrucura	FMNH75162	FMNH64469	FMNH75160
T. violaceus caligatus	FMNH190787	FMNH190786	
T. violaceus concinus	UMMZ132454	UMMZ210616	UMMZ132456
T. violaceus crissalis	FMNH248626		
T. violaceus ramonianus	LSUMNH71917	LSUMNH132155	LSUMNH153260
T. violaceus sallaei	UMMZ137725	UMMZ137722	UMMZ137724
T. violaceus violaceus	FMNH318854	FMNH260250	FMNH260249
T. viridis chionurus	NMNH461910	NMNH477622	NMNH484309
T. viridis viridis	FMNH318848	FMNH91968	FMNH120077

Table S4. 3 Parameters and AICc scores of all GLMM model ordered with decreasing number of parameters. Models included plumage differences as the dependent variable and subspecies identity as the within-subject random factor.

Model	Parameters	AICc
Global	Sympatry Genetic distance Clade Location Latitude Longitude Clade*Sympatry Location*Sympatry	893.133
1)	Sympatry Genetic distance Clade Location Clade*Sympatry Location*Sympatry	880.58
2)	Sympatry Genetic distance Clade Location Location*Sympatry	873.552
4)	Sympatry Genetic distance Location Clade Clade*Sympatry	876.845
5)	Sympatry Genetic distance Location Clade	872.261
6)	Sympatry Genetic distance	872.667
7)	Intercept	901.815

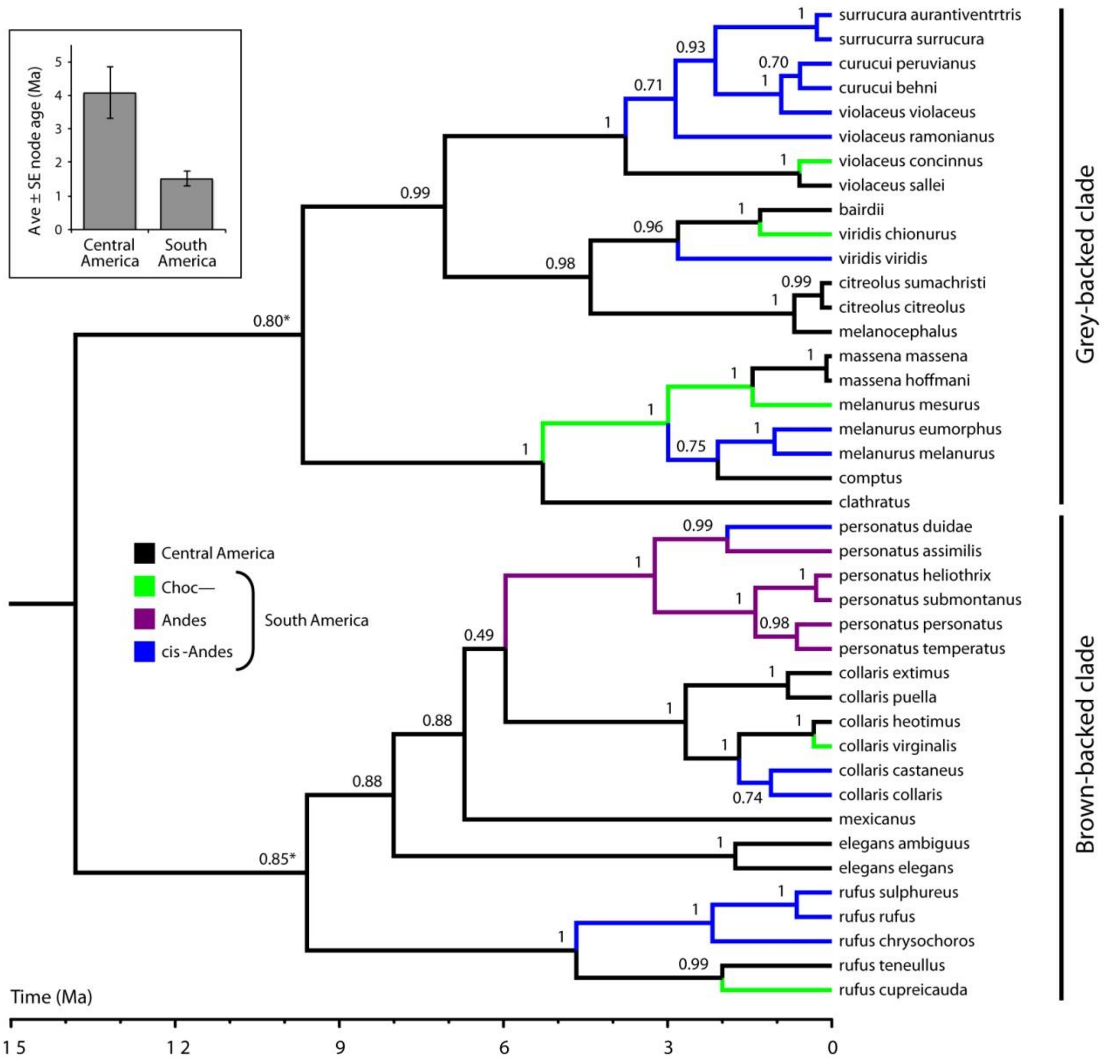

Figure S4. 1 Molecular phylogeny of 41 *Trogon* species/subspecies and ancestral state reconstruction of ancestral areas. Numbers on nodes correspond to posterior probability support, and asterisks mark nodes that receive posterior probability values of 1.0 when outgroups are included in the analysis. Branch colors show ancestral state reconstruction results based on parsimony, with ambiguous results resolved using maximum likelihood. Inset: Average node ages for Central American and South American (including Choco, Andes, *cis*-Andes) lineages show that diversification has been more recent in South America (t-test, $P = 0.008$).

Table S5. 1 Catalogue numbers for all specimens measured. AMNH = American Museum of Natural History, New York; FMNH = Field Museum of Natural History, Chicago; ROM: Royal Ontario Museum, Toronto; UMMZ = University of Michigan Museum of Zoology, Ann Arbor.

Scientific name	Common name	Male 1	Male 2	Male 3	Female 1	Female 2	Female 3
Acryllium vulturinum	Vulturine Guineafowl	FMNH_192683	ROM_34.9.6.1	FMNH_405746	ROM_33.6.20.1	FMNH_192686	FMNH_406226
Afropavo congoensis	Congo Peafowl	AMNH_763938	AMNH_305691	AMNH_763937	AMNH_763941	AMNH_305693	AMNH_305692
Agriocharis ocellata	Ocellated Turkey	UMMZ_95038	FMNH_40755	FMNH_13216	FMNH_120862	ROM_37192	AMNH_61172
Alectoris barbara Barbara	Barbary Partridge	FMNH_404276	FMNH_407988	FMNH_406930	ROM_33.9.1.125	FMNH_404277	FMNH_411638
Alectoris graeca	Rock Partridge	ROM_91811	ROM_36988	ROM_146344	ROM_146345	ROM_146343	FMNH_415114
Alectoris rufa	Red-legged Partridge	FMNH_408741	FMNH_408731	FMNH_408743	FMNH_408740	FMNH_409848	FMNH_408742
Alectura lathami	Australian Brush-turkey	FMNH_415316	FMNH_415320	FMNH_417123	FMNH_400782	AMNH_539307	AMNH_539306
Arborophila rufogularis	Rufous-throated Hill Partridge	ROM_37049	ROM_37050	ROM_37048	FMNH_84360	FMNH_84357	FMNH_217900
Arborophila torqueola torqueola	Common Hill-partridge	ROM_37045	ROM_37046	ROM_37044	ROM_37047	FMNH_84368	FMNH_426050
Argusianus argus	Great Argus	FMNH_414261	ROM_26510	ROM_37157	FMNH_414262	FMNH_40724	AMNH_544057
Bambusicola fytchii	Mountain Bamboo-partridge	UMMZ_140962	UMMZ_140961	UMMZ_140960	UMMZ_140940	UMMZ_140915	UMMZ_140932
Bambusicola thoracica	Chinese Bamboo-partridge	UMMZ_57477	ROM_29067	FMNH_404463	UMMZ_57478	FMNH_404472	FMNH_406543
Bonasa (Tetrastes) bonasia	Hazel Grouse	ROM_36721	FMNH_414729	FMNH_412918	ROM_36722	FMNH_416633	FMNH_412919
Bonasa umbellus	Ruffed Grouse	FMNH_131131	ROM_36770	ROM_29214	ROM_80226	ROM_145996	ROM_36772
Catreus wallichi	Cheer Pheasant	FMNH_426070	ROM_37101	ROM_01.10.1.18	FMNH_96808	ROM_67550	FMNH_16224
Chrysolophus amherstiae	Lady Amherst' Pheasant	FMNH_410562	ROM_23.2.27.1	ROM_68495	FMNH_111885	FMNH_67905	FMNH_408997
Chrysolophus pictus	Golden Pheasant	FMNH_109179	FMNH_88551	UMMZ_84354	UMMZ_54313	ROM_69042	ROM_28221
Coturnix coturnix	Common Quail	ROM_75193	ROM_75194	ROM_33.9.1.130	ROM_81613	ROM_91.11.1.900	ROM_37019
Coturnix japonica	Japanese Quail	ROM_37022	FMNH_406545	FMNH_411130	ROM_37023	FMNH_419107	FMNH_405133
Crax rubra	Great Curassow	FMNH_418523	ROM_112814	FMNH_15452	ROM_36563	FMNH_411741	FMNH_411742
Crossoptilon auritum	Blue Eared-pheasant	ROM_35.11.15.6	ROM_66902	FMNH_109187	FMNH_109188	FMNH_410201	-
Crossoptilon mantchuricum	Brown Eared-pheasant	ROM_21.3.6.2	ROM_34.3.23.5	ROM_37080	FMNH_392224	ROM_22.12.15.1	AMNH_543113

Francolinus francolinus	Black Francolin	FMNH_413367	ROM_36995	FMNH_420353	FMNH_420345	FMNH_420336	FMNH_420351
Francolinus pondicerianus	Grey Francolin	FMNH_410845	FMNH_410848	FMNH_414052	FMNH_414055	FMNH_414054	FMNH_414053
Francolinus squmatus	Scaly Francolin	FMNH_423915	FMNH_417588	FMNH_417590	FMNH_403913	FMNH_423907	FMNH_417587
Francolinus swainsonii	Swainson’s Francolin	ROM_121044	FMNH_410600	FMNH_423156	ROM_121043	ROM_91212	FMNH_486021
Gallus gallus	Red Junglefowl	FMNH_420755	FMNH_400745	FMNH_420759	FMNH_420737	FMNH_420742	FMNH_420770
Gallus lafayettei	Ceylon Junglefowl	FMNH_401144	FMNH_422530	FMNH_401145	FMNH_422528	AMNH_543371	AMNH_203777
Gallus sonneratii	Grey Junglefowl	FMNH_414948	FMNH_414949	FMNH_420789	FMNH_414947	FMNH_420785	FMNH_420802
Gallus varius	Green Junglefowl	FMNH_405246	FMNH_405166	FMNH_406655	FMNH_406656	FMNH_405247	AMNH_543402
Ithaginis cruentus	Blood Pheasant	FMNH_109175	FMNH_109176	FMNH_403880	FMNH_404607	FMNH_403882	FMNH_109177
Lophophorus impejanus	Himalayan Monal	FMNH_84350	ROM_01.10.1.37	ROM_37078	FMNH_84351	UMMZ_234309	ROM_37079
Lophophorus lhuysii	Chinese Monal	FMNH_109196	FMNH_88542	FMNH_88543	FMNH_88544	AMNH_423702	AMNH_543110
Lophophorus sclateri	Sclater's Monal	AMNH_543103	AMNH_543104	AMNH_543108	FMNH_97920	AMNH_543107	-
Lophura edwardsi	Edward’s Pheasant	FMNH_76414	AMNH_348673	-	UMMZ_119960	ROM_3510222	-
Lophura leucomelana	Kalij Pheasant	FMNH_210931	ROM_26812	ROM_29.1.20.1	FMNH_210937	FMNH_217897	FMNH_210934
Lophura nycthemera	Silver Pheasant	FMNH_408966	ROM_36.2.25.4	ROM_24112	ROM_1822810	ROM_19481	FMNH_408967
Lophura swinhoii	Swinhoe’s Pheasant	FMNH_405134	ROM_32029	ROM_35.12.17.6	UMMZ_119958	ROM_3471898	FMNH_405135
Meleagris gallopavo	Wild Turkey	FMNH_93516	ROM_37176	ROM_31973	FMNH_160406	ROM_34.5.8.3	ROM_37181
Numida meleagris	Helmeted Guineafowl	ROM_33.9.1.141	ROM_114469	FMNH_405724	FMNH_405726	FMNH_405719	FMNH_192654
Ortalis vetula	Plain Chachalaca	ROM_36570	ROM_36571	ROM_81801	ROM_36572	ROM_81800	FMNH_409461
Pavo cristatus	Indian Peafowl	ROM_26.3.23.144	FMNH_421426	ROM_37164	FMNH_420844	ROM_27.4.6.1	ROM_37165
Pavo muticus	Green Peafowl	FMNH_404960	FMNH_92678	ROM_37166	FMNH_404962	FMNH_405167	FMNH_404961
Perdix dauuricae	Daurian Partridge	FMNH_96819	FMNH_406733	FMNH_56309	FMNH_56305	FMNH_56312	FMNH_56308
Perdix hodgsoniae	Tibetan Partridge	FMNH_408819	FMNH_67884	AMNH_541962	FMNH_408818	FMNH_109182	FMNH_109183
Perdix perdix	Grey Partridge	ROM_80227	ROM_74165	ROM_146348	ROM_36.1.4.1	ROM_37006	ROM_134533
Phasianus colchius	Ring-necked Pheasant	FMNH_404491	ROM_67044	ROM_29588	ROM_37135	ROM_31.5.27.7	ROM_29589
Phasianus versicolor	Green Pheasant	FMNH_405140	FMNH_405142	FMNH_405141	FMNH_405143	FMNH_405138	FMNH_405139
Polyplectron bicalcaratum	Grey Peacock-pheasant	FMNH_400753	FMNH_401330	FMNH_415143	FMNH_415142	FMNH_400754	AMNH_409108

Polyplectron chalcurum	Bronze-tailed Peacock pheasant	AMNH_543975	AMNH_543979	AMNH_257149	AMNH_543980	AMNH_543981	AMNH_543974
Polyplectron emphanum	Palawan Peacock-pheasant	FMNH_426082	FMNH_416817	FMNH_416818	FMNH_404223	AMNH_544041	AMNH_544040
Polyplectron germaini	Germain's Peacock-pheasant	FMNH_89970	AMNH_417029	AMNH_544015	ROM_37154	AMNH_544017	AMNH_544019
Polyplectron inopinatum	Mountain Peacock pheasant	AMNH_543966	AMNH_543971	AMNH_804683	AMNH_543969	AMNH_203867	-
Polyplectron malacense	Malaysian Peacock-pheasant	AMNH_544026	AMNH_544022	-	ROM_3250	AMNH_203879	-
Pucrasia macrolopha	Koklass Pheasant	FMNH_40731	ROM_01.10.1.16	ROM_37099	ROM_37100	FMNH_416216	FMNH_416217
Rheinardia ocellata	Crested Argus	FMNH_UCMROO	AMNH_258935	AMNH_544046	FMNH_76415	AMNH_348697	-
Syrmaticus ellioti	Elliot's Pheasant	FMNH_96805	ROM_68392	ROM_95005	ROM_34.3.7.1	FMNH_39345	AMNH_543904
Syrmaticus humiae	Hume's Pheasant	FMNH_415486	FMNH_415488	FMNH_415485	FMNH_415492	FMNH_415489	FMNH_415496
Syrmaticus reevesii	Reeve's Pheasant	FMNH_88552	UMMZ_119966	ROM_37139	UMMZ_119967	ROM_34.3.7.2	ROM_34.7.9.4
Syrmaticus soemmerringii	Copper pheasant	FMNH_405149	ROM_24.3.13.392	ROM_37140	ROM_98.4.8.2	FMNH_96965	FMNH_405147
Tetrao tetrix	Eurasian Black Grouse	FMNH_67078	ROM_2925	ROM_3198	ROM_9085	ROM_146360	FMNH_406927
Tetrao urogallus	Western Capercaillie	FMNH_404587	FMNH_67034	ROM_36582	FMNH_401633	FMNH_406928	FMNH_408409
Tetraogallus himalayensis	Himalayan Snowcock	FMNH_410838	FMNH_60618	AMNH_804741	ROM_36984	FMNH_420101	FMNH_410836
Tetraogallus tibetanus	Tibetan Snowcock	FMNH_426040	FMNH_410841	FMNH_410842	FMNH_420097	FMNH_420095	AMNH_540543
Tetraophasis obscurus	Verreaux's Monal Partridge	FMNH_410198	FMNH_410199	FMNH_109172	FMNH_410196	AMNH_540578	AMNH_204527
Tetraophasis szechenyii	Szechenyi's Monal Partridge	FMNH_409970	FMNH_411061	AMNH_540588	FMNH_67913	AMNH_291992	AMNH_540581
Tragopan blythii	Blyth's Tragopan	FMNH_415463	FMNH_415461	FMNH_399352	FMNH_415132	FMNH_415462	FMNH_415465
Tragopan caboti	Cabot's Tragopan	FMNH_51135	FMNH_407536	ROM_10.2.21.24	FMNH_51136	FMNH_407663	ROM_156309
Tragopan satyra	Satyr Tragopan	FMNH_414243	FMNH_84323	FMNH_84321	FMNH_84327	FMNH_84325	AMNH_817845
Tragopan temminckii	Temminck's Tragopan	FMNH_88534	FMNH_88533	FMNH_88537	FMNH_88536	FMNH_88540	FMNH_88541

UCMROO = uncatalogued

Table S5. 2 Spectral parameters of cone visual pigments in avian species separated by eye type (UV range SWS1 or VIS range SWS1).

Order	Species	Photoreceptor *λmax* (nm)					References
		UV	VIS	SWS2	MWS	LWS	
Anseriformes	*Anas platyrhynchos*		415	452	506	567	1
	Branta canadensis		409	458	509	580	2
Apodiformes	*Sephanoides sphanoides*	371		444	508	560	3
Columbiformes	*Columbia livia*		404	452	506	566	4
Galliformes	*Coturnix coturnix*		418	450	505	567	5
	Gallus gallus		418	453	507	571	4
	Meleagris gallopavo		420	460	505	563	6
	Pavo cristatus		424	458	505	567	7
Gruiformes	*Grus americana*		404	450	499	561	8
Passeriformes	*Amadia fasciata*	370		447	500	563	9
	Corvus frugilegus				497	565	10
	Dolichonyx oryzivorus	372			505	564	11
	Erythrura gouldiae	370		440	500	562	9
	Leothrix lutea	355		454	499	568	12
	Lonchura maja	373		446	500	562	9
	Neochmia modesta	373		442	500	565	9
	Parus caeruleus	372		449	502	563	13
	Passer domesticus			445	503	563	14
	Ptilonorhynchus violaceus		410	454	511	562	15
	Serinus canaria	363		440	501	567	16
	Spinus tristis		399	442	512	580	17
	Sturnus vulgaris	362		449	504	563	18
	Taeniopygia guttata	359		427	505	566	4, 19
	Turdus merula	373		454	504	557	13
Procellariformes	*Puffinus pacificus*		406	450	503	566	20
	Puffinus puffinus		402	452			4
Psittaciformes	*Melopsittacus undulatus*	371		440	499	566	4
	Platycercus elegans	365		440	509	567	21
Spheniciformes	*Spheniscus humboldti*		403	450		543	22
Strigiformes	*Strix aluco*			463	503	555	23
Struthioniformes	*Rhea americana*			447	506	571	24
	Struthio camelus		405	445	506	570	24

Table S5. 3 Spectral absorption parameters for oil droplets and ocular media in avian eyes. See Methods for meaning of λcut, λmid and T50.

Order	Species	λcut (nm)			λmid(nm)			SWS1 Pigment	OM T50	Oil droplet reference	OM Reference
		C type	Y type	R type	C type	Y type	R type				
Accipitriformes	*Accipiter nisus*							VS	369		25
	Buteo buteo							VS	375		25
	Milvus milvu							VS	394		25
Anseriformes	*Anas platyrhynchos*	445	506	561	459	521	585	VS	371	1	1
	Branta canadensis		506	559		526	598	VS		2	
Apodiformes	*Apus apus*							VS	388		25
	Sephanoides sephanoides							UVS	315		3
Charadriiformes	*Larus marinus*							UVS	344		26
Columbiformes	*Columba livia*	448	514	586	470	542	613	VS	337	4	27
Falconiformes	*Falco tinnunculus*							VS	379		25
Galliformes	*Conturnix conturnix*	446	511	566	461	528	589	VS		5	
	Gallus gallus	443	505	561	460	523	586	VS	351	4	27
	Meleagris gallopavo							VS	355		6
	Pavo cristatus	449	511	569	462	525	592	VS	364	7	7
Gruiformes	*Grus americana*	448	522	576				VS		8	
Passeriformes	*Ailuroedus crassirostris*	421	508	558	438	526	580	VS	340	15	15
	Amadina fasciata	423	516	575	439	535	598	UVS	316	9	9
	Chlamydera maculata	428	515	571	449	533	595	VS	351	15	15
	Chlamydera nuchalis	421	515	568	440	530	590	VS	349	15	15
	Corvus frugilegus							VS	365		25
	Cyanistes (Parus) caeruleus	413	508	573	426	528	596	UVS	316	13	13

	Dolichonyx oryzivorus	412	502	561	429	519	584	UVS		11	
	Erythrura gouldiae	422	513	572	434	531	595	UVS	315	9	9
	Leothrix lutea	392	506	566	419	530	591	UVS		12	
	Lonchura maja	422	510	567	434	524	589	UVS	317	9	9
	Neochmia modesta	415	514	568	428	534	591	UVS	314	9	9
	Parus major							UVS	314		25
	Pica pica							VS	370		25
	Ptilonorhynchus violaceus	423	514	567	435	534	591	VS	344	15	15
	Scenopoetes dentirostris	424	514	567	438	532	589	VS		15	
	Sericulus chrysocephalus	418	511	567	431	528	589	VS	349	15	15
	Serinus canaria	414	506	578	431	531	604	UVS		16	
	Spinus tristis	417	523	579	432	537	596	VS		17	
	Sturnus vulgaris	399	515	573	419	536	595	UVS	337	18	18
	Taeniopygia guttata	414	510	571	432	537	597	UVS	321	4	25
	Turdus merula	414	515	570	429	532	593	UVS	343	13	13
	Turdus philomelos							UVS	335		25
Podicipediformes	*Podiceps cristatus*							VS	390		25
Procellariiformes	*Puffinus pacificus*	445	506	562	460	528	586	VS	335	20	20
Psittaciformes	*Melopsittacus undulatus*	411	507	566	429	544	592	UVS	320	4	27
	Neopsephotus bourkii							UVS	334		25
	Platycercus elegans							UVS	319		28
Strigiformes	*Aegolius funereus*							VS	335		25
	Asio otus							VS	356		25
	Athene cunicularia							VS	359		25
	Strix aluco							VS	353		25
Struthioniformes	*Rhea americana*	417	506	556	439	524	585	VS		24	
	Struthio camelus							VS	369		24

Table S5. 4 Ratio of photoreceptor densities in avian retinas. Photoreceptor with lowest proportion was always given 1.00.

Order	Species	SWS1	SWS2	MWS	LWS	Reference
Anseriformes	*Anas penelope*	1.00	2.10	4.28	4.17	29
	Aythya affinis	1.00	2.73	4.09	4.23	29
	Branta canadensis	1.00	3.16	4.18	5.92	2
Apodiformes	*Sephanoides sephaniodes*	1.00	2.60	4.40	3.00	3
Charadriiformes	*Anous minutus*	1.00	9.59	16.82	14.29	29
	Larus novaehollandiae	1.00	1.87	2.38	2.34	29
Columbiformes	*Streptopelia chinensis*	1.00	1.25	1.61	1.43	29
Coraciiformes	*Todiramphus sanctus*	1.00	1.32	1.55	6.36	29
Cuculiformes	*Eudynamys scolopacea*	1.00	2.28	3.65	3.11	29
Galliformes	*Gallus gallus*	1.00	1.48	2.48	2.01	30
	Pavo cristatus	1.00	1.88	2.20	2.11	29
Gruiformes	*Gallinula tenebrosa*	1.00	1.69	2.10	2.19	29
Passeriformes	*Ailuroedus crassirostris*	1.00	1.79	2.59	2.07	15
	Chlamydera nuchalis	1.00	1.84	2.84	2.94	15
	Entomyzon cyanotis	1.00	1.96	2.70	2.61	29
	Leiothrix lutea	1.00	2.50	2.50	5.50	12
	Manorina melanocephala	1.00	1.84	2.26	2.30	29
	Parus caeruleus	1.00	1.89	2.67	2.67	29
	Parus caeruleus	1.00	1.92	2.68	2.70	13
	Ptilonorhynchus violaceus	1.00	2.36	3.53	3.15	29
	Ptilonorhynchus violaceus	1.00	1.69	2.88	3.12	15
	Scenopoeetes dentirostris	1.00	2.40	3.09	2.77	15
	Sericulus chrysocephalus	1.00	1.71	3.71	3.93	15
	Spinus tristis	1.00	2.18	2.36	1.94	17
	Sturnus vulgaris	1.00	1.36	3.70	3.77	29
	Turdus merula	1.00	1.71	2.14	1.89	29
	Turdus merula	1.00	1.78	2.21	1.96	13
Pelecaniformes	*Phalacrocorax varius*	1.00	2.45	5.83	1.43	29
Procellariiformes	*Puffinus pacificus*	1.47	1.00	1.53	2.12	29
Psittaciformes	*Cacatua roseicapilla*	1.00	1.24	3.96	4.18	29
	Melopsittacus undulatus	1.00	1.89	2.94	2.48	29
	Platycercus eximius	1.00	1.88	3.60	3.87	29
	Trichoglossus chlorolepidotus	1.00	1.73	3.29	3.11	29
	Trichoglossus haematodus	1.00	1.28	2.86	2.63	29

Reference details at end of Supplementary material

1 Jane and Bowmaker 1988 J Comp Physiol A 162:225-235; 2 Moore et al. 2012 J Exp Biol 215:3442-3452; 3 Herrera et al. 2008 J Comp Physiol A 194:785-794; 4 Bowmaker et al 1997 Vis

Res 37:2183-2194; 5 Bowmaker et al 1993 Vis Res 33:571-578; 6 Hart et al 1999 Vis Res 39:3321-3328; 7 Hart 2002 J Exp Biol 205:3925-3935; 8 Porter et al. 2014 J Exp Biol 217:3883-3890; 9 Hart et al 2000 J Comp Physiol A 186:681-694; 10 Bowmaker 1977 Vis Res 17:1129-1138; 11 Beason and Loew 2008 Vis Res 48:1-8; 12 Maier and Bowmaker 1993 J Comp Physiol A 172:295-301; 13 Hart et al. 2000 J Comp Physiol A 186:375:387; 14 Hart and Hunt 2007 Am Nat 169:S7-S27; 15 Coyle et al 2012 J Exp Biol 215:1090-1105; 16 Das et al 1999 Vis Res 39:2801-2815; 17 Baumhardt et al 2012 Brain Behav and Evol 83:181-198; 18 Hart et al 1998 J Exp Biol 201:1433-1446; 19 Yokoyama et al 2000 PNAS 97:7366-7371; 20 Hart 2004 J Exp Biol 207:1229-1240; 21 Knott et al 2013 J Exp Biol 216: 4454-4461; 22 Bowmaker and Martin 1985 J Comp Physiol A 156:71-77; 23 Bowmaker and Martin 1978 Vis Res 18:1125-1130; 24 Wright and Bowmaker 2001 Vis Res 41:1-12; 25 Lind et al 2013 J Exp Biol 216:1819-1827; 26 Hastad et al 2009 J Comp Phys A 195:585-590; 27 Lind and Kelber 2009 Vis Res 49:1939-1947; 28 Carvalho et al 2011 Proc Roy Soc 278:107-114; 29 Hart 2001 J Comp Physiol A 187:685-698; 30 Kram et al 2010 PLoS one 5:e8992

Table S5. 5 Parameters used to reproduce the average VIS and average UV avian visual systems presented in Endler and Mielke (2005). These visual systems were used as the starting point for comparison of the various parameters.

Eye Type	Parameter	Ocular media (nm)	UV/VIS	SWS	MWS	LWS
UV		324				
	Peak sensitivities (nm)		367	444	501	564
	λ cut		NA†	411	511	572
	Bmid		NA	0.0278	0.023	0.022
VIS		352*				
	Peak sensitivities (nm)		412	452	505	565
	λ cut		NA	447	510	572
	Bmid		NA	0.0294	0.028	0.027

*Endler and Mielke (2005) indicate a value of 362nm for the ocular media cut-off point but we could only reproduce the photoreceptor curves from their supplemental material when using 352nm.

†Oil droplets associated with the SWS1 photoreceptor do not filter light between 300 and 700nm.

Table S5. 6 Summary of photoreceptor sensitivities of the four avian cone classes separated by eye type. Values were derived by compiling all known measurements of these parameters (See Table S5.2 for complete data and references).

Cone class	Eye type	Minimum *λmax* (nm)	Maximum *λmax* (nm)	Mean ± SD *λmax* (nm)	N
SWS1	UVS	355	373	368 ± 6	14
	VS	399	424	410 ± 8	14
SWS2	UV	427	454	444 ± 7	13
	VS	442	463	452 ± 6	17
MWS	UV	499	509	503 ± 3	14
	VS	497	512	505 ± 4	16
LWS	UV	557	568	564 ± 3	14
	VS	543	580	566 ± 9	17

Table S5. 7 Summary of oil droplet cut-off parameters of three avian cone classes and T50 of the ocular media, separated by eye type. Values were derived by compiling all known measurements of these parameters (See Table S5.3 for complete data and references).

Parameter	Eye type	λ Min (nm)	λ Max (nm)	λ Mean ± SD (nm)	N
OM T50	UVS	314	344	324 ± 11	15
	VIS	335	394	360 ± 17	24
λ cut C	UVS	392	423	413 ± 9	12
	VIS	417	449	433 ± 13	15
Bmid C	UVS	0.0187*	0.0273*		
	VIS	0.0380†	0.0318*		
λ cut Y	UVS	502	516	510 ± 4	12
	VIS	505	523	512 ± 6	16
Bmid Y	UVS	0.0294‡	0.0228*		
	VIS	0.0256*	0.0380†		
λ cut R	UVS	561	578	570 ± 5	12
	VIS	556	586	567 ± 8	16
Bmid R	UVS	0.0294‡	0.0187*		
	VIS	0.0170*	0.0190*		

* Calculated from b

† Obtained from literature

‡ Calculated from λ cut and λ mid

Table S5. 8 Photoreceptor density ratios values selected for comparisons from all known ratios with the justification for including these in our analyses (See Table S5.4 for complete data and references).

Order	Species	SWS1	SWS2	MWS	LWS	Reason for inclusion
Anseriformes	*Branta canadensis*	1.00	3.16	4.18	5.92	Largest SWS2 value (Excluding *A. minutus*)
Charadriiformes	*Anous minutus*	1.00	9.59	16.82	14.29	Most skewed overall
Columbiformes	*Streptopelia chinensis*	1.00	1.25	1.61	1.43	Smallest (Max/Mean)
Coraciiformes	*Todiramphus sanctus*	1.00	1.32	1.55	6.36	Largest (Max/Mean) (Excluding *A. minutus*)
Galliformes	*Pavo cristatus*	1.00	1.88	2.20	2.11	Classic visual system
Passeriformes	*Leiothrix lutea*	1.00	2.50	2.50	5.50	Most skewed Passerine
Passeriformes	*Average*	1.00	1.91	2.79	2.96	Average passerine
Pelecaniformes	*Phalacrocorax varius*	1.00	2.45	5.83	1.43	Most skewed MWS
Procellariiformes	*Puffinus pacificus*	1.47	1.00	1.53	2.12	SWS2 not SWS1 is smallest value

Table S5. 9 Summary of total dichromatism score changes of 70 species of the Order Galliformes when comparing the influence of changing light environments. Values reported describe the correlation between the scores (Pearson's r), how many species (out of 70) were assigned the same rank in the comparison (Equal rank), the average rank change (Rank change), the standard deviation of rank change (Rank SD), and the maximum rank change (Max change). The simulations were conducted using both the 'average UV' and 'average VIS' eye types. See Methods and Results section for more details. Main comparisons are in relation to an ideal illuminant (wavelength independent) and final comparison presents the largest pariwise differences, based on the lowest Pearson's r value.

UV Eye type	Pearson's r	Equal rank	Rank change	Rank SD	Max change	*VIS Eye type*	Pearson's r	Equal rank	Rank change	Rank SD	Max change
Forest Shade	0.9996	41	0.71	1.18	7	Forest Shade	0.9992	32	0.77	0.95	4
Woodland	0.9997	40	0.71	1.14	7	Woodland	0.9996	39	0.54	0.70	3
Blue Sky	0.9999	51	0.31	0.55	2	Blue Sky	0.9999	61	0.20	0.58	3
D65	0.9987	28	1.09	1.45	10	D65	0.9986	23	1.06	1.11	5
Gaps	0.9995	32	0.89	1.16	7	Gaps	0.9991	25	0.91	0.97	4
Cloudy	0.9996	37	0.77	1.16	7	Cloudy	0.9994	36	0.66	0.85	4
Sky vs D65	0.9986	28	1.17	1.56	10	Average vs D65	0.9986	23	1.06	1.11	5

Table S5. 10 Summary of total dichromatism score changes of 70 species of the Order Galliformes when comparing the influence of changing maximum photoreceptor sensitivity values. Values reported describe the correlation between the scores (Pearson’s r), how many species (out of 70) were assigned the same rank in the comparison (Equal rank), the average rank change (Rank change), the standard deviation of rank change (Rank SD), and the maximum rank change (Max change). The simulations were conducted using both the ‘average UV’ and ‘average VIS’ eye types and modifying the photoreceptor sensitivity parameter using the values presented in Table S6. See Methods and Results section for more details. Main comparisons are in relation to the average visual system and final comparison presents the largest pariwise differences, based on the lowest Pearson’s r value.

UV Eye type	Pearson’s r	Equal score	Rank change	Rank SD	Max change	*VIS Eye type*	Pearson’s r	Equal score	Rank change	Rank SD	Max change
SWS1 Max	0.9999	46	0.43	0.67	3	SWS1 Max	0.9995	35	0.69	0.83	3
SWS1 Min	0.9994	40	0.49	0.63	3	SWS1 Min	0.9995	45	0.51	0.79	3
SWS2 Max	0.9999	56	0.23	0.52	3	SWS2 Max	0.9999	54	0.26	0.53	3
SWS2 Min	0.9996	53	0.26	0.47	2	SWS2 Min	0.9999	63	0.11	0.36	2
MWS Max	0.9999	64	0.11	0.40	2	MWS Max	1.0000	66	0.06	0.23	1
MWS Min	1.0000	65	0.09	0.33	2	MWS Min	1.0000	58	0.17	0.38	1
LWS Max	0.9994	44	0.43	0.63	3	LWS Max	0.9996	39	0.54	0.70	3
LWS Min	0.9994	33	0.74	0.90	4	LWS Min	0.9992	46	0.43	0.65	2
All Max	0.9999	47	0.40	0.65	3	All Max	0.9994	32	0.74	0.86	4
All Min	0.9993	34	0.69	0.84	4	All Min	0.9988	39	0.66	0.95	5
All Max vs All Min	0.9986	26	1.00	1.19	6	All Max vs All Min	0.9966	25	1.17	1.45	8

Table S5. 11 Summary of total dichromatism score changes of 70 species of the Order Galliformes when comparing the influence of changing oil droplet cut-off values. Values reported describe the correlation between the scores (Pearson's r), how many species (out of 70) were assigned the same rank in the comparison (Equal rank), the average rank change (Rank change), the standard deviation of rank change (Rank SD), and the maximum rank change (Max change). The simulations were conducted using both the 'average UV' and 'average VIS' eye types and modifying the oil droplet cut-off parameter using the values presented in Table S5.7. See Methods and Results section for more details. Main comparisons are in relation to the average visual system and final comparison presents the largest pariwise differences, based on the lowest Pearson's r value.

UV *Eye type*	Pearson's r	Equal score	Rank change	Rank SD	Max change	*VIS* *Eye type*	Pearson's r	Equal score	Rank change	Rank SD	Max change
C Max	0.9998	55	0.26	0.56	3	C Max	1.0000	68	0.03	0.17	1
C Min	0.9999	60	0.17	0.45	2	C Min	0.9976	37	0.83	1.25	8
Y Max	1.0000	68	0.03	0.17	1	Y Max	0.9999	64	0.09	0.28	1
Y Min	0.9998	57	0.23	0.54	3	Y Min	1.0000	62	0.11	0.32	1
R Max	0.9999	60	0.14	0.35	1	R Max	0.9993	30	0.77	0.85	4
R Min	0.9992	40	0.63	0.94	4	R Min	0.9993	47	0.37	0.59	3
All Max	0.9998	55	0.29	0.64	3	All Max	0.9893	15	2.40	2.42	13
All Min	0.9992	44	0.57	0.93	4	All Min	0.9966	29	0.89	1.11	7
R Min vs All Max	0.9983	35	0.83	1.17	7	R Max vs All Max	0.9880	10	2.69	2.39	12

Table S5. 12 Summary of total dichromatism score changes of 70 species of the Order Galliformes when comparing the influence of changing ocular media absorbance curves. Values reported describe the correlation between the scores (Pearson's r), how many species (out of 70) were assigned the same rank in the comparison (Equal rank), the average rank change (Rank change), the standard deviation of rank change (Rank SD), and the maximum rank change (Max change). The simulations were conducted using both the 'average UV' and 'average VIS' eye types and modifying the ocular media absorption parameter by increments spanning the range of values presented in Table S5.7. See Methods and Results section for more details. Main comparisons are in relation to the average visual system and final comparison presents the largest pariwise differences, based on the lowest Pearson's r value.

UV Eye type	Pearson's r	Equal rank	Rank change	Rank SD	Max change	*VIS Eye type*	Pearson's r	Equal rank	Rank change	Rank SD	Max change
T314	1.0000	60	0.14	0.35	1	T335	0.9998	53	0.29	0.54	2
T334	1.0000	60	0.20	0.47	2	T375	0.9996	35	0.63	0.76	3
T344	0.9999	60	0.51	0.81	4	T395	0.9986	21	1.06	1.06	5
T314 vs T344	0.9998	42	0.60	0.92	4	T335 vs T395	0.9976	20	1.20	1.15	5

Table S5. 13 Summary of total dichromatism score changes of 70 species of the Order Galliformes when comparing the influence of changing photoreceptor densities. Values reported describe the correlation between the scores (Pearson's r), how many species (out of 70) were assigned the same rank in the comparison (Equal rank), the average rank change (Rank change), the standard deviation of rank change (Rank SD), and the maximum rank change (Max change). The simulations were conducted using both the 'average UV' and 'average VIS' eye types and modifying the photoreceptor density parameter using the values presented in Table S8. See Methods and Results section for more details. Main comparisons are in relation to the average visual system and final comparison presents the largest pariwise differences, based on the lowest Pearson's r value.

UV		Equal	Rank	Rank	Max	*VIS*		Equal	Rank	Rank	Max
Eye type	Pearson's r	rank	change	SD	change	*Eye type*	Pearson's r	score	change	SD	change
Branta canadensis	0.9987	32	0.77	0.85	3	*Branta canadensis*	0.9989	29	0.91	1.00	4
Anous minutus	0.9900	18	2.14	2.08	11	*Anous minutus*	0.9935	19	1.91	2.03	9
Average Passerine	0.0999	35	0.66	0.80	3	*Average Passerine*	0.9995	46	0.43	0.65	2
Leiothrix lutea	0.9995	44	0.51	0.76	3	*Leiothrix lutea*	0.9996	36	0.74	0.93	3
Pavo cristatus	0.9985	25	1.06	1.13	5	*Pavo cristatus*	0.9985	34	0.83	1.08	5
Phalacrocorax varius	0.9936	23	1.43	1.82	9	*Phalacrocorax varius*	0.9948	21	1.26	1.28	7
Puffinus pacificus	0.9924	12	1.74	1.59	6	*Puffinus pacificus*	0.9941	17	1.37	1.25	6
Streptopelia chinensis	0.9947	20	1.49	1.47	6	*Streptopelia chinensis*	0.9955	20	1.23	1.18	5
Todiramphus sanctus	0.9996	38	0.57	0.75	3	*Todiramphus sanctus*	0.9994	43	0.60	0.92	4
A. minutus vs P. pacificus	0.9660	11	3.40	3.12	13	*A. minutus vs P. pacificus*	0.9760	9	3.00	2.91	12

Table S5. 14 Summary of total dichromatism score changes of 70 species of the Order Galliformes when comparing the influence of changing the visual system. Values reported describe the correlation between the scores (Pearson's r), how many species (out of 70) were assigned the same rank in the comparison (Equal rank), the average rank change (Rank change), the standard deviation of rank change (Rank SD), and the maximum rank change (Max change). The simulations were conducted using the parameters of species for which the physical properties of visual systems have been completely characterized, in addition to the 'average UV' and 'average VIS' systems. See Methods and Results section for more details. Main comparisons are in relation to the average visual system and final comparison presents the comparison between the 'average UV' and 'average VIS', as well as the largest pariwise difference, based on the lowest Pearson's r value.

UV *Eye type*	Pearson's R	Equal score	Rank change	Rank SD	Max change	*VIS* *Eye type*	Pearson's R	Equal score	Rank change	Rank SD	Max change
M. undulatus	0.9986	34	0.86	1.13	5	*G. gallus*	0.9979	31	0.86	1.07	6
C. caerulus	0.9992	37	0.66	0.87	4	*P. cristatus*	0.9993	35	0.69	0.84	4
S. vulgaris	0.9989	28	0.89	1.00	4	*P. pacificus*	0.9879	17	1.91	1.93	8
T. merula	0.9978	35	0.97	1.29	6	*P. violaceus*	0.9969	33	0.86	1.07	6
Average UV vs Average VIS	0.9903	15	2.37	2.40	13						
P. cristatus vs *T. merula*	0.9847	12	3.17	2.85	14						

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