THE UNIVERSITY OF CHICAGO

BUILDING VISUAL SIGNAL COMPLEXITY THROUGH MODIFICATIONS OF COLOR AND MOTION

A DISSERTATION SUBMITTED TO
THE FACULTY OF THE DIVISION OF THE BIOLOGICAL SCIENCES
AND THE PRITZKER SCHOOL OF MEDICINE
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DEPARTMENT OF ECOLOGY AND EVOLUTION

BY
KRISTINA YURIEVNA FIALKO

CHICAGO, ILLINOIS
DECEMBER 2023

Моїм рідним присвячується, тим хто завжди поруч зі мною, і тим хто підтримує здалеку.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGMENTS

The production of a dissertation requires assembling a financially, intellectually and emotionally supportive village. The research herein and my growth as a scientist is thanks to a wonderful group of people.

First and foremost, this work would not have been possible without the guidance of my advisor, Trevor Price. The spark for this dissertation came from the very first email exchange between Trevor and I back in 2015 and many of the ideas that weaved their way into this research come directly from conversations we've shared through the years. It doesn't take very long in interacting with Trevor to realize that he will consider everyone's opinion on a scientific topic with the same level of sincerity and genuineness. He balances teaching and openness to be taught, which allows students under his mentorship to grow into independent scientists. The opportunity to work on these questions and the experiences I had in the process of answering them is something that I will forever be grateful for.

I truly had a dream team of scientists on my committee that combined their expertise to guide this thesis forward. Stephanie Palmer, Marcus Kronforst, Steve Pruett-Jones and Mark Westneat: your critical feedback, support, and enthusiasm have shaped the trajectory of this work, expanded the horizons of my research interests and contributed greatly to my development as a scientist. I will carry the lessons I learned from you all in any future endeavors.

Most of this work would not have been possible without the support I received from the administrative staff in the department of Ecology and Evolution at UChicago. Mary, Jeff, Mike and Bonnie keep the entire operation running and it was a pleasure to work with them all over the last 7 years. A special thanks goes to Audrey Aronowsky, who epitomizes the meaning of going above and beyond. Her sage wisdom and patience have gotten me through several situations both on campus and abroad and the graduate programs are very lucky to have her.

The opportunity to work in India has been an absolute privilege and I am indebted to the colleagues and friends I've made there. I am grateful to all the scientists at the Wildlife Institute of India that facilitated and aided in this research: Dhananjai Mohan, Suresh Kumar, Sandeep Gupta and especially to Pratap Singh who generously provided his song recordings for playback. Suresh Rana was one of the first people I met on the very first trip I took to the Himalaya and has been so generous with his knowledge and his time ever since. Shiv Kumar's pride and joy in the wildlife and landscapes of Lahul Spiti are contagious and I am grateful to him for sharing it with me. A particular thank you goes to Sonal Bathla for the permission to stay in Kalingcha as our home base in Manali and to Amar Singh and his family for their hospitality and logistical support. This place became a home away from home and I look forward to return again.

My path toward science was paved and enabled by many incredible mentors I had prior to graduate school. Milly Formby gave me my first fieldwork opportunity in 2014 when I was abroad, assisting with her research on black swans in Australia through the University of Melbourne. While I was an undergraduate at the University of California Berkeley, no experience was more formative than the time I spent at the Museum of Vertebrate Zoology. Jesyka Melendez was the best TA I ever had the pleasure to learn from and the friendship we developed while searching for mice in chaparral and poison oak modeled the type of field experience I wanted to emulate. My interest in birds at all is thanks to Carla Cicero, who I worked with as both a curatorial assistant and who mentored me during my first independent research project on spotted towhee songs. I am particularly grateful for the mentorship and friendship of Terri Barclay, who first gave me a foot in the door of the MVZ in the Prep Lab back in 2012 and that alone made all the rest of this possible.

My own research was possible thanks to the contributions of a fantastic group of field assistants. In the 2022 season, Julia Weiss, Antara Kulkarni, Winter Bell and Annika Munson were all put through the ringer and came to the field everyday with curiosity and enthusiasm.

The memories and data collected as a result of that field season are both things I look back on fondly.

A special shout-out goes to Jennifer Stevenson. She came with me to the Himalaya in 2017 and 2019 at a time when I was still learning on the go and provided the logistical support to make the research possible and the emotional support to build my confidence as a field biologist and leader. There's a piece of this work that is as much hers as it is mine.

There are many moments here where I highlight the people whose contributions made this research possible but that sentiment rings especially true when it comes to Chaman Lal and Jai Singh. Their support in the field has remained a steadfast element of this project since the first time I met them in 2016. I particularly appreciated their sense of humor and the grounding effect they had on me when I would come back from another frustrating day of failed behavioral experiments and they'd ask how my "bird movies" went.

The experience I have had in graduate school is defined by the people who I was surrounded by. The Price Lab has been my academic home base for the last 7 years and I've been privileged to get to work alongside Daniel Hooper, Shane DuBay, Alex White, Supriya, Laura Céspedes Arias, Francisco Henao Diaz, Tati Washington and affiliates (Abhimanyu Lele, Jacob Drucker, and Louise Bodt). The conversations we've shared through lab meetings and in-office chats have provided invaluable support and feedback. Thank you to the people at the Field Museum - John Bates, Shannon Hackett, Ben Marks and Chad Eliason - for both enabling me to use the collections in my research as well as your input and advice on the research over the years. While at times it was a strange home for a student interested in behavior, the people in the department of Ecology and Evolution and the broader Darwinian cluster have left an indelible mark. I am particularly grateful to my student community in EE, who demonstrated the strength in organizing towards common goals. A very special place in my heart is occupied by members of my 2016 Darwinian cohort for the journey that we have been on together: Hannah Whitehurst, Brooke Weigel, Peter Flynn, Ryan Fuller, Jacob Cooper, Ben Otoo, Katie Whitlow and Chloe Nash.

Several people have made an outsized impact on my time here. Very early on in graduate school, when I was going through a particularly difficult time, Mo was one of the first people with whom I felt I could honestly answer the question: "how are you". He encouraged me to take on larger roles and much of the confidence I've built is thanks to the steps he pushed me to take in those early years. Jackie is like an academic big sister who I could turn to for both career advice and overcoming personal demons when navigating academia. Anything I've learned about the importance of building an inclusive, ethical and progressive science I learned from Natalia and Supriya. Both of these women modeled a compassionate and critical approach towards science and intersectionality that the community should aspire to. When I first began exchanging research ideas with Valentina, it felt like a breath of fresh air. Her curiosity, breadth and empathy continue to inspire me. Heather is one of the sharpest people I know and the most generous with her time and knowledge. Throughout this whole process, she's never been farther than a phone call away and has taught me more about the value of resilience than anyone else. Since Laura joined the lab it's been difficult for me to remember a time when she wasn't in it. I'm incredibly grateful for her critical mind, her kindness, her friendship and the shared experiences we've had. And of course, Chloe. If at the end of this journey, all I walked away with was your friendship then the entire endeavor would have been worth it.

I do not have the words to express my profound gratitude for the support of my parents, Yuri and Nataliya, whose sacrifices, love and knowledge shaped me into the person I am. To my family members who couldn't be here to see the end of this, your actions have altered the trajectory of my life and I think of you every day.

Reaching the end of this road with my head still screwed on relatively straight is thanks entirely to my partner, Matthew Calvert. To walk alongside you through life is a dream I couldn't have imagined.

ABSTRACT

The use of color and movement are foundational aspects of animal visual communication, but the underlying causes of the diversity in color and display behaviors across species remain an outstanding evolutionary question. While traditionally studied in isolation, integrating color and motion to assess the entire visual phenotype is necessary to understand not only the relationship between these two components but to also elucidate what factors may be contributing to the variation observed in the natural world. The focus of this dissertation lies at the nexus of sensory ecology, behavioral ecology and kinematic methods to ask how color and display co-vary and to evaluate the role of the signaling environment in the diversification of both traits. Using field-based methods and a comparative approach, I analyze plumage variation, display behavior and light environment across 13 species of warblers in the Himalaya in the context of intraspecific aggression. In Chapter 2, I investigate the presence and use of a concealed visual signal across bush warblers and allies in the family Cettiidae and find that visual communication in cryptic, otherwise "drab" species may be much more prevalent than is currently appreciated or understood. In Chapter 3, I conduct a comparative study on the use of wing motions during territorial displays across 11 closely related bird species and ask whether species differences may be related to habitat brightness. This chapter provides one of the most detailed analyses on the shape of wing movements sampled from wild individuals and suggests that certain motions used during displays are highly conserved across species and are modified in modular ways. Lastly, in Chapter 4, I turn to evaluate plumage color variation in twelve *Phylloscopus* species and ask whether color differences can be explained by variation in light environment across habitats and use in display. The results from this chapter suggest that even in a system where color diversity is relatively simple, the influences shaping color diversification remain complex. The work in this dissertation endeavors to expand the scope of the type of species and contexts studied in visual communication by focusing on animals with relatively subtle variation in color

and to consider behaviors used during aggressive signaling. By combining field experiments, comparative analyses and natural history collections, this research provides a comprehensive insight into the complicated interplay between color and motion in a group of Himalayan warblers.

CHAPTER 1

INTRODUCTION

1.1 Background and Context

In 1948 Niko Tinbergen, one of the founders of the field of modern animal behavior, wrote, “..after a short time one is able to predict the nature of the display movement in a newly encountered species after merely viewing its morphological equipment…I am convinced that the correlation of structure and movement will be shown to be much more complex than is known at present.“ (Tinbergen 1948, pg 27). The morphological equipment and structures he referred to are various traits used in visual communication between animals, namely patterns, physical ornaments (wattles, crests, and dewlaps), and overwhelmingly, color. The staggering diversity of visual phenotypes has continued to engage and puzzle researchers (Cuthill et al. 2017) and the covariation between color and motion has remained a particularly difficult topic. The proposed relationship between color and motion is a fairly intuitive one – both are processed by an animal’s visual system and can communicate information about the individual possessing them such as quality (Byers et al. 2010; Barske et al. 2011; Weaver et al. 2018; Ribeiro et al. 2019; White 2020), identity (Macedonia et al. 2013), or status (Pärt and Qvarnström 1997; Bókony et al. 2006; Senar 2006; Galván and Sanz 2008; Kenyon and Martin 2023). While the observation that color and motion are interconnected is not a novel one, until quite recently the bodies of work on each topic have remained largely divorced (Rosenthal 2007).

Part of this is because both components are independently complex. The study of color alone has spanned developmental biology, neurobiology, optical physics, biochemistry, genomics, visual ecology, behavior and evolution. From an animal communication perspective, understanding what data is important when considering “color” requires understanding what type of sensory information is available to the species in question. This is no trivial task, because the visual systems of most organisms differ from our own (Bennett et al. 1994). Birds, for example, have a tetrachromatic color vision system (Cuthill 2006; Bennett and Théry 2007; Kelber 2019) and their visual range extends into UV wavelengths imperceptible to humans. A field in its own right, advancements in our understanding of avian color vison (Vorobyev and Osorio 1998; Vorobyev et al. 1998; Hart 2001; Kram et al. 2010; Baden and Osorio 2019) have enabled the development of avian color vision models (Vorobyev and Osorio 1998; Stoddard and Prum 2011) and other analytical tools (Troscianko and Stevens 2015; Maia et al. 2019) to model what visual information an avian receiver is likely processing. In the last decade, however, more attention has been called to the dynamic nature of visual communication (Hutton et al. 2015) and efforts to move away from studying color in isolation to incorporating the entire visual phenotype, including motion, have become more prominent (Hogan and Stoddard 2018; Simpson and McGraw 2018a,b; Miles and Fuxjager 2019; Echeverri et al. 2021).

Within the context of animal communication, studies of motion have also benefited from advances in technology, moving from qualitative behavioral descriptions (Andrew 1961a,b) to quantitative measures of body positioning and other display parameters using videography (Mathis et al. 2018; Simpson and McGraw 2018b; Ribeiro et al. 2019). In particular, the affordability and access to high speed cameras has enabled the study of behaviors that may be imperceptible or impossible to quantify to human observers. High-speed video analysis of blue-capped cordon-bleus (*Uraeginthus cyanocephalus*) reveals a “tap-dancing” behavior that is otherwise indiscernible to human eyes (Ota et al. 2015). Manakin species generate acoustic “clapping” sounds through deliberate wing movements and the mechanisms of these behaviors were only characterized after detailed review of high-speed video footage (Bostwick and Prum, 2003). These behaviors also reveal features that may be more salient to their intended receivers than to humans. For instance, the critical flicker fusion frequency for birds is higher than that for humans (above 130 Hz for some small birds and 50-100 Hz for humans, Boström et al. 2016), suggesting that our perception of rapid movements may be poorer than that of a bird. The advent and accessibility of these technologies means that the field is at a time uniquely suited to quantitatively assess how color and motion are related to one another in animal communication.

Considering both traits allow us to not only further understand the relationship between color and motion but also address broader evolutionary questions about signal diversification. Are motion and color subject to the same selective pressures, or do they evolve independently? Can the presence of one trait enable diversification in the other? What features of a display do receivers attune to and does this vary across contexts and environments? In the last few years, there have been a boom of quantitative assessments of the covariation of color and motion in birds. Several of these studies use behavioral and color descriptions from the literature (Miles and Fuxjager 2018, 2019) or by scoring color and motion traits from publicly available videos of the species of interest (Ligon et al. 2018; Miles and Fuxjager 2019; Kenyon and Martin 2022). Experimental, field-based studies on the covariation between motion and color have been concentrated primarily in hummingbirds (Hogan and Stoddard 2018; Simpson and McGraw 2018b,a, 2019). Reflecting the attention of the field as a whole, most studies focus on species that are quite resplendent in their coloration, such as the birds-of-paradise (Ligon et al. 2018; Miles and Fuxjager 2018) and hummingbirds (Hogan and Stoddard 2018; Simpson and McGraw 2018b,a, 2019). Further, the overwhelming majority of studies focus on a particular behavioral context: courtship displays in highly sexually selected, elaborate species. The attention to these areas is understandable, especially with respect to elucidating the evolutionary dynamics underlying visual signal diversification; these groups of bird possess some of the most extreme visual phenotypes (Clark 2009; McCoy et al. 2018; Scholes and Laman 2018; Venable et al. 2022) and are an obvious area of interest for biologists.

However, the focus on a single behavioral context in some of the most colorful, exaggerated species may obscure the evolutionary pressures that influence more subtle species or visual traits used in other signaling contexts. The call to study groups with more subdued features has been made for plumage color evolution (Marcondes and Brumfield 2019) and can be extended to the broader visual phenotype as well. This may be especially important when considering one of the more prevalent hypotheses in color diversification – the role of the signaling environment. The effects of the signaling environment can affect not only the production (Peters and Evans 2003; Hutton et al. 2015; Ramos and Peters 2017; Simpson and McGraw 2018b) and perception (Heindl and Winkler 2003; Douglas et al. 2007) of a visual signal but also influence its evolution (Endler 1992; Boughman 2002; Price 2017; Cummings and Endler 2018). The influence of habitat on color may be expected to have a greater impact in species with more subtle coloration, since variation in color is less likely due to intense sexual selection. Incorporating studies on such species would allow us to compare potential differences in evolutionary pressures on visual signals and develop a more predictive theory of color diversification.

The focus of this dissertation lies at the nexus of sensory ecology, behavioral ecology and kinematic methods to ask how color and display co-vary and to evaluate the role of signaling environment in the diversification of both traits. Using field-based methods and a comparative approach, I analyze plumage variation, display behavior and light environment across 13 species of warblers in the Himalaya in the context of intraspecific aggression. Below, I present an overview of the chapters included in this work:

1.2 Chapter Overview

1.2.1 Chapter 2: Use of visual display in a dense, cluttered environment

In this chapter I investigate the presence and use of a concealed visual signal across bush warblers and allies in the family Cettiidae. Using citizen science photographs from the Macaulay Library at Cornell University, I map the distribution of white underwing patches across the Cettiidae phylogeny. I compare these results with species descriptions in field guides and find that underwing coverts are rarely mentioned and the records of these patches appears to be vastly unreported. Using playback experiments on two species in the western Himalaya, I propose a behavioral context in which underwing patches may function – stereotyped wing motions during territorial displays. Overall, the work in this chapter challenges assumptions about what constitutes a viable environment for visual signaling and highlights a hitherto understudied way through which "drab", cryptic birds may be making themselves more conspicuous.

1.2.2 Chapter 3: Building visual signal complexity through discrete modifications of motion

Stereotyped movements are among the most distinguishable traits used in animal displays, but how these behaviors arise and diversify is a particularly challenging question. Using a combination of field observations, playback experiments and kinematic methods, I conduct a comparative study on the use of wing motions during territorial displays across 11 closely related bird species; 10 species of *Phylloscopus* warbler and 1 species of *Horornis* warbler. I propose a possible origin for the most common wing motion observed during displays and show how visual complexity is built across different species through discrete modifications of several traits. I then ask whether species differences may be related to habitat brightness. To date this chapter provides one of the most detailed analyses on the shape of wing movements sampled from wild individuals and suggests that certain motions used during displays are highly conserved across species.

1.2.3 Chapter 4: Evaluating light environment and display as contributors to color differences among related bird species

The aim in this chapter is to integrate the three major elements detailed previously: color signals, display behaviors and the sensory environment. While the relationship between achromatic plumage pattern and habitat brightness in *Phylloscopus* have been previously established (Marchetti 1993), I expand the scope to incorporate chromatic variation in plumage and the spectral shape of the light environment across an elevational gradient in the western Himalaya. Using spectroradiometry, I quantify color variation in 12 species of *Phylloscopus* warblers and model adjacent patch perception under avian visual model. I then test whether the color differences observed are influenced by different light regimes across two habitat extremes, quantified through irradiance measurements during the breeding season. Building upon the work in Chapter 3, I incorporate tail movements to then ask whether interspecific color variation is related to wing and tail use during display. The results from this chapter suggest that even in a system where color diversity is relatively simplified the influences shaping color diversification remain complex.

CHAPTER 2

USE OF VISUAL DISPLAY IN A DENSE, CLUTTERED ENVIRONMENT

2.1 Abstract

Animals living in dense vegetation are limited in their use of visual signals due to the transmission constraints in these dim, cluttered environments. Birds in such habitats are often drab in appearance and thought to rely predominately on acoustic signals for conspecific communication. Here, we investigate the presence and use of a concealed underwing patch in the family Cettiidae. We find that this distinct white patch is widely present in the genus *Horornis*, with mixed evidence for its presence in other genera. In response to simulated territorial intrusions, two species, *Horornis fortipes* and *Cettia castaneocoronata* perform wing-flicking displays which results in a flashing effect in *Horornis fortipes.* We review known functions of achromatic patches in birds from the literature and evaluate the possible hypotheses for how underwing patches may function in Cettiidae and in environments previously thought to be unprofitable for visual signaling.

2.2 Introduction

The use of visual displays in communication depends on clear lines of sight. When line of sight is obscured, animals can overcome transmission constraints through a variety of strategies to increase conspicuousness, including increasing display effort (Candolin et al. 2007; Michelangeli et al. 2015) or by displaying areas of high contrast on the body (Stuart-Fox et al. 2007). Animals can also reduce the distance the signal must travel, which may be accomplished by moving closer to the receiver or by the signaler positioning themselves in a more exposed area. Many birds in visually cluttered environments, such as species in reed beds or sagebrush, use display flights that enable them to communicate over longer distances (Craig 1974; Castrale 1983; Menezes and Santos 2020). These strategies can only go so far, however. When the environment severely limits the effectiveness of a signaling modality, it may be complemented or replaced by an alternative communication strategy. In acoustically noisy environments, anurans turn to the use of color and motions to enhance detectability (Amézquita and Hödl 2004; Preininger et al. 2009, 2013; Grafe et al. 2012). Conversely, when line of sight is obscured acoustic signals are predicted to play a greater role in communication (Bradbury and Vehrencamp 2011).

Understory environments present an additional challenge to visual communication as they are not only visually cluttered but also dimly lit. These environmental conditions have been suggested to result in a reliance on vocal communication over visual (Thorpe 1963; Catchpole 1973; Seddon 2005). Species living in these environments are often described as "drab" (Walther et al. 1999), a word typically meaning possessing plain, little-ornamented plumage that is not chromatically striking, such as brown, olive, or gray colors. In the understory, many species exhibit brown or black coloration (Gomez and Théry 2007) which make them cryptic in these habitats. Because many of these species have reduced or unnoticeable color ornaments, there are few studies that investigate the extent to which visual communication is used (however see Macedo et al. (2021) for use of dark plumage patches in territoriality and Carlos (2002) for use of white patches in flock cohesion in Thamnophilidae species). As Marcondes et al. noted, the dearth of studies on "drab" species leaves a gap in our understanding of color evolution (Marcondes and Brumfield 2019) and, we argue, how visual signals may function in different signaling environments.

This is particularly notable because more species may be using visual signals than previously expected. In a review of nocturnal and crepuscular animals, Penteriani and Delgado (2017) note the common use of achromatic (white) patches, which produce a high contrast in dark environments. In some species, such as nightjars (family Caprimulgidae), these white patches are placed on areas of the body that can be facultatively concealed or revealed, such as the wings and tail (Juan Aragonés et al. 1999). The visibility of these patches is therefore behaviorally mediated, requiring the study of how they are used in the wild to understand how they function.

In this study, we investigate the presence and use of a concealed visual trait – the underwing patch – in the family Cettiidae. This family consists of 29 - 31 species across 7 genera distributed across southeast Asia, Europe and Africa (Alström et al. 2011, 2013; Winkler, D. W., S. M. Billerman, and I. J. Lovette 2020). Known commonly as the bush-warblers and allies, most species in this family are commonly described as skulking, drably colored passerines that inhabit dense forest undergrowth and other thick vegetation close to the ground. All are sexually monomorphic in plumage, with the typical bush warblers (*Horornis* and *Cettia*) and stubtails (*Urosphena*) possessing mostly brown and whitish plumage while the tesias (*Tesia*) are mainly olive-green and gray. The exceptions in drab coloration are mostly found in the *Abroscopus* and *Tickellia* warblers, and in the tailorbirds (*Phyllergates*) which have bright yellow underparts, olive green upperparts and some red head ornamentation. With the exception of *Abroscopus* and *Tickellia*, which move more frequently between forest strata, most species in Cettiidae forage and breed in dense understory habitats. These species are notable for their elusive nature, with most work on communication in this clade conducted primarily on song (Luschi and Seppia 1996; Hamao and Ueda 2000; Park and Park 2000; Alström et al. 2007; Hamao et al. 2008; Xia et al. 2010, 2011, 2013b, 2014, 2015; Wei et al. 2017). However, visual components in the form of wing motion have been noted during territorial interactions (Luschi and Seppia 1996; Xia et al. 2013a). As such, Cettiidae presents a compelling system to ask whether species are using visual signals in dark, dense environments. We focus specifically on the presence of white plumage patches, as these are expected to provide the highest contrast in dimly lit environments. We first investigate the presence of underwing plumage patches across Cettiidae using publicly available photographs. We then study the use of wing motions during intraspecific competition in two species: *Horornis fortipes* – a typical bush warbler, and *Cettia castaneocoronata* – a relatively more colorful species during their breeding season.

2.3 Methods

2.3.1 Image collection

To measure whether species had white underwing patches we used publicly available images deposited in the Macaulay Library (https://macaulaylibrary.org/) at the Cornell Lab of Ornithology. Using the scientific name for every species in Cettiidae we searched the database for all available photographs of that species. We then parsed through all photos and selected any in which the wing is lifted above the midline of the body and the ventral feathers of the wing are visible. All qualifying images can be found in table S2.1 (n = 39). We defined the presence of a white underwing patch by the following criteria: the feathers on the underwing coverts had to be white or whitish in coloration and they had to contrast with adjacent flank feathers and surrounding primaries. If at least one individual of a species met these criteria, we labeled that species as possessing a white underwing patch. For every species across Cettiidae we looked for any information on underwing covert coloration from the species descriptions in the online version of Handbook of the Birds of the World. If underwing coverts were mentioned, we recorded the color described for that species. To examine the distribution of white underwing patches across Cettiidae, we plotted the available data for underwing patch presence from both the photographs and field guide using the phylogeny from Alstrom et al. (2011).

2.3.2 Study area and experimental approach

To study the use of wing motions during intraspecific competition, we conducted playback experiments in the Manali Wildlife Sanctuary, Himachal Pradesh, India (32.25°N, 77.17°E, spanning 2000m - 3600m, between April 22 – May 4, 2019 and April 25 – May 30, 2022). We located territorial males between the hours of 0500 - 1110 and positioned a Bluetooth speaker (Ultimate Ears WONDERBOOM) in the bird's territory. Because discerning the wing movements in these birds can be challenging, we employed two camera setups. The first consisted of a solo camera (Sony RX10 DSC III) set to film at 60 frames per second. The purpose of this setup was to film the territory owner for as long as possible, allowing us to measure the rate of wing motion used in response to playback. The second setup consisted of a synchronized 3-camera array set to film at 480 frames per second. The purpose of the second camera setup was to record the behavior at a high frame rate, allowing us to capture a prolonged view of the underside of the bird wing.

Playback trials were organized in two parts: establishing a filming focal point and recording of the behavior itself. During the initial phase, we simulated a territorial intrusion by playing the song of the focal species. If the territory owner responded, we played the song for 5 minutes and observed where the individual would perch in the territory. Once the focal point was identified, we placed the three camera-array at least 3 meters from the focal point, one pointed 90 degrees to the focal point and the other two arranged 45 degrees and 135 degrees, respectively. The other camera remained at least 6 meters from the focal point. We left the setup undisturbed for 10 minutes and then began the trial.

During the second phase we first played a song for 10 minutes. If the bird reacted by responding or approaching, the experiment continued. When the bird entered the focal point within the cameras frame of view the array was activated, filming the behavior simultaneously from three different perspectives. The entire playback session lasted for 10 minutes, during which we collected several behavior videos.

Throughout this time we continued recording the behavior of the bird using the single-camera setup throughout the duration of the trial. If the individual continued to be responsive through the first trial (i.e.: did not retreat or fly away), the trials were repeated after a 5-minute rest, conducting no more than 3 trials for each individual. Post behavioral trial we calibrated the filming area by placing a 3' x 5' checkerboard and XRite ColorChecker Passport close to the focal point where the bird perched, which provide a scale visible from all camera viewpoints.

2.3.3 Behavioral analysis

To calculate the rate of wing motion, we used the trim function in Quicktime Player (Apple Computer) to extract the timestamps when the individual first appears on screen and when it leaves the field of view for videos recorded on the solo 60 fps camera. This yielded a measure of total display time. Within this display time we counted how many wing flicks an individual performs. To distinguish wing motions used in response to playback from the wing movements used in locomotion, we did not count wing flicks if the bird moved more than its body length immediately after completing the behavior. Individuals had to complete at least 5 wing flicks in a row to be included in analysis.

To record the presence of white underwing patches we extracted frames from each 480 fps video using the `extractFrames` function in StereoMorph (Olsen and Westneat 2015). We then isolated a single wing flick per individual, which we define by the frame in which the wing begins the upstroke to when it returns to the starting position and ceases motion. We then selected the frame in which the wing reaches maximum extension, transitioning from the upstroke to the downstroke. This gives us the most clear view of the underside of the wing. Each individual recorded was then scored on whether they possessed white underwing coverts or not.

To test for differences between the two species we ran an analysis of variance on wing flick rate. All statistical analyses were conducted in R (version 4.2.2, R Core Team 2022).

2.4 Results

2.4.1 Presence of white underwing patches

We looked through all available photographs of 29 species in the Macaulay Library (https://macaulaylibrary.org/) at the Cornell Lab of Ornithology. 16 species had photographs where the wing was in a position in which underwing coverts could be evaluated. Of the 16 species assessed, 9 species had white underwing patches and 5 species did not have white underwing patches (Figure 2.1). The genus *Horornis* accounted for 7 of the species with white underwings. *Cettia cetti* and *Urosphena squameiceps* also showed white underwing coverts, although the extent of white appeared reduced in the latter. Underwing covert descriptions from field guides were only available for 5 species in Cettiidae (Figure 2.1). Of these, two species (*Horornis acanthizoides* and *Urosephena pallidipes*) are noted to have white underwing coverts. All species in *Abroscopus* have yellow underwing coverts, however the extent to which these may be distinct patches remains to be determined. In the available images, some species, such as *Abroscopus albogularis* and *Abroscopus schisticeps* have white flank feathers, which provides a contrast against the adjacent yellow underwing coverts. However, *Abroscopus superciliarus* has yellow flank and belly coloration, which result in a continuous ventral color.

2.4.2 Territorial wing motion rate and duration

All *Horornis fortipes* (n = 11) and *Cettia castaneocoronata* (n = 3) studied performed wing motions in response to territorial playbacks. The two species differed significantly in the rate of wing motion (Figure 2.2, *H. fortipes* n = 4, *C. castaneocoronata* n = 3, ANOVA: $F_{1,5} = 80.27$, $P < 0.001$).

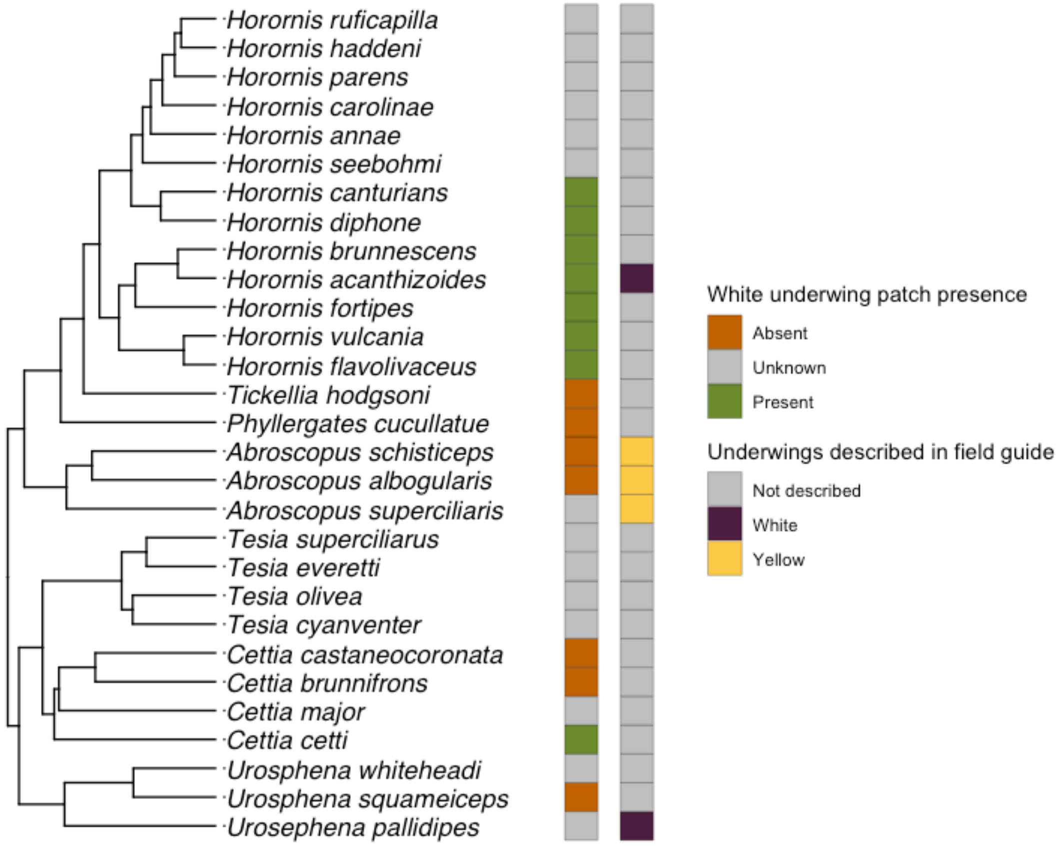

Figure 2.1: **Distribution of underwing patches across Cettiidae.** Presence of white underwing patches and field guide descriptions for Cettiidae (phylogeny from Alström et al. 2011). Of the 16 species with available underwing images from the Macaulay Library at the Cornell Lab of Ornithology, 9 species have white patches beneath the wing and 7 do not. Underwing covert descriptions are largely absent from the Handbook of the Birds of the World (Winkler, D. W., S. M. Billerman, and I. J. Lovette 2020) for Cettiidae species.

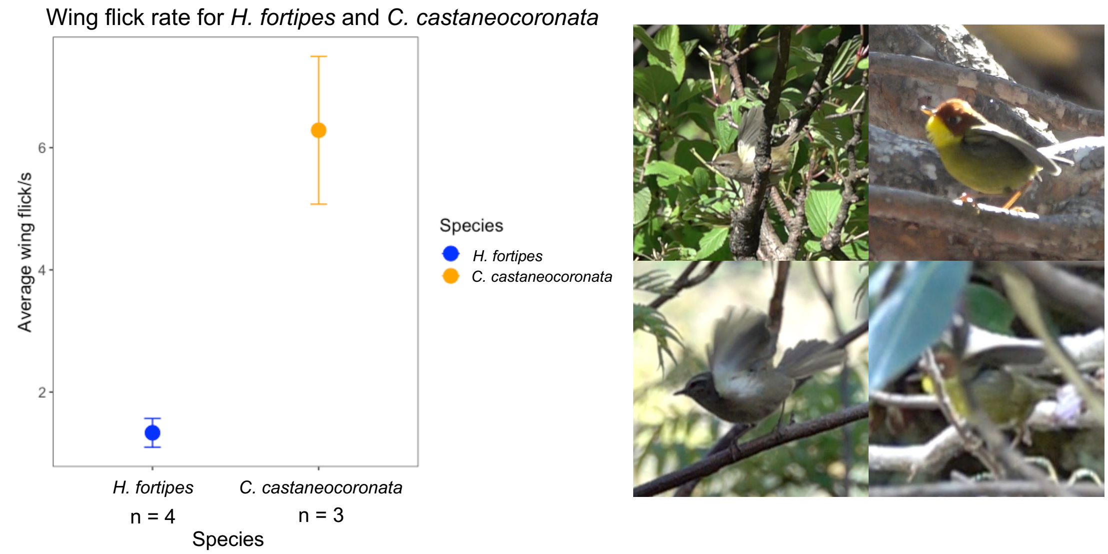

Figure 2.2: **Wing flick rates in Cettiidae.** *Left* Territorial wing flick rates for *Horornis fortipes* and *Cettia castaneocoronata*. Both species use wing motion in response to playback, and *C. castaneocoronata* moves its wings faster than *H. fortipes*. *Right* The point of maximum wing extension for two individuals of each species. The white underwing patch is clearly visible in both *H. fortipes* individuals (left column) and absent in *C. castaneocoronata* (right column).

2.5 Discussion

Species living in the understory are often cryptic in both plumage and behavior; as a consequence we know relatively little about the use of communication modalities other than song. Here, we investigate one component of a visual display – use of a facultatively hidden white patch – across the bush warblers in Cettiidae. We find that 10 species possess white underwing patches, which are distributed across the *Horornis* (n = 7), *Cettia* (n = 1) and *Urosphena* (n = 2) genera (Figure 2.1). Only five of the 29 Cettiidae species examined had underwing covert color recorded in their species descriptions, which is striking for *Horornis* because all species with available photographs showed evidence of white underwing patches, suggesting this trait may be common across the genus. In *Horornis fortipes*, all individuals studied during the breeding season displayed white underwing coverts (n = 11, Figure 2.2), but description of this patch is absent from most modern field guides inspected (Grimmett et al. 2012, 2016; Clement 2020; MacKinnon et al. 2022) with the exception of Baker (1991). We also found one record of underwing descriptions for this species from Rickett and La Touche (1898). Underwing patches appear to have been overwhelmingly missed because they are flashed too quickly for the eye to detect and are hidden beneath the wing on museum study skins. This patch placement presents a way through which species may balance conspicuousness and crypsis pressures by concealing strongly contrasting achromatic plumage in areas that can be behaviorally revealed.

The extent to which understory species use visual signals is poorly resolved. By definition, drab birds are visually non-distinctive, a feature often attributed to their environments, which are both dimly lit and present constraints on long-distance visual signal transmission. Nonetheless, in response to playback we found that both *Horornis fortipes* and *Cettia castaneocoronata* perform stereotyped wing flicking displays, similar to those described for many other passerines including the closely related Phylloscopidae warblers (Andrew 1961a,b; Marchetti 1993). The two species differed in their rate of wing motions (Figure 2.2), although this may be largely driven by differences in their wing morphology. In both species the rate of wing flicking is well below the flicker fusion frequency of insectivorous birds in dim light (Boström et al. 2016), suggesting that conspecifics should be able to resolve the presence of underwing patches when present. In *H. fortipes*, the combination of patch and rapid wing motion produces a flashing effect. The use of an achromatic patch may serve the same effect as in nocturnal species, increasing contrast and detectability in light restricted environments. Diurnal birds in understory habitats are unlikely to experience the same extent of light restriction as nocturnal species, but these habitats nonetheless present distinct light environments; in one measure of a tropical forest, understory habitats received 0.1 – 1.9% of the light intensity experienced in full sun conditions (Bazzaz and Pickett 1980). While we have documented the presence of these patches across several species in Cettiidae, the function of them remains a mystery. Use of wing motion during territorial displays present one avenue through which they may be visible but white patches in birds have been documented across a variety of contexts. We review several of these functions (Table 2.1) with respect to underwing patch presence in Cettiidae and outline future studies that can test these hypotheses.

2.5.1 Foraging

Many arthropod species detect potential threats visually and respond by initiating an escape response involving sudden motion away from the perceived threat (Holmqvist and Srinivasan 1991; Galatowitsch and Mumme 2004). Some insectivorous bird species exploit this prey response and have evolved several traits to enhance its effectiveness, including rapid wing and/or tail motion (Hailman 1960; Selander and Hunter 1960; Root 1967; Harrison 1976; Robinson and Holmes 1982; Jabłoński 1999; Hayslette 2003; Mumme 2014), body pivots (Harrison 1976; Jabłoński 1999; Jablonski and McInerney 2005) and contrasting wing and/or tail patches (Hailman 1960; Root 1967; Harrison 1976; McLean 1989; Jabłoński 1999;

Mumme 2002, 2014). One possible function for white underwing patches in Cettiidae may be to enhance foraging performance. Evidence in support of this hypothesis are that all species are insectivorous and commonly use wing motion during foraging bouts (Winkler, D. W., S. M. Billerman, and I. J. Lovette 2020). However, birds that use contrasting markings to enhance foraging are also associated with flush-pursuit and flycatching foraging behaviors, catching most prey through aerial maneuvers after they have been flushed (Robinson and Holmes 1982; Holmes and Recher 1986; Van Remsen and Robinson 1990). Most species in Cettiidae occupy a different foraging niche than flush pursuit foragers, instead taking prey items from the ground or in dense vegetation and rarely pursue prey via flight (Winkler, D. W., S. M. Billerman, and I. J. Lovette 2020). Of the species that do have records of flycatching or other aerial behaviors (genera *Abroscopus*, *Tickellia* and *Phyllergates*), these notably lack white underwing coverts. It therefore appears unlikely that white markings in Cettiidae function similarly to flush-pursuit species. Properly assessing the role of white underwing patches on Cettiidae foraging performance requires additional field observations to calculate the proportion of foraging behaviors associated with wing movement and experimentally manipulating the size of white underwing patches to test effects on prey capture success.

2.5.2 Flock formation and cohesion

White plumage patterns have been associated with both flock formation (Moynihan 1962; Armstrong 1971; Kushlan 1977; Brooke 1998; Beauchamp and Heeb 2001) and flock cohesion (Moynihan 1962; Wiley and Haven Wiley 1971; Brooke 1998). However, with the exception of the *Abroscopus* warblers (Chen et al. 2022), which do not have white underwing patches, species in *Cettia*, *Urosphena* and *Horornis* are not recorded as frequent members of mixed species flocks (Winkler, D. W., S. M. Billerman, and I. J. Lovette 2020), making underwing patch use in flock formation and cohesion unlikely. To test the role of white underwing patches in flock cohesion, further studies on flocking propensity across Cettiidae are required.

2.5.3 Predator deterrence and evasion

Bright or strongly contrasting plumage may be costly because it makes the individual more conspicuous to predators. Conversely, some species appear to use contrasting white markings to signal directly to predators to discourage further pursuit (Woodland et al. 1980; Alvarez 1993; Randler 2006, 2007; Jones and Whittingham 2008; Stang and McRae 2009; Ramesh and Lima 2019). Known as pursuit-deterrence signals (Woodland et al. 1980; Hasson 1991), these behaviors function to alert the predator that it has been detected and that further pursuit would be unprofitable. Most support for the pursuit-deterrence hypothesis comes from species that display white markings on the tail (Alvarez 1993; Randler 2007; Jones and Whittingham 2008; Stang and McRae 2009; Ramesh and Lima 2019) or rump (Woodland et al. 1980) and increase the rate of display when in the presence of a predator. To date, there have been no studies providing evidence for the use of wing patches in birds as a pursuit deterrent signal. If underwing patches in Cettiidae function as pursuit deterrence signals, we would predict that species with white underwing patches should increase rates of wing-flicking and patch exposure in response to a predator stimuli and that these behaviors should be proportional to predator distance (Hasson 1991).

An alternative function of white markings in response to predation is predator evasion. The rapid reveal of conspicuous coloration in motion and concealment at rest - termed flash markings – may serve to hinder detection of the prey object by the predator (Cott 1940; Edmunds 1974) and has been shown experimentally to be an effective escape mechanism in computer simulation trials (Murali 2018; Loeffler-Henry et al. 2021). There is little experimental or behavioral evidence available on the use of flash markings in predator evasion in Passerines, however, the presence of white rump patches in pigeons (*Columba livia*) strikingly reduces the proportion of successful falcon captures compared to those without rump patches (Palleroni et al. 2005). Testing the predator-evasion hypothesis would require 1) categorizing the main predation pressures for Cettiidae species, and 2) experimentally reducing underwing patches to test whether patch presence impacts rates of predation.

2.5.4 Individual quality

Perhaps the most well studied use of plumage patches has been in the context of sexual selection as markers of individual quality (Hill and McGraw 2006). These can be broadly split into intrasexual signals, such as male-male competition, and intersexual signals, relating to mate choice. We will briefly summarize the use of white plumage in both contexts.

Intrasexual signals of quality are typically studied from the perspective of status signals (e.g. badges of status) or indicators of dominance (Senar 2006). Variation in white plumage has been associated with greater access to food resources (Crowhurst et al. 2012; González-García et al. 2018), body condition (Galván and Sanz 2008), testosterone level (Moreno et al. 2014; Cantarero et al. 2017), and access to territories in intrasexual competition (Pärt and Qvarnström 1997; van Dongen and Mulder 2007; Jones et al. 2017). The outcome of these intrasexual competitions can result in greater access to resources or mates, but white plumage may also be assessed independently in mate choice by both sexes. Female mallards show a preference for males with larger white patches (Weidmann 1990; Omland 1996) and female great tits with more immaculate white cheek patches breed earlier and have more high quality offspring (Ferns and Hinsley 2004; Remeš and Matysioková 2013). White plumage patches can vary along three traits, size (Hanssen et al. 2006; McGlothlin et al. 2007; Moreno et al. 2014), intensity (Hanssen et al. 2006; McGlothlin et al. 2007; Igic et al. 2018) and immaculateness (Ferns and Hinsley 2004; Galván and Sanz 2008, 2009), all of which may be used when assessing individual quality in both intrasexual competition and mate selection. Some species in Cettiidae, such as *Cettia cetti*, showed considerable variation in the amount of white underwing plumage (Table S1). Further studies are required to assess whether this variation may be an indicator of individual quality or may be due to other factors, such as geographic variation. Unraveling whether these patches are functioning in sexual selection will require several studies including quantifying the natural variation, testing whether patch traits affect competitive outcomes between males, assessing female preference for patch size, brightness and immaculateness and testing whether underwing patch traits affect offspring survival and other measures of reproductive success.

2.5.5 Conclusions

Drab species, such as those living in the understory, are often overlooked when considering the evolution and function of visual traits such as color ornaments. In this study, we explored the potential role of a concealed underwing patch within the family Cettiidae. These patches, predominantly found in the genus *Horornis*, have heretofore been relatively undescribed. Through simulated territorial intrusions, we observed wing-flicking displays, resulting in a distinctive flashing effect in *Horornis fortipes*. The presence of underwing patches across Cettiidae challenge previous assumptions about the limited role of visual signals in densely vegetated environments, emphasizing the potential importance of achromatic patches in habitats traditionally thought to be unprofitable for visual communication. Understanding the function of white underwing patches requires considerable behavioral and experimental work and invites further investigation into the communicative strategies employed by birds living in such conditions.

Function	**Patch location**	**References**
Foraging	Wings and tail	Hailman 1960; Selander and Hunter 1960; Root 1967; Harrison 1976; Robinson and Holmes 1982; McLean 1989; Jabłoński 1999; Mumme 2002, 2014; Hayslette 2003; Galatowitsch and Mumme 2004; Jablonski and McInerney 2005
Flock formation and cohesion	Wings, tail, rump	Moynihan 1962; Armstrong 1971; Wiley and Haven Wiley 1971; Kushlan 1977; Brooke 1998; Beauchamp and Heeb 2001
Predator deterrence and evasion	Tail, rump	Woodland et al. 1980; Alvarez 1993; Palleroni et al. 2005; Randler 2006, 2007; Jones and Whittingham 2008; Stang and McRae 2009; Ramesh and Lima 2019
Aggression and territoriality	Wings, tail, throat, head	Pärt and Qvarnström 1997; van Dongen and Mulder 2007; Galván and Sanz 2008; Crowhurst et al. 2012; Moreno et al. 2014; Cantarero et al. 2017; Jones et al. 2017; González-García et al. 2018
Mate choice	Wing, neck	Weidmann 1990; Omland 1996; Ferns and Hinsley 2004; Remeš and Matysioková 2013

Table 2.1: Functions of white plumage markings.

APPENDIX

2.A Supplementary Data

Supplementary tables for this chapter can be viewed at `https://figshare.com/s/eaba219aa91c039e827a`

CHAPTER 3

BUILDING VISUAL SIGNAL COMPLEXITY THROUGH DISCRETE MODIFICATIONS OF MOTION

3.1 Abstract

Aggressive interactions between conspecifics are commonly associated with stereotyped display movements, which serve to efficiently inform receivers of motivation. Consequently, once an effective aggressive display has evolved, it is unclear why it should be altered through subsequent speciation events. Here we study 11 closely related bird species to evaluate the extent of display evolution, and to infer the underlying causes of any differences. We use high-speed videography of territorial behavior to quantify differences in wing motion intensity and form. We show that a likely precursor to the display is movement of the wing during foraging; this motion is then amplified during displays. As expected, both rate and form of the display are similar across species. Differences arise through slight modifications in form associated with wing shape evolution, loss of display ($N = 1$), expansion of behavioral repertoire ($N = 2$), gain or loss of color patches (2x), and changes in location of the color patch (2 locations). We relate some of these differences to habitat, which differ discretely and dramatically in light intensity. We conclude that display evolution proceeds largely in a modular fashion. The basic conventional signal is maintained across species, enabling modifications to appear without loss of efficacy.

3.2 Introduction

Displays to conspecifics are used in a wide range of social situations, including to attract mates (Mitoyen et al. 2019), repel competitors (van Staaden et al. 2011), and communicate between parent and offspring (Kilner et al. 1999). Differences between species have been documented in association with both mate attraction (Prum 2010; Ligon et al. 2018; Miles and Fuxjager 2018, 2019; Simpson and McGraw 2019; McGinley et al. 2022) and territorial advertisement (Fleishman 1992; Ord et al. 2013; Clark et al. 2015; Jenssen 2015). The question of how and why these differences arise has been asked for a long time (Tinbergen 1960) and recent comparative analyses have shed some insight. Notably, Endler (1992), building on earlier studies by sensory biologists (e.g. Lythgoe 1979) argued that an animal's communication system (signals and sensory receptors) should be adapted to optimize transmission and reception. Accordingly, when signaling environments differ, traits associated with communication experience selection pressures to be better suited for the specific features of these different signaling environments. There is accumulating evidence that this process, termed sensory drive, affects the evolution of color and other visual signals (Marchetti 1993; Price 2017; Cummings and Endler 2018), especially in the aquatic environment. More recently, differences in display movements have also been connected to environmental features (Ord et al. 2007; Ramos and Peters 2017; Miles and Fuxjager 2018; Menezes and Santos 2020; McGinley et al. 2022). For example, birds-of-paradise signaling on the forest floor have larger behavioral repertoires than those in higher microhabitats (Ligon et al. 2018; Miles and Fuxjager 2018) and wolf spiders alter the timing and total courtship effort under different light environments (McGinley et al. 2022).

A third form of display, beyond courtship and territorial advertisement is associated with close range aggressive interactions (Hurd and Enquist 2001). In this case, for several reasons, we a priori expect limited diversification across species. First, the influence of environment differences should have less impact on transmission at short-range. Second, unlike those used to attract mates, short range displays should remain simple in order to transmit an unambiguous signal of intent (Morris 1957; Cullen and Huxley 1966). Third, unlike courtship (Ryan 1990), such displays are less likely to be important in transmitting species identity, as these displays are used intraspecifically as an escalatory step once a challenger has been identified through other means, such as song or call notes in birds.

Despite these considerations, diversification of short-range aggressive displays may be promoted in various ways. First, if habitat differences are extreme then signal transmission may still be affected. Terrestrial habitats are not as variable along a chromatic axis as aquatic habitats (Cummings and Endler 2018) but can vary considerably in brightness based on habitat type (Marchetti 1993; Bortolotti et al. 2011) and structure (Bazzaz and Pickett 1980; Gomez and Théry 2004; Medina et al. 2017). In dim light conditions the tradeoff between temporal and spatial resolution becomes exacerbated (Lythgoe 1979). Poor motion discrimination in dark environments can lead to pressures to exaggerate critical features of a motion-based display.

Second, differences between species that arose outside of the context of threat may stimulate receivers. The responses to these motions can then be exploited, such as if the signaler exaggerates the motion to induce increased reactions in the receiver (the principle of sensory or perceptual bias, Ryan and Cummings 2013). Starting from a relatively small difference, exaggeration can then take displays along different trajectories. For example, Irwin et al. (2001) argued that small initial differences in song of neighboring populations had become amplified as the songs were selected to become more complex. Third, Tinbergen (1948) noted “I am convinced that the correlation of structure and movement will be shown to be much more complex than is known at present.” This raises the possibility that display may subsequently evolve to exhibit or amplify (Hasson 1989) color patches, which may have evolved previously in response to sexual selection (Hill 2006; Senar 2006), sensory drive (Marchetti 1993), perceptual biases (Burley and Symanski 1998) or other processes (Savalli

1995). Fourth, display may be limited by the morphological and physiological adaptations that have evolved in response to natural selection pressures. For example, Gómez-Bahamón et al. (2020) show that two subspecies of the Fork-tailed flycatcher (*Tyrannus savana*) differ in the sonations made with their outer wing feathers during aggressive and other displays. The differences in feather morphology appear to have evolved in response to the demands of seasonal migration in one subspecies, whereas the other is a year-round resident.

We focus on wing movement, which is one of the most commonly used motions during avian threats (Tinbergen 1960; Andrew 1961a,b; Kenyon and Martin 2022), presumably because wings are so easily moved. For birds, movement against a background is an inevitable part of foraging for food. The motion per se draws attention (Rushton et al. 2007) and while this may attract predators it can also communicate location. For example, Moynihan (1962) suggested that conspicuous colors and motions help maintain flock cohesion, although experimental tests have yet to confirm this (Carlos 2002). The precursors for aggressive displays are typically thought to derive from intention movements (Daanje 1951), undergoing further elaboration and ritualization. However, movements associated with basic functions, such as foraging, can also function as evolutionary precursors for signals (Bradbury and Vehrencamp 2011).

In a study in Kashmir, India, Marchetti (1993) found that different forest types, as defined by dominant tree species, varied significantly in brightness. Different warbler species in the genus *Phylloscopus* are intimately associated with these habitats (Price 1991). Marchetti showed that species in the darkest habitat (conifer) have the brightest wing-bars, whereas species in the most open environments have no wing-bar at all. She argued that increased patch brightness functions to enhance conspicuousness in dark environments. Additionally, she showed that species with wing bars perform wing flicking displays, while those without do not, echoing the argument made by Tinbergen (1948) that form (plumage ornaments) and motion are expected to be correlated.

We test predictions that emerge out of considerations of the selection pressures constraining the evolution of threat displays (Hurd and Enquist 2001), to evaluate possible roles of sensory drive (Endler 1992), perceptual bias (Ryan 1990), and morphological constraints arising out of natural selection pressures. We first show that wing movements are used during foraging by all species outside the context of flight and then ask how these movements are altered in rate and form among different species during threat displays. To assess a role for sensory drive, we measure habitat brightness across the elevational gradient, as brightness has previously been correlated with plumage complexity (Marchetti 1993) and is expected to impact perception of motion-based signals (Warrant 1999; Boström et al. 2016). Because migration distance, habitat type and foraging behavior are all correlated with measures of wing morphology (Sheard et al. 2020), we evaluate the role of these ecological factors in the evolution of the display. We show that the essential form of the display remains similar across species, attributed to a conserved perceptual bias, plus large variation among individuals within each species. Despite display similarity among species, small differences can be related to wing shape evolution, and some species have added a novel display, or lost the display altogether, associated with large difference in the signaling environment.

3.3 Materials and Methods

3.3.1 Study system

The family Phylloscopidae (leaf warblers) contains about 81 species (Winkler et al. 2020), which vary in mass from 5-12 g. In all species, individuals spend much of their time foraging for insects in trees and bushes (e.g., in a non-breeding season study, *Phylloscopus trochiloides*, consumed one arthropod every 14 seconds throughout the day (Price 1981). We studied 11 species that breed along a limited altitudinal gradient (2,000-4,000m; Price et al. 1997; Figure 3.1) in the west Indian Himalayan state of Himachal Pradesh (Price et al. 2003). In this study, we also included the related brown-flanked bush warbler, *Horornis fortipes*. All species are partial or complete migrants, spending the non-breeding season at lower altitudes and latitudes.

All species have similar plumages, possessing greenish-olive to brown upperparts and pale underparts. Many species have a light stripe of unmelanized feather keratin across the tip of the greater covert feathers, producing a wing bar. Wing bar size varies between species (Figure 3.1, Price and Pavelka 1996) and for the one species where it has been studied (*Phylloscopus humei*) wing-bar size is about 10% larger in males than females (Scordato et al. 2012). Color of the sexes is similar, as assessed spectrophotometrically (Chapter 4). *Horornis fortipes* has brown upper plumage and pale underparts. This species has a large white patch beneath the wing, extending from the underside of the underwing covert feathers to the upper body (Chapter 2). The patch is fully concealed when the wing is closed. In both genera plumages do not vary seasonally, except for feather wear, which can reduce the size of wing bars over time (Scordato et al. 2012).

3.3.2 Field methods

We studied warbler behaviors during the breeding season in the Manali Wildlife Sanctuary, Himachal Pradesh, India (32.25 °N, 77.17 °E, spanning 2000m - 3600m, between April 22 – June 22, 2019 and April 25 – May 30, 2022) and at Nain Gahar village, Himachal Pradesh, India (32.73 °N, 76.86 °E between June 11 - 21, 2019 and June 15 – July 8, 2022). We also visited two sites in Arunachal Pradesh (26.97 °N, 92.92 °E and 27.06 °N, 93.03 °E) and one site in Andhra Pradesh (17.81 °N, 82.49 °E) during the non-breeding season (December 22, 2021 – January 22, 2022). We collected two sets of data: the first on rate of wing movement during foraging and territorial intrusions (Table S3.1), and the second on form of the display. Rate of wing movement was collected because it was qualitatively apparent that movement increases during aggressive responses (call note rate similarly increases,

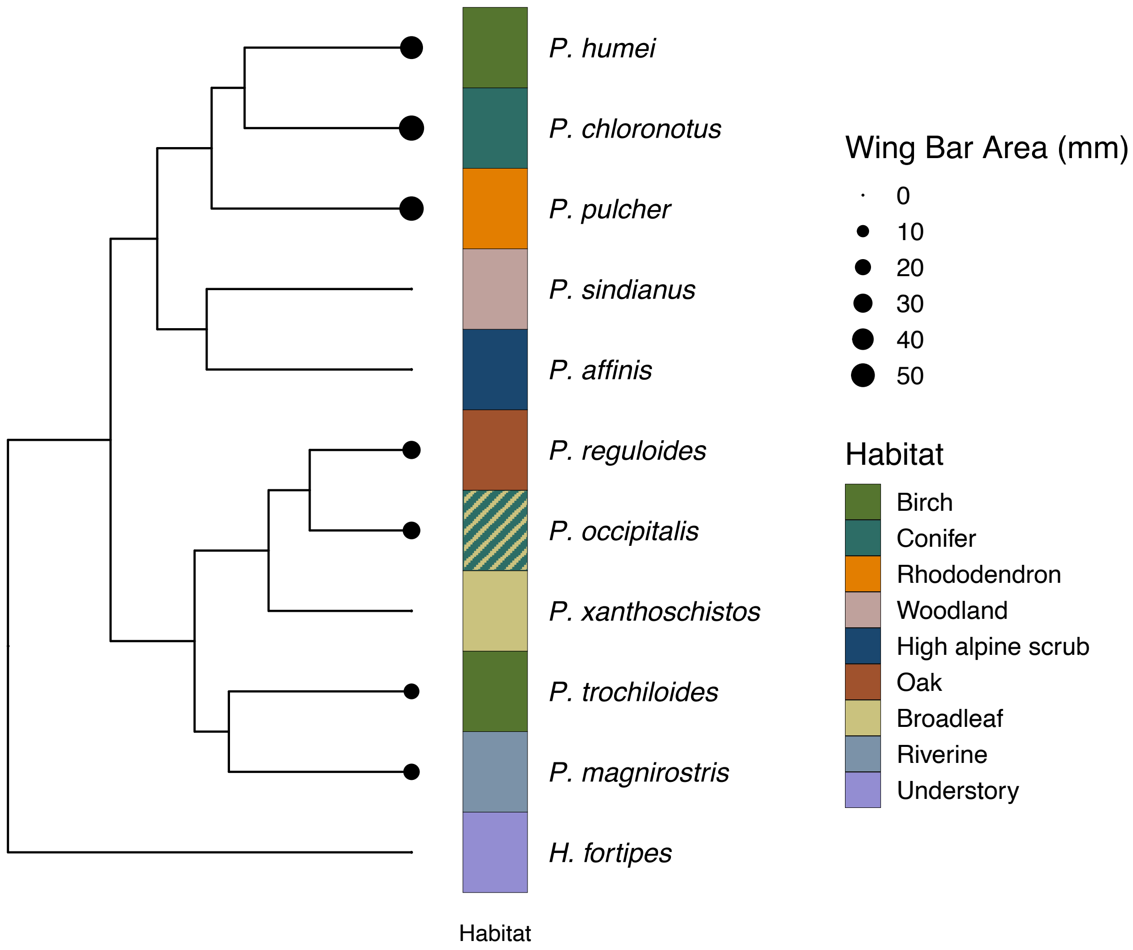

Figure 3.1: **Evolutionary relationships for the 11 species studied** (phylogeny from Price et al. 2014). Size of the point at the tip corresponds to each species wing bar size (Price and Pavelka 1996) and is color coded by primary habitat during the breeding season.

Wheatcroft 2015). Display form was collected to quantitatively assess whether displays vary and explicitly address the question of how displays have evolved across species.

To document the use of wing movements during foraging, we opportunistically filmed individuals. When a species of interest was detected, we used a single Sony RX10 DSC III camera mounted on a tripod set at 60 frames per second (fps) and filmed the individual for as long as possible. Birds were identified to species at the time of filming or when reviewing the video footage through call notes, songs, plumage, or a combination of these traits.

Most of the data comes from territorial playback experiments. During the breeding season, we located singing males between 0500 - 1100. Experiments consisted of two parts. During Part I we established a filming focal point and observed the territory owner's response. We placed a Bluetooth speaker (Ultimate Ears WONDERBOOM) in the target individual's territory and played that species song to simulate a territorial intrusion. If the territory owner responded by singing back and approaching the speaker, we continued to play the song for 5 minutes to observe where the individual would perch in the territory. This was to maximize the likelihood that the camera setup would capture the behaviors of interest. In total, we attempted 376 behavioral trials. Of those, 45% (N=160) were terminated during Part I due to either poor filming conditions or lack of response from the territory owner.

Part II: Once a consistent focal point was established, we set up two camera teams. The first team consisted of a single person with a camera (Sony RX10 DSC III) mounted on a tripod, filming the target bird at 60 fps continuously during the trial. This allows for an extended view of the display and was used to calculate wing flick rate and record all the motions present in the species display repertoire. The second camera team operated a high-speed camera assembly, which consisted of three Sony RX10 DSC III cameras mounted on tripods, each equipped with a Ziv TRS-10 Timer Remote set to the same channel, allowing for simultaneous remote triggering. We used three cameras to increase the chances of capturing displays during which the bird is oriented laterally (defined as the line from beak to tail running perpendicular to the camera lens). The cameras were placed at least 3 meters from the focal point, in an arc with each camera separated by 45° from the next one. The cameras were set to film at 480 fps on a delayed trigger. This mode continuously films until the trigger is pressed, at which point the prior two seconds of footage are written to the SD card, thereby allowing the capture of display behaviors without a response delay from the observer. Both setups were left undisturbed for 10 minutes before the trial started. During the trial the two observers remained 8 meters away from the focal point.

During the behavioral trials, we played a target species song for 10 minutes. In 38% of trials (N = 216 total trials) the bird did not respond, at which point the trial was deemed unsuccessful and ended (N = 78 terminated trials). For clarification, this differs from the termination described in part I; here the individual responded during the pre-trial period (Part I) but then ceased responding after the camera array was set up and trials began. Because of set-up time and the 10-minute undisturbed period, approximately 20-25 minutes could elapse between song playbacks.

If the bird responded by calling or singing back or by approaching the speaker during this time, the trial continued. We triggered the high-speed camera assembly when the bird perched near the focal point, within the camera's frame of view. The single camera team filmed the bird for as long as possible until sight of the bird was lost, at which point camera recording was paused. The playback trial continued until the end of the 10-minute period, accumulating as many 2 second videos as possible when the birds displays at the focal point. If the bird continuously displayed throughout the time of the first trial, we would leave the camera array in place and begin a 5-minute pause period. After the pause period, the trial was repeated up to a maximum of 3 times.

After behavioral trials, we calibrated the filming area. In every video we placed a 3"x 5" checkerboard and XRite ColorChecker Passport as close to the area where the bird perched. The checkerboard is moved throughout the filming area, pointing to each of the camera views. These tools are used to provide a scale visible from any camera angle.

3.3.3 Light measurements

In both field sites, we deployed Onset light and temperature loggers (HOBO Pendant MX2202 Temperature/Light Data Logger), resulting in 5-13 samples per habitat across the two field locations (Table S3.2). Light loggers were mounted horizontally with the light sensor facing the sky on either horizontal branches in woodlands (birch, conifer, rhododendron, oak) or on PVC pipes staked in the ground in understory and open habitats. Loggers were configured to record light and temperature every minute. Data from the loggers were downloaded to the HOBOconnect app via Bluetooth at the time of collection.

3.3.4 Analysis

Wing motion

From the single 60 fps camera, we measured wing flick rate in two contexts: foraging and territorial response. Videos were selected for foraging analysis if the individual could be seen actively searching for or capturing prey. Territorial responses were filmed at the time of simulated territorial intrusion experiments. We calculated rate as the number of wing flicks an individual performs divided by the total amount of time the bird is present on screen. Using the trim function on QuickTime Player (Apple Computer) with video playback at half speed, we analyzed the video frame by frame to quantify wing flicks. To separate flicks from wing movements used in locomotion we only counted wing flicks when the bird hopped less than one body length during the observation sequence. Total display time is the difference in the timestamp when the individual leaves the frame of view and the timestamp when the focal individual first appears in the frame. We only selected individuals that completed at least 5 wing flicks during the course of the display time. For individuals that left the frame and reappeared over the course of a video recording we took the first display sequence in which the bird performed at least 5 wing flicks.

To quantify the form of the display during the territorial playback experiments, we used only the high frame rate videos in which the bird is in a lateral orientation. We determined lateral orientation visually and then confirmed orientation by viewing the angle from the other two cameras, leaving us with a sample size of 45 individuals from 10 species, reduced from a total high-frame rate dataset of 96 individuals across 15 species. We then extracted frames using the `extractFrames` function in StereoMorph (Olsen and Westneat 2015). We isolated each individual wing flick, defined by the frame in which the wing begins the upstroke to when it returns to the starting position after the downstroke. We described shape using 15 time points for each lateral display. We numbered the frames from 1 (initiation) to the end of the flick; the number of frames varied from 35-45. We first identified three time points from each video – the initiation and end of the wing flick (usually close to the initiation point but often not the exact same position, determined by the point at which the wing stops moving) and the point of maximum wing extension, when the wing transitions from the upstroke to the downstroke (time points 1, 15 and 7, respectively, Figure 3.2). From these we added 12 additional time points by extracting frames uniformly dispersed between the 1-7 (5 points) and 8-15 (7 points).

All statistical analyses were conducted in R (version 4.2.2, R Core Team 2022). We used the `labelFrames` function in StereoMorph to place a landmark on the tip of the 8th primary feather for each of the 15 frames. Each wing flick is then described using 15 "homologous" landmarks, creating a shape capturing the trajectory of wing motion. The landmarks describing the trajectory shapes were scaled and aligned using the Generalized Procrustes Analysis (GPA) in the R package borealis (Angelini 2022) to remove variables of size, rotation and orientation, leaving a set of aligned coordinates that capture variation in shape. We performed a principal component analysis (PCA) on the aligned coordinates and visualized

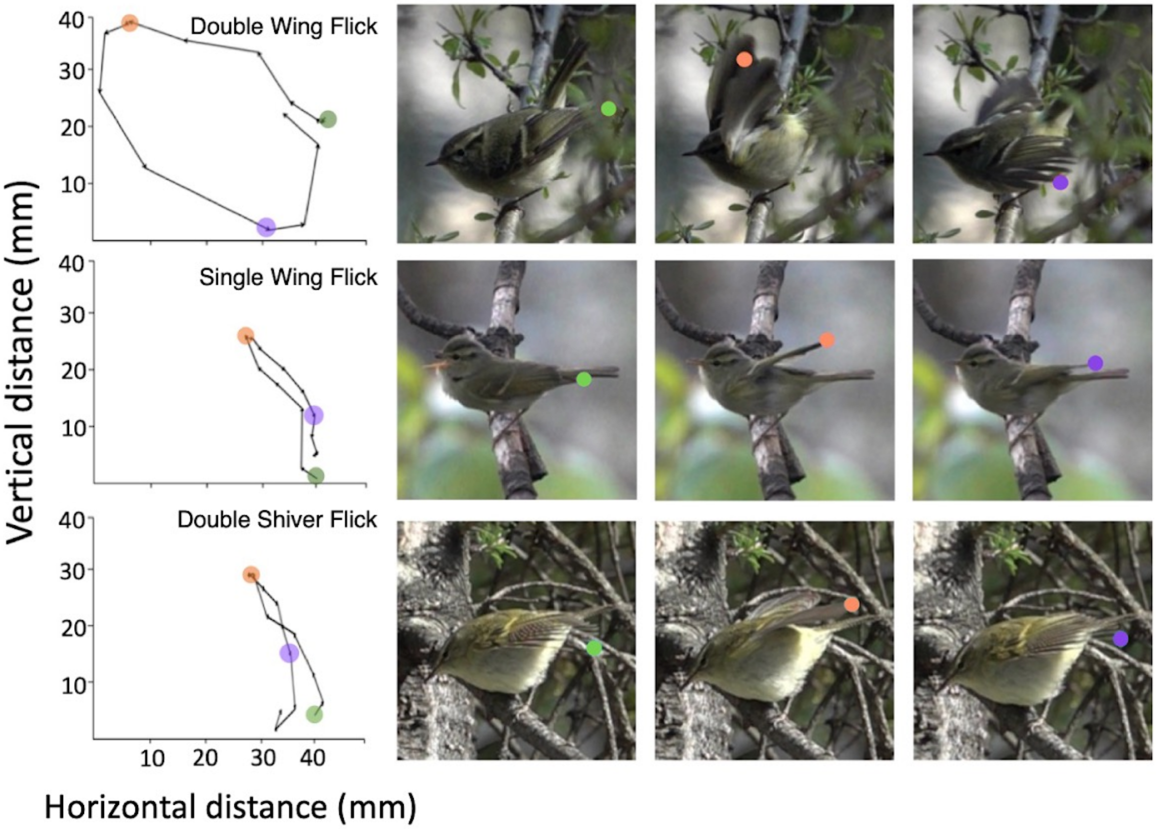

Figure 3.2: *Left* Trajectories for the displays observed in the warblers studied. Plotted is the distance moved in 15 equal time intervals. The dots correspond to 3 time points. L1 (green): when the wing flick begins. L5 (orange): when the wing reaches the upstroke:downstroke transition. L13 (purple): A sample landmark showing how this position can differ depending on the type of motion used in display. *Right* Video frames for each labeled point. From the top, species are *Phylloscopus chloronotus*, *Phylloscopus reguloides*, *Phylloscopus pulcher*. Video examples of these behaviors can be found in the supplementary data.

the location of each individual's trajectory by plotting the first two PCA axes. We plotted convex hulls around the data points in the morphospace generated by PC1 and PC2, the most significant axes of variation. We used the lme4 package in R (Bates et al. 2015) to calculate percent variance between and within species display components for both PC1 and PC2.

To visualize how the shape of wing movement changes along PC1 and PC2, we plotted back transformations of the PC scores to their relative positions in the morphospace (Olsen 2017). The points along the outside of the backtransform shape correspond to the 15 landmarks used to describe the trajectory.

Morphological correlates

To test for the effect of wing morphology on movement we first examined the relationships between the display characteristics (PC1 scores, PC2 scores, territorial and foraging wing flick rates), morphological variables (Kipp's index, Tobias et al. 2022), wing bar size (Price and Pavelka 1996) and foraging behavior (proportion of flycatching, Price 1991; Ghosh et al. 2011) using Pearson's correlation coefficients. To account for potential non-independence among species due to shared evolutionary history, we also performed a PGLS analysis using the `gls` function from the nlme package in R (Pinheiro et al. 2023) with a maximum likelihood method and Brownian correlation structure. We used the time-calibrated phylogeny from (Price et al. 2014) and pruned it to include the 11 species used in this study (Figure 3.1).

Light measurements

We extracted the lux values from the logger files and log-transformed the data. To standardize for longer day lengths as the season progressed, we filtered the data to include times between 0600 - 1800, which is a time interval occurring after sunrise and before sunset through the entirely of the breeding season. We then took the average lux measurement per logger per day.

Results from habitats present in both locations were similar and we combined them. We fitted a linear mixed-effects model with habitat as a fixed effect and location and logger ID as nested random effects using the R package lme4 (Bates et al. 2015). We then performed a post-hoc pairwise comparison of the habitats using R package emmeans (Lenth 2023).

3.4 Results

We observed three discrete behaviors (Figure 3.2). We first analyzed a behavior, which we term the double wing flick, that is shared between all species. This behavior resembles motions used during takeoff, where both wings are moved simultaneously through rotation at the elbow and shoulder joints during the upstroke. During the downstroke, the humerus is extended horizontally from the body, resulting in the extension of the distal portion of the wing until it folds back to rest near the starting position. One species (*P. pulcher*) commonly conducts a double shiver flick, distinguished from the double flick by both shape (Figure 3.4) and rate (Figure S3.1). During this behavior the wings are extended horizontally from the body at the shoulder and undergo a series of rapid rotations at the elbow and wrist joint, resulting in a shivering motion. During territorial displays, this behavior is repeated and rarely interspersed with double wing flicks. Finally, two related species (*P. occipitalis* and *P. reguloides*) conduct a single wing flick, whereby one wing is raised vertically from the body at the elbow joint, but the wing does not undergo a horizontal extension. Instead, the wing is placed back to the starting position before alternating with the other. Both species intersperse single wing flicks with double wing flicks during both foraging and territorial displays (Table S3.3).

3.4.1 Wing flick rate

Phylloscopus affinis does not flick its wings at all in display, although it does so when foraging (Figure 3.3). All other species flick their wings significantly faster during territorial displays than during foraging (Figure 3.3, Table S3.4). All species, including *P. affinis*, have similar foraging wing flick rates ($F_{10,28} = 0.597$, P = 0.8). Once *P. affinis* is excluded, species do not differ significantly in territorial display wing flick rate ($F_{9,17} = 0.59$, P = 0.8, Table S3.5). Shiver flicks are the dominant behavior used by *P. pulcher* during territorial contexts, comprising 95% of the motions used during a display. Shiver wing flick rates are significantly faster than double wing flick rates (Figure S3.1). Shiver flicks are only used during territorial interactions, and we observed no instances of this behavior during foraging. Within the foraging context, single wing flicks do not differ significantly from double wing flicks in *P. occipitalis* and *P. reguloides*. However, single wing flicks used during territorial displays are significantly faster than those used during foraging (Figure S3.2).

3.4.2 Wing trajectory

We first analyzed double wing flicks. The primary axis of variation (PC1: 47% of the variance explained) describes reduced horizontal movement of the wing (Figure 3.4). Individuals with low values of PC1 move their wings more elliptically while those with high values of PC1 move it along a more constrained vertical axis. PC1 scores do not vary significantly among species (ANOVA: $F_{9,23} = 2.03$, P = 0.08, table S3.6). The second axis of variation (PC2: 18% of the variance explained) corresponds to an offset of the starting and ending points. Individuals with low values of PC2 tend to place their wings close to the point at which they initiate their wing flick, while those with high values of PC2 have more variability with where the final downstroke points land relative to where they start. Most of the variance is within versus between species (95% within for PC1 scores, 81% for PC2 scores). Despite this large variance among individuals within species, species differ

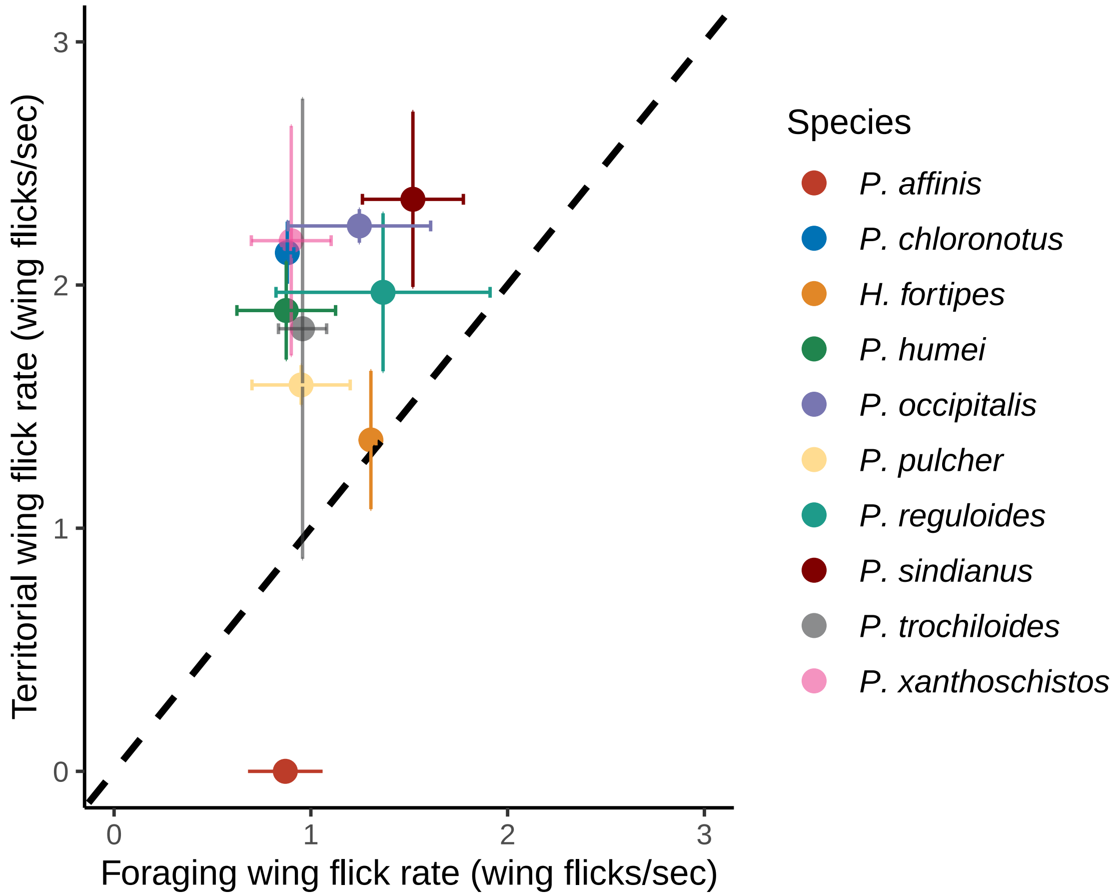

Figure 3.3: **Species territorial wing flick rate plotted against foraging wing flick rate**, with standard error. The black dashed line is the line of equality; 8 species flick wings faster in territorial interactions. Among the 9 species foraging and territorial rate are not correlated (r = 0.12, P = 0.3). For sample sizes for each species, see Table S1.

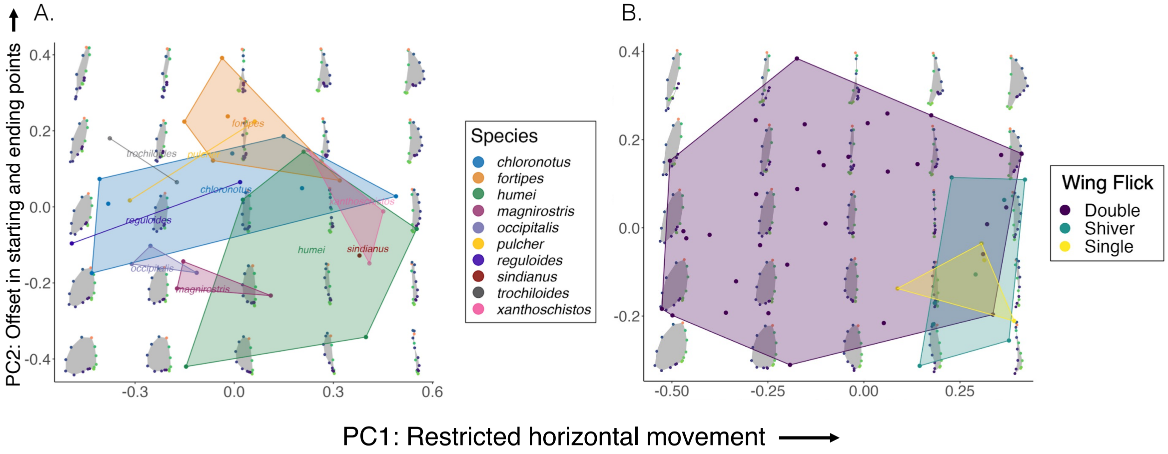

Figure 3.4: (A) Double wing flick shapes for individual males. The colored lines circumscribe the convex hull for each species (note that some species have a sample size of N = 2, so are connected by a line). Background (in grey) illustrates the trajectories; upstroke landmarks (points 1-6) are in green, the upstroke:downstroke transition (point 7) is shown in orange and downstroke landmarks (points 8-15) are in purple. PC1 (47% of the variance) describes a restriction in horizontal movement of the wing and PC2 (18%) represents an offset in the starting and ending points of the wing. (B) Principal component analysis was performed on the entire dataset for the three wing flick types. The convex hulls enclose all species for each wing flick type (double, as in the left plot, single: *reguloides*, *occipitalis*, shiver *pulcher*.) PC1 (44%) describes a restriction in horizontal movement of the wing and PC2 (15%) an offset in the starting and ending points of the wing.

significantly in wing flick shape along the PC2 axis (ANOVA: $F_{9,23} = 3.07$, P = 0.014, Table S3.6). Pairwise comparisons indicate that this is a consequence of large differences between *H. fortipes* and both *P. humei* and *P. magnirostris* (Table S3.7). Specifically, *H. fortipes* tends to bring the wing further down during the downstroke, overshooting the starting position.

Next, we included all three wing flick types in a single analysis, where we combined observations from all species to compare the three types. The single and shiver wing shape motions varied significantly from the double wing flick along PC1 (ANOVA: $F_{2,42} = 9.5$, P = 0.0004, a posteriori tests are in Table S3.8). Shiver and single wing flicks have higher PC1 scores relative to double wing flick because the upstroke and downstroke landmarks are closer together, with less horizontal motion. The two wing flick types overlap with the edges of the double wing flick space at extreme values of PC1 (Figure 3.4). Differences along the PC2 axis are not significant ($F_{2,42} = 3.06$, P = 0.06). Although shiver flicks (N = 8) occupy a larger area of the morphospace along PC2 (Figure 3.4) than single wing flicks (N = 4) this may be due to a larger sample size capturing more individual variation.

3.4.3 Correlation of morphology and movement

Mean PC2 scores of double wing flicks correlate with a species' Kipp's Index (r = 0.66, P = 0.03, PGLS, P = 0.04, Figure 3.5, Table S3.9): species with more rounded wings (lower Kipps Index) have higher variability in wing starting and ending position during display. All other tests of morphological and ecological correlates (wing bar size, proportion of flycatching behavior) are nonsignificant (Table S3.9).

3.4.4 Habitat

Habitats differ in brightness (Figure 3.6); a posteriori pairwise tests indicate that open is brighter than all other habitat types and understory is significantly darker than all other

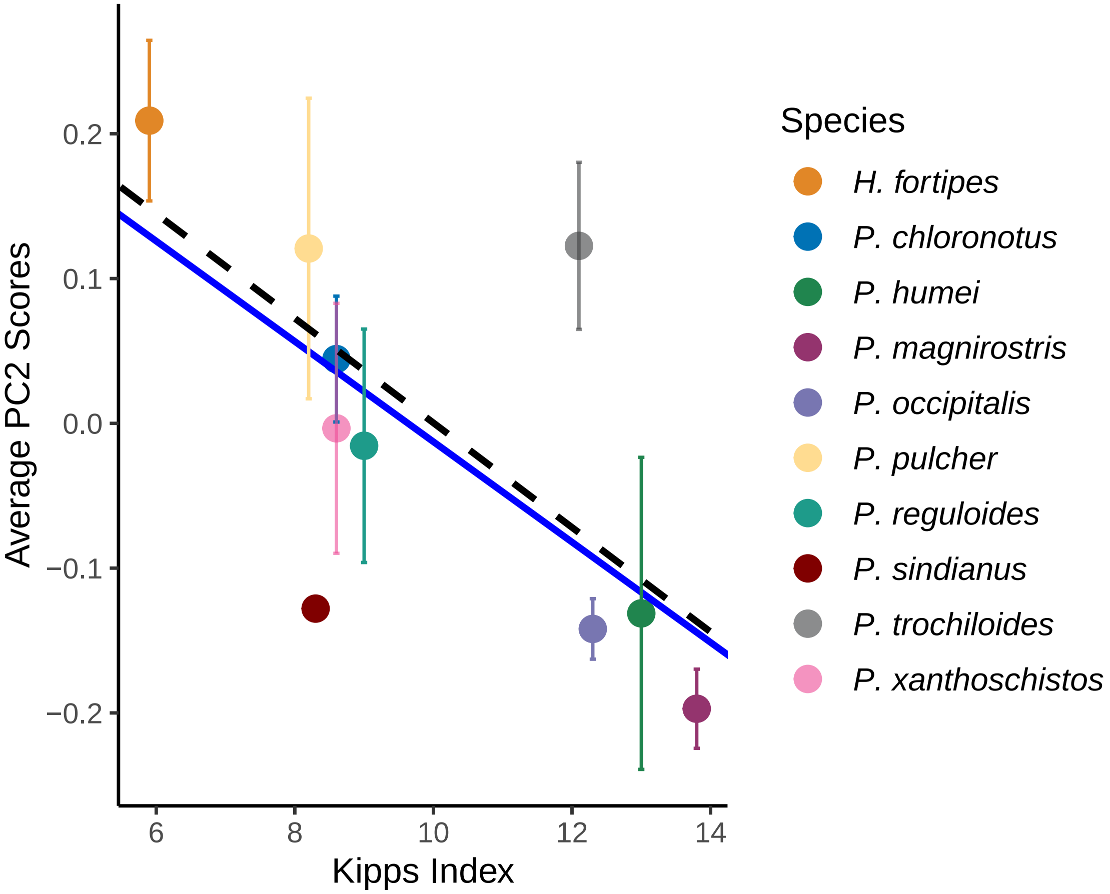

Figure 3.5: **Association between Kipps Index and PC2 scores** (as in (A) of Figure 3.4) for double wing flicks (r = 0.66, P = 0.03), with standard error. Ordinary least squares regression (solid line) (b = -0.03, P = 0.04, R2 = 0.44), phylogenetic least squares (dashed line, b = -0.04, P = 0.03). For sample sizes for PC2 scores see Table S10.

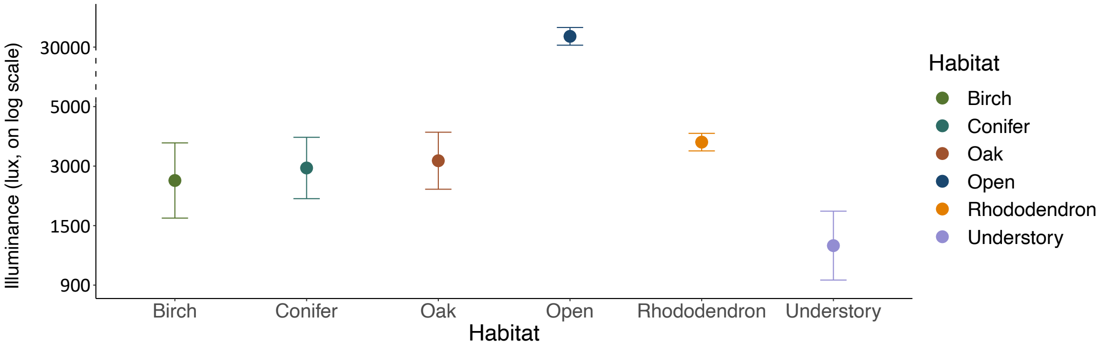

Figure 3.6: **Brightness for 6 different habitats in the western Himalaya** (mean ± standard deviation). For statistical tests see table S9. Pairwise Tukey tests indicate open and understory habitats are significantly brighter and darker, respectively, from birch, conifer, oak and rhododendron, which are not different from each other.

habitat types (Table S3.10). Conifer, birch, oak, and rhododendron did not vary significantly in brightness between each other.

3.5 Discussion

Motion is one of the most effective ways to capture attention (Abrams and Christ 2003; Franconeri and Simons 2003; Rushton et al. 2007). In birds, wing movement is perhaps the simplest way to increase visibility. If wing movements draw the attention of receivers, an increase in the rate of movement may elucidate stronger reactions, as in the principle of perceptual bias. We show here that 11 related warbler species all flick their wings when foraging, and all but 2 of these species increase wing flick rate when facing a simulated territorial intrusion (Figure 3.3). Because individuals can modulate rate of wing movement and given that most species increase the intensity of the behavior in response to threat, some role in communication is implicated. The wing motions may be communicating aggressive intent (Anderson et al. 2013), or used as cue to increase detectability, including serving as an amplifier of plumage patches when they are present (Hasson 1991; Bókony et al. 2006).

The wing movements we studied occur during short range aggressive interactions. They are present in all but one of the species we studied. Consequently, we expected the form of the display to remain largely consistent, inherited through their common ancestor. We found this to be the case: the primary display (the double wing flick) follows a similar shape trajectory in all species, with 95% and 80% of the variation occurring among individuals within species than among species for PC1 and PC2 shape scores, respectively. The large variation within species may reflect differences in individual aggressive motivation (Hurd and Enquist 2001), nesting stage (Gowaty 1981) and/or fighting ability (Jonart et al. 2007), with all these factors likely to operate in all species. We presume the overall similarity in the display reflects an underlying general constraint of a wing designed for flight. However, three species use a different display as well as the double wing flick, in which the wing shows relatively less horizontal movement.

Despite the widespread use of the display across species and its expected efficacy in close-range interactions, the display has been modified in four distinct ways: 1) slight changes associated with wing morphology differences, 2) loss of the display altogether, 3) integration with a color patch, and 4) presence of additional displays. We first consider the origins of the shared display and why it remains similar across species, and then evaluate the drivers of differences among species.

3.5.1 Perceptual bias

All species flick their wings when foraging (Figure 3.3), a behavior that is shared across sexes and seasons. One proposed function for regular wing flicking is prey flushing, typically described in flush-pursuit foragers, which rely on motion of wings and tails to flush insects (Jabłoński 1999; Mumme 2002; Jablonski and McInerney 2005). In the Phylloscopidae the proportion of flush-pursuit behaviors is generally low and some species feed almost entirely on resting insects. For example, in *P. affinis* 96% of prey captures involve picking insects from the foliage (Price 1991), yet it regularly flicks its wings when foraging (Figure 3.3).

Movement in general is an effective means of increasing detection (Rushton et al. 2007) and the wings are easily flicked even when a bird is stationary, and it seems likely that an important function of wing movement is communication to conspecifics. If individuals are attuned to a particular motion used in one context, such as foraging, the use of this motion in different context, such as threat, should continue to elicit a response. The perceptual bias generates attention to these motions, which then become co-opted and exaggerated into components of the threat displays. In this way, interactions specific to males during the breeding season arise out of movements common to both sexes used throughout the year.

3.5.2 Ecological constraints

If social and natural selection pressures together affect morphology, altered ecologies are expected to impact social displays. Here we have found that species with more pointed wings are more likely to start and end their wing flick from the same place, while species with more rounded wings are less consistent in where the wing is placed at the beginning and end of the flick. In the Phylloscopidae species with rounded wings both forage in denser vegetation and have shorter migration distances (Marchetti et al. 1995). *H. fortipes*, also included in our study, has the most rounded wing, forages in particularly dense vegetation, and is an altitudinal migrant (Olsson et al. 2006; Clement 2020). Hence, we attribute natural selection pressures associated with foraging and migration to drive morphological differences, which have affected the overall form of the display.

3.5.3 Sensory drive

In Kashmir, Marchetti (1993) observed that *Phylloscopus* species with wing-bars inhabited darker environments than those without wing-bars, which she attributed to sensory drive. She argued that in darker habitats, species maintain visibility by becoming brighter in appearance. *P. affinis* is the one species without wing-bars held in common between that study and ours. This species breeds above treeline in high alpine scrub (Price 1991), which is substantially brighter than all other habitats we studied (Figure 3.6), reflecting the open composition of this habitat with little to no tree cover. Further, this species does not flick its wings in display (Marchetti 1993) implicating a role for sensory drive in not only affecting plumage, but also display. Note that the lack of wing flicking in this species is not a consequence of reduced aggressive responses. Indeed, in our experiment, the territory owner responded very aggressively, singing back, approaching (Supplementary Video 1), and even attacking the speaker, but it never flicks its wings. One distinctive feature of *P. affinis* is the prominent yellow (carotenoid based) underparts (Figure 3.1). It appears that conspicuousness in this species is driven largely by the yellow coloration, and that wing motion during display may be unnecessary or even disadvantageous in the open habitat. It bears noting that the two other species without wing-bars both flick their wings. One, *P. xanthoschistos*, has yellow underparts, and the second, *P. sindianus* lives in relatively open habitats, whose light environment we were not able to measure but is likely to be intermediate between that of open habitat and dense woodland.

H. fortipes inhabits thick undergrowth which is substantially darker than all other habitats (Figure 3.6). *H. fortipes* has no wing-bar, but does have a white patch under the wing, which is only exposed when the wing is raised (Chapter 2). Despite using a very similar motion to that of the other species in our study, the patch is placed in a completely different location, and may function as a flash display at close quarters (Chapter 2). These features suggest adaptation to the specific features of this habitat.

Overall, despite the similar form of the display across species, the location, size, color and presence of the plumage patch varies, and at least some of this variation may be explained by the light environment. These results reject a hypothesis proposed by Tinbergen (1948) that display movements and color patches should be closely correlated. Instead, patches have evolved in the context of a relatively invariant display. The one exception to this pattern which tests and supports a role for sensory drive is *P. affinis*, which lives in the most open environment and has dropped the display and also has no wing-bar.

3.5.4 Additional displays

In addition to the baseline double wing-flick, a small clade within the Phylloscopidae have a display in which species alternate moving single wings (see Table S3.3 for example sequence) (del Hoyo et al. 2020a,b). The clade includes both *P. reguloides* and *P. occipitalis* from this study. These single wing flicks are often intermingled with double wing flicks during both foraging and aggressive displays (Table S3.3). While the origins of the single wing flick are obscure, it is used by both males and females during foraging throughout the year. These species form large flocks in the winter (Macdonald and Henderson 2008; Hariharan et al. 2022), where wing motions may serve to facilitate flock cohesion or communication. The rate of the single wing flicks increases during male aggressive interactions (Figure S3.2) so the display functionally operates in the same way as the double wing flick. However, the single wing flick is distinctive in its trajectory, where the distal portion of the wing remains unextended and most of the motion is concentrated in lifting the wing at the wrist joint. This results in relatively less horizontal movement than the double flick (Figure 3.4).

The other display, employed by *P. pulcher* is different. This display, the shiver double flick, is used only in the breeding season and largely replaces that of the double wing flick (Supplementary Video 2). The shiver flick is characterized by faster movement (Figure S3.1), achieved through a series of rotations at the wrist joint. This also results in relatively less horizontal motion than the double wing flick (Figure 3.4), although the motion itself is different from the single wing flick. It resembles the motions used by young birds of all species when they are begging for food (Supplementary Video 3), but the reasons why it has been established as an aggressive display in this species alone remain obscure.

3.5.5 Conclusions

Our ability to dissect display movements using high speed video and advances in shape analysis borrowed from morphometrics shows that rather than diversify across species, the form of the primary aggressive display has been largely conserved, with only slight modifications associated with wing morphology. Aggressive displays are expected to be simple in form in order to convey an unambiguous message (Hurd and Enquist 2001), e.g. through changes in rate. Once such a display efficiently conveys a message there appears to be little reason for it to be modified. Nevertheless, we find that the primary display has been built on to generate differences among species, through either its complete loss, by the addition or subtraction of color patches on the wing, or by addition of qualitatively different displays. Some of these differences can be related to the light environment. Given environments vary in many ways light intensity, such as foliage structure and background color, we anticipate that future detailed studies of habitat will further our understanding of the origin of qualitatively different displays, and their link to color patch evolution.

APPENDIX

3.A Supplementary Data

The supplementary tables and video files for this chapter can be viewed at `https://figshare.com/s/37cbf252176a0b138284`

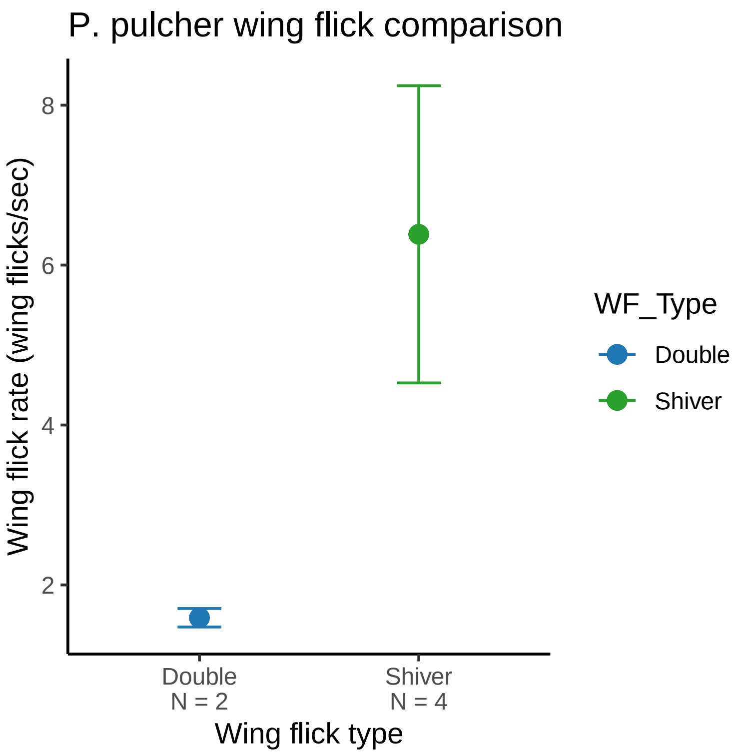

Figure 3.A.1: **Territorial wing flick rates for the two types of wing flicks used by *Phylloscopus pulcher*.** The bars show standard deviations from the mean. Shiver flicks are faster than double flicks. (ANOVA: $F_{1,4} = 11.82$, P $= 0.03$).

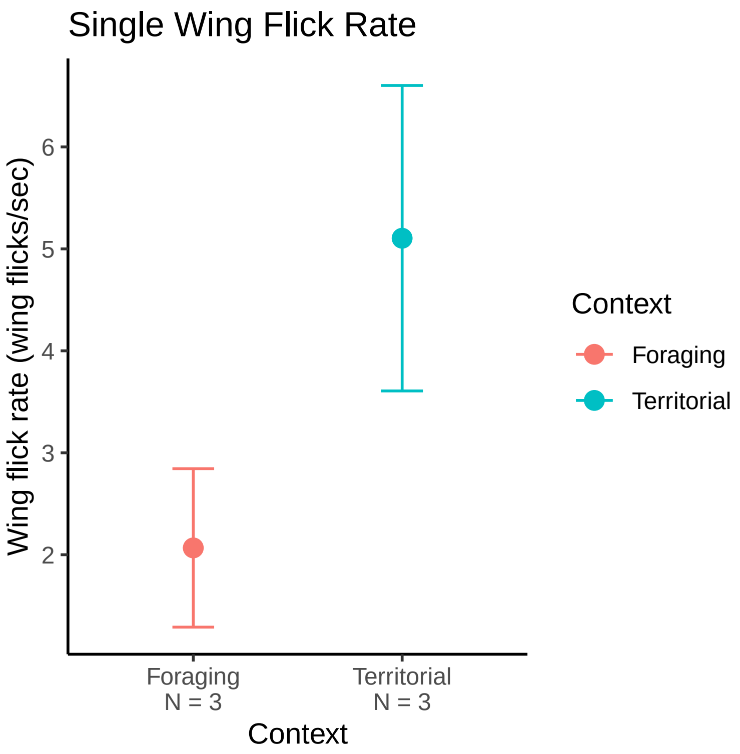

Figure 3.A.2: **Single wing flick rates for foraging and territorial displays used by *Phylloscopus occipitalis*.** The bars show standard deviations from the mean. Single wing flick rate is faster during territorial contexts compared to foraging (ANOVA: $F_{1,4} = 9.719$, P = 0.04).

CHAPTER 4

EVALUATING LIGHT ENVIRONMENT AND DISPLAY AS CONTRIBUTORS TO COLOR DIFFERENCES AMONG RELATED BIRD SPECIES

4.1 Abstract

Understanding the diversity of color in nature has been one of the more elusive evolutionary problems. In the terrestrial environment, comparative analyses have associated color differences between species to light environment, background color and receiver perceptual abilities. However, these only account for a small fraction of color diversity, and it has been difficult to explain why a certain species is the color it is. How a color patch is displayed behaviorally also impacts perception and incorporating motion may help elucidate patterns in color diversity. Here we examine color variation across 12 very similar species of warblers belonging to the genus *Phylloscopus*. Most species have pale patches on the wing bars, and some also have white outer tail feathers. We quantify variation in plumage color and model perception of these patches under light conditions found in species habitats. To ask whether color may be related to behaviors during signaling, we investigate patch use during territorial display through playback experiments and high-speed video recording. We find little evidence that irradiance or different display motions affect the color of patches. Instead, differences in tail and wing coloration may be a consequence of their potential use in different signaling functions. In general, the many factors affecting colors and the many adaptive solutions possible likely mean that species should regularly occupy unique positions in color, pattern, and display space. This implies weak correlations in comparative analyses are to be expected and making detailed studies of individual species particularly important.

4.2 Introduction

Understanding what drives diversification in animal signals has proved to be a particularly challenging topic. Why, for example, does the Wilson's bird-of-paradise (*Cicinnurus respublica*) possess a feather-less blue head, while its closest relative, the Magnificent bird-of-paradise (*Cicinnurus magnificus*) have feathered, rufous head coloration? Substantial differences in animal colors may result from the many possible color variants that can each elicit favorable responses from receivers (Arak and Enquist 1993). Given the relentless pressure of social selection (West-Eberhard 1983), even small color differences may become exaggerated, leading to dramatic differences between species that can be uncorrelated with environmental features (Lande 1981; Schluter and Price 1993; Mendelson et al. 2014). This reasoning likely explains differences among males in strongly sexually-selected radiations, such as the birds-of-paradise (Price 2017). However, despite the innumerable possibilities for diversification, ecological factors do make it more likely that some signals are favored over others. For example, in the birds-of-paradise, display repertoires are more complex in species dwelling near the forest floor (Ligon et al. 2018; Miles and Fuxjager 2018) while acoustic repertoires increase for species in higher forest strata (Ligon et al. 2018) likely due to different transmission pressures along a vertical gradient in tropical forests.

Most families contain bird species that are much less differentiated from each other than the birds-of-paradise. With respect to color and color patterns, males and females in such families may be very similar or even identical (Dunn et al. 2015). Such groups are considered to be subject to weak sexual selection, and diversification in social signals correspondingly limited (Seddon et al. 2013; Dale et al. 2015). Accordingly, a relatively larger fraction of species' color and pattern variation may be correlated with ecological factors; these include predation pressure (Bliard et al. 2020), thermoregulation (Rogalla et al. 2022), camouflage (Mason et al. 2023) and habitat (Gomez and Théry 2004; Beco et al. 2021). Studying clades in which there is relatively little variation between species is a promising route to develop a more predictive theory of color and pattern evolution and to elucidate the role of ecology in these processes (Marcondes and Brumfield 2019). Comparative and experimental studies assessing the association of color and ecology in such groups may provide a baseline model against which arbitrary divergence in more sexually selected groups can be evaluated.

The most influential model used to elucidate the role of environment in color and pattern evolution is sensory drive (Endler 1992), which emphasizes that the conditions of an animal's environment are expected to affect both its sensory system and its signaling traits. Since its proposal, evidence has accumulated showing support for sensory drive (reviewed in Cummings and Endler 2018). The strongest support in the visual modality comes from aquatic environments, which experience stark gradients in available light spectra due to scattering of wavelengths at different depths influencing both which colors fish species evolve to perceive (Cummings and Partridge 2001; Carleton et al. 2005; Fuller et al. 2005; Maan et al. 2006; Veen et al. 2017) and which colors species carry (Endler 1991; Boughman 2001; Fuller 2002; Maan et al. 2006; Cummings 2007; Seehausen et al. 2008).

Color in the environment has been quantified in two ways. Radiance measures the spectral distribution of light emanating from a point source, whereas irradiance measures the spectral distribution of light assumed to be illuminating the object. Hence, units for radiance are photons/second/solid angle for each nanometer wavelength, whereas for irradiance the units are photons/second for each nm. wavelength. In the sensory drive literature, the effects of both radiance and irradiance have been considered in affecting color pattern evolution. Comparisons of an animal with its background and of patches within an animal rely on radiance, which provide a measure of how similar two patches or objects are under the same viewing conditions. These have been important in assessments of camouflage as well as signaling traits (Endler and Théry 1996; Heindl and Winkler 2003a; Uy and Endler 2004; Endler and Mappes 2017). Irradiance is used to describe how various signaling environments differ in their available light spectra, such as the spectral distribution along a depth gradient in aquatic environments (Cummings and Partridge 2001; Seehausen et al. 2008) and along different forest geometries in terrestrial environments (Endler 1993). Because an object or animal's radiance can be estimated from the irradiance, most studies measure the latter when testing the relationship between color and environment (Heindl and Winkler 2003b,a; Gomez and Théry 2004; Uy and Endler 2004).

In the terrestrial environment, habitat irradiance has been associated with chromatic variation among bird species. Species in “closed” environments, such as forests, are on average "redder" (McNaught and Owens 2002) and show a higher diversity of within plumage coloration (Shultz and Burns 2013, 2017) than species in open habitats. Within forests, a strong stratification in both chromatic (color) and achromatic (brightness) axes occurs along a gradient from canopy to understory, with a decreasing proportion of low wavelength (‘blue’) light and decrease in overall light intensity as one moves to the understory (Endler 1993; Théry 2001). Correspondingly species in the canopy have higher within-plumage chromatic diversity and more UV reflectance than species occurring in the understory (Gomez and Théry 2004; Shultz and Burns 2013, 2017). It is worth noting that an animal's coloration can vary along several dimensions. First, for any given location in the body species can differ in color, such as the variation in crown coloration between the Wilson's bird-of-paradise and Magnificent bird-of-paradise noted previously. Second, species are rarely uniformly colored, but instead consist of a mosaic of patches of two or more colors.

Differences between species coloration in large patch areas have been associated with habitat irradiance as described previously (Gomez and Théry 2004, 2007; Shultz and Burns 2013, 2017; Marcondes and Brumfield 2019) but the relationship between different patches within the same individual and the light environment is more complicated. In Wire-tailed Manakins *Pipra filicauda*, the within-bird brightness and color contrasts differ between light conditions such that visual contrast is enhanced when viewing adjacent patches at close range but overall body contrast is reduced against the background, suggesting birds may be balancing crypsis and conspicuousness pressures (Heindl and Winkler 2003a). Gomez and Thery (2007) found that canopy birds had more local brightness and color contrasts on the wings and tail while understory species had more local color contrasts on the head, tail and chest but the distribution of brightness contrasts differed between males and females, with the latter having brightness contrasts focused on the head and chest. The placement of contrasting patches is notable, as its been suggested that species in darker environments may be modulating conspicuousness through movement (Marcondes and Brumfield 2019).

How a patch is moved can affect the perception of a color or may make certain colors more likely to be used. Several studies have shown how color and display covary, mostly in highly sexually selected groups including hummingbirds (Hogan and Stoddard 2018; Simpson and McGraw 2018a,b, 2019), manakins (Endler and Théry 1996), birds-of-paradise (Ligon et al. 2018; Miles and Fuxjager 2018), and peacocks (Dakin and Montgomerie 2009; Dakin et al. 2016), as well as in toucans (Miles and Fuxjager 2019). Despite this connection, the understanding of why specific patches are the color they are has proven elusive. We propose two plausible adaptive reasons for why display should affect patch color.

1. Different locations of the body may be incorporated more easily into displays. Some areas of the body, such as the wings and tail on birds, can be moved easily and with greater control which can serve to amplify a color signal (Hasson 1991) or reinforce the information communicated in color with information through motion (Johnstone 1996). Other areas, such as the head, belly and back, are easily visible to receivers. Cardosa and Mota (2022) showed that in 53 species of finches the color saturation of the yellow breast was on average sexually dimorphic, whereas the yellow rump was sexually monomorphic. They argued the breast color was used in display by males to females, whereas rump color was involved in flock cohesion. We may predict that colors used in displays should be placed in areas of the body in which they are prominently visible or areas that can be incorporated with movements used in communication.

2. If there is a tradeoff in conspicuousness and camouflage, highly conspicuous color signals may be placed on areas of the body in which they can be facultatively concealed or revealed. Coverable badges, for example, are used in intrasexual displays and can be behaviorally modulated depending on context (Hansen and Rohwer 1986). Areas such as the rump, outer retrices, underwing coverts and flanks can be concealed when the bird is at rest and revealed through movement.

In this paper, we use the leaf warblers (Phylloscopidae) as a model system to study chromatic and achromatic variation between species and sexes, addressing roles for irradiance, display and their possible interaction as a cause of color differences, couched in the context of the explanations above. The Phylloscopidae are monomorphic and different species are similar in appearance, with the most striking difference being the number of pale plumage patches (white or yellow) on olive, brown or greenish plumage (Price and Pavelka 1996). Variation in the quantity of patches (on the wing, crown, rump, and tail in the most patterned species) has been attributed to sensory drive along an achromatic (bright-dark) axis (Marchetti 1993). Species living in dark habitats, notably conifer, have more pale patches than species living in open woodlands or high alpine scrub (Marchetti 1993).

We studied 12 species of *Phylloscopus* warbler that breed across an altitudinal range of 2,000-4,000 meters within the west Indian Himalayan region of Himachal Pradesh (Price et al. 1997, 2003). Species have restricted altitudinal distributions, closely associated with specific habitats (Price 1991; Ghosh-Harihar and Price 2014). We quantify the distribution of color across species, and within individuals by looking at the back, belly, greater covert feathers (wing bar and adjacent areas) and retrices. Most species (Figure 4.1) have a lighter portion at the distal end of the greater covert feathers that forms a distinct patch due to an absence of melanin and deposition of carotenoid (Price and Pavelka 1996), called the wing bar. The rest of the feather is darker, often brown or olive green in coloration and we refer to this as the area adjacent to the wing bar. Some species (Figure 4.1 also have varying extents

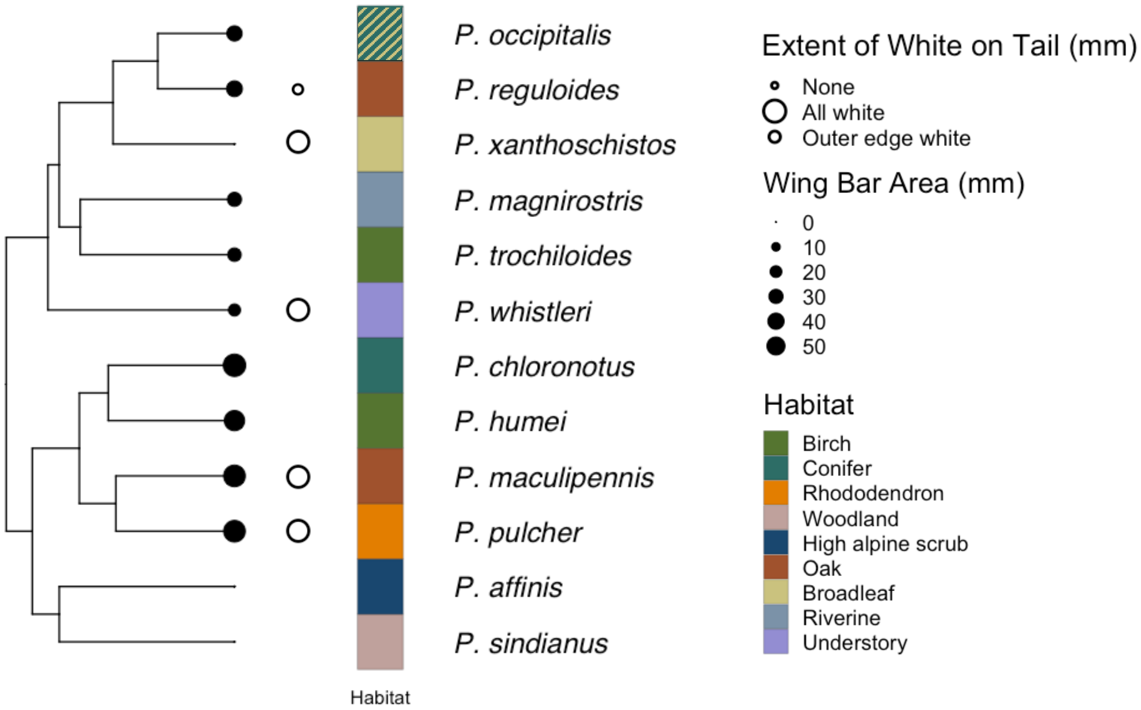

Figure 4.1: **Evolutionary relationships for 12 *Phylloscopus* species in the western Himalaya**. Filled circles at the tips of the phylogeny correspond to the wing bar size of each species and open circles correspond to the extent of white on the outer retrices. The colored squares represent the primary habitat of each species during the breeding season. Phylogeny is pruned from Alstrom et al. 2018

of white in the outer tail feathers and we considered these patches in addition to non-white retrices.

After quantifying the color and variability of patch types across species, we then ask how adjacent patches are perceptible to an avian receiver. When assessing an individual, color patches are not viewed in isolation but against other areas of the body. This can potentially lead to different pressures on discriminability depending on the function of the color patch. Adjacent areas in a plumage can affect perception of the focal patch, especially in intraspecific signaling. For example, "super-black" plumage adjacent to lighter patches in bowerbirds have invoked this mechanism as means of increasing brilliance in the receiver's eye (McCoy et al. 2018). We focus our analyses on three pairs of adjacent patches: the back and belly, the wing bar and adjacent area and the white and nonwhite areas of the tail. The back and belly plumage encompass the largest area of the bird and the contrast between them is responsible for countershading, a feature important in camouflage (Thayer 1896). The wing bar, a patch formed by the lighter tips of the greater covert feathers, is known to function as a signal in inter and intrasexual interactions in *Phylloscopus humei* (Marchetti 1998). The area immediately adjacent to the wing bar can affect the perception of the focal patch and this contrast may be under different pressures in different signaling conditions. Finally, the function of white tail feathers in *Phylloscopus* is unknown, but white tail markings in other bird species have been related to foraging (Jabłoński 1999; Mumme 2002, 2014), flock cohesion (Beauchamp and Heeb 2001) and predator deterrence (Randler 2016; Ramesh and Lima 2019). Thus in this system we have three pairs of patches that may serve different functions (back-belly: camouflage, possibly intraspecific signaling, wing bar-adjacent area: intraspecific signaling, white-nonwhite tail: possibly foraging, flocking, predator signaling). If enhanced contrast is important in color patches used in intraspecific signaling then we predict differences between the three patch comparisons, with wing bars and adjacent areas having the greatest contrast. If contrast is important in camouflage via countershading, species living in the same habitat types should have more similar contrasts than other species.

The “color” of an object is dependent on both the properties of the object and the illuminant under which it is viewed under. Differences in the available light spectra may affect both the perceived color of a plumage patch as well as the contrast between adjacent patch types. To ask whether differences in signaling environment influence differences in color across species and plumage patch types we first characterize the light environment during the breeding season by measuring irradiance. Light spectra in forests are strongly influenced by geometry (Endler 1993), so different characteristics of tree species may affect which light regimes are possible. For example, if a forest type has a largely discontinuous canopy, then both "forest shade" and "small gap light" environments (Endler 1993) would be absent from that habitat. We focused on 5 habitats: birch, conifer, oak, understory, and rhododendron and ask whether these habitats present distinct chromatic light environments. We then use avian visual models to investigate whether adjacent plumage contrasts differ under different light regimes.

Lastly, we turn to the role of motion as a contributor to color variation by looking at how species use their plumage patches during territorial displays. Male *Phylloscopus* warblers perform stereotyped wing and tail motions in response to intraspecific challengers during the breeding season (Marchetti 1993; Fialko and Price 2024), presenting an avenue through which color patches may function. In our investigation we compare wing patches, which contain carotenoid pigments making them appear yellowish, with tail patches, which are always white in the species that carry them. We ask whether 1) color differences between the wing and tail are related to differences in wing and tail use during display and 2) whether interspecific differences in patch contrasts between wing bars-adjacent area and white-nonwhite tails are related to differences in wing and tail movement between species. For example, under the reasoning of Tinbergen (1948) species with white tail patches should display those patches whereas those without should not or should do in a different way. Species with greater wing and tail contrasts are predicted to have more vigorous wing and tail movements.

4.3 Methods

4.3.1 Plumage measurements

Plumage characteristics were quantified from specimens at the Field Museum of Chicago. We used an Ocean Insight Flame spectrometer with a PX-2 pulsed xenon light source to measure plumage reflectance from 300 to 700 nm, encompassing the avian visual spectrum, in one nm intervals (data available in Table S4.1. Measurements were taken at a 90° incidence angle to the feather surface with a QR200-7-UV-VIS bifurcated reflection probe outfitted with a custom probe holder. The reflectance values are taken relative to a Spectralon 99% reflection standard. We focused on five plumage regions: back, belly, greater covert feathers (wing bar and adjacent area), and rectrices (tail feathers). For back and belly measurements we sampled randomly over the plumage. On the greater covert feather, the wing bar and the area adjacent to the wing bar were measured based on the distinct boundary between the unmelanized (wing-bar) and melanized parts of the covert (Price and Pavelka 1996). However, three species (*P. affinis*, *P. xanthoschistos*, *P. sindianus* Figure 4.1) have no discernable wing bars. For these species we measured the distal tip of the greater covert feathers as the "wing bar" and the proximal region of the feather 4 mm away from the tip as the area adjacent. These areas corresponded to the same location on the greater covert feathers as in the species with visually distinct wing bars. For tail measurements we sampled the area on the outer vane of the outermost left rectrix. However, 5 species (Figure 4.1) have varying extent of white in the outer rectrices and for these we took two separate tail reflectances: white and non-white. If the outermost left rectrix had both white and non-white areas we took the white and nonwhite samples from the same feather. However, if the outermost rectrix was all white then we took nonwhite tail measurements from the next tail feather that showed non-white area (typically the third rectrix). For each patch type we took five replicates and averaged across them.

We measured 72 individuals across 12 species of *Phyllosocpus*. For wing bar, area adjacent to the wing bar, back and belly plumage areas we measured 3 males and 3 females per species. For tail measurements we measured 3 males and 3 females for 11 species with the exception of *P. affinis* in which we only measured 2 females due to tail damage in the third specimen (n = 71 individuals for tail). Five species showed varying extent of white on the outer retrices – we measured reflectance of these areas for 3 males and 3 females of *P. maculipennis*, *P. whistleri*, *P. pulcher* and *P. xanthoschistos*. For *P. reguloides* only males were measured because the extent of white on females was too narrow to capture with the spectrometer.

4.3.2 Color quantification

All color analyses were conducted using pavo (Maia et al. 2013, 2019) in R (R Core Team 2022). We first calculated the average reflectance of each patch per individual across the five replicates and smoothed the spectra using locally weighted scatterplot smoothing (LOESS) with a span of 0.03, using the `procspec` function in pavo. Spectra were then centered to remove brightness by subtracting the mean reflectance across all 401 values and then binned to 20 nm intervals. We then ran a Principal component analysis using all individuals and all patches across all species to evaluate differences in color and variability between all patch types and species. To test for differences in patch plumage color across species we extracted the PC1 and PC2 scores and subset the data by patch type (Table S4.2). We then ran a two-way analysis of variance (ANOVA) for both PC1 and PC2 scores for each of the six plumage regions with sex * species, using individuals as replicates. We also ran multivariant analysis of variance (MANOVA) on each of the adjacent patch comparisons (wing bar-adjacent area, back-belly and white-nonwhite tail).

We performed a second analysis by averaging reflectance spectra for each sex and species, resulting in a single measure for each patch type for males and females across 12 species. To assess how variable each patch type is we repeated the principal component analysis after preparing the data by binning and centering spectra in the same way described previously. After extracting PC1 and PC2 scores we ran an F-test of variance between each of the patch types (Table 4.2). Because different areas of the body may be under different selection pressures for coloration we did local PCA analyses on each of the three patch pairings (back-belly, wing bar-adjacent area, white-nonwhite tail) to visualize color variation and distribution.

4.3.3 Visual models

To analyze whether adjacent patches are discriminable to an avian receiver and to measure the contrast between adjacent patches we modeled patch perception under and avian visual model. First, we estimated photoreceptor catches using a blue tit avian visual model (Hart et al. 2000) under a white light illuminant using the `vismodel` function in pavo. From these photoreceptor catches we calculated color distances between adjacent patches using the `coldist` function in pavo based on the receptor-noise model (Vorobyev and Osorio 1998). These color distances are measured in units of "just noticeable differences", with a JND > 1 taken to imply that the patch comparison would be discernable to an avian receiver. This JND is based on experiments with the Red-billed leiothrix, *Leiotrix lutea*, based on responses to colored lights in a small cage (Maier 1992; Vorobyev et al. 1998). Whether it is directly transferrable to field conditions is uncertain, and it may be that the experimentally assessed JNDs underestimate the difference required to distinguish color patches. On the other hand more recent work with chickens suggests close range discrimination can be achieved with a smaller difference than implied by the leiothrix experiments (Olsson et al. 2015). Hence, we use the JND as a guide only. We used the four cone catches to calculate chromatic contrasts and the double cone catch to calculate achromatic contrasts (here the Weber fraction, which forms the basis for the JND, is typically assumed to be the same as that for long wavelength single cone Olsson et al. 2018). While we focus most of our analysis and interpretation on chromatic contrasts the double cone is likely used in motion detection, and so achromatic contrasts may be applicable to display movements.

4.3.4 Light measurements

To determine ambient light conditions in the natural environment of these species we took irradiance measurements during the breeding season in the Manali Wildlife Sanctuary, Himachal Pradesh, India (32.25 ˚N, 77.17 ˚E, spanning 2000m – 3600m, May 27 – June 13,

2022) and at Nain Gahar village, Himachal Pradesh, India (32.73 °N, 76.86 °E, spanning 3100 – 3700 m, June 15 – July 8, 2022). Habitats were designated based on the primary associations of the species studied (Figure 4.1) so we focused on birch, conifer, oak, rhododendron, and understory. For the habitats based on plant species (birch, conifer, oak, rhododendron), we chose locations where the forest was largely a composed of the focal species and sampled areas in which the canopy cover did not include other species. For understory measurements we sampled areas in dense vegetation that corresponded to the habitat preferences of the bird species. Sample sites within a habitat were at least 20 meters apart. We sampled habitat light measurements between 0530 - 1135 in sunny conditions which we define as the sky $>$ 75% blue. Although ambient light conditions can vary greatly through the day (Foster and Nascimento 1994; Moyen et al. 2006) aggressive interactions and displays are largely confined to the morning. To sample irradiance, we used an Ocean Insight Flame spectrometer and P400-5-UV-VIS fiber optic probe, that were both calibrated prior to fieldwork by Ocean Insight for absolute irradiance measurements using a light source of known spectral power. Previous work has indicated that spectral variation in terrestrial environments is driven by forest geometry (Endler 1993), which varies primarily in the extent of sun penetration through the canopy. Rather than a priori assigning a light environment category to sites (i.e. forest shade, small gap, etc), in each forest type we measured two light conditions: sun and shaded. This allowed us to capture the range of available geometries. Shaded areas were defined as areas without direct sunlight, and we specifically sought for areas blocked by tree canopy. Sun areas were measured adjacent to shaded by looking for sunspots or sun flecks along the ground. The species we studied readily displayed across both shaded and sunny areas within the forest, moving actively between perches during territorial responses (pers. obs.). We measured irradiance from 300 – 700 nm. For each light condition at each habitat site we took 5 measurements with the fiber optic probe lifted at least 1.5 meters above the ground and above the measurer's head to avoid any effect of clothing or other objects. In both light conditions, measurements were taken away from large breaks in the canopy or forest edges and away from large obstructing objects such as tree trunks.

4.3.5 Light environment analysis

To account for the effects of mountain slope on the time when the sun crests over the highest ridge we filtered data to include times between 0730 – 1135. We converted spectral data from watts to photon flux using the `irrad2flux` function in pavo. For each light condition, we averaged the measurements taken at the same sample site and smoothed the spectra using locally weighted scatterplot smoothing (LOESS) with a span of 0.03 again using the `procspec` function in pavo. We then extracted a set of colorimetric variables from the data, including average relative brightness ('B2' in pavo). Brightness, or more specifically, luminance has previously been shown to differ between habitats which correlate with patch number (Marchetti 1993). This itself may affect the evolution of color differences. For example, brighter patches may simply evolve different colors as a correlated response and the luminance of the signaling environment may affect the kind of displays that are used. To test for differences between habitat luminance we conducted a two-way ANOVA for average relative brightness (B2) on habitat*light condition.

To assess whether habitats differed in their spectral shape, we removed effects of brightness by subtracting the mean reflectance across all 401 values and then binned the spectra to 20 nm intervals. Similar to the methods for plumage color, we ran a principal component analysis on all locations samples and extracted the principal components describing the majority of the variation: PC1 and PC2 (Table S4.4). We then conducted a two-way ANOVA for both PC1 and PC2 on habitat*light condition.

To ask whether differences in light environment could affect perception of plumage color, we focused on the habitats where spectral shapes between sun and shade differed the most: conifer and rhododendron. We averaged irradiance samples for conifer sun, conifer shade, rhododendron sun and rhododendron shade to obtain an average spectrum for each of these habitats and light conditions. Using the same adjacent patch comparisons as before, we asked how chromatic contrast discriminability changes across these four light conditions, which represent the range of variability across all habitats. We ran four visual models using the same parameters as described in the previous section but changed the illuminant from white light to the four irradiance comparisons: conifer shade, conifer sun, rhododendron shade and rhododendron sun. As before we calculated color distances between adjacent patches using the `coldist` function in pavo for each visual model. We filtered the data to only include species patches with chromatic contrasts of 1.5 JND and below, assuming that contrasts greater than 1.5 are unlikely to be significantly affected by changes in illuminant . Using a linear regression analysis, we compared chromatic contrasts between sun and shaded conditions for the two habitat types.

4.3.6 Display behavior

During the breeding season, males defend individual territories. When challenged by other conspecific males, the two birds perform a threat display consisting of rapid wing and tail motion. To quantify these behaviors, we performed playback experiments to species during the breeding season and recorded wing and tail motion using a high-speed camera array. Additional details about the playback experiments and recording setup can be found in Chapter 2.

4.3.7 Motion analysis

Similar to the methods described in Chapter 2, we carefully selected high frame rate videos in which the bird is in a lateral orientation to the camera, thereby excluding many experiments. We extracted frames from each video using the `extractFrames` function in StereoMorph (Olsen and Westneat 2015) and isolated an individual wing or tail flick. In previous work we studied shapes of the wing flick, which followed three discrete forms. First, a double wing flick, whereby both wings are moved in a coordinated fashion is conducted by all species in our study, except for one which does not move its wings in display at all (*P. affinis*). Second, one species (*P. pulcher*) conducts a shiver flick, where both wings are moved more rapidly and over a shorter horizontal distance than the standard double flick. Third, two related species (*P. occipitalis* and *P. reguloides*) conduct single wing flicks, where one wing is flicked in sequence before switching to the other wing (Table S3.3).

We used the `labelFrames` function in StereoMorph to place landmarks on the tip of the beak, the eye, the tip of the 8th primary feather and the tip of the outer tail feather for every frame over the course of the wing flick. We incorporated beak and eye as these two features are easily identified and form a point of reference for the entire bird. For the wing and tail we measured duration of one entire flick, in milliseconds, from the number of frames the flick took (video recordings are at 480 frames per second). To calculate the absolute displacement of the wing and tail, we used checkerboards placed in the filming area as a reference scale bar. We measured absolute wing and tail displacement by measuring the difference between the highest and lowest points for each body part during the duration of a flick. We then plotted the absolute vertical displacement of the wing and tail over time to analyze the relationship between wing and tail movement and to compare how this relationship changes between the three wing flick types.

Due to variability in filming conditions, we were not always able to include a checkerboard in the filming area. To expand the available dataset and to account for differences in bird location in the frame, distance to camera and size differences between species, we used a Generalized Procrustes Analysis (GPA) (Gower 1975; Webster and Sheets 2010) to align and scale all landmarks. For this analysis, we summarize each wing and tail flick by using 15 frames sampled at approximately equally dispersed time points over the course of the behavior. This allows us to compare how landmark placement varies during similar points in the behavior while accounting for differences in total duration between individuals, species and the three wing flick types. Once all landmarks had been transformed, we took new measurements of relative vertical wing and tail displacement. To ask whether variability in plumage contrast may be associated with use of body part during display motion we ran correlations of relative wing and tail displacement with chromatic and achromatic contrasts of wing bar-adjacent area, back-belly and white-nonwhite tail.

4.4 Results

4.4.1 Plumage variation

Description of pattern

We quantified the color of six patches for 12 species of *Phylloscopus*: back, belly, greater covert feathers (wing bar and adjacent area), and rectrices (white and non-white tail feathers) and summarized reflectance curves using Principal component analysis. Loadings on PC1 of all patches in the global analysis correspond to the proportion of short versus long wavelengths in the reflectance curves. Species with higher values of PC1 have a greater proportion of reflectance above 500 nm, which corresponds to a sharp jump in the spectral curve for patches that have carotenoid-based coloration (yellow and orange) compared with patches that are more olive-green and brown (Figure 4.2). Loadings on PC2 correspond to an increase in wavelength reflectance at opposite extremes of the spectrum. A species with a plumage patch that has high values of PC2 have a greater proportion of reflectance in both the UV and long wavelengths, a signature of carotenoid pigment-based reflectance (MacDougall and Montgomerie 2003). The first two principal components together account for 96% of the variance (PC1: 85%, PC2 11%). In the three restricted PCA analyses of the three adjacent patch pairings (back-belly, wing bar-adjacent area, white-nonwhite tail) the loadings on PC1 and PC2 for back-belly and wing bar-adjacent area showed the same general pattern as the global analysis (Figure 4.2). In the white-nonwhite tail analysis PC1 loadings corresponded to more equal wavelength reflectance (65% of the variance) while PC2 loadings matched that of prior analyses, describing a greater proportion of UV and longer wavelength reflectance (Figure 4.2).

Two-way analysis of variance on sex * species using individuals as replicates showed that species differ significantly ($P < 0.001$) in all patches for both PC1 and PC2 (Table 4.1, post-hoc Tukey tests in Table S4.5). Males and females did not differ in patch color for most plumage areas with the exception of back patches, which differed between the sexes in PC1 ($F_{1,48} = 5.99$, $P = 0.018$). The interaction term for sex * species was marginally significant for both belly ($F_{11,48} = 2.05$, $P = 0.044$) and tail patches ($F_{11,48} = 2.02$, $P = 0.048$) along PC2. Multivariate analysis of variance on patch pairs paralleled the results for the two-way ANOVAs (Table 4.1).

With respect to patch variance belly plumage is the most variable followed by wing bars (Table S4.6) with back plumage being the least variable. F-tests comparing the variances of principal components between adjacent patch pairs indicate that wing bars are significantly more variable than the adjacent areas on the greater covert feathers along both PC1 and PC2 (Table 4.2). Belly plumage is significantly more variable than back plumage (Table 4.2) and white areas of the tail are more variable than nonwhite areas of the tail (Table 4.2).

Patch discriminability

To assess the contrast and discriminability of adjacent patches we modeled all patch types under an ideal illuminant (equal proportion white light). The chromatic contrast between the white and nonwhite areas of the tail all have a JND > 1 (Figure 4.3). This is to be expected as we are comparing white against brownish-green areas in the five species with noticeable areas of white in the tail. For the greater covert feathers, all species with discernable wing bars have chromatic contrasts greater than the discriminability threshold

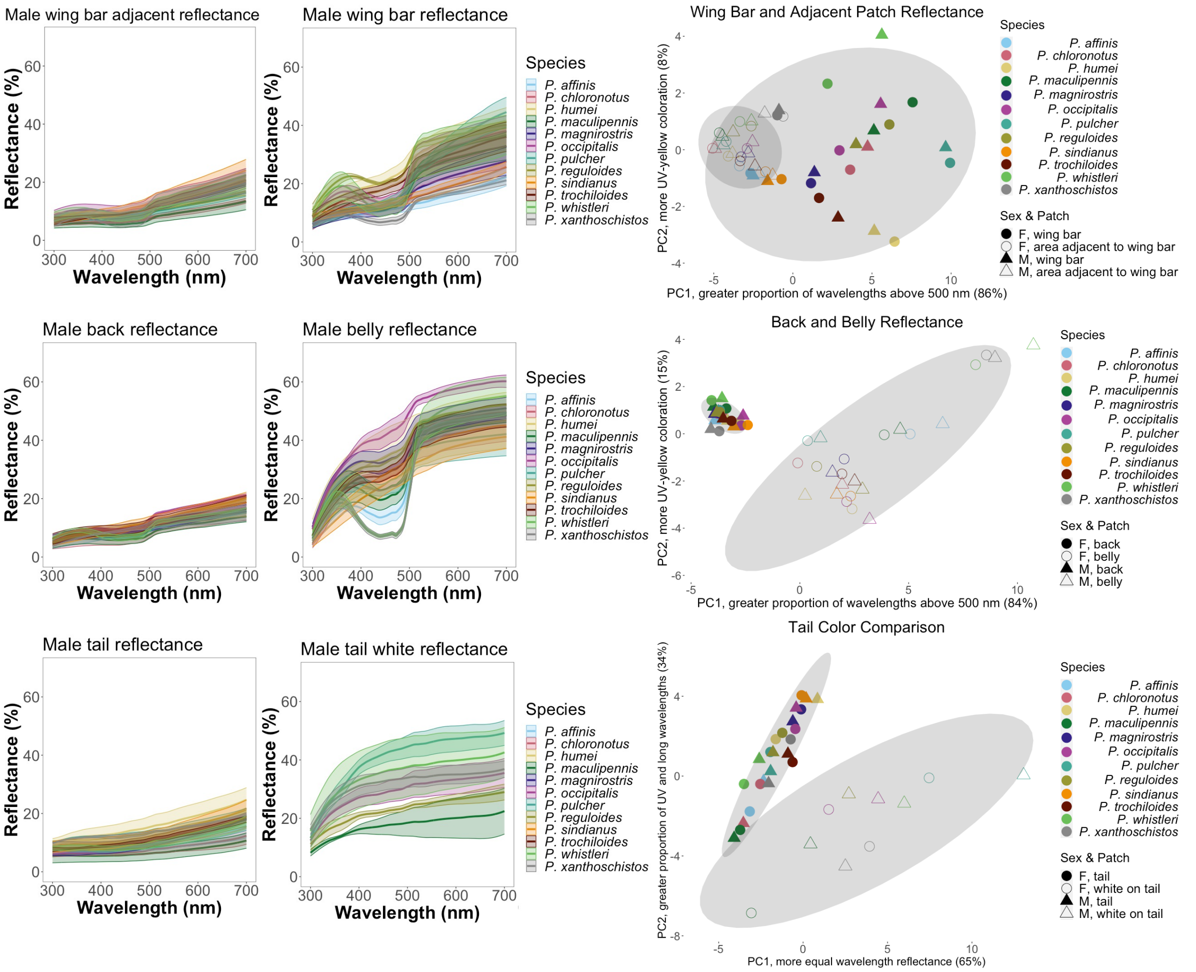

Figure 4.2: **Color variation in *Phylloscopus* warblers.** Row A: Average reflectance spectra (solid lines) and their standard deviation (shading) for male wing bars (middle), and adjacent areas (left, N = 3 individuals per species). Plot of PC2 vs PC1 of the wing bar and adjacent patch reflectances (N = 144, being based on 3 measurements of two traits from 72 individuals). Shape denotes sex (circle for females, triangle for males) and fill denotes patch type (solid shapes are wing bars, open shapes are adjacent areas). PCs are based on means for each sex by species. In the PC analyses, all spectra are first standardized for brightness. The grey ellipses are 95% predictive intervals for each patch type. When comparing the two adjacent wing patches, wing bars are more variable than adjacent feather areas. Row B: Average reflectance spectra for male back reflectance (left), belly reflectance (middle), and a PC plot of standardized reflectances for back (solid) and belly (open) comparisons. Belly plumage colors are more variable than back plumage. Row C: Average reflectance spectra for male tails (left) and white tail areas (middle) only for those species with white in the tails. A PC plot of white and nonwhite tail standardized reflectances is on the right. PC scores for each set of plumage patch comparisons can be found in Table S4.3

of JND $>$ 1 with the exception of *P. reguloides* (both sexes) and *P. trochiloides* females. The three species that do not have discernable wing bars (*P. affini*s, *P. xanthoschistos*, *P. sindianus*, Figure 4.1) all have chromatic contrasts of JND $<$ 1 between the distal and proximal areas of the greater covert feathers, which matches human visual assessment.

Several chromatic contrasts between the back and belly vary between both sexes and species, some falling below JND = 1 (Figure 4.3). However, all patch comparisons have achromatic contrasts greater than the discriminability threshold of JND = 1, with the exception of the three species without discernable wing bars (*P. sindianus*, *P. xanthoschistos* and *P. affinis*). In sum, all patches should be discriminable along a brightness axis to an avian receiver, and in many species along a chromatic axis as well. The average achromatic contrast is greatest for back and belly comparisons and is the least variable between species (Figure 4.3), because all species possess darker back plumage and lighter belly plumage.

Source of Variation		*df (Degrees of Freedom)*	*Mean Square*	*F*	*P*	*Test Statistic (Pillai's Trace)*
ANOVA for PC1 scores of wing bar reflectance	**Species**	11	42.60	13.512	**3.04e-11 *****	-
	Sex	1	0.23	0.072	0.789	-
	Species x Sex	11	2.46	0.781	0.657	-
	Residuals	48	3.15	-	-	-
ANOVA for PC2 scores of wing bar reflectance	**Species**	11	4.946	12.513	**1.11e-10 *****	-
	Sex	1	0.669	1.693	0.199	-
	Species x Sex	11	0.303	0.765	0.672	-
	Residuals	48	0.395	-	-	-
ANOVA for PC1 scores of area adjacent to wing bar reflectance	**Species**	11	4.444	14.309	**1.13e-11*****	-
	Sex	1	0.36	1.160	0.287	-
	Species x Sex	11	0.467	1.502	0.162	-
	Residuals	48	0.311	-	-	-
ANOVA for PC2 scores of area adjacent to wing bar reflectance	**Species**	11	0.6454	26.371	**<2e-16*****	-
	Sex	1	0.0124	0.508	0.479	-
	Species x Sex	11	0.0196	0.803	0.637	-
	Residuals	48	0.0245	-	-	-

Table 4.1 beginning.

Source of Variation		***df (Degrees of Freedom)***	***Mean Square***	***F***	***P***	***Test Statistic (Pillai's Trace)***
MANOVA results for PC1 and PC2 scores of wing bar and area adjacent to wing bar reflectance	**Species**	11	-	12.33	**<2e-16 *****	1.17
	Sex	1	-	0.625	0.54	0.01
	Patch	1		309.963	**<2e-16 *****	0.87
	Species x Sex	11	-	0.99	0.548	0.19
	Species x Patch	11	-	11.24	**<2e-16 *****	1.13
	Sex x Patch	1	-	1.073	0.35	0.02
	Species:Sex:Patch	11	-	0.521	0.96	0.11
	Residuals	96	-	-	-	-
ANOVA for PC1 scores of back reflectance	**Species**	11	1.7479	6.610	**1.42e-06*****	-
	Sex	1	1.5863	5.999	**0.018***	-
	Species x Sex	11	0.2602	0.984	0.474	-
	Residuals	48	0.2644	-	-	-
ANOVA for PC2 scores of back reflectance	**Species**	11	1.1841	37.319	**<2e-16*****	-
	Sex	1	0.0189	0.595	0.444	-
	Species x Sex	11	0.0455	1.434	0.189	-
	Residuals	48	0.0317	-	-	-
ANOVA for PC1 scores of belly reflectance	**Species**	11	86.72	24.569	**4.78e-16*****	-
	Sex	1	13.61	3.855	0.0554	-

Table 4.1 continued.

Source of Variation		***df (Degrees of Freedom)***	***Mean Square***	***F***	***P***	***Test Statistic (Pillai's Trace)***
	Species x Sex	11	0.93	2.049	**0.0437***	-
	Residuals	48	0.45	-	-	-
MANOVA results for PC1 and PC2 scores of back and belly reflectance	**Species**	11	-	19.66	**<2e.2-16*****	1.38
	Sex	1	-	1.21	0.054	0.02
	Patch	1		982.15	**<2e-16*****	0.95
	Species x Sex	11		1.65	**0.04***	0.32
	Species x Patch	11		12.96	**<2e-16*****	1.19
	Sex x Patch	1		4.23	**0.02***	0.08
	Species:Sex:Patch	11		1.38	0.12	0.27
	Residuals	96				
ANOVA for PC1 scores of tail reflectance	**Species**	11	2.7520	8.445	**5.95e-08*****	-
	Sex	1	0.0167	0.051	0.822	-
	Species x Sex	11	0.3740	1.148	0.348	-
	Residuals	47	0.3259	-	-	-
ANOVA for PC2 scores of tail reflectance	**Species**	11	0.16570	5.780	**8.18e-06*****	-
	Sex	1	0.02257	0.787	0.3795	-
	Species x Sex	11	0.05778	2.015	**0.0481***	-
	Residuals	47	0.02867	-	-	-

Table 4.1 continued.

Source of Variation		***df (Degrees of Freedom)***	***Mean Square***	***F***	***P***	***Test Statistic (Pillai's Trace)***
ANOVA for PC1 scores of white tail reflectance	**Species**	5	10.071	4.698	**0.00534****	-
	Sex	1	4.249	1.982	0.17453	-
	Species x Sex	3	1.467	0.684	0.57203	-
	Residuals	20	2.144	-	-	-
ANOVA for PC2 scores of white tail reflectance	**Species**	5	7.032	15.215	**3.16e-06*****	-
	Sex	1	3.827	8.280	0.00931	-
	Species x Sex	3	1.388	3.003	0.05469	-
	Residuals	20	0.462	-	-	-
MANOVA results for PC1 and PC2 scores of white tail reflectance	**Species**	11	-	12.23	**< 2.2e-16 *****	1.34
	Sex	1	-	20.37	**1.288e-07 *****	0.38
	Patch	1	-	480.97	**< 2.2e-16 *****	0.94
	Species x Sex	11	-	1.52	0.075660	0.40
	Species x Patch	5	-	7.68	**1.235e-09 *****	0.73
	Sex x Patch	1	-	6.42	**0.002833 ****	0.16
	Species:Sex:Patch	3	-	2.51	**0.024724 ***	0.20
	Residuals	67	-			

Table 4.1 continued.

Source of Variation		***df (Degrees of Freedom)***	***Mean Square***	***F***	***P***	***Test Statistic (Pillai's Trace)***
ANOVA for PC1 scores of rump reflectance	**Species**	11	34.79	17.514	**4.28e-13*****	-
	Sex	1	0.01	0.005	0.943	-
	Species x Sex	11	2.04	1.027	0.439	-
	Residuals	47	1.99	-	-	-
ANOVA for PC2 scores of rump reflectance	**Species**	11	5.684	26.012	**2.48e-16*****	-
	Sex	1	0.209	0.958	0.333	-
	Species x Sex	11	0.244	1.118	0.369	-
	Residuals	47	0.219	-	-	-

Table 4.1: **ANOVA and MANOVA results of PC1 and PC2 scores of *Phylloscopus* patch reflectance**

Phylloscopus color variation summary

First, we find that species vary in the color of individual patches, with some marginally significant differences between the sexes (Table 4.1). Some areas of the plumage are more variable across species than others, with the belly and wing bar being especially variable in comparison to back and adjacent areas (Table 4.2, Figure 4.2). Lastly, species differ in how contrasting adjacent patches are to each other, with some possessing plumage areas that are chromatically near or below the discriminability threshold (Figure 4.3). Having described the color variation within and across species, we now turn to consider how this variation may be perceived across habitats.

4.4.2 Light environment variation

Habitat color

We measured sun and shade irradiance across 5 different habitat types (Figure 4.4). The loadings of PC1 on all habitats and light conditions correspond to a step function around 430 nm such that habitats with negative PC1 scores have a greater proportion of UV and short wavelengths and those with positive PC1 scores have a greater proportion of longer wavelengths. PC1 accounts for 96% of the variance in the data. The loadings of PC2 correspond to a difference between middle or extreme wavelength reflectance: habitats with negative PC2 scores have more wavelength reflectance between 400-500 nm while those with greater PC2 scores have a greater proportion of short and long wavelengths. PC2 describes 3% of the variance. In a two-way ANOVA for color descriptors summarized by the first two

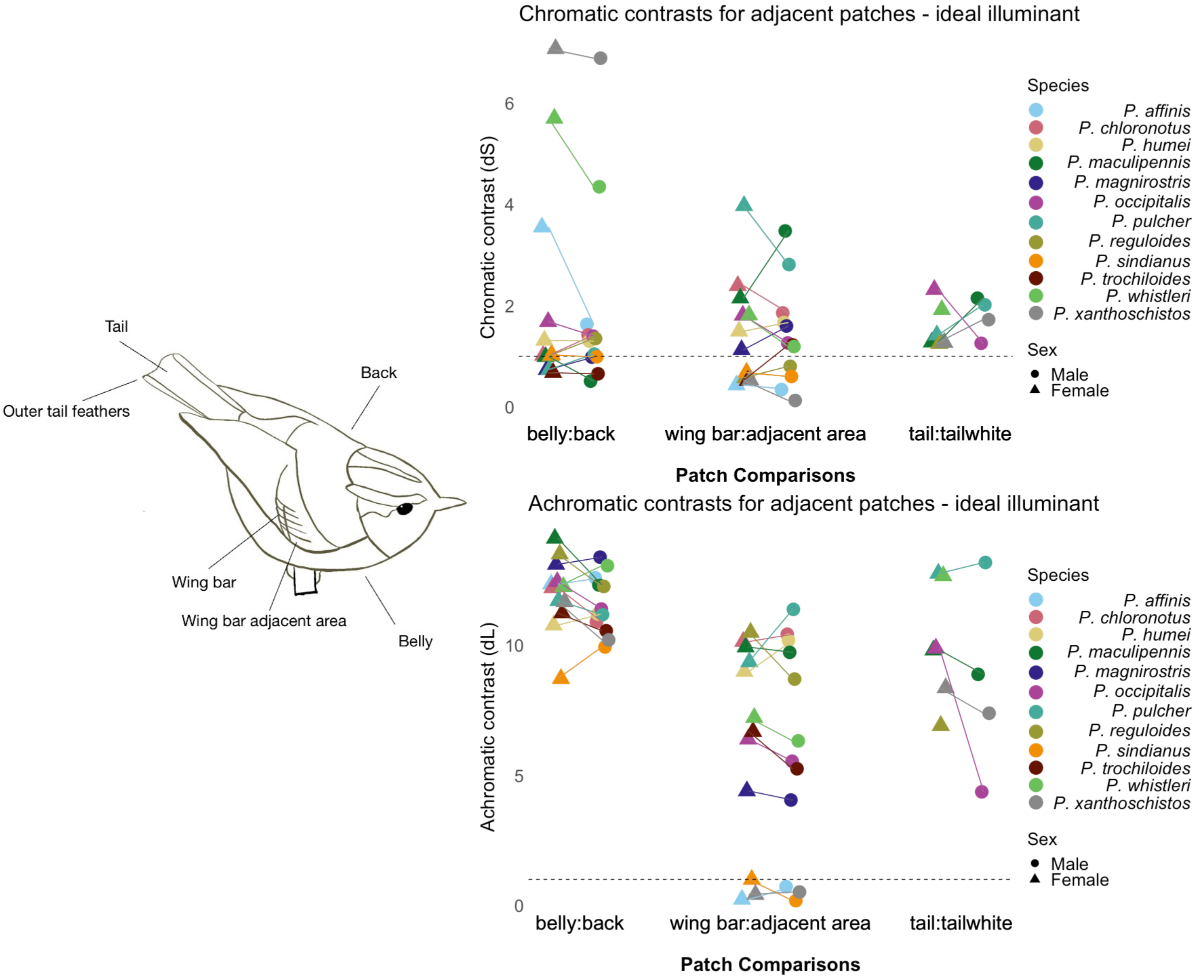

Figure 4.3: **Adjacent patch discriminability in an avian visual model.** A. Location of adjacent plumage patches . B. Chromatic contrasts for the three adjacent patch comparisons in an avian visual model under an ideal illuminant (equal energy white). JND values are available in Table S4.7. The black dashed line denotes a just noticeable difference (JND) of 1 under the assumptions of Vorobyev et al. (1998). Points that lie above the black line indicate that these adjacent patches should be chromatically distinct to a nearby avian viewer. Lines connect males (circles) and females (triangles) of each species. C. Achromatic contrasts for the three adjacent patch comparisons in an avian visual model. Same as above, where the black dashed line represents a JND of 1. All patches have an achromatic contrast of JND > 1. Note that *P. xanthoschistos*, *P. sindianus* and *P. affinis* do not have discernable wing bars. Several species do not have discernable tail patches either, but they are not included in this figure

Comparison	**F-statistic**	**P-value**	**95% confidence interval**
Wing bar PC1 vs area adjacent to the wing bar PC1	9.14	1.37 e -06	3.95, 21.13
Wing bar PC2 vs area adjacent to the wing bar PC2	8.21	3.75 e -06	3.55, 18.97
Belly PC1 vs Back PC1	42.59	1.55 e -13	18.42, 98.46
Belly PC2 vs Back PC2	49.42	3.00 e -14	21.38, 114.24
Nonwhite tail PC1 vs white tail PC1	0.23	0.005	0.065, 0.641
Nonwhite tail PC2 vs white tail PC2	0.02	2.95 e -12	0.006, 0.059

Table 4.2: Results of F-tests comparing the variances of Principal Component 1 (PC1) and Principal Component 2 (PC2) scores for different plumage patches and their respective adjacent parts.

PCs on light condition (sun/shade) * habitat the two light conditions differ significantly from each other along PC1, with sun having a greater proportion of long wavelengths than shade (Table 4.3). In sunlight, conifer habitats differ significantly in PC1 from rhododendron, birch and oak (Table S4.8). Habitats or light conditions did not vary significantly in PC2 (Table 4.3).

Luminance

As expected in the two-way ANOVA, sun is brighter than shade ($F_{1,36} = 92.155$, $P < 0.001$, Figure 4.5). However, both habitat ($F_{4,36} = 6.574$, $P < 0.0001$) and habitat * light ($F_{4,36} = 4.776$, $P = 0.003$) condition also vary significantly (Table S4.9). Post-hoc pairwise Tukey tests (Table S4.9) indicate that rhododendron in sun is brighter than conifer ($P <$

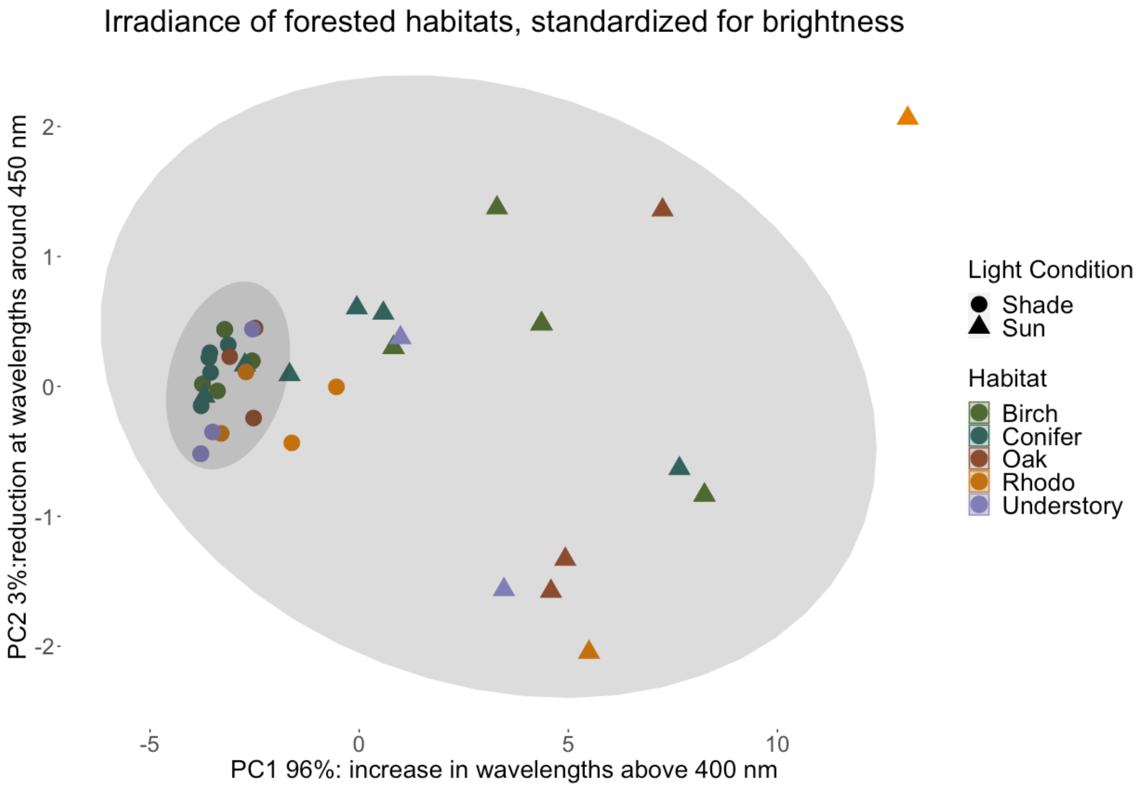

Figure 4.4: **PCA of spectral shape color variation across 5 habitats.** Shape denotes light condition, where circles represent shaded areas and triangles represent sunny areas. Colors correspond to the habitat type determined by dominant tree type. In the PC analyses, all spectra are first standardized for brightness. The grey ellipses are 95% predictive intervals for each light condition.

Source of Variation		***df (Degrees of Freedom)***	***Mean Square***	***F***	***P***
ANOVA for PC1 scores of habitat irradiance	**Light condition**	1	482.7	92.12	**2.45e-11*****
	Habitat	4	26.2	4.99	**0.0027 ****
	Light condition * habitat	4	15.8	3.02	**0.03 ***
	Residuals	35	5.2	-	-
ANOVA for PC2 scores of habitat irradiance	**Light condition**	1	0.03	0.05	0.82
	Habitat	4	0.49	0.78	0.54
	Light condition * habitat	4	0.19	0.30	0.88
	Residuals	35	0.63	-	-

Table 4.3: **ANOVA of PC1 and PC2 scores for habitat irradiance**

0.00001), birch (P = 0.001) and understory sun conditions (P = 0.006) but shaded habitats do not differ significantly from one another in brightness (Table S4.9). When comparing sun and shade conditions within a habitat, rhododendron (P < 0.0001), birch (P < 0.0001) and oak (P = 0.012) differ significantly in brightness (Table S4.9), meaning these habitats have two very distinct light regimes. Sun and shade conditions did not differ significantly for understory or conifer habitats.

In summary, rhododendron and conifer habitats encompass all the significant variation associated with spectral shape, brightness and between light conditions and we use the spectra from these habitats to evaluate how patch appearance might change under different illuminants.

4.4.3 Effects of light environment on plumage

We use avian visual models to test discriminability of patches in sun and shade in both rhododendron and conifer. Chromatic discriminability does not vary significantly across

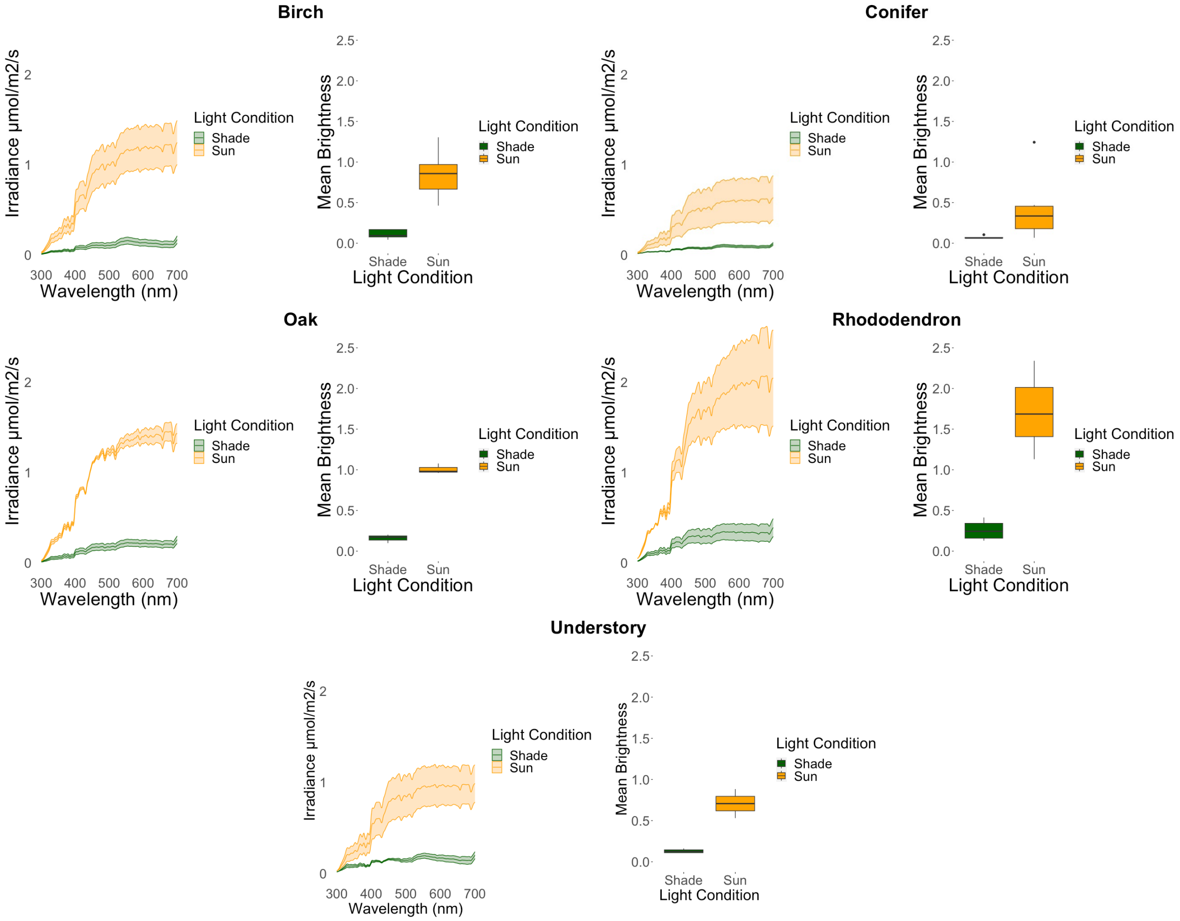

Figure 4.5: **Irradiance spectra (left) and associated boxplots (right) for shade (green) and sun (orange) light conditions for 5 habitat types.** Each habitat is measured between 0730 - 1300 (birch: shade n = 8, sun n = 8, conifer shade n = 5, sun n = 6, oak shade n = 3, sun = 3, rhododendron shade n = 4, sun n = 3, understory shade n = 4, sun n = 2). Irradiance spectra means are represented by solid lines and shading around the line corresponds to the standard error. Box plots show the distribution of the mean relative irradiance over the spectral range with the line representing the median brightness, the colored areas above and below the line showing the third and first quartiles respectively, the top and bottom whiskers extending to the largest and smallest data value within the inner fence and points corresponding to data falling outside the inner fence. In an analysis of variance for brightness, habitats ($F_{4,36}$ = 6.574, P < 0.001), sun/shade condition ($F_{1,36}$ = 92.155, P < 0.001) and their interaction ($F_{4,36}$ = 4.776, P = 0.003) are all statistically significant. Post-hoc pairwise Tukey tests (Table S4.9) indicate that rhododendron, birch and oak differ significantly in mean brightness between sun and shaded light conditions. Sun and shade conditions are not significantly different for understory or conifer habitats.

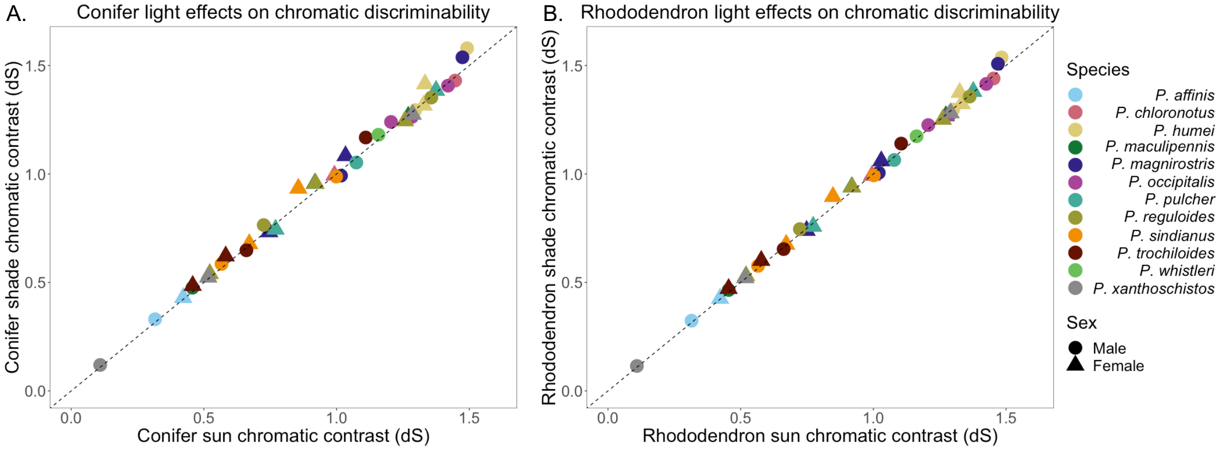

Figure 4.6: **Correlation of chromatic contrasts in sun and shade** for conifer (left) and rhododendron (right), as illustrated in Figure 4.3. Data have been filtered to include those with a JND < 1.5. Chromatic discriminability does not vary significantly across light condition. The very tight correlations with little scatter ($r > 0.99$ in both plots) indicate little influence of light environment (sun/shade) on perception.

light condition in either conifer or rhododendron (Figure 4.6). The chromatic contrasts in sun and shade were very tightly correlated in both light conditions ($r > 0.99$), indicating that the light environment has very little influence on the perception of color patches even between light conditions that are distinct in brightness from each other.

4.4.4 Display

Given we find little evidence that irradiance differences between environments have affected coloration, we now turn to ask if differences in display are important. We focus on tail and wing motions, because the large color differences between tail (white) and wing bar (yellowish) are consistent across species. All species conduct double wing flicks, but only two species add a single wing flick and one a shiver flick (Chapter 2). The three wing flick types: double flick, single flick, and shiver flick, differed significantly in duration of both wing and tail motion (ANOVA $F_{2,10} = 14.34$, P $= 0.0006$, Figure 4.7). The maximum amplitude of tails differs between the three wing flick types ($F_{2,10} = 32.26$, P < 0.0001) but not maximum wing amplitude ($F_{2,10} = 2.88$, $P = 0.103$). The timing of maximum absolute amplitude of wings and tails appear to be related in both double and shiver wing flicks (Figure 4.7), suggesting that the two body parts move as a unit during display with the tail perhaps serving as a counterbalance to wing motion (Gatesy and Dial 1996). Single wing flicks are slower to reach maximum vertical displacement than the other two wing flick types ($F_{2,10} = 16.87$, $P < 0.001$) and have little tail motion (Figure 4.7).

When considering the relative motion of wings and tails from the GPA aligned landmarks double wing flick displays have greater horizontal and vertical motion in both wings and tails than shiver and single wing flicks, which are more restricted to vertical displacement (Figure 4.8). When testing the association between vertical wing and tail displacement with chromatic and achromatic tail and wing patch contrasts, we find that vertical tail and wing displacement are not correlated with achromatic tail or wing contrasts (tail: $r = 0.008$, $P = 0.99$, wing: $r = 0.45$, $P = 0.43$). Vertical tail displacement is not correlated with tail chromatic contrast ($r = 0.35$, $P = 0.55$) but vertical double wing displacement is correlated with wing chromatic contrasts, albeit with borderline significance ($r = 0.90$, $p = 0.03$, Figure 4.9). Given the four tests, we interpret this p-value cautiously.

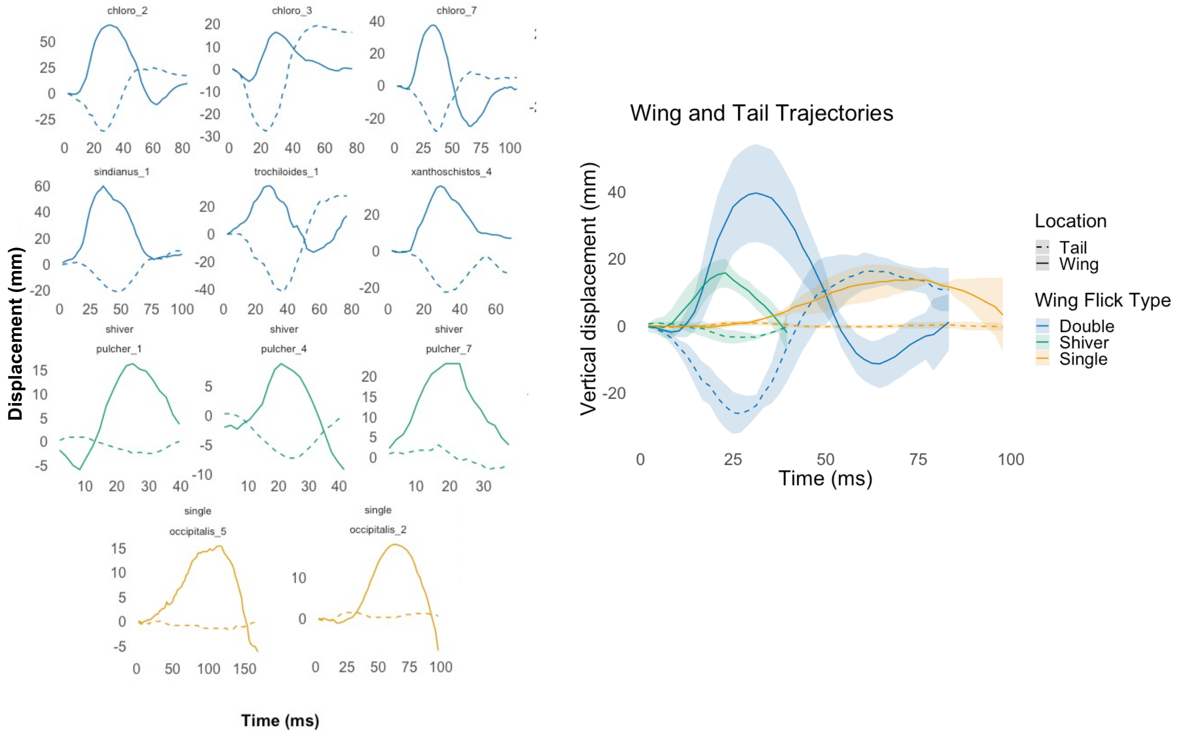

Figure 4.7: **Wing and tail trajectories during territorial displays**. A. Example individual wing and tail trajectories for several species, showing wing and tail displacement over the duration of a single wing flick for double (blue), single (yellow) and shiver (green) wing flick types. B. Comparison of duration and displacement for the three wing flick types (line type) for wings (red) and tails (blue) with standard deviation (shaded).

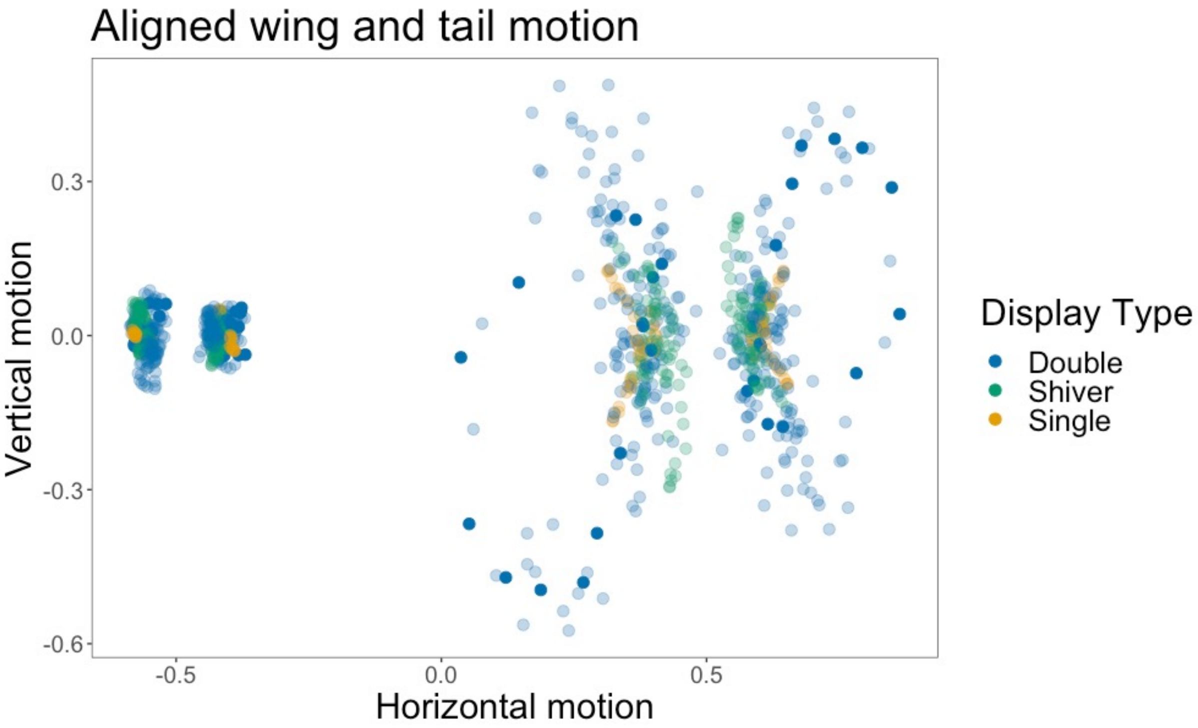

Figure 4.8: **Aligned landmarks during the duration of a single wing flick.** From left to right the landmarks represent beak, eye, wing and tail, respectively. Each point corresponds to the location of an individual's landmark during a single time point during the wing flick, color coded by wing flick type. One individual has been highlighted in the opaque points with the rest of the data represented by transparent points. Most of the motion is concentrated in the wing and tail during wing flicks and species performing double wing flicks have greater horizontal and vertical wing and tail displacement (blue) than species performing shiver (green) or single wing flicks (yellow).

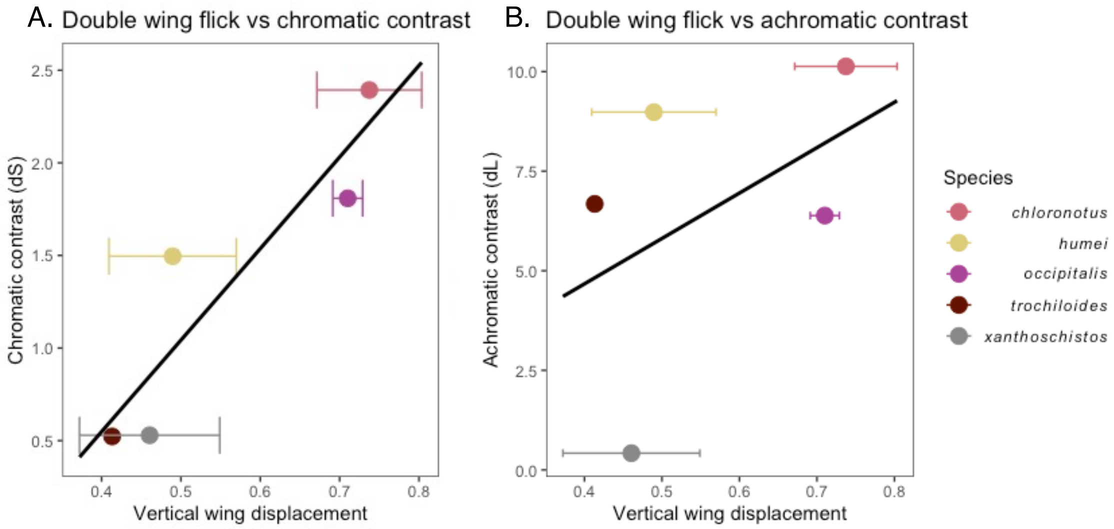

Figure 4.9: **Correlation of vertical wing displacement for double wing flicks and wing contrasts.** A. The vertical displacement for double wing flicks is correlated with wing chromatic contrasts, albeit with borderline significance ($r = 0.90$, $p = 0.03$). B. Vertical displacements for double wing flicks is not correlated with wing achromatic contrasts.

4.5 Discussion

We tested two possible explanations for color variation among similar species in a system where plumage variation along the achromatic axis (patch quantity and wing bar brightness) has been related to a light-dark environmental axis; darker species (less patterned and including presence/absence of a wing bar) occupy more open, brighter habitats while brighter species (more patterned) occupy darker, forested habitats (Marchetti 1993). First, despite variation in habitat spectral shape and brightness, we found little evidence that plumage patch chromatic contrast is altered significantly between and within the habitats. This suggests that differences in species colors cannot be explained as adaptations to specific light conditions in their signaling environments, as would be predicted by a sensory drive hypothesis. Second, we show that variation in tail and wing motion is not correlated with differences in plumage patch contrast, suggesting that how patches are used in display is not driving the color differences. Together these findings imply we must look elsewhere for explanations for the color differences we have documented. We assess both the irradiance and display hypotheses in turn to evaluate what may be happening in this system. We then evaluate alternative hypotheses for what factors may be driving plumage color variation in *Phylloscopus.*

4.5.1 Relationship between color and irradiance

In avian visual models, plumage patch discriminability across *Phylloscopus* is nearly identical across habitats and light conditions (Figure 4.6). Our results support the proposition that, in the terrestrial environment, spectral gradients in light have only a small influence on color differentiation (Cummings and Endler 2018). Unlike the aquatic environment, spectral shape variation along a vertical axis (canopy to undergrowth) is relatively limited (Endler 1993; Théry 2001). In forests the differences in the spectral composition of light has been shown to be driven by variation in forest geometry, with little effect from the tree species the forest is composed of (Endler 1993; Théry 2001). Our results confirm these findings by showing that spectral shape differences across six habitats in sunlight vary little, and in shade hardly at all. Sunny areas in conifer habitats did show significant differences in spectral shape from several other habitats, which we attribute to a relatively homogenous light environment between sunny and shaded areas in conifer. This is particularly evident when comparing the brightness differences between the sunny and shaded areas (light conditions) across habitats (Figure 4.5). Further, spectra vary more between sun and shade than across habitat types. This implies that birds in most habitats regularly experience similar light regimes which extensively overlap between habitats. The small differences between habitats and larger differences within lead one to expect all species to adapt in a similar way to irradiance spectra.

More generally, we note that differences in spectral shape may be irrelevant to discrimination of color patches because of the phenomenon termed relational color constancy.

Foster and Nascimento (1994) showed that across a range of daylight spectra, the ratio of cone catches from one location (e.g., the wing bar in our case) to another (e.g., the plumage adjacent to the wing bar) stays approximately constant for each cone, so the ratio between two cones also stays constant, and it is this ratio that affects chromatic discrimination. The critical feature of relational color constancy is that it does not require some way to assess the illuminant, which is needed for true color constancy, where the percept of a given patch does not change across environments. A great deal of effort has gone into trying to understand how the illuminant may be assessed in humans (e.g., the brightest spot in the scene is likely to be close to white, and reflect the entire spectrum; Foster 2011), but this complication is not required in discrimination tasks. We expect relational color constancy to apply even more strongly to birds because their cone absorbance spectra are of narrower bandwidth (e.g., Price et al. 2019) and are enhanced by their oil droplets (Vorobyev et al. 1998). Under relational color constancy, the appearance of both patches may change as one moves between environments (i.e., the plumage itself could change color and not remain constant), but the JND distance between the two patches will not. Relational color constancy has been confirmed for the chicken (*Gallus gallus*) and other animals (Olsson et al. 2016; Olsson and Kelber 2017).

While we found no correlation of color with irradiance, some comparative studies have identified weak correlates of color with light gradients, notably darker habitats have a higher proportion of species with red-shifted hues (McNaught and Owens 2002; Gomez and Théry 2004, 2007). One explanation could be that blue-shifted colors appear brighter in the canopy than the understory (Endler 1993). Alternatives include habitat differences that are not related to the light environment and effects of background. For example, in an intra-specific study Simpson and McGraw (2018b) found that red individuals were more often in darker habitats, but suggested this reflected an association of red with dominance, giving access to these habitats, rather any direct effect of the light environment.

4.5.2 Relationship between color and motion

An alternative explanation for variation in color across species and patches is that colors are linked in some way to display. Both color and motion are components of visual signals and the connection between these two elements has been long recognized (Tinbergen 1948; Burtt and Jr. 1979) and tested empirically more recently (Miles et al. 2017; Hogan and Stoddard 2018; Ligon et al. 2018; Simpson and McGraw 2018a, 2019; Miles and Fuxjager 2019). This may account for the differences in color variation between patch types. For example, wing motion may be communicating aggressive intent or information about individual quality and the message reinforced by an individual's wing bar color (Moller and Pomiankowski 1993). Carotenoid colors have long been thought to be condition indicators (McGraw and Hill 2000), perhaps most likely socially imposed by aggressive interactions (Pryke and Andersson 2003). The size of the wing-bar has been shown to correlate with dominance (Marchetti 1993), and is condition dependent (Scordato et al. 2012). While the effect of color per se of the wing bar or other plumage areas on aggressive outcomes has not been tested in *Phylloscopus* there is evidence to suggest that subtle variation in coloration may be particularly salient to these species. Based on experiments with chickens, Osorio et al. (1999) found yellows and greens to be especially well separated in birds and concluded (p.2958) that "differences between the yellowish-green plumages that separate various *Phylloscopus* warblers (Sylvidae) that are difficult for humans to differentiate may be much more noticeable for the birds themselves".

Whether the color differences between species can be related to display is more debatable. However, we found that across five species the vertical wing displacement during the display they hold in common (double wing flicks) is significantly correlated with wing chromatic contrasts (Figure 4.9, albeit this finding needs confirmation through more study. This finding suggests some connection between display and color, although the overwhelming impression is that variability within species is much greater than that between species (Chapter 3).

We found that the double wing display is always associated with tail movements. We assume that reasons for tail movement are largely biomechanical, providing a counterbalance to the wing movements (Gatesy and Dial 1996) as maximum depression of the tail and wing maximum elevation of the wing are closely associated in time (Figure 4.7). As when we consider double wing flicks alone (Chapter 3), joint movements of the tail and wing show a large degree of variation within species (Figure 4.7, top line) and relatively less between species. Both the ubiquitous presence of tail movements when the wings are moved in the double wing flick display, and similarity of the display across species together suggest that this aspect of display cannot explain presence of white tail patches, or chromatic variation across species in these patches.

However, one species conducts shiver wing displays with more rapid movements of the wings in a more horizontal plane and two species conduct single wing displays, which also show less horizontal movement than the double wing flicks (Chapter 3). These displays are associated with virtually no tail movement (Figure 4.7). Of the three species that perform these displays, two have white in the tail (*P. pulcher* and *P. reguloides*), suggesting that one contributing factor to the evolution of these alternative wing displays is a reduction in tail exposure during the display.

Overall, we find that both hypotheses tested in this study can only make – at best – small contributions to explain the color variation documented in Phylloscopus. We now briefly consider alternatives, focusing on other sensory ecological explanations and differences in how plumage patches may function.

4.5.3 How color may be affected by environment

Color variation may be related to camouflage (Endler and Mappes 2017). The upperparts of all species are greenish, which is generally thought to result in crypsis against leaves (Brooke 2010), but chromatic differences among the species are small (Figure 4.2).

All species have pale underparts and dark (melanized) upperparts and the achromatic contrasts between back and belly are strong and relatively similar across species (Figure 4.3). This has been attributed to counter-shading, whereby an individual becomes camouflaged by masking the shadows cast on its underparts (Thayer 1896). If belly and back coloration were both driven by camouflage pressures we would expect that both should be similarly variable across species. Instead, we find the belly plumage is exceptionally variable across species; the back much less so (Table S4.6). This suggests that belly coloration may be under different selection pressures than the rather invariable back plumage, such as use in intraspecific signaling as inferred to be the case for finches (Cardoso and Mota 2022).

Habitats may vary along axes other than irradiance. The radiance, or color of the background may influence the perception of plumage patches due to the contrast of the bird against the background (Gomez and Théry 2007). Our study focused on the total light environment (irradiance) because *Phylloscopus* species are interacting at short range during the relevant signaling contexts and are assumed to be assessing patches against other parts of the plumage. However contrast between background and patch may be involved (Lind 2016). However, the spectral composition of various terrestrial radiances have been found to be largely invariable (Chiao et al. 2000), making this an unlikely axis upon which sensory drive is acting.

Features of the habitat may also affect the evolution of visual perception systems. Sensory biases describe how a species trait preference may arise due to features in its sensory environment (Ryan and Keddy-Hector 1992; Ryan and Cummings 2013). Spectral tuning differences in different species of surfperch arise due to preferences for specific foraging environments, which vary in background luminance (Cummings 2007). In turn, males have diverged in their courtship coloration that matches perceptual sensitivities for each species (Cummings 2007). Alternatively, sensory biases may arise from attenuation for a specific feature; the preference for orange spots in male guppy (*Poecilia reticulata*) coloration have been related to sensory biases arising from a preference for a particular food source – orange fruit (Rodd et al. 2002). Notably, the buff-barred warbler, *Phylloscopus pulcher*, has noticeably orange wing-bars (extreme rightmost points in the PC plot in Figure 4.2). *P. pulcher* is a rhododendron specialist, and rhododendron has orange under-leaves, as shown by the limited radiance data we have collected (data not shown). Birds foraging for insects resting on the underside of rhododendron leaves will be constantly evaluating prey against an orange background, and this may create a sensory bias leading birds to prefer more orange coloration. This is a speculative hypothesis and does not account for the variation in wing bar coloration across other species, nor variation in other plumage areas.

4.5.4 How color may be affected by function

Our findings contrast with those of Fitzpatrick (1998) who used a large comparative study of many bird species to show a relatively weak but significant association of white in the tail and use of the tail in display, suggesting that for some species tail white has indeed evolved in association with displays. In our case it appears that, if anything, unusual displays have evolved to minimize tail white exposure. Other hypotheses have been proposed for the evolution of tail patches (Randler 2016), some of which appear unlikely in the *Phylloscopus*. For example, the white tail may be used in prey flushing (Mumme 2022), but a study of foraging indicates that prey is infrequently caught in the air (maximum of 8% in the case of *P. whistleri*) and there is no correlation of white patch with those species that were or were not observed flycatching (Ghosh-Harihar and Price 2014). A plausible hypothesis relates to flock cohesion and communication. Several of the species with white in the tail are known to flock in the nonbreeding season, some in quite gloomy habitats. For example, *P. pulcher* often forages deep in dark rhododendron forests, and sometimes it has appeared to us as if the white tail feathers are moving in the forest with no bird attached.

A striking feature of the within bird pattern is that the tail patch is always white, whereas the other patches are always yellowish, containing at least some carotenoid. Comparing tail patch with wing-bar, we suggest this reflects different functions of the two patches. Tail patches are concealed except during flight, and act as conspicuous flashes as the tail is spread. Hence the tail is intimately tied to motion, which is detected achromatically (by the double cones), and white should be most conspicuous against a dark background. The presence of flash markings (patches on the plumage that can be concealed and exposed) have been correlated with flocking behavior in shorebirds (Brooke 1998). Testing this association required experiments during the nonbreeding season, when many *Phylloscopus* species join mixed-species foraging flocks to test whether white tail patches correlate with flocking propensity. In contrast, the yellowish wing-bar is constantly exposed on the greater covert feathers. Given the role of wing bar size in conspecific aggression in *Phylloscopus* and the use of carotenoid coloration in aggression more generally (Kenyon and Martin 2022, 2023) it is likely that wing bar color functions in aggressive interactions. Thus, the color of these two patch types may be driven by different selection pressures and should be considered as modular units. The extent to which, if any, they interact to stimulate a receiver during a composite visual display such as the behaviors studied here remains to be tested.

4.5.5 Conclusions

In this study we addressed two main hypotheses in shaping plumage coloration: spectral variation in the environment and use in display. We find little evidence that light environment or different display motions affect the color of patches. Plumage chromatic contrasts remain invariable across the two habitat extremes measured. Moreover we find no correlation between the variation in tail motion and presence of white in the tail – on the contrary our results suggest that species with white in the tail use alternate displays that minimize tail exposure. Vertical wing displacement is weakly correlated with wing bar chromatic contrasts but this result warrants further study. Overall, we propose that the variation observed in wing and tail coloration may be attributed to their different roles in signal function and suggest possible modularity in evolutionary pressures affecting color on different parts of the body.

APPENDIX

4.A Supplementary Data

Supplementary tables for this chapter can be viewed at `https://figshare.com/s/ae26a8e21924cf101655`

CHAPTER 5

CONCLUSION AND FUTURE DIRECTIONS

5.1 Conclusion

At the time of writing, approximately 75 years have passed since Tinbergen's observation that color and motion traits are likely connected (Tinbergen 1948). As the fields of sensory biology and behavioral ecology continue to orient themselves towards understanding this relationship it is helpful to assess where the field stands (Introduction) and what questions remain unanswered. This dissertation aimed to address the relationship between color and display directly as well as expand the scope of the types of species and contexts that have heretofore been the focus of study. We focused on a group of "drab", superficially similar species in the western Himalaya, an area that is relatively understudied. By combining field-based observations and experiments with comparative analyses, and natural history collections, the results of this work offer not only additional data toward elucidating the relationship between visual signaling traits but also suggest new research directions.

The first conclusion of this work is that the use of visual communication in cryptic, otherwise "drab" species may be much more prevalent than is currently appreciated or understood. In the first comparative study of underwing plumage patches across the Cettiidae bush warblers, we found that these plumage markings are common across several genera. More strikingly, descriptions of these plumage patches are largely absent from field guides, indicating that they likely have gone unnoticed. The function of these patches remains unclear but behavioral observation and playback experiments across two species in the western Himalaya suggest the use of wing motions during territorial display as a possible avenue through which patches may be viewed. In the case of these understory species, it appears that the placement of highly contrasting white markings beneath the wing may balance conspicuousness and crypsis pressures, enabling their reveal only when behaviorally electing to do so. Furthermore, it raises the possibility that visual communication is being used under conditions previously thought to be unprofitable.

The second primary conclusion is that visual signal complexity in aggressive displays of *Phylloscopus* is built in a modular fashion. We find that the primary double wing flick display is largely consistent with respect to interspecific comparisons. There is greater within-species variation in wing motion, suggesting that wing flicking may play a role in communicating something about the internal state of the individual. The interspecific variation found is discrete rather than continuous – three species have added new behaviors to their repertoires that are distinct in the shape and rate of motion from the shared double wing flick. Additionally, a fourth species has dropped wing motion altogether. Why species have evolved additional display types remains a future research direction.

The third conclusion addresses the hypothesis put forth by Tinbergen directly and challenges it – we find scarce evidence that wing and tail motion in *Phylloscopus* is correlated with differences in plumage contrast. To address this, we quantified plumage color variation across 12 species of *Phyllosocpus* for the first time, in addition to measuring spectral shape variation in the form of irradiance across 5 habitat types in the western Himalaya. This work provides an additional perspective to the study published 30 years ago by Marchetti that concluded achromatic plumage variation in *Phylloscopus* is related to habitat brightness (1993). Our results indicate that the signaling environment (sensory drive) cannot account for the variation observed in plumage color and that the effects of light environment on the perception of color across habitats is rather limited.

The work within this dissertation has concerned itself with the relationship between motion and color of the animal and asked what influence the light of the sensory environment has on the observed variation in these traits. However, one limitation of this work is we have thus far treated the sensory environment as a static object. In the final section, I outline an area for future study that incorporates the role of motion not only within the focal animal but in the sensory environment as well.

5.2 Future Directions

5.2.1 Incorporating background complexity and motion

Most of the work concerning the effects of the sensory environment on visual signals have focused on the relationship between the irradiance or radiance of the environment and the reflectance of the color in question. In other words, the axis of variation is related to the spectral composition of the available light, the resulting color of the background and the resulting color of the focal species. The work in this dissertation has followed in this direction. However, variation in spectral composition and background color is only one axis upon which the sensory environment can vary. The spatial organization of the background (Hulse et al., 2020) and its motion (Ord, 2012; Ramos and Peters, 2017a) are other variables that should affect the perception of a visual phenotype.

Imagine in your mind's eye the image of a tree canopy. This scene will likely be composed of leaves, branches, perhaps gaps of sky or small objects located further from your focal plane of view. The experience will unlikely be a homogenous block of green color, however the scene being recreated when modeling a background with point samples of radiance captures just that. Instead, natural scenes in forested habitats are often spatially variable, with differing levels of complexity, varying in the size, structure and placement of their branches, leaves and other objects (Figure 5.1). The extent to which these scenes significantly and biologically meaningfully vary in this spatial complexity and at what scales is a relatively untapped question in sensory biology generally and the sensory drive hypothesis specifically. The influence of habitat spatial heterogeneity on the visual signal phenotype is an emerging area (Hulse et al. 2020; Wilgers et al. 2022). Male darters (*Etheostoma* spp) appear to match their patterning to that of their microhabitat, a correlation not found

Figure 5.1: **Lateral view of foliage in four primary habitats.** Forest habitats present an ideal environment in which to test for differences in spatial complexity of sensory backgrounds

for female darters (Hulse et al. 2020). The authors conclude that this is the result of a female preference driven by the efficient coding hypothesis (Redies 2007), whereby aesthetic preferences arise due to the ease of neural processing of certain stimuli, such as natural scenes. Another study testing the interaction between ornamentation, courtship behavior, and signaling environment complexity on female choice in wolf spiders found that the signaling environment influences the interaction between ornamentation and behavior. In complex signaling environments, males reduced their display effort but maintained the same mating success, despite both visual traits independently influencing mating success (Wilgers et al. 2022). Variation in habitat spatial complexity has been noted for some time in *Anolis* lizards (Powell and Leal 2014; Steinberg and Leal 2016; Fleishman et al. 2022) although it has not yet been directly quantified and tested. Finding ways to quantify and test the effects of background heterogeneity alone presents an avenue for future research.

However, analogous to how our understanding of a visual phenotype is incomplete without considering the role of motion, quantifying spatial complexity in habitats without incorporating how they are moved only captures part of the sensory environment. In this area, a great deal of work has been done on *Anolis* and other species of lizards. The effect of background noise due to movement on visual displays was noted and tested by Fleishman over 30 years ago (Fleishman 1992). Despite continued work on the effects of background motion on detection (Peters 2008; Fleishman and Pallus 2010; Pallus et al. 2010; Steinberg and Leal 2016; Bian et al. 2021), display output (Ord et al. 2007; Ord and Stamps 2008; Woo and Rieucau 2013; Ramos and Peters 2017; Bian et al. 2019; Peters and Ramos 2022) and development of methods (Peters et al. 2008; Peters 2013; Bian et al. 2018), this body of research has not broken through to other taxa. This is rather surprising with respect to birds, especially given the breadth of research on avian visual biology and presents a fruitful opportunity for future work.

REFERENCES

Abrams, R. A. and Christ, S. E. (2003). Motion onset captures attention. *Psychol. Sci.*, 14:427–432.

Alvarez, F. (1993). Alertness signalling in two rail species. *Anim. Behav.*, 46:1229–1231.

Anderson, R. C., DuBois, A. L., Piech, D. K., Searcy, W. A., and Nowicki, S. (2013). Male response to an aggressive visual signal, the wing wave display, in swamp sparrows. *Behav. Ecol. Sociobiol.*, 67:593–600.

Andrew, R. J. (1961). The displays given by passerines in courtship and reproductive fighting: a review (part a). *Ibis*, 103a:549–579.

Andrew, R. J. (2008). The displays given by passerines in courtship and reproductive fighting: A review. *Ibis*, 103a:315–348.

Angelini, D. (2022). borealis: Tools for reproducible geometric morphometric analysis.

Arak, A. and Enquist, M. (1993). Hidden preferences and the evolution of signals. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 340:207–213.

Armstrong, E. A. (2008). Social signalling and white plumage. *Ibis*, 113:534.

Baden, T. and Osorio, D. (2019). The retinal basis of vertebrate color vision. *Annu Rev Vis Sci*, 5:177–200.

Baker, K. (1991). *An Identification Guide to the Warblers of Europe, Asia and North Africa.* Christopher Helm.

Barske, J., Schlinger, B. A., Wikelski, M., and Fusani, L. (2011). Female choice for male motor skills. *Proc. Biol. Sci.*, 278:3523–3528.

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.*, 67:1–48.

Bazzaz, F. A. and Pickett, S. T. A. (1980). Physiological ecology of tropical succession: A comparative review. *Annu. Rev. Ecol. Syst.*, 11:287–310.

Beauchamp, G. and Heeb, P. (2001). Social foraging and the evolution of white plumage. *Evol. Ecol. Res.*, 3:703–720.

Beco, R., Silveira, L. F., Derryberry, E. P., and Bravo, G. A. (2021). Ecology and behavior predict an evolutionary trade-off between song complexity and elaborate plumages in antwrens (aves, thamnophilidae). *Evolution*, 75:2388–2410.

Bennett, A. T. D., Cuthill, I. C., and Norris, K. J. (1994). Sexual selection and the mismeasure of color. *Am. Nat.*, 144:848–860.

Bennett, A. T. D. and Théry, M. (2007). Avian color vision and coloration: Multidisciplinary evolutionary biology. *Am. Nat.*, 169:S1–S6.

Bian, X., Chandler, T., Laird, W., Pinilla, A., and Peters, R. (2018). Integrating evolutionary biology with digital arts to quantify ecological constraints on vision-based behaviour. *Methods Ecol. Evol.*, 9:544–559.

Bian, X., Chandler, T., Pinilla, A., and Peters, R. A. (2019). Now you see me, now you don't: Environmental conditions, signaler behavior, and receiver response thresholds interact to determine the efficacy of a movement-based animal signal. *Frontiers in Ecology and Evolution*, 7.

Bian, X., Pinilla, A., Chandler, T., and Peters, R. (2021). Simulations with australian dragon lizards suggest movement-based signal effectiveness is dependent on display structure and environmental conditions. *Sci. Rep.*, 11:6383.

Bliard, L., Paquet, M., Robert, A., Dufour, P., Renoult, J. P., Grégoire, A., Crochet, P.-A., Covas, R., and Doutrelant, C. (2020). Examining the link between relaxed predation and bird coloration on islands. *Biol. Lett.*, 16:20200002.

Bortolotti, G. R., Stoffel, M. J., and Galvan, I. (2011). Wintering snowy owls bubo scandiacus integrate plumage colour, behaviour and their environment to maximize efficacy of visual displays. *Ibis*, 153:134–142.

Boström, J. E., Dimitrova, M., Cindy, O. C., Håstad, Qvarnström, A., and Ödeen, A. (2016). Ultra-rapid vision in birds. *PLoS One*, 11:e0151099.

Bostwick, K. S. and Prum, R. O. (2003). High-speed video analysis of wing-snapping in two manakin clades (pipridae: Aves). *J. Exp. Biol.*, 206:3693–3706.

Boughman, J. W. (2001). Divergent sexual selection enhances reproductive isolation in sticklebacks. *Nature*, 411:944–948.

Boughman, J. W. (2002). How sensory drive can promote speciation. *Trends Ecol. Evol.*, 17:571–577.

Bradbury, J. W. and Vehrencamp, S. L. (2011). *Principles of Animal Communication*. Sinauer, 2nd edition.

Brooke, M. D. E. L. (1998). Ecological factors influencing the occurrence of 'flash marks' in wading birds. *Funct. Ecol.*, 12:339–346.

Burley, N. T. and Symanski, R. (1998). "a taste for the beautiful": latent aesthetic mate preferences for white crests in two species of australian grassfinches. *Am. Nat.*, 152:792–802.

Burtt, E. H. and Jr. (2018). *The Behavioral Significance of Color*. Routledge.

Byers, J., Hebets, E., and Podos, J. (2010). Female mate choice based upon male motor performance. *Anim. Behav.*, 79:771–778.

Candolin, U., Salesto, T., and Evers, M. (2007). Changed environmental conditions weaken sexual selection in sticklebacks. *J. Evol. Biol.*, 20:233–239.

Cantarero, A., Laaksonen, T., Järvistö, P. E., López-Arrabé, J., Gil, D., and Moreno, J. (2017). Testosterone levels in relation to size and uv reflectance of achromatic plumage traits of female pied flycatchers. *J. Avian Biol.*, 48:243–254.

Carleton, K. L., Parry, J. W. L., Bowmaker, J. K., Hunt, D. M., and Seehausen, O. (2005). Colour vision and speciation in lake victoria cichlids of the genus pundamilia. *Mol. Ecol.*, 14:4341–4353.

Carlos, A. B. P. (2002). Is the white-flanked antwren (formicariidae: Myrmotherula axillaris) a nuclear species in mixed-species flocks? a field experiment. *Journal of Field Ornithology*, 73:74–81.

Castrale, J. S. (1983). Selection of song perches by sagebrush-grassland birds. *Wilson Bull.*, 95:647–655.

Catchpole, C. K. (1973). The functions of advertising song in the sedge warbler (acrocephalus schoenobaenus) and the reed warbler (a. scirpaceus). *Behaviour*, 46:300–320.

Chen, C.-C., Liao, C.-C., and Walther, B. A. (2022). Interspecific competition and facilitation coexist in mixed-species bird flocks of montane coniferous forests in taiwan. *J. Avian Biol.*, 2022.

Chiao, C. C., Cronin, T. W., and Osorio, D. (2000). Color signals in natural scenes: characteristics of reflectance spectra and effects of natural illuminants. *J. Opt. Soc. Am. A Opt. Image Sci. Vis.*, 17:218–224.

Clark, C. J. (2009). Courtship dives of anna's hummingbird offer insights into flight performance limits. *Proc. Biol. Sci.*, 276:3047–3052.

Clark, D. L., Macedonia, J. M., Rowe, J. W., Stuart, M. A., Kemp, D. J., and Ord, T. J. (2015). Evolution of displays in galápagos lava lizards: comparative analyses of signallers and robot playbacks to receivers. *Anim. Behav.*, 109:33–44.

Clement, P. (2020). *Brownish-flanked Bush Warbler (Horornis fortipes)*. Cornell Lab of Ornithology.

Cott, H. B. (1940). Adaptive coloration in animals. 540.

Craig, A. J. F. K. (1974). Reproductive behaviour of the male red bishop bird. *Ostrich*, 45:149–160.

Crowhurst, C. J., Zanollo, V., Griggio, M., Robertson, J., and Kleindorfer, S. (2012). White flank spots signal feeding dominance in female diamond firetails, stagonopleura guttata. *Ethology*, 118:63–75.

Cullen, J. M. (1966). E. ritualization of animal activities in relation to phylogeny, speciation and ecology: Reduction of ambiguity through ritualization. *Philos. Trans. R. Soc. Lond.*, 251:363–374.

Cummings, M. E. (2007). Sensory trade-offs predict signal divergence in surfperch. *Evolution*, 61:530–545.

Cummings, M. E., Endler, J. A., and editor: Rebecca C. Fuller, H. (2018). 25 years of sensory drive: the evidence and its watery bias. *Curr. Zool.*, 64:471–484.

Cummings, M. E. and Partridge, J. C. (2001). Visual pigments and optical habitats of surfperch (embiotocidae) in the california kelp forest. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.*, 187:875–889.

Cuthill, I. C. (2006). *Color perception*, pages 3–40. Harvard University Press.

Cuthill, I. C., Allen, W. L., Arbuckle, K., Caspers, B., Chaplin, G., Hauber, M. E., Hill, G. E., Jablonski, N. G., Jiggins, C. D., Kelber, A., Mappes, J., Marshall, J., Merrill, R., Osorio, D., Prum, R., Roberts, N. W., Roulin, A., M, T. N. R. H., Sherratt, Skelhorn, J., P, M. S. M., Stevens, Stoddard, M. C., Stuart-Fox, D., Talas, L., Tibbetts, E., and Caro, T. (2017). The biology of color.

Daanje, A. (1951). On locomotory movements in birds and the intention movements derived from them. *Behaviour*, 3:48–98.

Dakin, R., McCrossan, O., Hare, J. F., Montgomerie, R., and Kane, S. A. (2016). Biomechanics of the peacock's display: How feather structure and resonance influence multimodal signaling. *PLoS One*, 11:e0152759.

Dakin, R. and Montgomerie, R. (2009). Peacocks orient their courtship displays towards the sun. *Behav. Ecol. Sociobiol.*, 63:825–834.

Dale, J., Dey, C. J., Delhey, K., Kempenaers, B., and Valcu, M. (2015). The effects of life history and sexual selection on male and female plumage colouration. *Nature*, 527:367–370.

de L Brooke, M. (2010). Unexplained recurrent features of the plumage of birds. *Ibis*, 152:845–847.

Douglas, J. M., Cronin, T. W., Tsyr-Huei, N. J. C., and Dominy (2007). Light habitats and the role of polarized iridescence in the sensory ecology of neotropical nymphalid butterflies (lepidoptera: Nymphalidae). *J. Exp. Biol.*, 210:788–799.

Dunn, P. O., Armenta, J. K., and Whittingham, L. A. (2015). Natural and sexual selection act on different axes of variation in avian plumage color. *Sci Adv*, 1:e1400155.

Echeverri, S. A., Miller, A. E., Chen, J., McQueen, E. W., Plakke, M., Spicer, M., Hoke, K. L., Stoddard, M. C., and Morehouse, N. I. (2021). How signaling geometry shapes the efficacy and evolution of animal communication systems. *Integr. Comp. Biol.*, 61:787–813.

Edmunds, M. (1974). *Defence in Animals: A Survey of Anti-predator Defences.* Longman.

Endler, J. A. (1991). Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vision Res.*, 31:587–608.

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *Am. Nat.*, 139:S125–S153.

Endler, J. A. (1993). The color of light in forests and its implications. *Ecol. Monogr.*, 63:1–27.

Endler, J. A. and Thery, M. (1996). Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. *Am. Nat.*, 148:421–452.

Ferns, P. N. and Hinsley, S. A. (2004). Immaculate tits: head plumage pattern as an indicator of quality in birds. *Anim. Behav.*, 67:261–272.

Fialko, K. and Price, T. D. (2024). Building visual signal complexity through discrete modifications of motion. *MS*.

Fleishman, L. J. (1992). The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Am. Nat.*, 139:36–61.

Fleishman, L. J. and Pallus, A. C. (2010). Motion perception and visual signal design in anolis lizards. *Proc. Biol. Sci.*, 277:3547–3554.

Fleishman, L. J., Perez-Martinez, C. A., and Leal, M. (2022). Can sensory drive explain the evolution of visual signal diversity in terrestrial species? a test with anolis lizards. *Am. Nat.*, 200:236–249.

Foster, D. H. and Nascimento, S. M. (1994). Relational colour constancy from invariant cone-excitation ratios. *Proc. Biol. Sci.*, 257:115–121.

Franconeri, S. L. and Simons, D. J. (2003). Moving and looming stimuli capture attention. *Percept. Psychophys.*, 65:999–1010.

Fuller, R. C. (2002). Lighting environment predicts the relative abundance of male colour morphs in bluefin killifish (lucania goodei) populations. *Proc. Biol. Sci.*, 269:1457–1465.

Fuller, R. C., Carleton, K. L., Fadool, J. M., Spady, T. C., and Travis, J. (2005). Genetic and environmental variation in the visual properties of bluefin killifish, lucania goodei. *J. Evol. Biol.*, 18:516–523.

Galatowitsch, M. L. and Mumme, R. L. (2004). Escape behavior of neotropical homopterans in response to a flush–pursuit predator. *bitr*, 36:586–595.

Gatesy, S. M. and Dial, K. P. (1996). Locomotor modules and the evolution of avian flight. *Evolution*, 50:331–340.

Ghosh, M., Singh, P., and Mohan, D. (2011). Seasonal variation in foraging ecology of three species of overwintering leaf warblers (genus phylloscopus) in the himalayan foothills. *J. Ornithol.*, 152:869–877.

Gomez, D. and Théry, M. (2004). Influence of ambient light on the evolution of colour signals: comparative analysis of a neotropical rainforest bird community. *Ecol. Lett.*, 7:279–284.

Gomez, D. and Théry, M. (2007). Simultaneous crypsis and conspicuousness in color patterns: Comparative analysis of a neotropical rainforest bird community. *Am. Nat.*, 169:S42–S61.

Gowaty, P. A. (1981). Aggression of breeding eastern bluebirds (sialia sialis) toward their mates and models of intra-and interspecific intruders. *Anim. Behav.*, 29:1013–1027.

Gower, J. C. (1975). Generalized procrustes analysis. *Psychometrika*, 40:33–51.

Grafe, T. U., Preininger, D., Sztatecsny, M., Kasah, R., Dehling, J. M., Proksch, S., and Hödl, W. (2012). Multimodal communication in a noisy environment: a case study of the bornean rock frog staurois parvus. *PLoS One*, 7:e37965.

Grimmett, R., Inskipp, C., and Inskipp, T. (2012). *Birds of India, Pakistan, Nepal, Bangladesh, Bhutan, Sri Lanka, and the Maldives*. Princeton University Press, 2 edition.

Grimmett, R., Inskipp, C., Inskipp, T., and Baral, H. S. (2016). *Birds of Nepal: Second Edition*. Bloomsbury USA, revised edition edition.

Hailman, J. (1960). A field study of the mockingbird's wing-flashing behavior and its association with foraging. *Wilson Bull.*, 72:346–357.

Hamao, S. and Ueda, K. (2000). Simplified song in an island population of the bush warbler cettia diphone. *J. Ethol.*, 18:53–57.

Hamao, S., Veluz, M. J. S., Saitoh, T., and Nishiumi, I. (2008). Phylogenetic relationship and song differences between closely related bush warblers (cettia seebohmi and c. diphone). *The Wilson Journal of Ornithology*, 120:268–276.

Hansen, A. J. and Rohwer, S. (1986). Coverable badges and resource defence in birds. *Anim. Behav.*, 34:69–76.

Hanssen, S. A., Folstad, I., and Erikstad, K. E. (2006). White plumage reflects individual quality in female eiders. *Anim. Behav.*, 71:337–343.

Hariharan, P., Bangal, P., Sridhar, H., and Shanker, K. (2022). Habitat use by mixed-species bird flocks in tropical forests of the western ghats, india. *J. Trop. Ecol.*, 38:393–400.

Harrison, C. J. O. (1976). Some aspects of adaptation and evolution in australian fan-tailed flycatchers. *Emu*, 76:115–119.

Hart, N. S. (2001). The visual ecology of avian photoreceptors. *Prog. Retin. Eye Res.*, 20:675–703.

Hart, N. S., Partridge, J. C., Cuthill, I. C., and Bennett, A. T. (2000). Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the blue tit (parus caeruleus l.) and the blackbird (turdus merula l.). *J. Comp. Physiol. A*, 186:375–387.

Hasson, O. (1989). Amplifiers and the handicap principle in sexual selection: a different emphasis. *Proc. R. Soc. Lond. B Biol. Sci.*, 235:383–406.

Hasson, O. (1991). Sexual displays as amplifiers: practical examples with an emphasis on feather decorations. *Behav. Ecol.*, 2:189–197.

Hayslette, S. E. (2003). A test of the foraging function of wing-flashing in northern mockingbirds. *Southeastern Naturalist*, 2:93–98.

Heindl, M. and Winkler, H. (2003). Interacting effects of ambient light and plumage color patterns in displaying wire-tailed manakins (aves, pipridae). *Behav. Ecol. Sociobiol.*, 53:153–162.

Hill, G. E. (2006). *Female Mate Choice for Ornamental Coloration*, pages 137–200. unknown.

Hogan, B. G. and Stoddard, M. C. (2018). Synchronization of speed, sound and iridescent color in a hummingbird aerial courtship dive. *Nat. Commun.*, 9:5260.

Holmes, R. T. and Recher, H. F. (1986). Search tactics of insectivorous birds foraging in an australian eucalypt forest. *Auk*, 103:515–530.

Holmqvist, M. H. and Srinivasan, M. V. (1991). A visually evoked escape response of the housefly. *J. Comp. Physiol. A*, 169:451–459.

Hulse, S. V., Renoult, J. P., and Mendelson, T. C. (2020). Sexual signaling pattern correlates with habitat pattern in visually ornamented fishes. *Nat. Commun.*, 11:2561.

Hurd, P. L. and Enquist, M. (2001). Threat display in birds. *Can. J. Zool.*, 79:931–942.

Hutton, P., Seymoure, B. M., McGraw, K. J., Ligon, R. A., and Simpson, R. K. (2015). Dynamic color communication.

Igic, B., D'Alba, L., and Shawkey, M. D. (2018). Fifty shades of white: how white feather brightness differs among species. *Naturwissenschaften*, 105:18.

Irwin, D. E., Bensch, S., and Price, T. D. (2001). Speciation in a ring. *Nature*, 409:333–337.

Jenssen, T. A. (2015). Evolution of anoline lizard display behavior. *Integr. Comp. Biol.*, 17:203–215.

Johnstone, R. A. (1996). Multiple displays in animal communication: ‘backup signals’ and ‘multiple messages’. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 351:329–338.

Jonart, L. M., Hill, G. E., and Badyaev, A. V. (2007). Fighting ability and motivation: determinants of dominance and contest strategies in females of a passerine bird. *Anim. Behav.*, 74:1675–1681.

Jones, J. A., Tisdale, A. C., H, J. L. B. M., Larkin, Smalling, C. G., and Siefferman, L. (2017). Multiple plumage ornaments as signals of intrasexual communication in golden-winged warblers. *Ethology*, 123:145–156.

Jones, K. A. and Whittingham, M. J. (2008). Anti-predator signals in the chaffinchfringilla coelebsin response to habitat structure and different predator types. *Ethology*, 114:1033–1043.

Kelber, A. (2019). Bird colour vision – from cones to perception. *Current Opinion in Behavioral Sciences*, 30:34–40.

Kenyon, H. L. and Martin, P. R. (2022). Aggressive signaling among competing species of birds. *PeerJ*, 10:e13431.

Kenyon, H. L. and Martin, P. R. (2023). Color as an interspecific badge of status: A comparative test. *Am. Nat.*, 202:433–447.

Kilner, R. M., Noble, D. G., and Davies, N. B. (1999). Signals of need in parent–offspring communication and their exploitation by the common cuckoo. *Nature*, 397:667–672.

Kram, Y. A., Mantey, S., and Corbo, J. C. (2010). Avian cone photoreceptors tile the retina as five independent, self-organizing mosaics. *PLoS One*, 5:e8992.

Kushlan, J. A. (1977). The significance of plumage colour in the formation of feeding aggregations of ciconiiforms. *Ibis*, 119:361–364.

Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci. U.S.A.*, 78:3721–3725.

Lenth, R. V. (2023). Estimated marginal means, aka least-squares means [r package emmeans version 1.8.5].

Ligon, R. A., Diaz, C. D., L, J. M. J., Troscianko, Stevens, M., Moskeland, A., Laman, T. G., and 3rd, E. S. (2018). Evolution of correlated complexity in the radically different courtship signals of birds-of-paradise. *PLoS Biol.*, 16:e2006962.

Lind, O. (2016). Colour vision and background adaptation in a passerine bird, the zebra finch (taeniopygia guttata). *R Soc Open Sci*, 3:160383.

Luschi, P. and Seppia, C. D. E. L. (1996). Song-type function during territorial encounters in male cetti's warblers cettia cetti. *Ibis*, 138:479–484.

Lythgoe, J. N. (1979). *The Ecology of Vision.* Clarendon Press.

Maan, M. E., Hofker, K. D., van Alphen Jacques J M, O., and Seehausen (2006). Sensory drive in cichlid speciation. *Am. Nat.*, 167:947–954.

Macdonald, D. W. and Henderson, D. G. (2008). Aspects of the behaviour and ecology of mixed-species bird flocks in kashmir. *Ibis*, 119:481–493.

MacDougall, A. K. and Montgomerie, R. (2003). Assortative mating by carotenoid-based plumage colour: a quality indicator in american goldfinches, carduelis tristis. *Naturwissenschaften*, 90:464–467.

Macedo, G., Bravo, G. A., Marcondes, R. S., Derryberry, E. P., and Biondo, C. (2021). Differences in plumage coloration predict female but not male territorial responses in three antbird sister species pairs. *Anim. Behav.*, 182:107–124.

Macedonia, J. M., Clark, D. L., Riley, R. G., and Kemp, D. J. (2013). Species recognition of color and motion signals in anolis grahami: evidence from responses to lizard robots. *Behav. Ecol.*, 24:846–852.

MacKinnon, J. and Nong, Y. X. (2022). *Guide to the Birds of China.* Oxford University Press, annotated edition edition.

Maia, R., Eliason, C. M., Bitton, P. P., Doucet, S. M., and Shawkey, M. D. (2013). pavo: An r package for the analysis, visualization and organization of spectral data. *Methods Ecol. Evol.*, 4:906–913.

Maia, R., Gruson, H., Endler, J. A., and White, T. E. (2019). pavo 2: New tools for the spectral and spatial analysis of colour in r. *Methods Ecol. Evol.*, 10.

Maier, E. J. (1992). Spectral sensitivities including the ultraviolet of the passeriform bird leiothrix lutea. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.*, 170:709–714.

Marchetti, K. (1993). Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature*, 362:149–152.

Marchetti, K. (1998). The evolution of multiple male traits in the yellow-browed leaf warbler. *Anim. Behav.*, 55:361–376.

Marchetti, K., Price, T., and Richman, A. (1995). Correlates of wing morphology with foraging behaviour and migration distance in the genus phylloscopus. *J. Avian Biol.*, 26:177–181.

Marcondes, R. S. and Brumfield, R. T. (2019). Fifty shades of brown: Macroevolution of plumage brightness in the furnariida, a large clade of drab neotropical passerines. *Evolution*, 73:704–719.

Mason, N. A., Riddell, E. A., Romero, F. G., Cicero, C., and Bowie, R. C. K. (2023). Plumage balances camouflage and thermoregulation in horned larks (eremophila alpestris). *Am. Nat.*, 201:E23–E40.

Mathis, A., Mamidanna, P., Cury, K. M., Abe, T., Murthy, V. N., Mathis, M. W., and Bethge, M. (2018). Deeplabcut: markerless pose estimation of user-defined body parts with deep learning. *Nat. Neurosci.*, 21:1281–1289.

McCoy, D. E., Feo, T., Harvey, T. A., and Prum, R. O. (2018). Structural absorption by barbule microstructures of super black bird of paradise feathers. *Nat. Commun.*, 9:1.

McGinley, R. H., Starrett, J., Bond, J. E., and Hebets, E. A. (2023). Light environment interacts with visual displays in a species-specific manner in multimodal-signaling wolf spiders. *Am. Nat.*, 201:472–490.

McGlothlin, J. W., Duffy, D. L., Henry-Freeman, J. L., and Ketterson, E. D. (2007). Diet quality affects an attractive white plumage pattern in dark-eyed juncos (junco hyemalis). *Behav. Ecol. Sociobiol.*, 61:1391–1399.

McGraw, K. J. and Hill, G. E. (2000). Carotenoid-based ornamentation and status signaling in the house finch. *Behav. Ecol.*, 11:520–527.

McLean, I. G. (1989). Feeding behaviour of the fantail (rhipidura fuliginosa). *Notornis*, 36:99–106.

McNaught, M. K. and Owens, I. P. F. (2002). Interspecific variation in plumage colour among birds: species recognition or light environment? *J. Evol. Biol.*, 15:505–514.

Medina, I., Delhey, K., Peters, A., Cain, K. E., Hall, M. L., Mulder, R. A., and Langmore, N. E. (2017). Habitat structure is linked to the evolution of plumage colour in female, but not male, fairy-wrens. *BMC Evol. Biol.*, 17:35.

Mendelson, T. C., Martin, M. D., and Flaxman, S. M. (2014). Mutation-order divergence by sexual selection: diversification of sexual signals in similar environments as a first step in speciation. *Ecol. Lett.*, 17:1053–1066.

Menezes, J. C. T. and Santos, E. S. A. (2020). Habitat structure drives the evolution of aerial displays in birds. *J. Anim. Ecol.*, 89:482–493.

Michelangeli, M., Tuomainen, U., Ulrika, B. B. M. C., and Wong (2015). Habitat alteration influences male signalling effort in the australian desert goby. *Behav. Ecol.*, 26:1164–1169.

Miles, M. C., Cheng, S., and Fuxjager, M. J. (2017). Biogeography predicts macroevolutionary patterning of gestural display complexity in a passerine family. *Evolution*, 71:1406–1416.

Miles, M. C. and Fuxjager, M. J. (2018). Synergistic selection regimens drive the evolution of display complexity in birds of paradise. *J. Anim. Ecol.*, 87:1149–1159.

Miles, M. C. and Fuxjager, M. J. (2019). Phenotypic diversity arises from secondary signal loss in the elaborate visual displays of toucans and barbets. *Am. Nat.*, 194:152–167.

Mitoyen, C., Quigley, C., and Fusani, L. (2019). Evolution and function of multimodal courtship displays. *Ethology*, 125:503–515.

Moller, A. P. and Pomiankowski, A. (1993). Why have birds got multiple sexual ornaments? *Behav. Ecol. Sociobiol.*, 32:167–176.

Moreno, J., Gil, D., Cantarero, A., and López-Arrabé, J. (2014). Extent of a white plumage patch covaries with testosterone levels in female pied flycatchers ficedula hypoleuca. *J. Ornithol.*, 155:639–648.

Morris, D. (1957). “typical intensity” and its relation to the problem of ritualisation. *Behaviour*, 11:1–12.

Moyen, F., Gomez, D., Doutrelant, C., Pierson, J., and Théry, M. (2006). Interacting effects of signalling behaviour, ambient light and plumage colour in a temperate bird, the blue tit parus caeruleus. *Rev. Ecol.*, 61:367–382.

Moynihan, M. (1962). *The Organization and Probable Evolution of Some Mixed Species Flocks of Neotropical Birds*. Smithsonian Institution.

Mumme, R. L. (2002). Scare tactics in a neotropical warbler: White tail feathers enhance flush–pursuit foraging performance in the slate-throated redstart (myioborus miniatus). *Auk*, 119:1024–1035.

Mumme, R. L. (2014). White tail spots and tail-flicking behavior enhance foraging performance in the hooded warbler. *Auk*, 131:141–149.

Murali, G. (2018). Now you see me, now you don’t: dynamic flash coloration as an antipredator strategy in motion. *Anim. Behav.*, 142:207–220.

Ohlson, J., Fjeldså, J., and Ericson, P. G. P. (2008). Tyrant flycatchers coming out in the open: phylogeny and ecological radiation of tyrannidae (aves, passeriformes). *Zool. Scr.*, 37:315–335.

Olsen, A. M. (2017). Feeding ecology is the primary driver of beak shape diversification in waterfowl. *Funct. Ecol.*, 31:1985–1995.

Olsen, A. M. and Westneat, M. W. (2015). Stereomorph: An r package for the collection of 3d landmarks and curves using a stereo camera set-up. *Methods Ecol. Evol.*, 6:351–356.

Olsson, P., Lind, O., and Kelber, A. (2015). Bird colour vision: behavioural thresholds reveal receptor noise. *J. Exp. Biol.*, 218:184–193.

Olsson, P., Lind, O., and Kelber, A. (2017). Chromatic and achromatic vision: parameter choice and limitations for reliable model predictions. *Behav. Ecol.*, 29:273–282.

Olsson, P., Wilby, D., and Kelber, A. (2016). Quantitative studies of animal colour constancy: using the chicken as model. *Proc. Biol. Sci.*, 283:20160411.

Olsson, U., Alström, P., Gelang, M., Ericson, P. G. P., and Sundberg, P. (2006). Phylogeography of indonesian and sino-himalayan region bush warblers (cettia, aves). *Mol. Phylogenet. Evol.*, 41:556–565.

Omland, K. E. (1996). Female mallard mating preferences for multiple male ornaments. *Behav. Ecol. Sociobiol.*, 39:361–366.

Ord, T. J., Peters, R. A., Clucas, B., and Stamps, J. A. (2007). Lizards speed up visual displays in noisy motion habitats. *Proc. Biol. Sci.*, 274:1057–1062.

Ord, T. J. and Stamps, J. A. (2008). Alert signals enhance animal communication in “noisy” environments. *Proc. Natl. Acad. Sci. U. S. A.*, 105:18830–18835.

Ord, T. J., Stamps, J. A., and Losos, J. B. (2013). Convergent evolution in the territorial communication of a classic adaptive radiation: Caribbean anolis lizards. *Anim. Behav.*, 85:1415–1426.

Osorio, D., Vorobyev, M., and Jones, C. D. (1999). Colour vision of domestic chicks. *J. Exp. Biol.*, 202:2951–2959.

Ota, N., Gahr, M., and Soma, M. (2015). Tap dancing birds: the multimodal mutual courtship display of males and females in a socially monogamous songbird. *Sci. Rep.*, 5:16614.

Palleroni, A., Miller, C. T., Hauser, M., and Marler, P. (2005). Predation: Prey plumage adaptation against falcon attack. *Nature*, 434:973–974.

Pallus, A. C., Fleishman, L. J., and Castonguay, P. M. (2010). Modeling and measuring the visual detection of ecologically relevant motion by an anolis lizard. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.*, 196:1–13.

Park, S.-R. and Park, D. (2000). Song type for intrasexual interaction in the bush warbler. *Auk*, 117:228–232.

Penteriani, V. and Delgado, M. D. M. (2017). Living in the dark does not mean a blind life: bird and mammal visual communication in dim light. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 372.

Peters, R. A. (2008). Environmental motion delays the detection of movement-based signals. *Biol. Lett.*, 4:2–5.

Peters, R. A. (2013). *Noise in Visual Communication: Motion from Wind-Blown Plants*, pages 311–330. Springer Berlin Heidelberg.

Peters, R. A. and Evans, C. S. (2003). Design of the jacky dragon visual display: signal and noise characteristics in a complex moving environment. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.*, 189:447–459.

Peters, R. A. and Ramos, J. (2022). Properties of an attention-grabbing motion signal: a comparison of tail and body movements in a lizard. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.*, 208:373–385.

Pinheiro, J., Bates, D., and Team, R. C. (2023). nlme: Linear and nonlinear mixed effects models.

Powell, B. J. and Leal, M. (2014). Brain organization and habitat complexity in anolis lizards. *Brain Behav. Evol.*, 84:8–18.

Preininger, D., Boeckle, M., Freudmann, A., Starnberger, I., Sztatecsny, M., and Hödl, W. (2013). Multimodal signaling in the small torrent frog (micrixalus saxicola) in a complex acoustic environment. *Behav. Ecol. Sociobiol.*, 67:1449–1456.

Preininger, D., Boeckle, M., and Hödl, W. (2009). Communication in noisy environments ii: visual signaling behavior of male foot-flagging frogs staurois latopalmatus. *Herpetologica*, 65:166–173.

Price, T. (1991). Morphology and ecology of breeding warblers along an altitudinal gradient in kashmir, india. *J. Anim. Ecol.*, 60:643–664.

Price, T. and Pavelka, M. (1996). Evolution of a colour pattern: history, development, and selection. *J. Evol. Biol.*, 9:451–470.

Price, T., Zee, J., Jamdar, K., and Jamdar, N. (2003). Bird species diversity along the himalaya: a comparison of himachal pradesh with kashmir. *J. Bombay Nat. Hist. Soc.*, 100:394–410.

Price, T. D. (1981). the ecology of the greenish warbler phylloscopus trochiloides in its winter quarters. *Ibis*, 123:131–144.

Price, T. D. (2017). Sensory drive, color, and color vision. *Am. Nat.*, 190:157–170.

Price, T. D., Helbig, A. J., and Richman, A. D. (1997). Evolution of breeding distributions in the old world leaf warblers (genus phylloscopus). *Evolution*, 51:552–561.

Price, T. D., Hooper, D. M., Buchanan, C. D., Johansson, U. S., Tietze, D. T., Alström, P., Olsson, U., Ghosh-Harihar, M., Ishtiaq, F., Gupta, S. K., Martens, J., Harr, B., Singh, P., and Mohan, D. (2014). Niche filling slows the diversification of himalayan songbirds. *Nature*, 509:222–225.

Price, T. D., Stoddard, M. C., K, N. I. S. S., and Bloch (2019). Understanding how neural responses contribute to the diversity of avian colour vision. *Anim. Behav.*, 155:297–305.

Prum, R. O. (2010). Phylogenetic analysis of the evolution of display behavior in the neotropical manakins (aves: Pipridae). *Ethology*, 84:202–231.

Pryke, S. R. and Andersson, S. (2003). Carotenoid-based status signalling in red-shouldered widowbirds (euplectes axillaris): Epaulet size and redness affect captive and territorial competition. *Behav. Ecol. Sociobiol.*, 53:393–401.

Ramesh, D. and Lima, S. L. (2019). Tail-flashing as an anti-predator signal in small wintering birds. *Behav. Ecol. Sociobiol.*, 73:67.

Ramos, J. A. and Peters, R. A. (2017). Motion-based signaling in sympatric species of australian agamid lizards. *Journal of Comparative Physiology A*, 203:661–671.

Randler, C. (2006). Is tail wagging in white wagtails, motacilla alba, an honest signal of vigilance? *Anim. Behav.*, 71:1089–1093.

Randler, C. (2007). Observational and experimental evidence for the function of tail flicking in eurasian moorhen gallinula chloropus. *Ethology*, 113:629–639.

Randler, C. (2016). Tail movements in birds-current evidence and new concepts. *Ornithol. Sci.*, 15:1–14.

Redies, C. (2007). A universal model of esthetic perception based on the sensory coding of natural stimuli. *Spat. Vis.*, 21:97–117.

Ribeiro, P. H. L., Guaraldo, A. C., H, L. T. M. R., and Manica (2019). Variation within and between courts in visual components of swallow-tailed manakin (chiroxiphia caudata) display. *J. Ornithol.*, 160:485–496.

Rickett, C. B. and Touche, J. D. D. L. (2008). Further observations on the birds of the province of fohkien, china. *Ibis*, 40:328–333.

Robinson, S. K. and Holmes, R. T. (1982). Foraging behavior of forest birds: The relationships among search tactics, diet, and habitat structure. *Ecology*, 63:1918–1931.

Rodd, F. H., Hughes, K. A., Grether, G. F., and Baril, C. T. (2002). A possible non-sexual origin of mate preference: are male guppies mimicking fruit? *Proc. Biol. Sci.*, 269:475–481.

Rogalla, S., Shawkey, M. D., and D'Alba, L. (2022). Thermal effects of plumage coloration. *Ibis*, 164:933–948.

Root, R. B. (1967). The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr.*, 37:317–350.

Rosenthal, G. G. (2007). Spatiotemporal dimensions of visual signals in animal communication. *Annu. Rev. Ecol. Evol. Syst.*

Rushton, S. K., Bradshaw, M. F., and Warren, P. A. (2007). The pop out of scene-relative object movement against retinal motion due to self-movement. *Cognition*, 105:237–245.

Ryan, M. J. (1990). Sexual selection, sensory systems and sensory exploitation. *Oxford surveys in evolutionary biology*, 7:157–195.

Ryan, M. J. and Cummings, M. E. (2013). Perceptual biases and mate choice. *Annu. Rev. Ecol. Evol. Syst.*, 44:437–459.

Ryan, M. J. and Keddy-Hector, A. (1992). Directional patterns of female mate choice and the role of sensory biases. *Am. Nat.*, 139:S4–S35.

Savalli, U. M. (1995). *The Evolution of Bird Coloration and Plumage Elaboration*, pages 141–190. Springer US.

Schluter, D. and Price, T. (1993). Honesty, perception and population divergence in sexually selected traits. *Proc. Biol. Sci.*, 253:117–122.

Scholes, E. and Laman, T. G. (2018). Distinctive courtship phenotype of the vogelkop superb bird-of-paradise lophorina niedda mayr, 1930 confirms new species status. *PeerJ*, 6:e4621.

Scordato, E. S. C., Bontrager, A. L., and Price, T. D. (2012). Cross-generational effects of climate change on expression of a sexually selected trait. *Curr. Biol.*, 22:78–82.

Seddon, N. (2005). Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution*, 59:200–215.

Seddon, N., Botero, C. A., Tobias, J. A., Dunn, P. O., Macgregor, H. E. A., R, J. A. C. R. D., Uy, Weir, J. T., Whittingham, L. A., and Safran, R. J. (2013). Sexual selection accelerates signal evolution during speciation in birds. *Proc. Biol. Sci.*, 280:20131065.

Seehausen, O., Terai, Y., Magalhaes, I. S., Carleton, K. L., Mrosso, H. D. J., Miyagi, R., der Sluijs, I., Schneider, M. V., E, H. M. M., Tachida, Imai, H., and Okada, N. (2008). Speciation through sensory drive in cichlid fish. *Nature*, 455:620–626.

Selander, R. and Hunter, D. (1960). On the functions of wing-flashing in mockingbirds. *Wilson Bull.*, 72:205–214.

Senar, J. C. (2006). *Color Displays as Intrasexual Signals of Aggression and Dominance.* unknown.

Sheard, C., Neate-Clegg, M. H. C., Alioravainen, N., Jones, S. E. I., Vincent, C., MacGregor, H. E. A., Bregman, T. P., Claramunt, S., and Tobias, J. A. (2020). Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nat. Commun.*, 11:2463.

Shultz, A. J. and Burns, K. J. (2013). Plumage evolution in relation to light environment in a novel clade of neotropical tanagers. *Mol. Phylogenet. Evol.*, 66:112–125.

Shultz, A. J. and Burns, K. J. (2017). The role of sexual and natural selection in shaping patterns of sexual dichromatism in the largest family of songbirds (aves: Thraupidae). *Evolution*, 71:1061–1074.

Simpson, R. K. and McGraw, K. J. (2018). Two ways to display: male hummingbirds show different color-display tactics based on sun orientation. *Behav. Ecol.*, 29:637–648.

Simpson, R. K. and McGraw, K. J. (2019). Interspecific covariation in courtship displays, iridescent plumage, solar orientation, and their interactions in hummingbirds. *Am. Nat.*, 194:441–454.

Stang, A. T. and McRae, S. B. (2009). Why some rails have white tails: the evolution of white undertail plumage and anti-predator signaling. *Evol. Ecol.*, 23:943–961.

Steinberg, D. S. and Leal, M. (2016). Visual motion detection and habitat preference in anolis lizards. *Journal of Comparative Physiology A*, 202:783–790.

Stoddard, M. C. and Prum, R. O. (2011). How colorful are birds? evolution of the avian plumage color gamut. *Behav. Ecol.*, 22:1042–1052.

Thayer, A. H. (1896). The law which underlies protective coloration. *Auk*, 13:124–129.

Thorpe, W. H. (1963). Antiphonal singing in birds as evidence for avian auditory reaction time. *Nature*, 197:774–776.

Tinbergen, N. (1948). Social releasers and the experimental method required for their study. *Wilson Bull.*, 60:6–51.

Tinbergen, N. (1960). Comparative studies of the behaviour of gulls (laridae): a progress report1). *Behaviour*, 15:1–69.

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Claire, A. G. V., Phillips, Marples, N. M., Montaño-Centellas, F. A., Leandro-Silva, V., Claramunt, S., Darski, B., G, T. P. F. B., Bregman, Cooney, C. R., C, E. J. R. H. E., Capp, Varley, Z. K., Friedman, N. R., Korntheuer, H., Corrales-Vargas, A., Trisos, C. H., Weeks, B. C., Hanz, D. M., Töpfer, T., Bravo, G. A., Remeš, V., Nowak, L., Carneiro, L. S., R, A. J. M., Matysioková, B., Baldassarre, D. T., Mart´-Salinas, A., D, P. M. W. J., Chapman, Daly, B. G., Sorensen, M. C., Neu, A., Ford, M. A., J, L. M. R., Silveira, F., Kelly, D. J., Annorbah, N. N. D., Pollock, H. S., Grabowska-Zhang,

A. M., McEntee, J. P., Gonzalez, J. C. T., G, M. C. M. C., Muñoz, Powell, L. L., A, T. J. J. G., Matthews, Johnson, O., Brito, G. R. R., Zyskowski, K., Crates, R., G, M. H. M., Zevallos, J., Hosner, P. A., Bradfer-Lawrence, T., Maley, J. M., Stiles, F. G., Lima, H. S., Provost, K. L., Chibesa, M., Mashao, M., Howard, J. T., Mlamba, E., Chua, M. A. H., Li, B., Gómez, M. I., Garc´, N. C., Päckert, M., Fuchs, J., Ali, J. R., Derryberry, E. P., Carlson, M. L., Urriza, R. C., Brzeski, K. E., Prawiradilaga, D. M., Rayner, M. J., Miller, E. T., Bowie, R. C. K., Lafontaine, R.-M., Scofield, R. P., Lou, Y., Somarathna, L., Denis, M. L., Illif, Neuschulz, E. L., Mathias, D. M. T., Dehling, Cooper, J. C., Pauwels, O. S. G., Analuddin, K., Fjeldså, J., Seddon, N., Sweet, P. R., DeClerck, F. A. J., Naka, L. N., Brawn, J. D., Aleixo, A., Böhning-Gaese, K., Rahbek, C., Fritz, S. A., Thomas, G. H., and Schleuning, M. (2022). Avonet: morphological, ecological and geographical data for all birds. *Ecol. Lett.*, 25:581–597.

Troscianko, J. and Stevens, M. (2015). Image calibration and analysis toolbox - a free software suite for objectively measuring reflectance, colour and pattern. *Methods Ecol. Evol.*, 6:1320–1331.

Uy, J. A. C. and Endler, J. A. (2004). Modification of the visual background increases the conspicuousness of golden-collared manakin displays. *Behav. Ecol.*, 15:1003–1010.

Veen, T., Brock, C., Rennison, D., and Bolnick, D. (2017). Plasticity contributes to a fine-scale depth gradient in sticklebacks' visual system. *Mol. Ecol.*, 26:4339–4350.

Venable, G. X., Gahm, K., and Prum, R. O. (2022). Hummingbird plumage color diversity exceeds the known gamut of all other birds. *Commun Biol*, 5:576.

Vorobyev, M. and Osorio, D. (1998). Receptor noise as a determinant of colour thresholds. *Proc. Biol. Sci.*, 265:351–358.

Walther, B. A., Clayton, D. H., and Gregory, R. D. (1999). Showiness of neotropical birds in relation to ectoparasite abundance and foraging stratum. *Oikos*, 87:157–165.

Warrant, E. J. (1999). Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summation. *Vision Res.*, 39:1611–1630.

Weaver, R. J., Santos, E. S. A., Tucker, A. M., Wilson, A. E., and Hill, G. E. (2018). Carotenoid metabolism strengthens the link between feather coloration and individual quality. *Nat. Commun.*, 9:73.

Webster, M. and Sheets, H. D. (2010). A practical introduction to landmark-based geometric morphometrics. *The Paleontological Society Papers*, 16:163–188.

Wei, C., Price, T. D., Liu, J., Alström, P., and Zhang, Y. (2017). The evolutionary origin of variation in song length and frequency in the avian family cettiidae. *J. Avian Biol.*, 48:1295–1300.

Weidmann, U. (1990). Plumage quality and mate choice in mallards (anas platyrhynchos). *Behaviour*, 115:127–141.

Wheatcroft, D. (2015). Repetition rate of calls used in multiple contexts communicates presence of predators to nestlings and adult birds. *Anim. Behav.*, 103:35–44.

White, T. E. (2020). Structural colours reflect individual quality: a meta-analysis. *Biol. Lett.*, 16:20200001.

Wiley, R. H. and Wiley, R. H. (1971). Cooperative roles in mixed flocks of antwrens (formicariidae).

Wilgers, D. J., Watts, J. C., and Hebets, E. A. (2022). Habitat complexity and complex signal function – exploring the role of ornamentation. *Behav. Ecol.*, 33:307–317.

Winkler, D. W., Billerman, S. M., and Lovette, I. J. (2020). Leaf warblers (phylloscopidae). *Birds/World.*

Woo, K. L. and Rieucau, G. (2013). Efficiency of aggressive and submissive visual displays against environmental motion noise in jacky dragon (amphibolurus muricatus). *Ethol. Ecol. Evol.*, 25:82–94.

Woodland, D. J., Jaafar, Z., and Knight, M.-L. (1980). The "pursuit deterrent" function of alarm signals. *Am. Nat.*, 115:748–753.

Xia, C., Huang, R., Wei, C., Pinwen, Y. N., and Zhang (2011). Individual identification on the basis of the songs of the asian stubtail (urosphena squameiceps). *Chin. Birds*, 2:132–139.

Xia, C., Liu, B., Wang, D., Lloyd, H., and Zhang, Y. (2015). Reliability of the brownish-flanked bush warbler's soft song in male-male conflict. *Avian Research*, 6:1–6.

Xia, C., Liu, J., Alström, P., Wu, Q., and Zhang, Y. (2013). Is the soft song of the brownish-flanked bush warbler an aggressive signal? *Ethology*, 119:653–661.

Xia, C., Wei, C., Lloyd, H., Liu, J., Wu, Q., and Zhang, Y. (2014). Dawn singing intensity of the male brownish-flanked bush warbler: Effects of territorial insertions and number of neighbors. *Ethology*, 120:324–330.

Xia, C., Xiao, H., and Zhang, Y. (2010). Individual variation in brownish-flanked bush warbler songs. *Condor*, 112:591–595.