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MS ENVIRONMENTAL BIOLOGY
CAPSTONE PROJECT

by

Kaily Taylor-Meek N.

A Project Presented in Partial Fulfillment
of the Requirements for the Degree
Masters of Science
in Environmental Biology

REGIS UNIVERSITY
May, 2023

MS ENVIRONMENTAL BIOLOGY
CAPSTONE PROJECT

by

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CHAPTER 1. LITERATURE REVIEW

Functional trait ecology of ducks, geese, and swans (Anseriformes: Anatidae)

What are functional traits, and how are they applied in ecology? Traits and their functionality can be a point of contention in the scientific community and have been for decades. The definition of a trait has been challenged since the first collected specimens were used to try and make explicit connections of form and function. However, this has become more difficult with incorporating interactions and studying different scales of ecology (Calow, 1987; Violle et al., 2007). Including ecosystem interactions have created a juxtaposition of beliefs, which falls between adaptationists, who consider all traits to be functional, and those who believe that not all traits are functional, such as the Panglossian Paradigm (Gould & Lewontin, 1979). The adaptationist paradigms execute a methodology centered on all traits performing some function, reinforcing the idea that form and function are inherently joined (Fryer, 1988). At the same time, Gould & Lewontin, (1979) present a challenge to the adaptationist paradigm, where not all traits have adapted by one constraint or specific purpose but can result from non-adaptive evolution. Despite this ongoing controversy, this review will focus on those traits with which function is empirically associated. This review will evaluate the role of functional feeding traits across ducks, geese, and swans (Anseriformes: Anatidae): the methodology of their study, their usefulness in assessing biodiversity ecosystem health, their morphological traits associated with avian feeding ecology and their applications to current phylogenetic hypotheses for this group of birds.

Definition and Study of Functional Traits

Functional traits are quantitative measurements of organismal phenotypes that impact or influence their ecology and behavior, enabling organisms to adapt to their environment and

occupy specific ecological niches, such as by specializing in different types of food or habitats (Calow, 1987; Dawson et al., 2021; Díaz et al., 2013; Geber & Griffen, 2003; Kearney et al., 2021; Violle et al., 2007). Understanding functional traits provides insights into an organism's adaptations, ecological strategies, and responses to environmental changes. These traits can include physiological, morphological, behavioral, or life-history features that are relevant to an animal's ecological role and fitness (Kearney et al., 2021; Nock et al., 2016; Pigot et al., 2016; Violle et al., 2007). Organisms, regardless of their habitats or ecological niches, face various environmental changes, such as changing climatic conditions, pollution and human disturbance, which can be mitigated or intensified as a result of their traits (Ollerton et al., 2014; Pulliam et al., 2020; Renfrew et al., 2005; Sliwinski & Koper, 2012). In addition, microevolutionary forces affecting populations in some given environment, like genetic drift, founder effects, and bottleneck effects, influence the expression of genes associated with functional traits (Geber & Griffen, 2003; Gomulkiewicz et al., 2018). Ultimately when environmental and evolutionary effects are impacted, we see a consequence of the fitness of individuals in a given species (Bregman et al., 2016; Grabenstein et al., 2022; Pigot et al., 2016). Overall, functional traits are essential for the survival and success of organisms in their respective habitats and play a critical role in shaping their ecological interactions and evolutionary trajectories (Fründ et al., 2013; Gagic et al., 2015; Hancock et al., 2022; Imran et al., 2021; Lavorel & Grigulis, 2012; Pigot et al., 2020; Vandewalle et al., 2010; Zhang et al., 2022).

Measuring the functional traits of organisms and understanding the magnitude of their effects remain challenging due to a lack of consensus and accepted methodology (Barabás et al., 2022; Calow, 1987; Kearney et al., 2021; Nock et al., 2016; Violle et al., 2007). Nevertheless, quantifying these parameters is crucial for a broader understanding of the underpinning

mechanisms and roles that influence biodiversity in communities and ecosystem interactions. Scientists use different methodologies to study how functional traits affect survivorship, fecundity, and developmental rates (Calow, 1987; Violle et al., 2007). Some methods focus on indirect impacts, while others interpret the relationship between traits and their direct effects. For instance, direct impacts of functional traits on ecosystem interactions include the ability of bees to pollinate specific plant species, while indirect impacts encompass the effects of that pollination on the structure and function of the entire ecosystem (Fründ et al., 2013; Gagic et al., 2015). In addition to these methods, advanced integrated models such as ARTificial Intelligence for Ecosystem Services (ARIES) and Social Values for Ecosystem Services (SolvES) can utilize existing datasets to evaluate the ecosystem services supplied by functional traits (Zhao et al., 2020). Quantifying the magnitude to which a functional trait imparts functionality to an organism or ecosystem is critical in understanding the mechanisms and roles that influence biodiversity (Kearney et al., 2021).

Functional Trait Ecology

Functional traits are critical components of ecosystem functioning and are extensively studied due to their ecological relevance, contribution to ecosystem services, and associations with environmental pressures and ecological niches (Barabás et al., 2022; Carlucci et al., 2020). Examining functional trait ecology at the community level allows for a broader understanding of the relationship between community assemblages and ecosystem-level ecological functions and their impact on biodiversity in a system (Cadotte et al., 2015; Dehling et al., 2022). Functional trait ecology considers the life histories and functional traits of species present within a community, providing essential indicators of community structure, ecosystem health, and their ability to respond to and affect community interactions (Barabás et al., 2022; Carlucci et al.,

2020; Gomulkiewicz et al., 2018). This approach considers complex relationships between functional traits, community structure, and the services they provide, which cannot be explained by purely trait-based responses that disregard the entirety of the system. Therefore, a community-wide approach to examining functional traits is essential for studying the ecosystem services provided by these traits.

Ecosystem services and their evaluation alongside functional traits have been documented in many species and represent their functional roles that impact different ecosystem services through social and ecological interactions (Cadotte et al., 2011; Cardinale et al., 2011; Díaz et al., 2006, 2013; Fell et al., 2022; Gagic et al., 2015; Kandziora et al., 2013). Ecosystem services comprise many biotic and abiotic processes and are commonly categorized into four groups. These categories include provisioning, such as food and fresh water; regulating, which involves disease control and climate response; supporting soil health by retaining water and cycling nutrients through functional traits; and cultural services, including education, heritage, and traditions. Additionally, biodiversity services can encompass all four categories and are sometimes considered a separate entity (Birkhofer et al., 2015; Bregman et al., 2016; Echeverri et al., 2020; Kandziora et al., 2013; O'Higgins et al., 2020; McPhearson et al., 2013).

These processes collectively support the stability, resilience, resistance, and efficiency of the ecosystem, and functional traits can also have cascading effects on many of these ecosystem services (Díaz et al., 2006, 2013; McPhearson et al., 2013). Evaluating plant and animal functional trait variation provides insight into direct provisions of material and non-material goods (Díaz et al., 2006, 2013). For example, a plant's root and leaf morphology can impact the rate and efficiency of nutrient uptake and chlorophyll production or select fungi with increased enzymes to promote nutrient turnover, which both impact provisioning, supporting, and

regulating services such as carbon sequestration, soil fertility through decomposition and food production (Cadotte et al., 2011; Díaz et al., 2006; Imran et al., 2021; Lavorel & Grigulis, 2012; Zhang et al., 2022). Additionally, tree functional traits can impact many plants in the environment through light acquisition, increased wood density, and leaf area, impacting growth (Fell et al., 2022). Increasing tree growth and leaf coverage provide a habitat that increases avian diversity, which offers cultural services through aesthetics, recreation, and bird watching (Zhao et al., 2020).

Functional traits provide essential information for pinpointing the contribution of individual species and their communities to biodiversity and forecasting shifts in abundance and range across various organisms (Callow, 1987; Kearney et al., 2021). Effective management practices should include the capability to monitor changes in functional traits, which can serve as an indicator of broader environmental changes (Gómez et al., 2021). This ability can help to identify potential impacts on ecosystem services and biodiversity (Díaz et al., 2006, 2013). Thus, understanding the interactions between functional traits and ecosystem services is critical for effective ecosystem management and conservation. By identifying the functional traits that are key drivers of ecosystem services and have been broadly studied across organisms, we can better predict how changes in environmental conditions, land use, or species composition may affect ecosystem services provision. Birds are one group of organisms where ecological value and functional traits are extensively studied.

Avian Functional Trait Ecology and Feeding Ecology

Birds have been the subject of extensive research to understand their functional traits and ecological value. These traits are strongly linked to resource acquisition and contribute to bird ecology. For example, bird morphology and behavior are associated with resource acquisition,

such as pollination, pest control, and seed dispersal (Navalón et al., 2022; Pigot et al., 2016; Zweers, 1991). Feeding ecology is influenced by multiple traits and environmental factors, including food availability, climate, habitat disruption, and human encroachment (Buckner et al., 2018; Guillemain et al., 2002; Olsen, 2017). Traits associated with feeding behaviors include foraging, flight, migration, vocalization, and nesting (Hong et al., 2023; Sheard et al., 2020; Weeks et al., 2022). For example, a bird's beak shape and size can determine its feeding strategy and the types of food it can consume, while wings and feathers affect flight capability, which is important for many aspects of its ecology, such as finding food or avoiding predators (Nock et al., 2016; Rosamond et al., 2020; Tucker & Rogers, 2014). Additionally, specialized features like zygodactyl feet with strong nails and modified rectrices enable climbing and bracing on trees, requiring less gripping power and energy in prolonged exposure to vertical positioning for foraging (Manegold & Töpfer, 2013; Van Wassenbergh et al., 2022).

Migration timing and distance are influenced by wing shape, body size, and metabolic rate (Che et al., 2021; Hedenström, 2008; Pigot et al., 2020; Sheard et al., 2020; Zavalaga et al., 2007). Vocalizations serve as means of communication, species recognition, and mate attraction (Guillemain et al., 2002; Rosamond et al., 2020; Wood et al., 2017). Nesting traits such as size, shape, and location, impact reproductive success, predator avoidance, and thermal regulation (Guillemain et al., 2001; Rosamond et al., 2020). Although functional trait studies in birds aim to answer big questions in evolution and ecological interactions, the appropriate context of the trait and the environment in which it occurs is crucial to consider (Peña et al., 2022). Functional traits play a crucial role in shaping avian behavior and adaptation to different environments and ecological niches, with aspects of the bill being most intensively studied.

The morphology of bird beaks is closely related to their feeding habits and is well-documented. Beaks are a key morphological trait that helps birds capture and process food, and there are several generalized associations between beak shapes and diets (Olsen, 2017; Peña et al., 2022; Pigot et al., 2016; Tobias et al., 2022; Zweers, 1991). For example, nut and seed eaters such as finches have strong conical bills, bills with hooked ends function for tearing meat adapted for birds of prey, and large elongated beaks are found primarily in frugivores. Long, thin, pointed beaks are associated with fish eaters, and small, sharp beaks are typically found with insectivores with some exceptions (Hurlbert et al., 2021; Pigot et al., 2020; Rosamond et al., 2020; Tobias et al., 2022). Thin and narrow bills used like a straw belong to hummingbird nectarivores, and curved, thin, blunt, and flat bills are filter feeders, mainly found in dabbling ducks (Olsen, 2017; Pigot et al., 2020; Tobias et al., 2022).

These morphological traits generally associated with feeding are not solely related to foraging and have additional functional roles. For example, bills play a role in thermoregulation as well, and there is a relationship between the size of a bird's bill and its geographical location (Greenberg et al., 2012; Tattersall et al., 2009). Larger bills are found in species in tropical regions to dissipate heat, while species in colder areas have smaller bills relative to their body size to retain heat (Greenberg et al., 2012; Tattersall et al., 2017). In fact, some birds, like the Toco toucan (*Ramphastos toco*), use vasomotor on the surface of their bills to thermoregulate (Tattersall et al., 2009). Therefore, considering bill thermoregulation is an important aspect when studying beak morphology and its relationship to feeding habits. Overall, beak morphology provides insights into the evolution and adaptation of different species to their environments and food sources, which is particularly relevant given recent studies have revealed that thermoregulation in bills may be more common than previously known (Greenberg et al., 2012;

Smit et al., 2013; Tattersall et al., 2009, 2017). However, the path and divergence that lead to these adaptations are not necessarily the same; different relationships are driving a variety of feeding ecology found in birds. Studies have shown that ecology, and morphological traits have correlations, but a singular focus or limited view of traits can often lead to forcing relationships (Miles et al., 1987). Quite often, there is a disproportionate focus on bills when studying functional traits in birds, which leads to neglecting other traits occurring simultaneously toward the same function. The focus on the bill is likely due to its wide variety among species, its association with feeding ecology, and its relative ease in quantifying.

However, the bill is an integrated part of the avian cranium, which possesses an additional and complimentary suite of functional roles. For example, the boobies and gannets (Sulidae) are aquatic birds that dive for foraging. One species, the Blue-footed Booby (*Sula nebouxii*), dives into the water at speeds of 60 mph when foraging, and these intense speeds and impact force are mitigated by a functional trait of air sacs in the skull to protect the brain (Redrobe, 2015; Zavalaga et al., 2007). Plunge-diving species of kingfishers (Alcedinidae) showcase a similar array of functional traits in their skulls and bills (Crandell et al., 2019; Eliason et al., 2020). Another example of complicated interactions is found in woodpeckers (*Picidae*), whose thicker skulls are capable of sustaining impact and rapid movement into the hard surface of a tree; although this is for foraging, it also serves as dwelling construction and mating behaviors (Van Wassenbergh et al., 2022). Understanding these relationships of cranial features and how they impact each other is essential for understanding the ecological roles of birds and their importance in maintaining ecosystems. This review has illustrated in other organisms that there are often many interactions occurring when evaluating the functionality of traits, and the same is true specifically in the case of a cosmopolitan group like waterfowl.

Functional Feeding Traits in Waterfowl (Anatidae)

The waterfowl (Anatidae) represent a globally distributed family of birds that includes 174 species and comprises 97.7% of all birds in the order Anseriformes (Gill et al., 2023). These species are highly specialized and generally depend on aquatic habitats for efficient foraging and avoiding predators (Che et al., 2021; Guillemain et al., 2002; Li & Clarke, 2016; Olsen, 2017; Sun et al., 2017). Waterfowl exhibit a diverse range of feeding ecologies, including filter-feeding, diving, dabbling, and grazing. Their diets consist of submersed and emergent vegetation, seeds, roots, tubers, invertebrates, and small vertebrates, and their specialized feeding behaviors enable many species to coexist in the same habitat without competing for the same food resources (Guillemain et al., 2002; Olsen, 2017; Sun et al., 2017; Winemiller et al., 2015). Understanding the functional traits of waterfowl is essential for their conservation and management, maximizing the economic benefits of hunting and other forms of utilization, and quantifying their ecological roles (Green & Elmberg, 2014; Whelan et al., 2015).

Functional ecology is crucial for understanding the ecological and economic importance of waterfowl. By studying anatid functional traits, such as their feeding behavior, habitat preferences, and migration patterns, researchers can better comprehend the roles they play in their ecosystems and the impacts they have on other species. This knowledge is essential for the effective conservation and management of waterfowl populations and for identifying potential threats, such as habitat loss or changes in climate, and developing strategies to mitigate them (Birkhofer et al., 2015; Carlucci et al., 2020; Cavender-Bares et al., 2009; Sun et al., 2017; Vandewalle et al., 2010).

Studies of anatid feeding functional ecology have varied in their approach, examining morphology, such as tongue and bill shape, and exploring relationships between body size, skull

morphology, vigilance, and bill location (Guillemain et al., 2001, 2002; Li & Clarke, 2016; Olsen, 2017). However, despite these well-defined morphological traits, their direct connection to foraging ecology and discrete guilds remains unclear. Waterfowl exhibit a range of feeding guilds, showcasing their adaptability in utilizing diverse feeding strategies to meet their nutritional needs and exploit available food sources. To address this diversity, researchers have classified waterfowl based on feeding groups, including Diving-Graspers, Filter-Feeding, Grazing, and Mixed: feeding and grazing; Buckner et al., 2018; Guillemain et al., 2001, 2002; Li & Clarke, 2016; Olsen, 2017; Wood et al., 2017). For example, some waterfowl species, like diving ducks, employ the Diving-Graspers strategy by diving underwater to capture prey such as fish or invertebrates. Others, like certain species of waterfowl mentioned in the Mixed: feeding and grazing guild, have a broader diet that includes animal and plant matter, allowing them to feed on tiny aquatic organisms and aquatic vegetation. Meanwhile, certain species within the Mixed: feeding and grazing guild have a diet incorporating animal and plant matter, allowing them to feed on tiny aquatic organisms and vegetation.

Various studies further contributed to the understanding of waterfowl feeding behavior. Li and Clarke, (2016) investigated four feeding groups to explore the systematics of cranial and hyolingual functions associated with different feeding behaviors, Olsen (2017) observed three functional feeding groups: diving, grazing/dabbling, and filter feeding, and Wood et al., (2017) examined six different feeding groups in their study of waterbird assemblages, encompassing species from all of Anseriformes. It is worth noting that specialized filter-feeding and diving ecologies can occasionally overlap within the *Aythya* tribe (Li & Clarke, 2016). By categorizing waterfowl into distinct feeding guilds, researchers have shed light on the diversity of feeding strategies within this avian group, enhancing our understanding of their ecological roles and

adaptations, although their exact connections to functional traits and their evolutionary origins have not been fully resolved.

In particular, the unresolved phylogeny of Anatidae presents a challenge in understanding the origins of their functional traits across space and time. Several studies have investigated phylogenetic relationships within the family (Buckner et al., 2018; Donne-Gouss et al., 2002; Eo et al., 2009; Gonzalez et al., 2009; Johnson & Sorenson, 1999; Peters et al., 2005; Sraml et al., 1996; Sun et al., 2017), but the entirety of relationships within this group are still unclear. Despite this existing gap in knowledge, the study of their functional traits remains vital in evaluating their ecological and economic value. Future research should focus on resolving their phylogenetic relationships and studying their functional traits in the context of environmental change, which could help inform conservation and management strategies for these vital waterbirds.

Implications and Future Research

The waterfowl family Anatidae is a diverse group of birds with a global distribution, highlighting their ability to adapt to various habitats and their importance as indicators of environmental change. Their functional traits are critical components of ecosystem functioning, providing valuable ecosystem services and indicating the health of community structures. In this review, I evaluated the functional feeding traits of Anatidae, pinpointing the need for a comprehensive phylogenetic tree to evaluate ecosystem health through biodiversity and ecosystem services. There are growing trends in functional trait studies from an evolutionary context, including Anatidae (Buckner et al., 2018; Navalón et al., 2022; Olsen, 2017; Pigot et al., 2020; Sobral, 2021; Winemiller et al., 2015). However, comprehensive species-level phylogenetic trees are currently lacking in waterfowl, which limits our understanding of their evolutionary history and

the role of functional traits in ecosystem services (Cavender-Bares et al., 2009; Che et al., 2021; Olsen, 2017; Sun et al., 2017; Tobias et al., 2022). Several studies have resolved portions of the phylogeny of waterfowl (Buckner et al., 2018; Donne-Gouss et al., 2002; Eo et al., 2009; Gonzalez et al., 2009; Johnson & Sorenson, 1999; Peters et al., 2005; Sraml et al., 1996; Sun et al., 2017), but a complete phylogeny has not yet been inferred. Once this goal is accomplished, we can more robustly study functional traits in evolutionary and ecosystem services contexts (Carlucci et al., 2020; Díaz et al., 2013).

Functional trait ecology allows us to understand species' roles in the community and if there is any overlap within ecological niches by acting as indicators of biodiversity response (Vandewalle et al., 2010; Volaire et al., 2020). Functional traits have already proven helpful in evaluating land use change response when combined with existing methods of biodiversity monitoring (Vandewalle et al., 2010). Studies tend to be biased towards morphology and less focused on developmental traits, which overlooks other essential aspects of functional morphology in Anatidae (Geber & Griffen, 2003; Violle et al., 2007). The bias in these studies has prevented a comprehensive understanding of ecosystem services. Therefore, focusing on functional traits related to diet, foraging and breeding habitat should be evaluated (Zurell et al., 2016). Along with the quantification of patterns over time and space (Voltaire et al., 2020), specifically species interactions across different trophic levels to provide an inference of trait functions (Tobias et al., 2022). A stronger focus on functional traits, their patterns, and interactions within their ecosystem will help predict environmental response variables (Cadotte et al., 2015). It's important to note that choosing the best morphology to study in the functional trait ecology of birds depends on the specific research goals and the ecological questions.

Integrating multiple morphological traits and their relationships can provide a more comprehensive understanding of bird ecology and functional adaptations.

Additionally, biodiversity loss is a pressing concern that requires immediate and precise conservation management plans to preserve ecosystem services (Birkhofer et al., 2015; Green & Elmberg, 2014; Kandziora et al., 2013; O'Higgins et al., 2020; McPhearson et al., 2013; Whelan et al., 2015). Quantifying the functional traits of all waterfowl species can provide the opportunity to comprehensively study ecosystem services provided by these species on a global scale (Díaz et al., 2006; Pigot et al., 2016; Sheard et al., 2020). However, a more inclusive approach is necessary to evaluate the nuances of waterfowl communities and their ecosystem services (Cadotte et al., 2011; Kandziora et al., 2013; Schirpke et al., 2017). By examining the global diversity of waterfowl and their interactions with their environments, we can better understand the functional ecology of this important family and inform conservation efforts to preserve their ecological and economic significance (Birkhofer et al., 2015; Carlucci et al., 2020; Peña et al., 2022; Sheard et al., 2020; Whelan et al., 2015).

Waterfowl conservation is important because these species are found on a cosmopolitan scale and provide many essential ecosystem services. This literature review has illustrated the importance of ecosystem services and impacts on biodiversity loss. To gain a better understanding of the family Anatidae's ecosystem services and nuances of their ecological community, we need broader and more inclusive studies that evaluate how the global diversity of waterfowl interacts with their environments (Callow, 1987; Kearney et al., 2021; Violle et al., 2007; Volaire et al., 2020). The synthesis of methods that combine functional traits and comprehensive evolutionary histories can lead to a more comprehensive understanding of the functional diversity of the family Anatidae. By developing a complete understanding of the

family Anatidae's functional traits, we can develop more effective conservation management plans and help protect the ecosystem services provided by these ecologically and economically essential birds (Birkhofer et al., 2015; Carlucci et al., 2020; Cavender-Bares et al., 2009; Green & Elmberg, 2014; Sun et al., 2017; Vandewalle et al., 2010; Whelan et al., 2015).

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CHAPTER 2. GRANT PROPOSAL

Boulder County Parks & Open Space

2022 Small Grant Program Report

Northern Flicker (*Colaptes auratus*) Hybridization in the Colorado Front Range Hybrid Zone

December 14th, 2022

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Section 1. Abstract

Hybrid zones are geographical regions where hybridization occurs between two closely related lineages, taxa, or species. Increased interest and studies in the hybridization of vertebrates are becoming more common in ecology and conservation to gauge evolutionary processes and population changes. One such hybrid zone in the Front Range of Colorado area affects breeding and population changes in the Northern Flicker, where three distinct phenotypes are present: red-shafted, yellow-shafted, and intermediate (hybrid). In this study, we will investigate the impact of urbanization and anthropogenic habitat conversion on the hybridization of Northern Flickers. The Denver Museum of Nature and Science (DMNS) ornithological collections will provide specimens for hybrid data over the last ~150 years. DMNS currently possesses hundreds of Northern Flicker specimens in their collection, spatially spanning the majority of their range and temporally spanning from 1877 to the present. Natural history collections allow us to evaluate and quantify trends through space and time with precision, accuracy, and minimal cost. We will use a scorecard for six plumage characteristics to quantify the extent of hybridization, or lack thereof, from each specimen in this collection. GIS models of urban development and hybridization trends will be mapped and overlaid across the Colorado Front Range in the hybrid zone to assess how these changes may have impacted the dynamics and frequency of hybridization. Using this information, we will provide a complete natural history of Northern Flickers through impacts on their ecology and evolution by urbanization, specifically biodiversity, and changes in hybridization dynamics.

Section 2. Introduction

Objectives

This study aims to evaluate Northern Flickers' hybridization over the last ~150 years, cataloging all specimens in the Denver Museum of Nature and Science Ornithological Collections by quantifying the phenotypic characteristics of hybridization. Furthermore, urbanization in the hybrid zone along the Front Range of Colorado will be evaluated to understand its impact on hybridization in this species.

Questions and Hypotheses

Q1. How has hybridization changed in the hybrid zone along the Front Range of Colorado between red-shafted and yellow-shafted Northern Flickers?

H1. The frequency and dynamics of hybridization between red- and yellow-shafted flickers have increased through time as these populations have continued to mix.

P1. We will observe more individuals with hybrid ancestry and more variable plumage traits toward the present.

H2. Urbanization will increase the frequency and alter the dynamics of flicker hybridization because urbanization facilitates the westward movement of yellow-shafted flickers.

P1. We will observe more individuals of hybrid ancestry in more heavily urbanized areas of the Colorado Front Range.

Specific Aim

To quantify the impact of urbanization and anthropogenic habitat conversion on the hybridization of Northern Flickers.

Anticipated Value

Using this information, we will provide a complete natural history of Northern Flickers through impacts on their ecology and evolution by urbanization, specifically spatial and temporal changes in hybridization dynamics.

Literature Review

Hybrid zones are geographical regions in which hybridization between two closely related lineages, taxa, or species, and these regions can provide insight into evolutionary processes (Grabenstein et al., 2022; Maxwell et al., 2021; Taylor et al., 2014; Todesco et al., 2016).

Secondary contact in hybrid zones influences ecological and evolutionary processes such as local adaption, speciation, and reproductive barriers (Allendorf et al., 2001; Maxwell et al., 2021; Short & Chapman, 1965; Wang et al., 2019). These processes and hybrid zones themselves have been shown to respond and shift in response to natural environmental changes (Allendorf et al., 2001; Buggs, 2007).

We see these environmental factors shaping hybrid zones especially in birds. Avian behavioral mechanisms and climate fluctuations are environmental factors that are known to increase secondary contact (Aguillon & Rohwer, 2022; Buggs, 2007). Secondary contact facilitates evolutionary roles such as introgression and the creation of hybrid zones associated with natural hybridization (Aguillon et al., 2018; Hruska & Manthey, 2021; Neri et al., 2018). In the Golden-winged (*Vermivora chrysoptera*) and Blue-winged Warbler (*V. cyanoptera*) hybrid zone, population sizes and duration of contact are driving population changes (Dabrowski et al., 2005). Golden-winged warblers are subject to increased introgression and hybridization when population sizes are lower (Allendorf et al., 2001; Dabrowski et al., 2005). Widespread environmental changes such as climate change and sexual selection pressures are known to alter

avian populations. Similarly, anthropogenic hybridization has unnaturally increased pressures through the translocation of plants and animals, fragmentation, and habitat modifications (Buggs, 2007; Grabenstein et al., 2022).

Increased anthropogenic disturbances are expected to further drive hybrid frequencies and shift species boundaries in response to range changes (Aguillon & Rohwer, 2022; Allendorf et al., 2001; Buggs, 2007; Grabenstein et al., 2022; Harr & Price, 2014). Black-capped (*Poecile atricapillus*) and Mountain (*Poecile gambeli*) Chickadees respond to landscape alterations by relocating to better resources (nesting, food, habitat), increasing competition, and interspecific interactions (Grabenstein et al., 2022; Grand et al., 2019; Taylor et al., 2015). Anthropogenic habitat conversion increases the frequency of hybridization between these two species, and when Black-capped and Mountain Chickadees hybridize, their fitness decreases, which impacts their ability to breed (Grabenstein et al., 2022). Increased interactions trigger range changes and shift hybrid zones, especially in regions experiencing major anthropogenic habitat conversion, such as metropolitan growth (Aguillon & Rohwer, 2022; Buggs, 2007; Grabenstein et al., 2022).

One such region that has undergone environmental and anthropogenic changes in the last ~150 years, and that comprises part of the Black-capped and Mountain Chickadees hybrid zone, is the Colorado Front Range. The Front Range is a geographic area spanning from Northern Colorado (Weld County) to Central Colorado (Pueblo County) along the eastern edge of the Rockies (Colorado: Department of Local Affairs, 2023; Cronin & Loevy, 2017). This region is home to the Northern Flicker (*Colaptes auratus*), a common North American woodpecker. Within this species, two subspecies hybridize in this region: *auratus*, commonly called yellow-shafted, and *cafer*, red-shafted (Aguillon & Rohwer, 2022). These taxa have low levels of genomic divergence, facilitating the identification of distinct regions affiliated with plumage

characteristics that vary between red-shafted, yellow-shafted, and hybrid individuals (Aguillon et al., 2021; Aguillon & Rohwer, 2022). Plumage characteristics include crown, nuchal patch presence, ear/cheek covert, throat, malar stripe, and wing/tail and are easily diagnosable in individuals without genomic sampling (Figure 1, Aguillon et al., 2018; Aguillon & Rohwer, 2022; Hudon et al., 2015). This contemporary hybrid zone has been studied continent-wide, but the study of the contact zone itself and its historical dynamics through time has not occurred. This study will evaluate how hybridization frequency and dynamics have changed in the last ~150 years along the Front Range of Colorado between red-shafted and yellow-shafted Northern Flickers. We will evaluate temporal changes in this hybrid zone based on plumage characteristics and quantify the impacts of anthropogenic habitat conversion on altering natural hybrid zones using a dataset of historical land cover for this region (Drummond et al., 2019).

The assessment of hybridization is crucial to documenting change in the life histories of Northern Flickers in the Hybrid zone in which Boulder County Parks & Open Space resides. Ecological studies focusing on natural communities assist in understanding the properties of communities that are more vulnerable or resistant to hybridization. Additionally, assessment of bird diversity influenced by human encroachment of park borders and wildlife areas will assist managers in creating plans for proposed changes to and around the parks.

Section 3. Methods

Use of Natural History Collections Collection

Denver Museum of Nature and Science (DMNS) ornithological collections will provide specimens for hybrid data over the last ~150 years. Currently, the DMNS contains 804 Northern flicker specimens in their collection. Hybridization is difficult to document accurately in the wild and museum specimens are ideal for DNA and morphological trait research. Natural history

collections enable us to evaluate and quantify trends through time and space with the precision and accuracy needed to assess hybridization (Justyn et al., 2020; Ottenburghs & Slager, 2020). All plumage data recorded from these specimens will be available to all interested researchers through the Arctos database.

Quantifying Hybridization at the Individual Level

We will collect data from individual study skins in the Denver Museum of Nature and Science's ornithology collection. We will retrieve data for each study skin from the DMNS database, Arctos, which included collection date (month and year), location, and GPS (latitude and longitude). Using a published standardized plumage scorecard to identify hybrid individuals and calculate hybrid scores for every Northern Flicker study skin in the collection (Aguillon & Rohwer, 2022; Short & Chapman, 1965).

Northern Flickers have six plumage characteristics in males and five in females that differ in color and shape: crown color, nuchal patch presence, ear/cheek covert color, throat color, malar stripe color (males), and wing/tail color (Figure 2, Aguillon & Rohwer, 2022; Flockhart & Wiebe, 2009; Short & Chapman, 1965). True yellow-shafted flickers have grey crowns, broad unrestricted nuchal patches, tan coverts, tan throats, black malar stripes (males), and bright yellow feather shafts in the wing and tail. True red-shafted flickers have brown crowns, absent nuchal patches, grey coverts, grey throats, red malar stripe (males), and salmon red feather shafts in the wing and tail. Hybrids will display intermediate colors and traits between red-shafted and yellow-shafted phenotypes. Each plumage characteristic was scored 0-4, with 0 considered pure yellow-shafted and 4 pure red-shafted. Individual plumage scores were converted into a single hybrid score per individual by summing the scores for each character and dividing male sums by

24 and female sums by 20 (accounting for plumage dimorphism) (Aguillon & Rohwer, 2022; Short & Chapman, 1965).

Quantifying Urbanization

We will utilize historical georeferenced land use and cover (LUCU) data in the Front Range of Colorado data to quantify urbanization through time along the flicker hybrid zone in this region. Rasters created by this study illustrate historical urbanization change and categorize multiple land classes across the entirety of the front range from 1937 – 1997 in two-decade increments. We will simplify these data into seven land classes (urban, agriculture, natural resources, vegetation, bare, water, no data) and then overlay coordinates of each study skin according to the year collected to extract dominant land use and percent of urban land cover for a 0.25 km buffer for each specimen, reflecting the estimated home range size for this species (Elchuk & Wiebe, 2003). Historical data use will be restricted to individuals inside the boundaries of the hybrid zone and the LUCU data.

Data Analysis of Hybridization Through Time and in Response to Urbanization

All statistical analyses will be performed in R version 4.0.2 (R Core Team, 2023). Hybridization rates at the population level will be determined by the number of hybrid observations divided by the number of observations each month, year, and decade. A generalized linear model of the proportion of hybrid individuals as a function of time will evaluate the extent of hybridization in the Front Range has changed through time. I will determine major gradients of plumage variation by ordinating the six plumage characteristics with principal components analysis (PCA). I will perform two separate PCAs, one for each sex, to account for the differing numbers of plumage traits in males and females. Using the first two gradients from each PCA, I will fit separate regressions of principal component scores against time to establish how plumage dynamics have

changed historically. To analyze the effects of urbanization on hybridization frequency and plumage dynamics in the hybrid zone, we will fit several similar generalized linear models and linear regressions to hybrid frequencies and plumage scores with two measures of urbanization as separate predictors. Predictors of dominant land use and percent urban land use will be quantified from each individual's home range (Elchuk & Wiebe, 2003). Dominant land use is quantified by land use of the largest presence and percent urban land use is quantified by the percent of urban land use for individuals in land use data boundaries (Drummond et al., 2019).

Project requirements and permits

An internship at DMNS grants access to collections without additional permissions or permitting.

Schedule

Date	Activity	Deliverables
12 / 1 — 12 / 29	Measure hybrid traits of Northern Flickers in the Denver Museum of Nature and Science Ornithological collection.	Produce data that is inputted into Arctos.
1 / 30 — 2 / 9	Organizing data and creating an analysis plan.	Produce graphs and visuals from data.
2 / 9 — 2 / 14	Write up results from data analysis	Produce poster for presentation
4 / 17	Regis University poster presentation	

Map

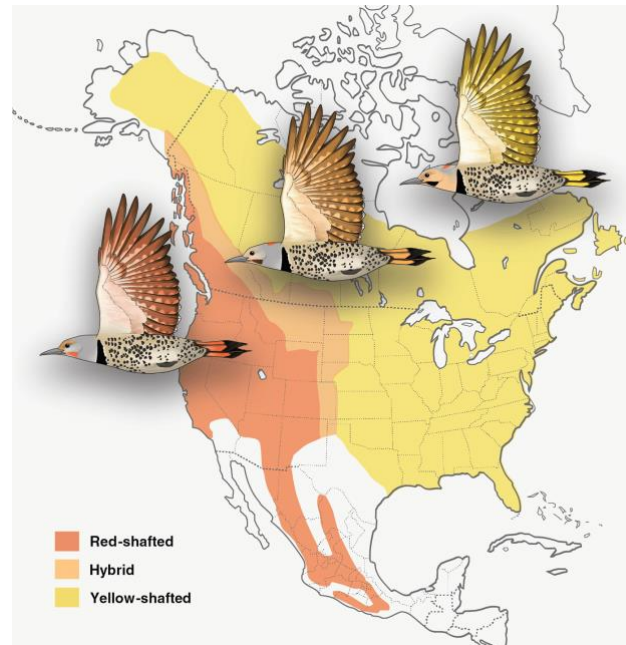


Figure 1: Illustration of color variation of the eastern yellow-shafted (*C. a. aurates*) and the western, red-shafted (*C.a. cafer*) subspecies and their hybrid overlaid with a map of their ranges. (Axelson, 2021). *Northern Flicker* illustrations by Megan Bishop.

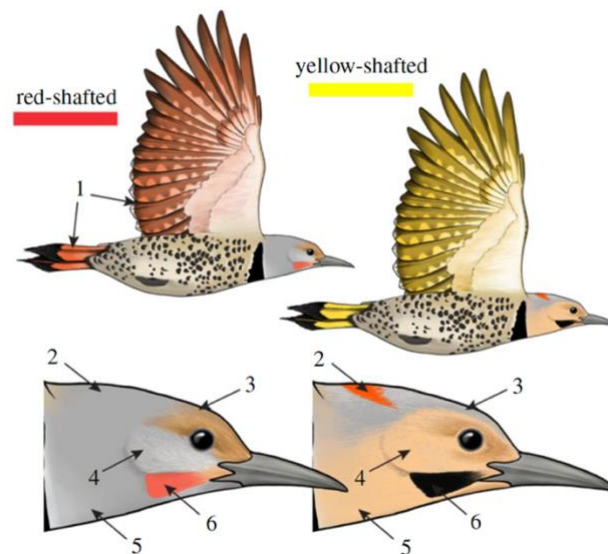


Figure 2: Illustration of color variation of red and yellow-shafted flickers: (1) wing and tail (shaft), (2) nuchal patch, (3) crown, (4) ear/cheek coverts, (5) throat and (6) malar stripe (male) (Aguillon et al., 2021). *Northern Flicker* illustrations by Megan Bishop.

Section 4. Budget

Item	Reason	Cost
Technology	XPS Desktop → <ul style="list-style-type: none"> – Processor: <i>12th Gen Intel® Core</i> – Memory: <i>32 GB</i> – Graphics Card: <i>NVIDIA® GeForce RTX, 3070, 8 GB, LHR</i> – Hard Drive: <i>1TB</i> 	\$2100 — \$2500
	Premium Support Plus → <ul style="list-style-type: none"> – <i>4 Years</i> 	\$539
	Dell Premier Multi-Device → <ul style="list-style-type: none"> – <i>Wireless Keyboard and Mouse</i> 	\$84
	Dell UltraSharp 27 Monitor → <ul style="list-style-type: none"> – <i>Dual monitors</i> 	\$410 x 2 = \$820
GIS Software	Arc Pro, GIS Professional Standard Package (2 years)	\$200 (\$100 yearly)
Office Supplies	Laminating sheets, gloves for handling specimens, Printer paper, and notebooks.	\$200
	TOTAL:	\$3,943 — \$4,343

Section 5, Qualification of Researchers

Kaily Taylor-Meek

4893 N. Raleigh St. | Denver, CO 80212 | 210.382.9655 | kmeek@regis.edu

EDUCATION

Regis University

April 2023

Master of Science, Environmental Biology

Metropolitan State University of Denver

May 2021

Bachelor of Arts, Biology, Cum Laude

Minor, Meteorology

SKILLS

Professional

- Participated in scientific conferences
- Handled hazardous waste and worked with contaminated testing instruments
- Entered and maintained all environmental data into laboratory notebooks
- Collaborated with research teams and resolved land management issues
- Researched and reviewed environment-based literature and publications
- NEPA and federal regulations, prepared and conducted EIS/EA assessments
- Data analysis and visualization in R
- Plant and Animal Identification
- Animal sampling (Seine Netting, Point Counts)
- Assessed and conducted wetland delineation
- Created impact remediation plans and mitigation activities
- Acquiring FAA drone license. (July 2023)

Software and Programming

- R within RStudio
- ArcPro
- HTML5 & CSS3
- Adobe Creative Suite (Illustrator, Photoshop, InDesign)
- Microsoft Office

RESEARCH EXPERIENCE

Graduate Researcher: Historical dynamics of the Northern Flicker

August 2021

(*Colaptes auratus*) hybrid zone in the Colorado Front Range

– May 2022

Denver Museum of Nature and Science, Regis University, Department of Biology

Graduate Researcher: Observations of Gambel Oaks' influence on plant communities and soil nutrients Client: Denver Mountain Parks and Highlands Ranch Community Association, Regis University, Department of Biology	August 2021 – May 2022
Graduate Researcher: The impact of social engagement on stereotypic behavior of captive bull Asian elephants (<i>Elephas maximus</i>) at night Client: Denver Zoo, Regis University, Department of Biology	August 2021 – December 2022
Graduate Researcher: What conditions promote winter feeding in large groups of Northern Shovelers in the Denver Metro Area? <ul style="list-style-type: none"> Lead in the conversion of a behavioral study to a conservation study. Mentored two undergraduate senior students on research development, field techniques and data management. Assisted in preparation for student presentation at MSU Denver Undergraduate Research Symposium 2022. 	June 2021 – June 2022
Undergraduate Researcher: Dynamics of Cooperative Feeding in Northern Shovelers Under the advisement of Christy Carello, Ph.D, Metropolitan State University of Denver	July 2020 – July 2021
Research Assistant: Convict Cichlids Under the advisement of Jennifer Gagliardi-Seeley, Ph.D, Metropolitan State University of Denver	January 2020 – May 2021

WORK EXPERIENCE

Intern—Zoology Collections Denver Museum of Nature and Science Denver, CO <ul style="list-style-type: none"> Using Arctos for data management Creating hybrid index scores for Northern Flickers Analyzing hybrid indices to determine temporal and spatial relationships to urbanization 	December 2022 – Current
Veterinary Technician Mead Veterinary Hospital Mead, CO <ul style="list-style-type: none"> General technician duties (surgery, radiology and laboratory) OSHA Safety Officer Handled, dispensed controlled substances and assisted in controlled substance inventory 	October 2017 – September 2018
Veterinary Technician Highlands Animal Clinic Denver, CO	June 2016 – December 2016

- General technician duties (surgery, radiology and laboratory)
- OSHA Safety Officer
- Handled, dispensed controlled substances

Veterinary Technician

March 2015 – June 2016

Valley Veterinary Clinic | Farmington, NM

- General technician duties including, not limited to: surgery, laser therapy treatment, assisting in acupuncture and ultrasound exams as well as front-desk duties
- Avian care and restraint
- AAHA point-of-contact 2016 inspection
- OSHA Safety Officer
- Ordering, maintenance and quality control of all in-house laboratory
- Accounts billing and receiving
- Handled, dispensed controlled substances

Veterinary Technician

October 2013 – March 2015

Aspen Tree Animal Caring Center | Durango, CO

- General technician duties (surgery, radiology and laboratory)
- Avian care and restraint
- Case Management: Invoicing and client communication (ClienTrax)
- Phone coverage and front office assistance
- Closing books, end-of-day shifts and deposits

PRESENTATIONS

City of Louisville Town Hall Meeting

April 2023

Coal Creek: Marshall Fire Effects on Biological Integrity

Disseminated by: Matthew Berta and Ceiteag Hennis

Louisville, CO

Metropolitan State University of Denver, Design for Life (CDES 390C)

February 2023

Professional Guest/Mentor

Denver, CO

Colorado Field Ornithologists Annual Convention

May 2022

What conditions promote winter feeding in large groups of Northern Shovelers in the Denver Metro Area?

Pueblo, CO

MSU Denver Undergraduate Research Symposium

April 2022

What conditions promote winter feeding in large groups of Northern Shovelers in the Denver Metro Area?

Disseminated by: Drew Bender and Laura Farnsworth,

MSU Denver Undergraduate Students
Denver, CO

Denver Mountain Parks and Highlands Ranch Community Association April 2022
Community effects of woody encroachment on mixed-grass prairies along the Front Range.
Douglas County, CO

Denver Mountain Parks & Highlands Ranch Community Association November 2021
Management Plan for mixed-grass prairies in for Daniels Park and Highlands Ranch Community Association.
Douglas County, CO

Metropolitan State University of Denver Animal Ecology (BIO 4550) October 2021
Professional Guest
Denver, CO

MSU Denver Undergraduate Research Symposium April 2021
Dynamics of Cooperative Feeding in Northern Shovelers
Denver, CO

TEACHING EXPERIENCE

Learning Assistant—Ornithology (BIO 4280), Spring 2021
Metropolitan State University of Denver

- Lead senior and junior student groups in research development
- Taught bird identification and field techniques
- Fostered group discussions on research readings
- Enhanced pedagogical skills in course development
- Implemented educational video projects for the Denver Audubon
- Prepared for this position by taking an education and pedagogical practices course

Teaching Assistant—Animal Behavior (BIO 3240), Spring 2020
Metropolitan State University of Denver

- Instruction in laboratories and management
- Coordination and maintenance of all lab and research equipment
- Advised junior and senior-level students on various research projects (building hypothesis, methods and supplies list)

GRANTS & HONORS

Metropolitan State University Biology Graduate Honoree May 2021
Selected by the Department Chair and the department faculty and staff

for exceptional academic achievements, leadership qualities and service contributions to MSU Denver and their communities.

Metropolitan State University Undergraduate Research Grant	January 2021
Birds of the World Digital Access Scholarship, Cornell Lab of Ornithology	August 2020 – August 2021
President Academic Achievement Scholarship, Metropolitan State University of Denver	August 2020 – August 2021
Provost Honor List, Metropolitan State University of Denver	August 2020 – August 2021

MEMBERSHIPS

American Ornithological Society	2021 – Current
Cornell Lab of Ornithology	2021 – Current
Denver Field Ornithologists	2020 – Current
Colorado Field Ornithologists	2020 – Current

VOLUNTEER

Iditarod: The Last Great Race | Anchorage, AK
Anchorage Checkpoint Veterinary Technician: 2015, 2016 & 2017 Races

La Plata County Humane Society | Durango, CO
Surgery Technician

Soul Dog Spay and Neuter Clinic | Four Corners Region
Surgery Technician

REFERENCES

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Regis University
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Professor,
Metropolitan State University of Denver
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Jennifer Gagliardi-Seeley, Ph.D
Professor,
Metropolitan State University of Denver
jgaglia1@msudenver.edu
303.548.4921

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chrysoptera) and Blue-winged (*V. pinus*) Warblers. *Conservation Genetics*, 6(5), 843–853.

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CHAPTER 3. JOURNAL MANUSCRIPT

Historical dynamics of the Northern Flicker (*Colaptes auratus*) hybrid zone in response to urbanization of the Colorado Front Range

Abstract

Hybrid zones play notable roles in ecological and evolutionary processes and can be impacted by environmental and anthropogenic factors. Increased anthropogenic disturbance is expected to spatially shift these zones and alter hybridization frequencies in many avian taxa, including the red- and yellow-shafted Northern Flickers. These taxa have low levels of genomic divergence and distinct plumage characteristics that vary between red-shafted, yellow-shafted, and hybrid individuals, allowing hybrids to be effectively scored genetically or morphologically. The Flicker hybrid zone has been extensively studied across the Great Plains from a historical and contemporary perspective, however, urbanization and human influences on Flicker hybridization are unknown. Our study evaluated how hybridization frequencies and dynamics of the flicker hybrid zone have changed in the last century along the Colorado Front Range. We quantified historical hybridization by scoring plumage characteristics using existing scoring methods from study skins and assessed this hybrid zone's spatial and temporal dynamics in conjunction with historical land-use data. Using ordination tools, Northern Flickers displayed a major gradient of plumage variation between pure red- and pure yellow-shafted individuals that correlated nearly perfectly with established hybrid index scores. Additionally, we observed nuanced sex biases in major plumage characteristics, where crown coloration covaried with differing plumage characteristics between sexes on the next greatest axis of variation. Hybridization frequency and plumage dynamics did not significantly change over time or in response to increased

urbanization in the Colorado Front Range. Our study demonstrates that anthropogenic habitat conversion has not notably altered the Northern Flicker hybrid zone since the late 1800s, emphasizing the long-term stability of hybridization in this region.

Introduction

Hybrid zones are geographical regions where hybridization occurs between two closely related lineages, taxa, or species (Todesco et al., 2016). Interest in and study of the hybridization of vertebrates are becoming more common in the fields of ecology, conservation, and evolutionary biology (Grabenstein et al., 2022; Maxwell et al., 2021; Taylor et al., 2014). Introgression in hybrid zones plays notable roles in many organisms, influencing ecological and evolutionary processes such as local adaption, speciation, and reproductive barriers (Allendorf et al., 2001; Maxwell et al., 2021; Short & Chapman, 1965; Wang et al., 2019). These processes and hybrid zones themselves can be influenced and reshaped by natural environmental changes (Allendorf et al., 2001; Buggs, 2007).

The impacts of these changes shaping hybrid zones are especially evident in birds. Avian behavioral mechanisms and climate fluctuations are environmental factors that are known to increase secondary contact (Aguillon & Rohwer, 2022; Buggs, 2007). Secondary contact facilitates evolutionary processes and is essential in the creation of hybrid zones associated with natural hybridization (Aguillon et al., 2018; Hruska & Manthey, 2021; Neri et al., 2018). In the Golden-winged (*Vermivora chrysoptera*) and Blue-winged Warbler (*V. cyanoptera*) hybrid zone, population sizes and duration of contact are driving population changes (Dabrowski et al., 2005). Golden-winged warblers are subject to increased introgression and hybridization when population sizes are lower (Allendorf et al., 2001; Dabrowski et al., 2005). Another example in warblers is within the Yellow-rumped Warbler (*Setophaga coronata*), which includes two

subspecies (Myrtle, *S. c. coronata*, and Audubon, *S. c. auduboni*) that differ in plumage and song. Where these two subspecies' ranges overlap in the northern Rockies, they are known to hybridize, leading to interbreeding in areas of secondary contact in the northern Rocky Mountains. This hybridization is likely shaped by ecological and behavioral factors like mate choice and territoriality (Brelsford, 2010; Toews et al., 2016). The Townsend's Warbler (*Setophaga townsendi*) and Hermit Warbler (*S. occidentalis*) are similar to the Yellow-rumped Warbler in that the two species overlap in the Washington Cascades and differ in physical appearance and behavior, leading to hybridization in areas of secondary contact in their respective ranges. Townsend's Warbler plumage phenotypes have moved moderately while Hermit Warbler phenotypes appear to be stable with the distribution of these phenotypes between closely related species (Wang et al., 2019). Widespread environmental changes such as climate change and sexual selection pressures are known to alter avian populations. Similarly, anthropogenic hybridization has unnaturally increased pressures through the translocation of plants and animals, fragmentation, and habitat modifications which have substantially threatened North American birds (Buggs, 2007; Grabenstein et al., 2022; Grand et al., 2019).

Increased anthropogenic disturbances and hybridization are expected to further drive hybrid frequencies and shift boundaries in response to range changes (Aguillon & Rohwer, 2022; Allendorf et al., 2001; Buggs, 2007; Grabenstein et al., 2022; Harr & Price, 2014). Hybridization in chickadees is directly related to human-induced landscape alterations (Grabenstein et al., 2022; Taylor et al., 2015). Black-capped (*Poecile atricapillus*) and Mountain (*Poecile gambeli*) Chickadees respond to landscape alterations by relocating to better resources (nesting, food, habitat), increasing competition, and interspecific interactions (Grabenstein et al., 2022; Grand et al., 2019; Taylor et al., 2015). Anthropogenic habitat conversion increases the frequency of

hybridization between these two species, and when Black-capped and Mountain Chickadees hybridize, their fitness decreases, which impacts their ability to breed (Grabenstein et al., 2022). This, bird populations may be negatively impacted through novel hybridization, especially in regions experiencing major anthropogenic habitat conversion, such as metropolitan growth (Aguillon & Rohwer, 2022; Buggs, 2007; Grabenstein et al., 2022).

Anthropogenic disturbances have also affected hybridization patterns in other bird species. For example, Mallards (*Anas platyrhynchos*), American Black Ducks (*Anas rubripes*), Mottled Ducks (*A. fulvigula*), and Mexican Ducks (*A. diazi*) hybridize in the Southern United States due to human alterations to their habitats, coastal marsh loss and increased hunting (Ford et al., 2017; Lavretsky et al., 2014; Peters et al., 2014). Similarly, in Europe, Chukars (*Alectoris chukar*) and Red-legged Partridges (*A. rufa*) engage in hybridization, which is believed to have been amplified by the release of farmed Chukars for hunting (Casas et al., 2012). These anthropogenic disturbances contribute to an elevated frequency of hybridization, potentially resulting in genetic swamping of parental species and a decline in genetic diversity within hybrid zones. Despite encountering reduced survival rates, hybrids exhibit the ability to sustain their current population by actively recruiting pure species, thereby leading to a noteworthy increase in hybridization frequency (Casas et al., 2012).

One region in particular that has undergone substantial environmental and anthropogenic changes in the last ~150 years is the Great Plains of North America. It is also home to several avian hybrid zones, including between the Lazuli and Indigo Buntings (*Passerina amoena* & *P. cyanea*), Bullock's and Baltimore Orioles (*Icterus bullockii* & *I. galbula*), Black-headed and Rose-breasted Grosbeaks (*Pheucticus melanocephalus* & *P. ludovicianus*) and the Spotted and Eastern Towhees (*Pipilo maculatus* & *P. erythrophthalmus*; Aguillon & Rohwer, 2022; Carling

& Zuckerberg, 2011; Mettler & Spellman, 2009; Short & Chapman, 1965; Walsh et al., 2020).

Within this region, the Colorado Front Range, the eastern mountain range of the Rockies spanning from Laramie, WY south to Pueblo, CO, has experienced relatively more significant amounts of change (Colorado: Department of Local Affairs, 2023; Cronin & Loevy, 2017).

The Front Range also includes the Northern Flicker (*Colaptes auratus*) hybrid zone, which has recently become the subject of extensive research. The Northern Flicker is a widespread North American woodpecker that includes two notable subspecies *auratus*, commonly called yellow-shafted, and *cafer*, red-shafted, with well-described plumage differences (Aguillon & Rohwer, 2022). Hybridization between these subspecies has been studied for decades, and previously was described to represent a stable hybrid zone in this region. These taxa have low genomic divergence, which facilitates the identification of distinct areas associated with plumage differences that vary between red-shafted, yellow-shafted, and hybrid individuals (Aguillon et al., 2021; Aguillon & Rohwer, 2022). Plumage characteristics include crown, nuchal patch presence, ear/cheek covert, throat, malar stripe, and wing/tail and are easily diagnosable in individuals without genomic sampling (Figure 1, Aguillon et al., 2018; Aguillon & Rohwer, 2022; Hudon et al., 2015). This contemporary hybrid zone has been studied continent-wide, but the study of the contact zone itself and its historical dynamics through time has not occurred (Moore & Buchanan, 1985; Short & Chapman, 1965).

This study represents the broadest temporal study of this hybrid zone and potential impacts of anthropogenic change on avian hybridization by evaluating how hybridization frequencies and dynamics have changed in the last 150 years along the Colorado Front Range between red-shafted and yellow-shafted Northern Flickers. Using study skins from natural history collections spanning over a century, we evaluated temporal changes of this hybrid zone based on plumage

characteristics. We also investigated impacts of urbanization on these frequencies and dynamics using a dataset of historical land cover for this region (Drummond et al., 2019). This hybrid zone has not been specifically studied in 40 years, a time frame in which we are already seeing striking shifts in avian populations and in which the Front Range region has profoundly urbanized (Moore & Buchanan, 1985). Given this increased urbanization, we expect that red- and yellow-shafted flickers are hybridizing more extensively in response to this habitat change and that plumage variation within hybrids has changed. Our study will revisit this hybrid zone over the last 150 years and specifically quantify the impacts of anthropogenic habitat conversion on altering natural hybrid zones.

Methods

Quantifying Hybridization at the Individual Level

We collected data from individual study skins in the Denver Museum of Nature and Science's (DMNS) ornithology collection. The DMNS collection includes specimens from the entire continental range of Northern Flickers, spanning a timespan between 1877 and 2023. We retrieved the locality and collection date for each study skin from the Arctos database, and we used a published standardized plumage scorecard to identify the extent of hybrid ancestry for each individual (Aguillon & Rohwer, 2022; Short & Chapman, 1965). There are six plumage characteristics in males and five in females that differ in color and shape: crown color, nuchal patch presence, ear/cheek covert color, throat color, malar stripe color (males), and wing/tail color (Figure 1; Aguillon & Rohwer, 2022; Flockhart & Wiebe, 2009; Short & Chapman, 1965). Each plumage characteristic was scored 0-4, with 0 considered pure yellow-shafted and 4 pure red-shafted. Individual plumage scores were converted into a single hybrid score per individual by summing the scores for each character and dividing male sums by 24 and female sums by 20

to account for plumage dimorphism (Aguillon & Rohwer, 2022; Short & Chapman, 1965). KTM scored each plumage characteristic on every specimen to remove inter-observer biases.

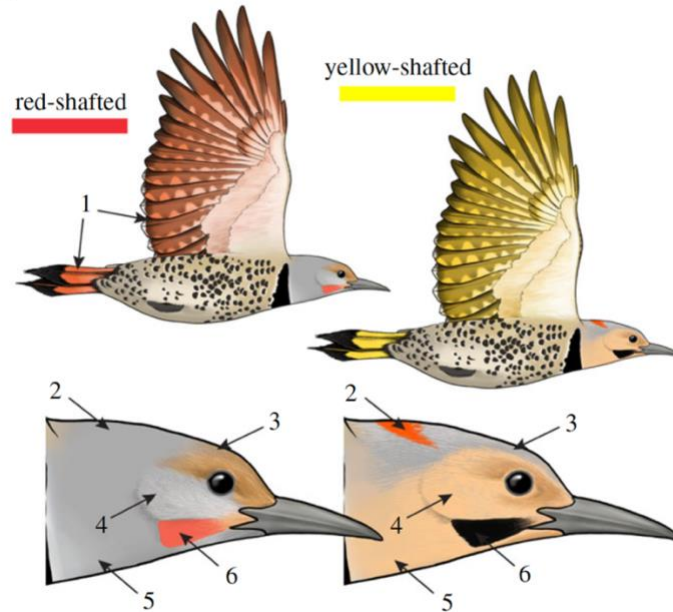


Figure 1: Illustration of color variation of red and yellow-shafted flickers: (1) wing and tail (shaft), (2) nuchal patch, (3) crown, (4) ear/cheek coverts, (5) throat and (6) malar stripe (male) (Aguillon et al., 2021). *Northern Flicker* illustrations by Megan Bishop.

Quantifying Urbanization

We used historical georeferenced land use and cover (LUCU) data to quantify the extent of urbanization through time along the Colorado Front Range. Drummond et al. (2019) described historical LUCU in the Colorado Front Range from 1937 to 1997 in two-decade increments, categorizing multiple land classes across the entirety of the region. We simplified these data to represent seven classes of land cover: urban, agriculture, natural resources, vegetation, bare, water, and no data. To spatially subset these data, we extracted data from the following counties in Colorado to define the extent of the Front Range region: Weld, Larimer, Boulder, Jefferson, Adams, Broomfield, Denver, Douglas, Arapahoe, El Paso, and Pueblo. We overlaid the coordinates of each study skin into twenty-year increments to extract dominant land use and percent of urban land cover for a 0.25 km buffer for each specimen, representing the typical

home range size for this species (Elchuk & Wiebe, 2003). Within each buffer, we recorded whether the dominant land cover was urban as a binary variable (urban = 1, other = 0), and we calculated the percent of urban land cover. Historical data prior to 1937 was not included and any individuals outside the boundaries of the Front Range and our land use data were excluded from downstream urbanization analyses.

Statistical Analyses

Ordination of Plumage Data

To ordinate the entirety of plumage variation of Northern Flickers, we performed a principal component analysis (PCA) on the plumage characteristics using the correlation matrix to establish gradients of plumage diversity in R (R Core Team, 2023). We removed immature individuals prior to these analyses, and we performed PCAs for each sex because adult males and females differed in the number of plumage characteristics (Aguillon & Rohwer, 2022). For each sex, we retained two axes for further analyses of plumage variation. Exploratory analyses on these principal components determined that PC1 scores for both sexes needed to be log-transformed for subsequent analyses to better meet the assumption of normality and we added a constant of the minimum PC1 score to each value to facilitate log-transforming negative numbers.

Analyses of Hybridization Through Time

We leveraged several analytical approaches to examine changes in the hybrid zone through time. Only flicker specimens collected from the Colorado Front Range were included in these analyses (and those with urbanization below). First, we converted the hybrid score from each individual to a binary variable to capture whether it showed hybrid ancestry (1) or not (0). We used the upper and lower 5% as cut-off values to indicate pure red (≥ 0.95), pure yellow (≤ 0.05), or hybrid

ancestry (> 0.05 and < 0.95 ; Wang et al., 2019). Hybrid individuals were scored as 1, and pure red or yellow individuals as 0. We assessed whether the frequency of hybridization changed through time by fitting a logistic regression with this binary variable as the response and year collected as the predictor. We tested whether this effect differed between the sexes by comparing this model to one with sex as a co-predictor and one with an additional interaction between sex and year collected, and the best model was chosen based on AIC values.

Analyses of Plumage Data Through Time

We assessed whether the PC scores of plumage variation changed through time using only flicker specimens collected from the Colorado Front Range. Using a linear regression, we fit our transformed PC1 plumage scores as the response and year collected as the predictor. We tested whether this effect differed between the sexes by comparing this model to one with sex as a co-predictor and one with an additional interaction between sex and year collected, and the best model was chosen based on AIC values. We also assessed PC2 plumage variable as the response and year collected as the predictor in two linear regressions separately for both sexes.

Analyses of Hybridization and Plumage Dynamics in Response to Urbanization

We similarly assessed the effects of urbanization on hybridization frequency and plumage variation and whether these effects differed between sexes. As described above, we fit a series of models with urbanization captured as a binary predictor (urban vs. other) and a continuous predictor (percent urban land cover). With these predictors, we fit the same suite of models to quantify the effects of urbanization and sex, with the binary hybrid ancestry variable in logistic regressions and PC scores in multiple linear regressions.

Results

Ordination of Plumage Characteristics

We calculated hybrid scores from 291 adult flicker specimens continent wide that were distributed throughout the last century, except for a notable gap throughout the 1950s and 1960s. We retained PC1 and PC2 from the ordinated plumage data for downstream analysis, and we found a consistent first major axis between the sexes with alternative nuanced plumage variation differing between the sexes on the second major axis. In both sexes, we found that the first two major axis explained the majority of variation, accounting for over half of all plumage variation. The first major axis of plumage variation (PC1) is loaded nearly identically between male and female flickers and explains comparable variance for each sex, 50.6% in males and 55% in females. All plumage characteristics were negatively loaded on PC1, indicating that it is essentially a red-to-yellow axis of variation with red-shafted birds on the negative end and yellow-shafted birds on the positive end. In fact, PC1 scores were essentially perfectly correlated to hybrid scores ($r = -0.99$), confirming that PC1 is a proxy for the published hybrid score card. The second major axis of plumage variation (PC2) captured nuanced differences of variation and covariation between male and female plumage traits, accounting for 15.1% of variation in males and 16.4% in females. The greatest difference between the male and female ordinations was in the loading of crown plumage. Males on the negative end of PC2 displayed a crown that is yellow-shafted but red-shafted wings and tails, and vice versa on the positive end of this axis. In contrast, females on the negative end of PC2 possess red-shafted crowns but yellow-shafted ear coverts and throat plumage, and vice versa on the positive end of this axis.

Hybridization Frequency through Time

All subsequent analyses were performed on a subset of specimens that explicitly occurred in the Colorado Front Range ($n = 201$). The best-fitting model for hybrid ancestry included sex as a interaction ($\Delta AIC > 2.1$), indicating that there was a difference in the frequency of hybrid ancestry between both sexes. The odds of a male displaying hybrid ancestry were 2.3 times greater than that of females (95% CI: 1.2 times – 4.4 times, $p = 0.013$). Despite there being differences in the number of hybrid males and females, there was a weak, non-significant effect of time. For each decade towards the present, the odds of an individual having hybrid ancestry increased by just 5.5% (Figure 2, 95% CI: 2.0% increase – 13.5% increase, $p = 0.153$).

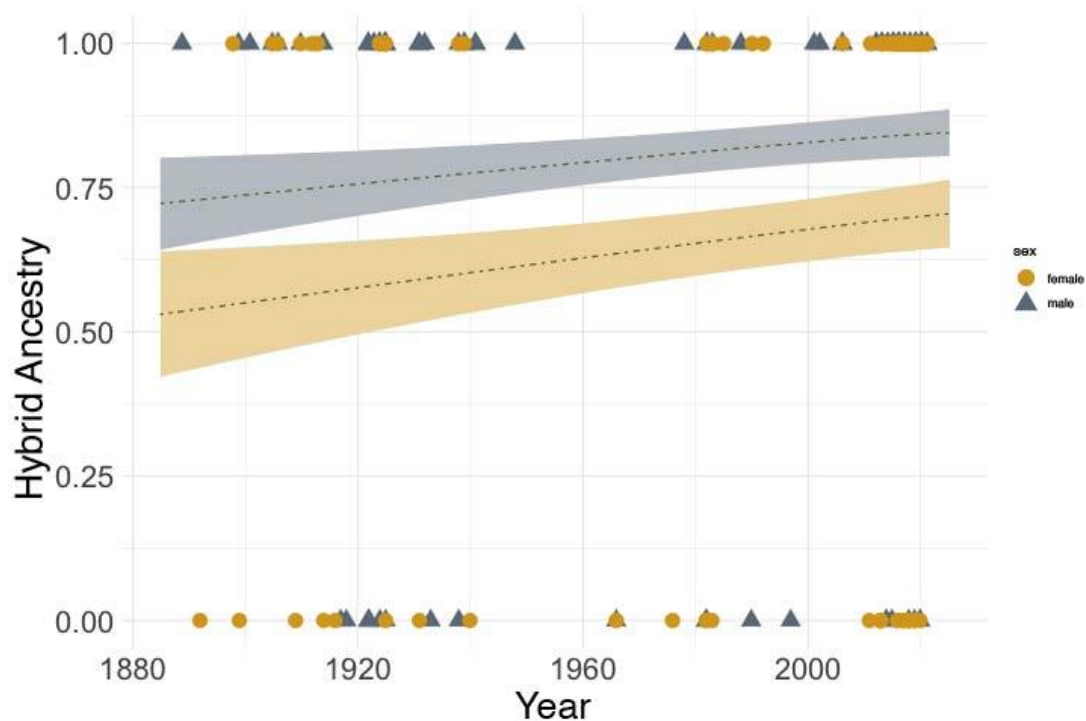


Figure 2. Hybridization frequency has not changed through time in the Northern Flicker hybrid zone. Points are color-coded and symbolized by triangles and circles to represent male and female specimens within the Front Range, respectively. The dashed line shows the best-fitting linear regression.

Plumage Dynamics through Time

Similar to hybrid frequency, we also observed no significant changes in plumage dynamics over time. Our best-fitting model for log-transformed PC1 scores included sex as a co-predictor

($\Delta AIC > 2.0$), indicating a sex-specific effect regarding red- or yellow-shafted plumage in the Front Range. This model showed that the plumage dynamics of flickers in this region have been relatively stable over the last 150 years. We found a weak non-significant trend of a 0.8% increase in median PC1 scores for each decade toward the present (Figure 3, 95% CI: 1.9% decrease – 3.4% increase, $p = 0.357$). Male median PC1 scores were 27.8 % greater than those of females, indicating that males showcased more hybrid plumage traits than females (Figure 3, 95% CI: 66.7% increase – 86.1% increase, $p = 0.040$). We found similar trends of stability for sex-specific PC2 scores. Males reported a weak non-significant trend of a 0.016 increase in mean PC2 scores for each decade toward the present (Figure 4, $p = 0.3$, 95% CI: 0.020 decrease – 0.053 increase) and females reported a weak non-significant trend of a 0.015 decrease in mean PC2 scores for each decade toward the present (Figure 5, $p = 0.547$, 95% CI: 0.064 decrease – 0.034 increase).

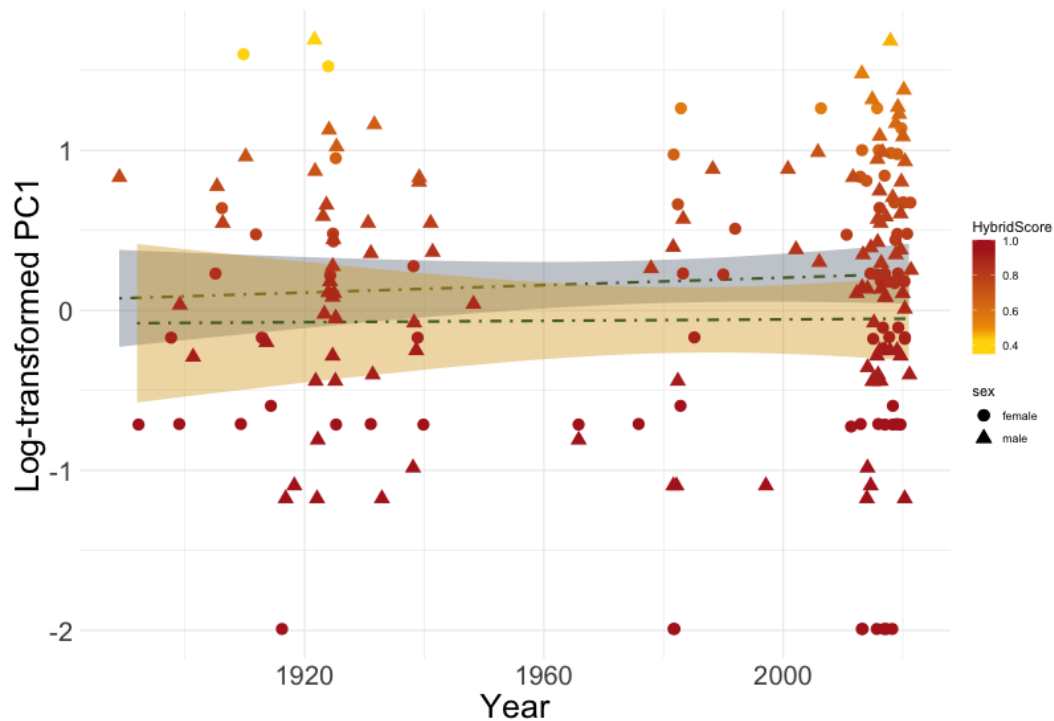


Figure 3. Plumage scores on PC1 were higher in males but did not significantly change over time. Triangles and circles represent male and female specimens, respectively. Points are color-coded according to individual hybrid

scores. The dashed line shows the best-fitting linear regression, with gray shading indicating the 95% confidence interval.

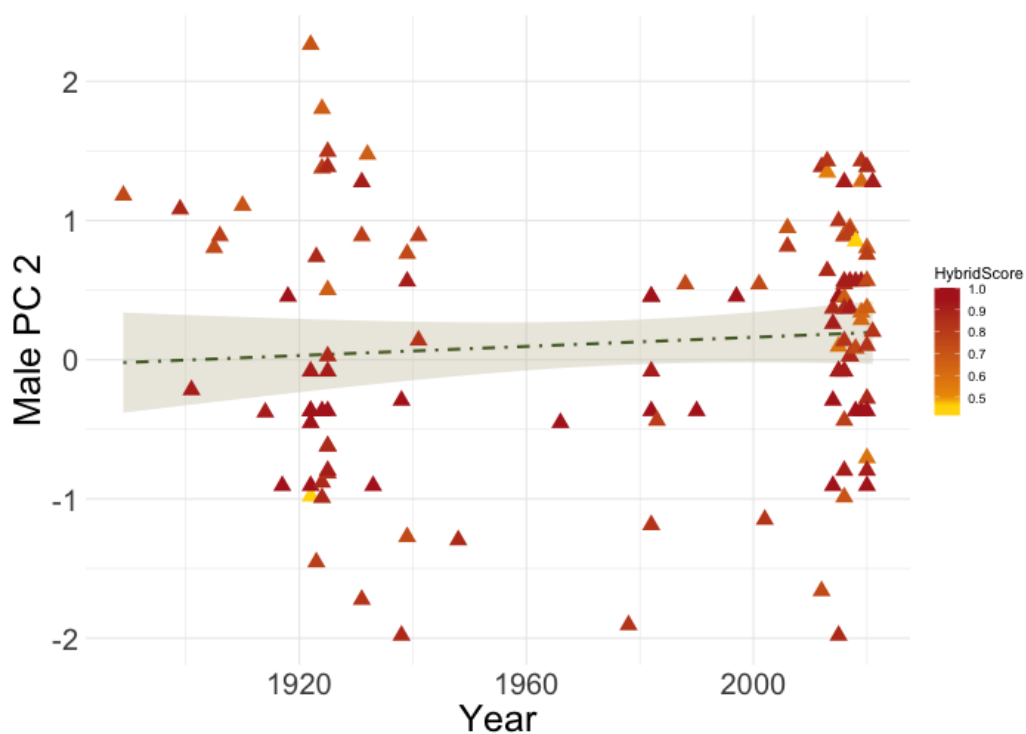


Figure 4. Plumage scores on male PC2 did not significantly change through time. Points are color-coded according to individual hybrid scores. The dashed line shows the best-fitting linear regression, with gray shading indicating the 95% confidence interval.

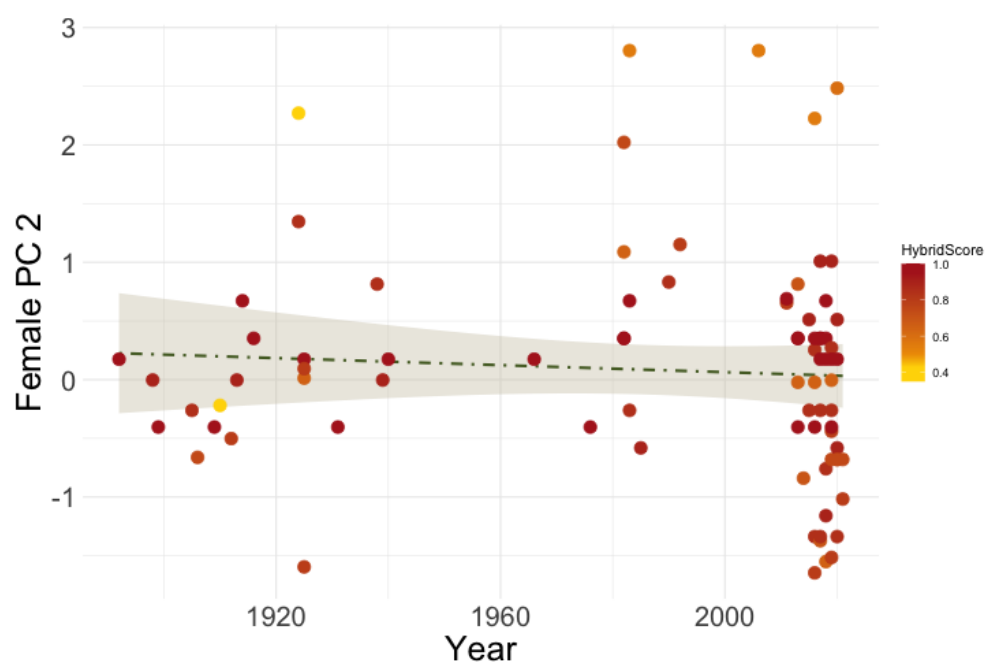


Figure 5. Plumage scores on female PC2 did not significantly change through time. Points are color-coded according to individual hybrid scores. The dashed line shows the best-fitting linear regression, with gray shading indicating the 95% confidence interval.

Hybridization Frequency in Response to Urbanization

All subsequent analyses were performed on a subset of specimens that explicitly occurred in the LUCU data ($n = 143$). We fit the same suite of models as above assessing the response of hybridization frequency to dominant land cover, but there were singularity issues due to there being no or very few non-hybrid females in urban areas, which distorted the model estimates. Therefore, we only considered models without the interaction and found the best-fitting model for hybrid ancestry included our binary urban variable and sex ($\Delta AIC > 1.4$), indicating that there was a difference in the frequency of hybrid ancestry between both sexes and between urban and non-urban areas. However, like all previous analyses, these differences were not significant. The odds of any individual displaying hybrid ancestry in an urban area were 2.6% greater than in non-urban areas (Figure 6, 95% CI: 85.5% decrease – 4.6-fold increase, $p = 0.976$). Despite there not being a strong effect of urbanization, we detect the same difference in the extent of hybrid ancestry between males and females in which males were more likely to possess hybrid plumages ($p = 0.065$). When we modeled urbanization as a continual effect of the percentage of land cover, our best model included the percent urban cover sex and their interaction. However, similar to previous analyses, we found no significant effects of urbanization and no notable impacts of sex for this model. As urban land cover increases by 1%, the odds of a male displaying hybrid ancestry increased by 2.3% (Figure 7, 95% CI: 0.4% decrease – 9.0-fold increase, $p = 0.070$). In contrast, the odds of a female displaying hybrid ancestry decreased by 1.8% (Figure 7, 95% CI: 7.6% decrease – 1.0-fold increase, $p = 0.367$).

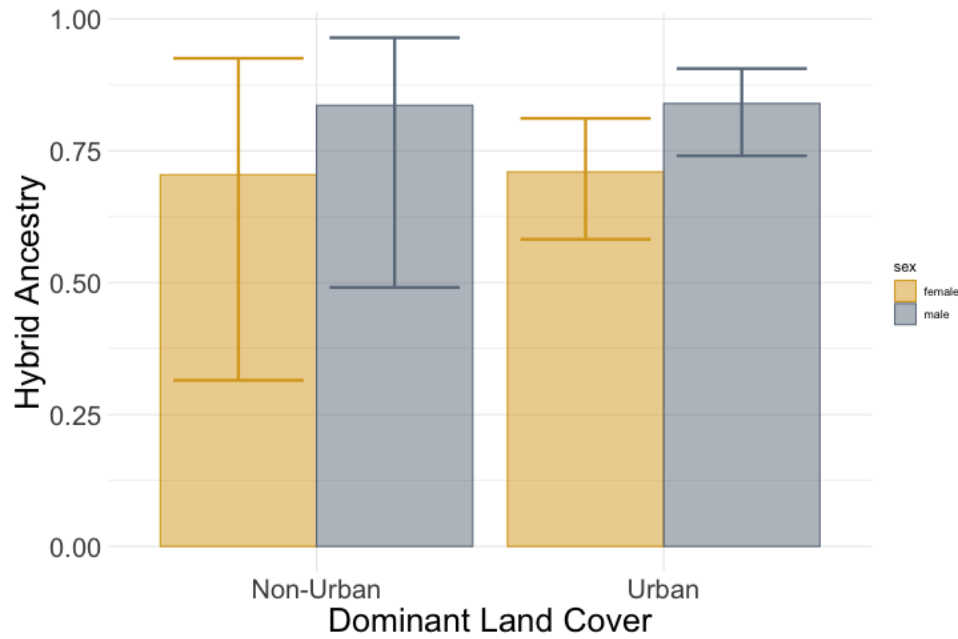


Figure 6. Hybrid ancestry difference is non-significant between both sexes and urban and non-urban areas. Bars are color-coded according to individual sex. Data points are hybrid ancestry of individuals for non-urban and urban areas, with 95% confidence intervals.

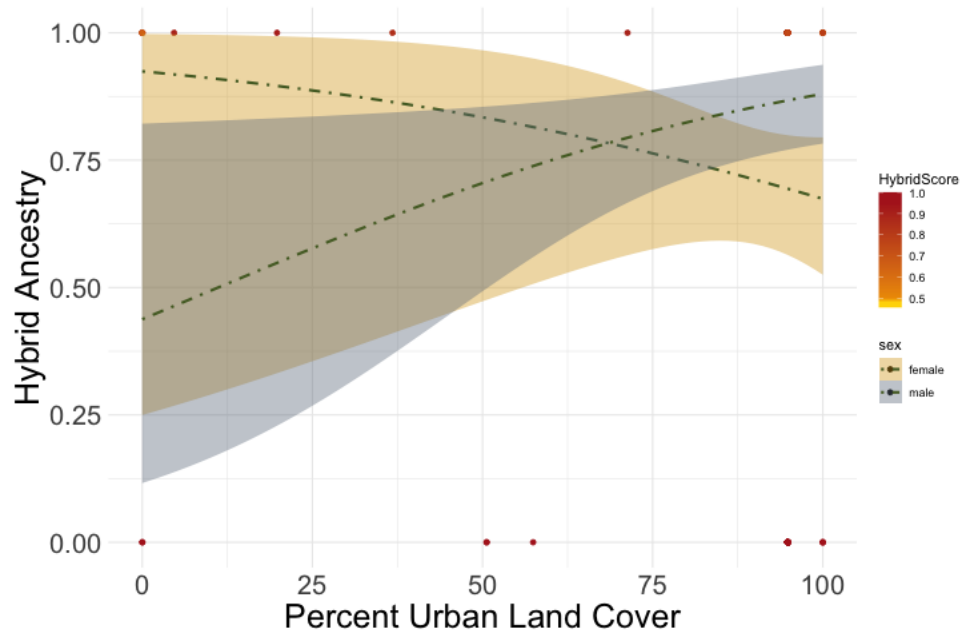


Figure 7. Hybrid ancestry increased in males and decreased in females in response to changes in urban land cover, albeit non-significantly. Points are color-coded according to individual hybrid scores. The dashed line shows the best-fitting linear regression, with gray shading indicating the 95% confidence interval for females and yellow shading indicating the 95% confidence interval for males. The seemingly small number of individuals is due to extensive overlap of points in the top and bottom right corners.

Plumage Dynamics in Response to Urbanization

The best-fitting model for log-transformed PC1 scores included percent urban land cover, sex, and their interaction ($\Delta AIC > 2.9$), indicating that there are sex-specific effects with regard to plumage dynamics and urban land cover in the Front Range. That said, PC1 scores were not significantly influenced by urban land cover in the Colorado Front Range. In males, median PC1 scores were significantly 34.2% higher in areas with dominant urban land cover than in other land covers (Figure 8, 95% CI: 83.7% decrease – 11-fold increase, $p = 0.039$). In female median PC1 scores were 37% less in areas with dominant urban land cover than in other land covers (Figure 8, 95% CI: 71.7% decrease – 40.2% increase, $p = 0.2557$). We found similar trends of urban land cover effects for sex-specific PC2 scores. Males reported a weak non-significant trend of 0.18 increase in mean PC2 scores are higher in areas with the dominant urban land cover than in other land covers (Figure 9, 95% CI: 0.513 decrease – 0.875 increase, $p = 0.605$), and females reported a weak non-significant trend of 0.70 increase in mean PC2 scores are lower in areas with the dominant urban land cover than in other land covers (Figure 10, 95% CI: 1.739 decrease – 0.346 increase, $p = 0.186$).

Similar to dominant urban land cover, we also found that plumage dynamics are not significantly influenced by the percent of urban land cover in the Colorado Front Range. Our best-fitting model for log-transformed PC1 scores included sex as an interaction ($\Delta AIC > 2.8$), indicating that there are sex-specific effects with regard to red- or yellow-shafted plumage and percent urban land cover in the Front Range. For each additional percent of urban land cover, male median PC1 scores significantly increased by 0.9% (Figure 11, 95% CI: 1.1% decrease – 3.0% increase, $p = 0.018$), whereas female median PC1 scores decreased by 0.3% with each additional percent of urban land cover (Figure 11, 95% CI: 1.3% decrease – 0.5% increase, $p = 0.3875$).

We found similar trends of urban effect for sex-specific PC2 scores. Males reported a weak non-significant trend of 0.003 increase in mean PC2 scores (Figure 12, 95% CI: 0.004 decrease – 0.010 increase, $p = 0.405$), and females reported a weak non-significant trend of 0.007 decrease in mean PC2 scores (Figure 13, 95% CI: 0.019 decrease – 0.004 increase, $p = 0.208$).

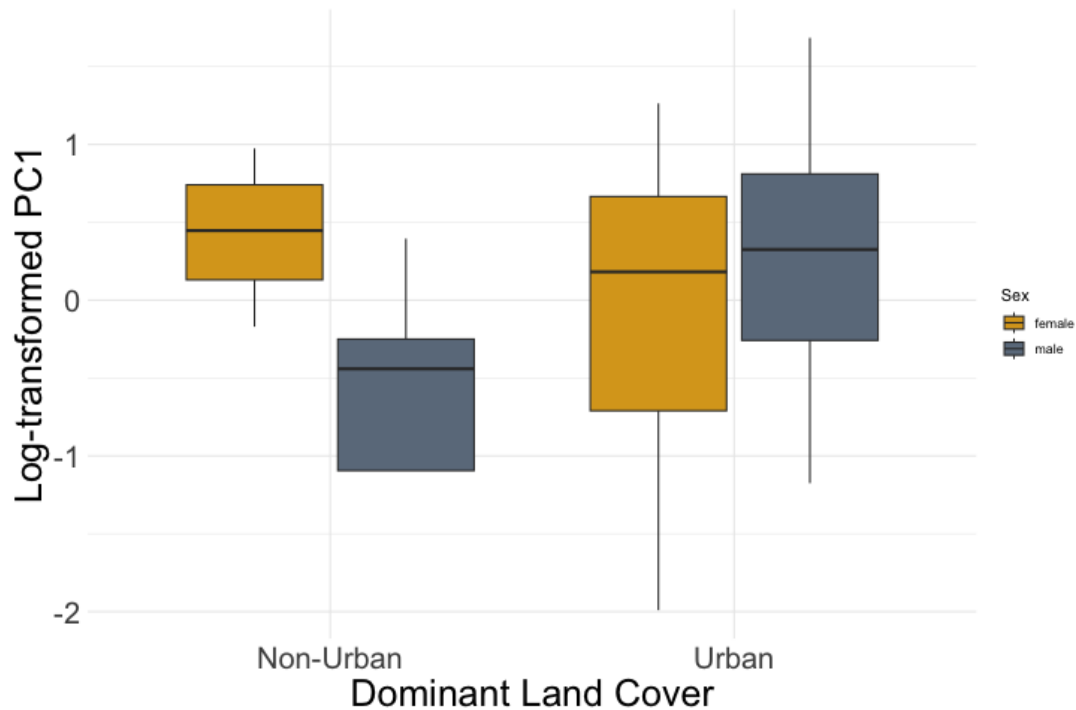


Figure 8. Dominant urban land cover on PC1 did not significantly change. Black bars represent the median amounts PC1 scores, whiskers indicate 1.5 interquartile above and below the median. Points show outliers from each set of data.

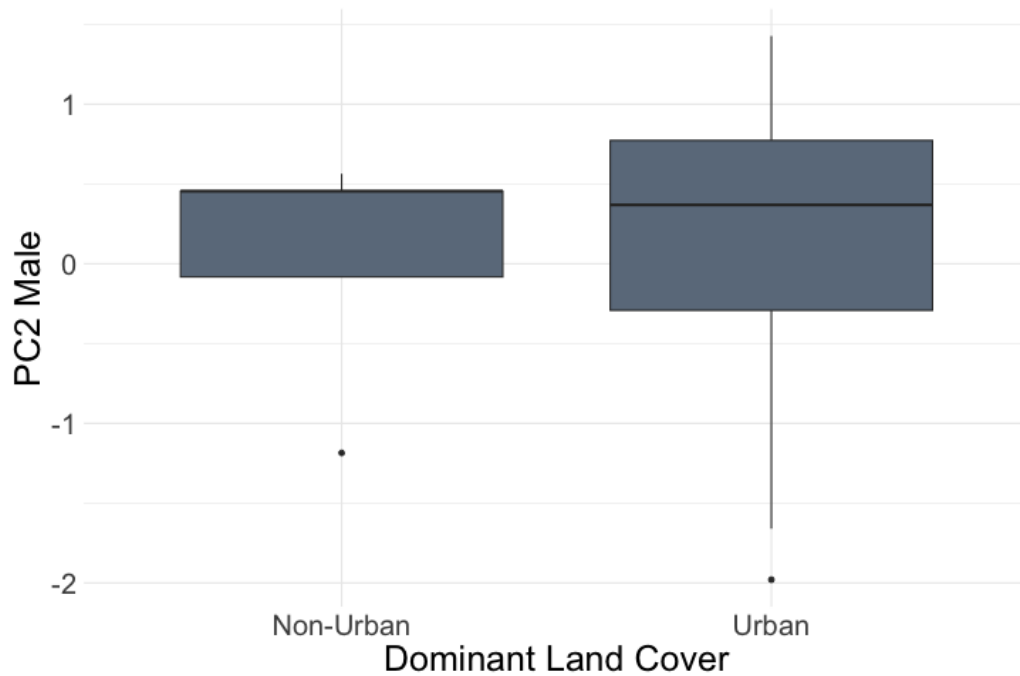


Figure 9. Dominant urban land cover on male PC2 did not significantly change. Black bars represent the median amounts PC1 scores, whiskers indicate 1.5 interquartile above and below the median. Points show outliers from each set of data.

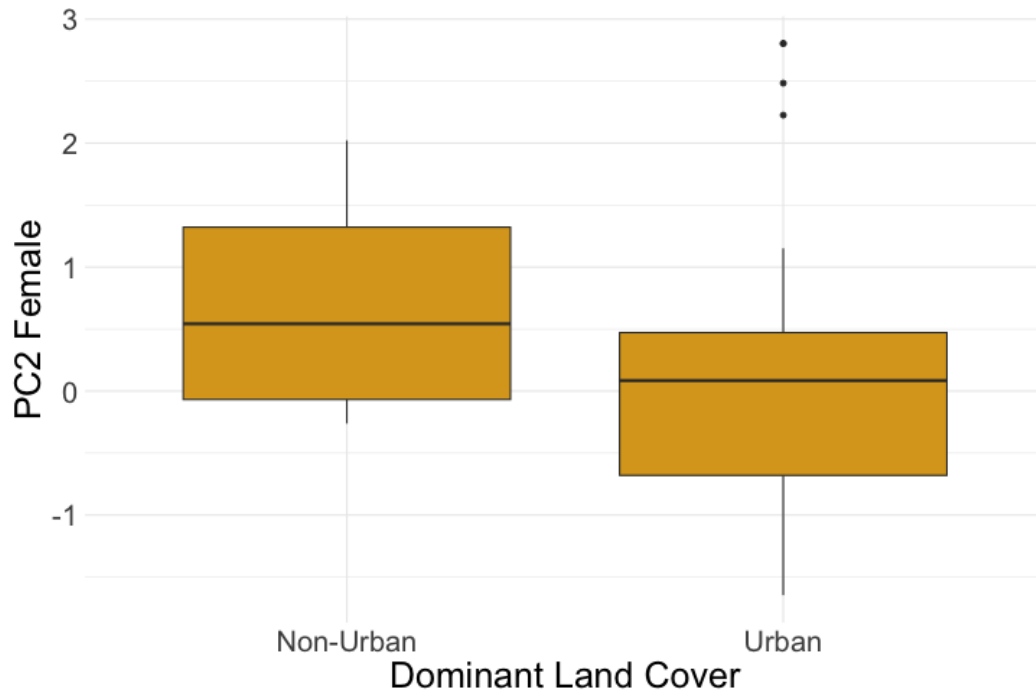


Figure 10. Dominant urban land cover on female PC2 did not significantly change. Black bars represent the median amounts PC1 scores, whiskers indicate 1.5 interquartile above and below the median. Points show outliers from each set of data.

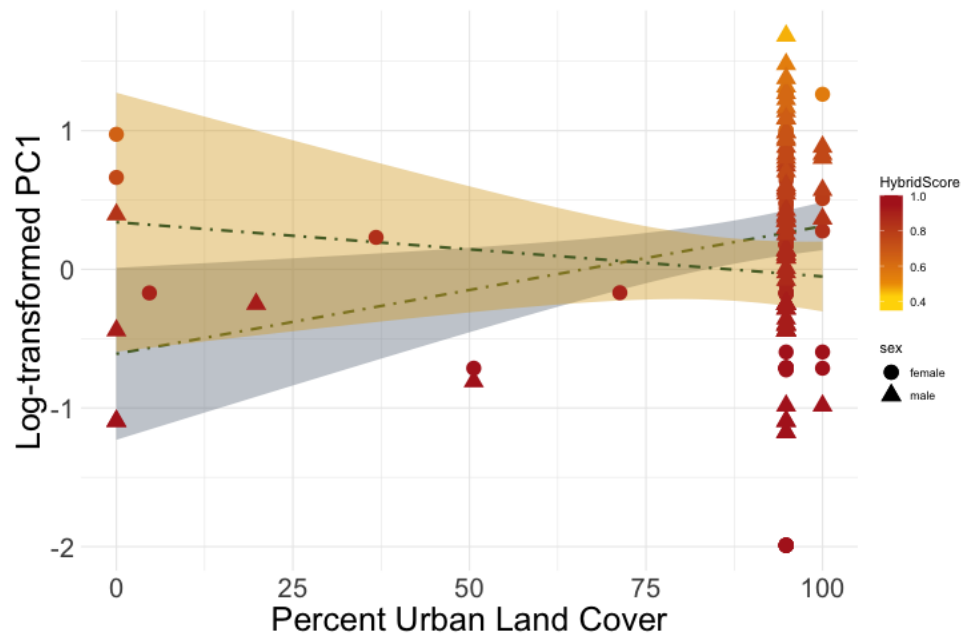


Figure 11. Plumage scores on PC1 did not significantly change with the percent urban land cover. Triangles and circles represent male and female specimens, respectively. Points are color-coded according to individual hybrid scores. The dashed line shows the best-fitting linear regression, with gray shading indicating the 95% confidence interval.

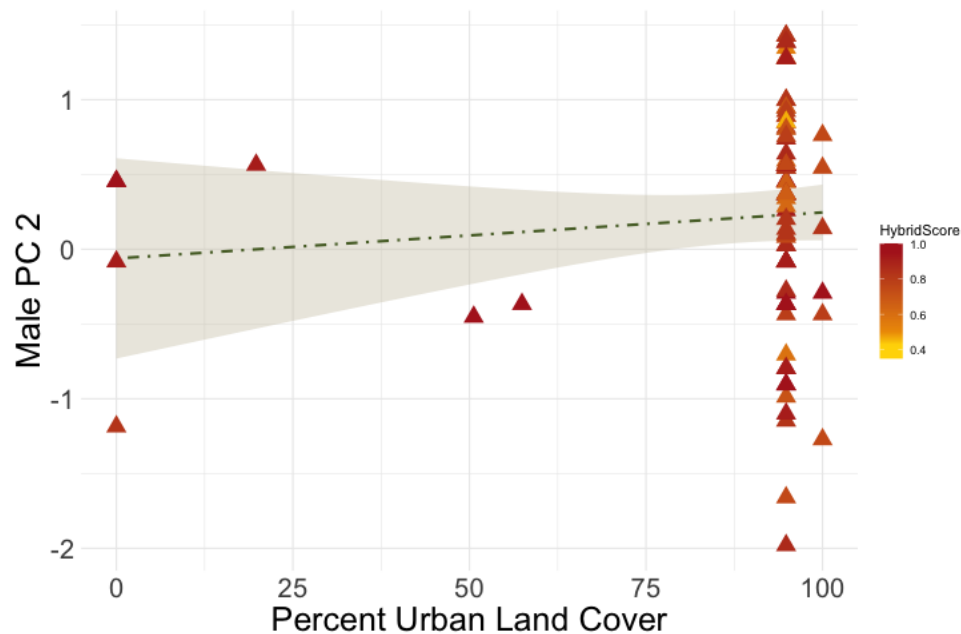


Figure 12. Plumage scores on male PC2 did not significantly change with the percent urban land cover. Points are color-coded according to individual hybrid scores. The dashed line shows the best-fitting linear regression, with gray shading indicating the 95% confidence interval.

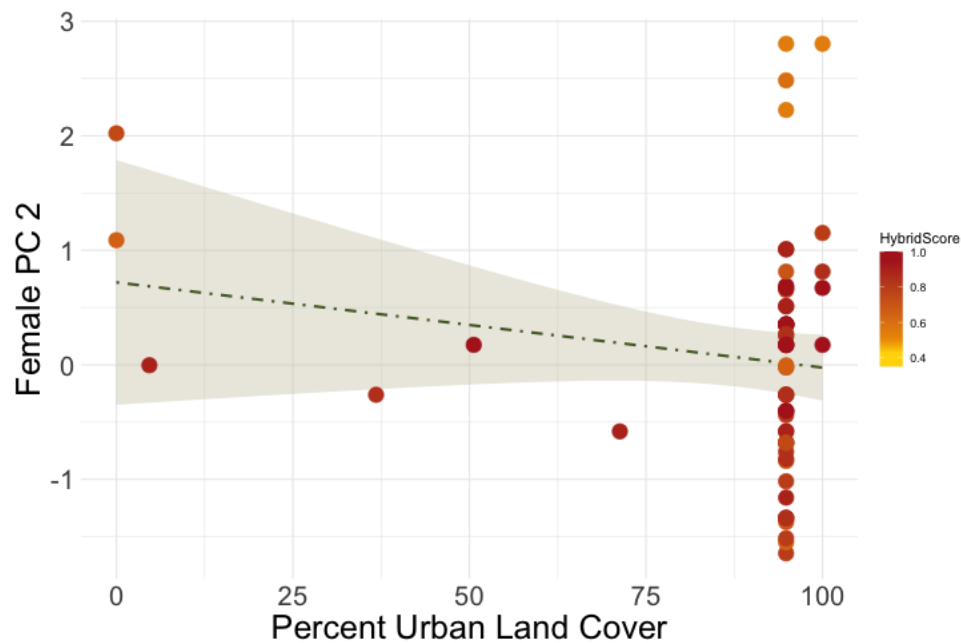


Figure 13. Plumage scores on female PC2 did not significantly change with the percent urban land cover. Points are color-coded according to individual hybrid scores. The dashed line shows the best-fitting linear regression, with gray shading indicating the 95% confidence interval.

Discussion

The goal of this study was to evaluate the hybridization dynamics of red and yellow-shafted Northern Flickers in response to urbanization over the last 150 years in the Colorado Front Range. We hypothesized that we would see an increase in hybridization and more individuals with hybrid ancestry toward the present in response to increasing urbanization of the Colorado Front Range. In contrast to these expectations, we found that plumage variation and hybridization frequency did not change significantly through time nor in response to urbanization. The Northern Flicker hybrid zone in the Colorado Front Range thus appears stable in response to profound anthropogenic change.

Ordination of Plumage Characteristics

The results of the principal component analysis (PCA) showed that there was notable variation in plumage dynamics between sexes among the first two major axes. The first major gradient of red-to-yellow plumage variation was consistent between sexes, but the second major axis of variation indicated differing covariation of crown plumage between the sexes. Males exhibit a yellow-shafted crown and red-shafted wings and tails, while females exhibit a yellow-shafted ear coverts and throat plumage with red-shafted crowns. The sex variation observed in crown plumage was found to be more prominent in hybrid males than females, and the origin of this plumage gradient are unknown. Aguillon et al. (2021) found that melanin and carotenoids were explicitly associated with malar stripes that were linked to the avian Z chromosome. While sexual dimorphism is documented in the malar stripe, at least three of our older female specimens showed increased melanin in this region. The effects of melanin were observed in the crown, ear coverts, and throat regions, while carotenoids influenced the wing and tail, and nuchal patch (Aguillon et al., 2021; Roulin & Jensen, 2015). This may explain the relationship in females between ear coverts, throat, and crown plumage traits, as they are solely impacted by melanin. Another possibility that could explain the observed difference is the known phenomenon where males tend to be more represented in natural history collections (Cooper et al., 2019), and this was the case in our sampling of the DMNS collection that included 173 male and 118 female Northern Flickers. Therefore, scientists using natural collections should attempt to resolve this bias when analyzing data and sampling sexes equally. Further exploration is warranted to better understand the potential role of this bias in the observed plumage variations. Moreover, hybridization can result in biased sex ratios influenced by fitness differences and genetic interactions, aligning with Haldane's rule (Schilthuizen et al., 2011). Haldane's rule is an

important principle that heterogametic offspring are more likely to experience reduced fitness or sterility in hybridization than homogametic offspring (Cowell, 2023; Maxwell et al., 2021; Schilthuizen et al., 2011). In the case of hybridizing Pied (*Ficedula albicollis*) and Collared (*F. hypoleuca*) Flycatchers, sex ratios have been observed to vary, potentially due to differences in hybrid fitness and genetic backgrounds (Nadachowska-Brzyska et al., 2013; Segami et al., 2022). Studies have shown infertile female offspring and male-biased sex ratio skews in females' nests mated to heterospecifics, suggesting reduced reproductive success for hybrid males (Neville et al., 2008; Segami et al., 2022). However, a hybridized population of Blue-winged (*Vermivora pinus*) and Golden-winged (*V. chrysoptera*) Warblers did not exhibit the same sex ratio pattern (Neville et al., 2008). Further investigations are needed to fully understand the underlying mechanisms of sex ratios in these avian species and the potential implications of Haldane's rule in hybridization between red-shafted and yellow-shafted flickers.

Hybridization and Anthropogenic Effects

Most notably, our analyses did not detect any significant changes in hybrid frequency or plumage dynamics within the Northern Flicker hybrid zone over the last 150 years. This finding is consistent with previous research in the Front Range area, which has found geographic stability in hybrid zones over time (Moore & Buchanan, 1985; Short & Chapman, 1965). Even though this area is rapidly urbanizing and experiencing significant habitat conversion, we may be observing stability in the hybrid zone because the Rocky Mountains is a physical barrier preventing further westward movement by yellow-shafted flickers. Or, this stability may be attributed to Northern Flickers' adaptability, as they are a primary cavity nester that is most abundant in high levels of urbanization (Tomasevic & Marzluff, 2017). Urbanization tends to favor omnivorous, granivorous, and cavity-nesting species like Northern Flickers, providing

ample opportunities to thrive in altered habitats (Chace & Walsh, 2006). This adaptability could be linked to their feeding strategies, as they forage on the ground in open areas commonly found in urban environments such as landscaping and parks. Furthermore, the Front Range area may also employ different conservation and management strategies contributing to the observed stability. Flickers rely on wood for cavities, which they can find in riparian and wooded areas or obtain through alternative sources such as telephone poles, building eaves, and existing cavities, regardless of the material (wood or otherwise). These factors likely contribute to the ongoing stability in the hybrid zone and the successful adaptation of Northern Flickers to urbanized environments.

Northern Flickers' lack of response to urbanization remains a puzzling question, as consistently negative results have been produced by this study. One possible explanation for the lack of change in plumage dynamics could be the stability of the Northern Flicker subspecies, consistent with previous studies suggesting a stable state for flickers (Moore & Buchanan, 1985; Short & Chapman, 1965). In contrast, chickadee species that also hybridized experienced unstable hybrid zones in response to urbanization, with studies revealing significant changes in plumage coloration and patterns (Grabenstein et al., 2022; McQuillan et al., 2017). While Black-capped and Mountain Chickadees, which are separate species with significant divergence (Aguillon et al., 2018; Grabenstein et al., 2022), experience fitness consequences due to hybridization, red and yellow-shafted flickers, as subspecies with low divergence, may not face the same challenges. In contrast, the stability of this hybrid zone through time appears more consistent with those of distinct species, as in the Black-throated Magpie-Jay (*Calocitta colliei*) and White-throated Magpie-Jay (*C. formosa*; Pizarro et al., 2023; Sánchez-González et al. 2021) and in *Pipilo* towhees (DeRaad et al., 2023). This variation in hybridization patterns is likely associated

with the extent of genomic divergence, stemming from the time since the divergence of the taxa in question (Pizarro et al., 2023; Sánchez-González et al., 2021).

Conclusion

Our study showed that Northern Flickers are in a stable hybrid zone over the last 150 years along the Colorado Front Range. Our results highlight the importance of natural history collections, which can inform us about the recent past and future of biodiversity (Cooper et al., 2019). As well as the importance of tracking hybrid zones because they can have conservation implications such as fitness consequences. Hybridization in certain groups raises conservation concerns, as evidenced by studies involving chickadees and *Vermivora* warblers. In the latter case, there is even a possibility of the Golden-winged Warbler's lineage assimilating into the Blue-winged Warbler (Dabrowski et al., 2005). However, in the case of the Northern Flicker, which exhibits stability within their hybrid zones, conservation and fitness consequences don't appear to be concerns. Despite what has been documented in other hybrid zones, flickers appear to be faring well in the face of habitat conversion and anthropogenic development. Low divergence between flicker subspecies could contribute to the lack of change in hybridization and plumage dynamics. This highlights the importance of understanding that hybridization may not necessarily be detrimental, particularly in cases where the species involved are not significantly divergent. Instead, it may simply be a natural occurrence, especially for birds like the Northern Flicker that do not represent distinct species. To bolster these findings, additional work could focus on quantifying the fitness of breeding individuals within this region, quantifying plumage traits through spectrophotometry, and more extensively sample historical specimens from this region. This would provide further insights into the overall health and adaptability of the flicker population and the robustness of using plumage as a proxy for hybrid ancestry. Furthermore, our

study underscores the notion that some natural hybrid zones have the capacity to withstand significant anthropogenic changes. It emphasizes that the response to such changes depends on the biological characteristics of the organisms themselves. Suggesting that these zones can be resilient to profound environmental changes (Moore & Buchanan, 1985; Short & Chapman, 1965).

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CHAPTER 4

Resolving the dichotomy of generational land use and modern inventions: Drilling in the Arctic National Wildlife Refuge

Introduction

The Arctic National Wildlife Refuge (ANWR) in northeastern Alaska covers roughly 19.5 million acres of wilderness that protects several unique ecosystems, such as forest and coastal plain tundra, freshwater wetlands, coastal marshes, boreal forests, barrier islands, and lagoons (Alaska State Office of the Audubon Society, 2020). Within the refuge, this critical habitat supports many notable plant and animal species, including polar bears, the Porcupine caribou herd, and over 200 species of migratory birds, such as eiders and ducks (Alaska, 2015; Bureau of Land Management, 2020). Most of the refuge is remote and undeveloped except for Indigenous people who still inhabit this region honoring their customs and traditions. The Coastal Plain 1002 Area has recently been opened for leases to drill for oil and gas. Proponents opposed to this drilling argue that this will impact the wildlife and culture of Indigenous groups. The Indigenous Gwich'in and Iñupiat Nations residing in these areas are impacted most by gas and oil development in their homelands. In order to protect cultural and natural resources, I argue that a tribal alliance that includes both Indigenous groups needs to work together to present a comprehensive plan that aims to benefit all parties and oversees development. If the path forward does include drilling, then increased protection of wildlife and mitigation of disturbances must employ best professional judgment to reduce impacts of drilling operations on sensitive species in the Coastal Plain 1002 Area. Ideally, the Bureau of Land Management (BLM) should relocate drilling away from the 1002 Area, but if that is impossible, a plan that specifically protects

critical habitat by allowing drilling only in the most disturbed areas will protect the area's biodiversity from degradation and support the financial benefits of increased oil exploration. Lastly, with increased revenue, funding should offset impacts in the way of education stipends to promote Indigenous peoples' involvement in maintaining land through research and legislation.

Background

Alaska remains an underexplored energy frontier, and the Alaskan economy relies heavily on the oil industry, which is its largest revenue generator (State of Alaska, 2022). Since 1980 when the U.S. Congress enacted the Alaska National Interest Lands Conservation Act (ANILCA), for the purposes of energy resource development, the future of ANWR has been the center of intense energy debate (Griffith et al., 2002). Opponents of oil extraction from ANWR advocate for untouched wilderness because they believe it is crucial to preserve the area's natural beauty and its wildlife, which are essential to maintaining the region's ecological integrity. This directly conflicts with the values of parties favoring oil and gas development underneath the refuge (Dister, 2022).

ANWR drilling is potentially one of Alaska's most significant revenue sources because the area is estimated to have approximately 10.4 billion barrels of oil (Attanasi, 2005; U.S. EIA, 2017). In 2017, Congress lifted the Alaska National Interest Lands Conservation Act (ANILCA) prohibition on oil and gas leasing and development in ANWR. The lifting of the ANILCA prohibition by Congress in 2017 was a controversial and partisan decision challenged by environmental and Indigenous groups in court (Dister, 2022). Under the direction of Congress, the United States Bureau of Land Management (BLM) created the Coastal Plain Oil and Gas Leasing Program, which proposed to sell two tracts of land (each at least 400,000 acres, Figure 1) in the 1002 Area located in the northwest area of ANWR's Coastal Plain region (Bureau of

Land Management, 2020). The first sale would occur by the end of 2021, and the second would conclude before December 2024.

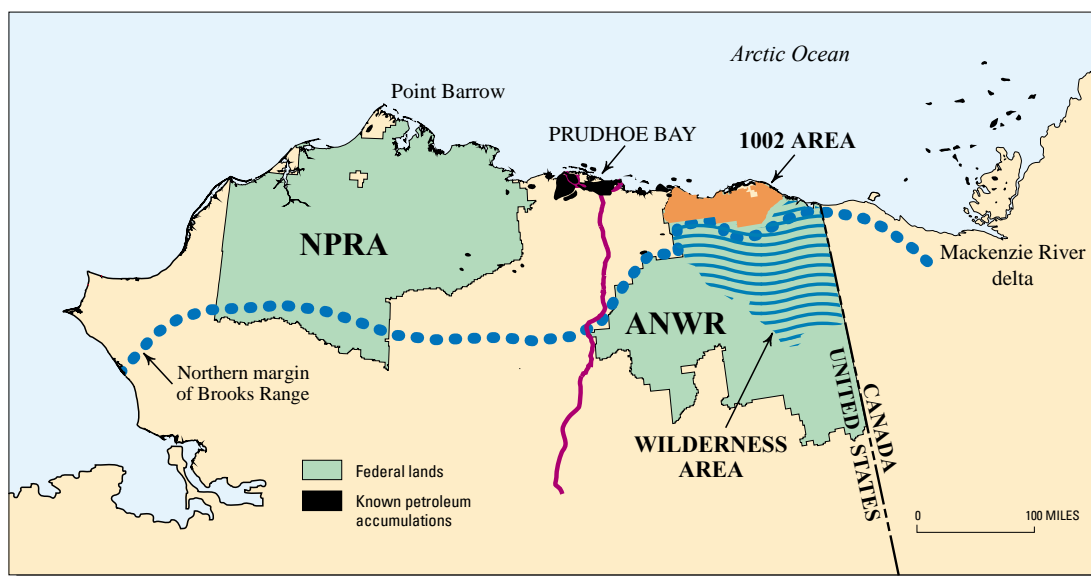


Figure 1. Map of northern Alaska showing locations of the Arctic National Wildlife Refuge (ANWR), the 1002 area, and the National Petroleum Reserve—Alaska (NPRA) (Alaska Region of the U.S. Fish and Wildlife Service, 2015).

In January 2021, policymakers auctioned the first lease in ANWR's coastal and central regions, both of which hold vast oil reserves. Conflict on this decision was almost immediate since the refuge is one of the last places in the United States free from development. It is a vital haven for wildlife and Indigenous peoples who depend on it for their way of life. The oil and gas operations proposed in these areas would be overseen by generally permissive provisions under the Naval Petroleum Reserves Production Act (NPRA) of 1976 (Bureau of Land Management, 2020; Dister, 2022). However, this act does not offer the in-depth review that the National Environmental Policy Act (NEPA) process would traditionally apply. The NPRA provides specific guidance and authority for managing the Naval Petroleum Reserve lands, including environmental review and public involvement provisions (NPRA, 1976). NEPA is a broader law that applies to all federal agencies and requires them to consider the environmental impacts of

their proposed actions, including those that may affect federal lands, and to involve the public in the decision-making process. The lack of these provisions triggered an onslaught of lawsuits just as presidential leadership changed, further complicating the fate of these leases. Furthermore, environmental groups questioned the validity and accuracy of the Environmental Impact Statement (EIS) used to assess the impacts of drilling (Bureau of Land Management, 2020). In the summer of 2021, the new Biden presidential administration evaluated BLM actions and ultimately determined that legal deficiencies existed in the EIS. This decision was based on concerns about the scientific integrity and adequacy of the previous EIS, which was completed during the Trump administration and was criticized for downplaying or ignoring the potential impacts of oil and gas development on climate change, wildlife, and Indigenous rights (Alaska State Office of the Audubon Society, 2020; Dister, 2022). Ultimately these shortcomings halted the Coastal Plain Oil and Gas Leasing Program until a comprehensive analysis of environmental impacts under NEPA was completed (Order No. 3401, 2021). In the interim, the Knik Arm Service, the only oil company to participate in the lease, requested that BLM rescind its lease. However, canceling leases in ANWR has not changed significant public interest. Recent polls of Alaskan citizens show that only 30% support oil and gas development in the refuge, with the remainder advocating for its protection (Marlon et al., 2022). Given the stark conflict about how to manage ANWR's significant oil reserves and natural resources, ANWR's future depends on the ability of stakeholders to work together within the legislative process.

However, the dichotomy between wild places and development does not have to be hard-edged when determining how to manage the ANWR. Legislation being considered by Congress has the dubious task of partitioning resources driven by divergent stakeholder values. Such legislation must balance job creation, preserve traditional Indigenous lands, protect wildlife, and preserve

Alaska's beauty and resources. Solutions will require creativity, sacrifice, and cooperation among all stakeholders.

Stakeholders of the Arctic National Wildlife Refuge

Oil and Gas Industry

Oil and gas companies invested in ANWR advocate for energy jobs and opportunities to subsidize America's dependency on foreign oil reserves. For example, the Alaska Industrial Development and Export Authority, Alaska's Department of Natural Resources, and Power the Future are focused on becoming reliant on local rather than foreign natural resources. Proponents of crude oil extraction from under the 1002 Area have suggested that the industry could create a significant number of jobs, potentially at least 4,000 (Attanasi, 2005; Dister, 2022; Green, 2021). The American Petroleum Institute (API), the largest national trade association representing the oil and natural gas industry in the United States, has been a vocal proponent of drilling in the ANWR. API has argued that the opening of the 1002 Area in the ANWR to oil and gas exploration and development would provide a significant boost to domestic energy production, create jobs and economic growth, and generate revenue for the federal government and the State of Alaska (Green, 2021; State of Alaska, 2022).

Federal Land Management

The development of oil and gas resources in the Arctic National Wildlife Refuge (ANWR) is a complex issue that involves balancing economic interests with environmental concerns. Several federal agencies, including the BLM, U.S. Fish and Wildlife Services (USFWS), National Park Service (NPS), and Environmental Protection Agency (EPA), are involved in managing the ANWR and have varying values and positions on drilling.

The BLM has attempted to balance the health, diversity, and productivity of the ANWR with the implementation of a Coastal Plain oil and gas program (Bureau of Land Management, 2020).

The Department of the Interior directed the BLM to protect surface resources and find alternatives to energy development that did not inflict significant environmental impacts. In addition to the economic benefits of oil and gas development, the BLM also explored impacts on endangered species and greenhouse gas emissions. Because preliminary results found many impacts on the landscape and wildlife under all action alternatives explored by the BLM (BLM, 2021), a supplemental EIS was ordered to investigate best professional practices to reduce environmental disruption (Dister, 2022).

The USFWS and the NPS support the decision for a supplemental EIS regarding the potential impacts of oil and gas development on the ANWR's fragile ecosystems and wildlife (Associated Press, 2017; Bureau of Land Management, 2021; Dister, 2022). These agencies have pointed out that the ANWR is one of the last remaining intact ecosystems in the United States and is home to numerous species that are critical to the region's ecology and cultural heritage (Bureau of Land Management, 2020). The EPA has also expressed concern about air and water pollution and its effects on local communities (Alaska, 2015; Bureau of Land Management, 2020; Gwich'in Steering Committee, 2023).

As the situation stands, the BLM aims to work with Indigenous communities and environmental groups to craft a maintenance and mitigation plan to sustainably develop the ANWR for oil and gas (Dister, 2022). This plan is designed to extend the protection of wild places beyond the BLM's current policies (Bureau of Land Management, 2020). The maintenance and mitigation plan aims to protect wildlife habitat and reduce environmental impacts by implementing best professional practices and enforcing current protections, such as The Endangered Species Act,

the Migratory Bird Treaty Act, and the Marine Mammal Protection Act (Alaska, 2015; Bureau of Land Management, 2020). Currently, these acts protect polar bears, Porcupine caribou, and migratory birds, all responding negatively to land fragmentation, noise, air, and water pollution (Alaska, 2015; Bureau of Land Management, 2020). Finally, the management plan will incorporate adaptive management strategies, such as regular monitoring and evaluation of management actions and other adjustments based on changing natural resource conditions. For example, if monitoring data show that a particular mitigation measure is ineffective, the plan will be adjusted accordingly to ensure that alternative best practices are implemented.

Environmental Groups

Environmental groups are essential in advocating for environmental protection and sustainability, raising awareness about environmental issues, and mobilizing public support and action. Environmental stakeholders focus on the preservation and protection of habitat for all native wild animal and plant species in Alaska's wild lands and waters against degradation from land development. Environmental group stakeholders in this region include The Wilderness Society, Defenders of Wildlife, and Alaska Wilderness League. These organizations work to create and enforce conservation policies that protect terrestrial and aquatic wildlife in the region and value the application of scientific principles to the conservation of organisms and resources in the American Arctic and Sub-Arctic areas. In the case of development in ANWR, environmental groups are working towards preventing or mitigating negative impacts on natural resources.

Environmental groups argue that the introduction of machinery and drilling in the 1002 Area will disrupt wildlife and have long-term effects on the natural landscape (Allred et al., 2015). For example, noise disturbance and drilling construction are environmental stressors that severely

alter migratory pathways of caribou and birds by fragmenting contiguous habitat, enhancing invasive plant establishment, and altering wildlife behavior (Allred et al., 2015). Habitat fragmentation will compromise the protected corridors used by Porcupine caribou for migration to calving grounds on the Coastal Plain (Alaska, 2015; Allred et al., 2015; Bureau of Land Management, 2020; Gwich'in Steering Committee, 2023), loss of which may stifle their reproduction by increasing calf mortality (Alaska 2015). Migratory birds are also sensitive to environmental change in the ANWR because they depend solely on this flyway for rest, refueling, and breeding grounds. Over 200 species have been documented in ANWR, with more than half using the refuge specifically for breeding, and at least seventy species specifically nesting in the Coastal Plain area (Alaska 2015). Disturbance from oil and gas development would also strip the habitat of its native vegetation and disrupt food webs resulting in alterations to the natural cycle (Fraley, 2021). Through their work, environmental advocacy groups help ensure that the environment is given the attention and protection it needs to thrive for future generations.

Non-Indigenous Communities

Similarly, discussions of resource partitioning among non-Indigenous Alaskan residents have revealed divisions between economic development and subsistence uses of land (Wallace, 2005). Proponents of oil and gas development argue that increased revenue would significantly impact Alaskan residents and Indigenous communities to create generational wealth and a higher standard of living (State of Alaska, 2022). Subsidies are a major source of economic support for many individuals and families in the state. Increased oil and gas production from the 1002 Area could help boost revenues and provide even larger dividends to Alaskan residents. The state's oil and gas revenues provide all eligible Alaskan residents an annual dividend, managed and

distributed by the Alaska Permanent Fund (Alaska Permanent Fund Corporation, 2023; U.S. Energy Information Administration, 2017).

However, Alaskans who rely on wildlife products (e.g., fish, hide, antlers, and ivory) for sustenance or their livelihoods are concerned that increased oil and gas development will further disrupt resources (Fraley, 2021). Fishing is culturally and historically linked to Alaska's rich history, and current industrial activities such as seismic surveys and drilling are disrupting commercial and subsistence fishing for salmon, halibut, and other species including the endangered Bowhead whale (Audubon Alaska, 2023; Fisheries, 2023). Oil and gas development could disrupt these traditional subsistence activities and jeopardize the economic well-being of Alaskan residents and Indigenous communities.

Indigenous Communities

Indigenous Alaskan communities live with the land through culture, spirituality, hunting, and fishing but hold diverse interests that lie along a continuum between generational land use and modern technology (Wallace, 2005). The ANWR is a significant area of land for the Gwich'in people as it is their ancestral home and an important part of their cultural and spiritual identity (Gwich'in Steering Committee, 2023). The Gwich'in Steering Committee, created in 1988, aims to protect the Porcupine caribou herd by protecting ecosystems along its migration path in the Coastal Plain of the ANWR (Gwich'in Steering Committee, 2023). Protection will ensure the long-term conservation of the herd, which the Gwich'in People rely on to sustain their way of life. Conversely, the Iñupiat Nation sees the value in drilling in the ANWR because landowners adjacent to the refuge will benefit from development through jobs, economic development, revenue shares, and infrastructure improvements (Dister, 2022; Lumen Learning, 2018, Ch 1).

In contrast, the Iñupiat Nation, another Indigenous community, has historically supported drilling in the Arctic National Wildlife Refuge (ANWR) because of the benefits drilling would provide to their economy standard of living, and lifestyle. The Iñupiat Nation has generally called for consultation and engagement with the federal government and other stakeholders in decision-making regarding drilling in ANWR. They have also advocated for measures to ensure that any development is conducted to minimize environmental harm and protect their cultural and subsistence practices (Wallace, 2005). The Iñupiat Nation has expressed concerns about the potential harm to the wildlife, their subsistence practices and the potential negative impacts on their cultural and spiritual connections to the land. Thus, any development in the region should be approached carefully and with the involvement of the Iñupiat Nation and other stakeholders. Approaching the decision pragmatically, the Iñupiat Nation believes that carefully regulated oil development can promote ecological preservation and healthy living conditions while meeting energy needs (Voice of the Arctic Iñupiat, 2023). The Iñupiat Nation encourages culturally responsible development in which drilling can be done in an environmentally responsible way that minimizes the impact on the natural habitat and wildlife (Dister, 2022). Oil and gas development offers job opportunities while stimulating the local economy and funding community services such as healthcare, education, roadways, clean water, and utilities that are the cornerstone of healthy living conditions (Dister, 2022; Voice of the Arctic Iñupiat, 2023). The Iñupiat Nation has worked with the current U.S. presidential administration and the Bureau of Land Management to advise on the latest EIS regarding these natural, oil, and gas resources to convey community needs.

Resolution

After conducting a thorough stakeholder analysis, it is clear that many groups are vested in the potential oil and gas development in the Arctic National Wildlife Refuge (ANWR). While some stakeholders, such as oil and gas companies, are in favor of drilling for economic reasons, others, such as environmental organizations, are against it due to concerns about the impact on wildlife and the environment. In order to come up with a resolution that accounts for the concerns and interests of all stakeholders, it is important to engage in meaningful dialogue and collaboration. This includes creating a tribal alliance among Indigenous groups in the area, exploring alternative drilling technologies, and investing in research to better understand the impacts of drilling on the environment. By involving all stakeholders in the decision-making process and finding a resolution that considers their concerns, it is possible to create a sustainable solution that benefits all parties involved. It is important to keep in mind that the long-term impact of drilling in the ANWR area is uncertain, and it is crucial to take a cautious and collaborative approach to minimize negative impacts on the environment and wildlife.

Tribal Council

First, the creation of a tribal alliance in which all Indigenous groups, regardless of opinion, work as a collective will result in a shared vision. Currently, tribes and existing tribal alliances focus on debating each other and lobbying the government individually. This separation of effort creates divisiveness among communities and minimizes the effect of tribal input on decisions made by the federal government which is far removed from the conflict. A tribal alliance would allow multiple tribal governments to use their collective voices to influence decisions made by the federal government. Any resolution from the tribal alliance will be a collaborative effort to express common voices that would simultaneously recognize cultural traditions and economic

empowerment. One facet the alliance could work on is exploring options to provide jobs that would provide income similar to that of drilling, such as those in the renewable energy or resource management sectors. Ultimately the tribes who are directly impacted by drilling in ANWR should be deciding on the resolution, not just the federal government.

Oil and Gas

As outlined in the 2020 Coastal Plain Oil and Gas Leasing Program Record of Decision, there are several alternatives to the leases. If the path forward does include drilling, then best professional judgment will need to be employed along with the newest technology to reduce impacts on wildlife. Oil and gas companies leasing land will implement protocols for minimizing surface disturbance by using advanced drilling technologies, such as directional drilling, that can reach underground resources without requiring large surface areas for drilling equipment as well as protecting sensitive areas by implementing exclusion zones or buffer areas where drilling activity would not be allowed (Lavis, 2018).

Provisions for wildlife and policies will need to be written to minimize surface disturbance and maintain compliance with these policies. As stated in the EIS alternative action 2.5

Environmentally Preferred Alternative (BLM, 2020), leases should be reduced by more than 50% from 1,563,500 acres to 800,000 acres. Leasing land for drilling only on the edge of the refuge will also minimally disrupt critical habitat and migratory pathways. In addition, calving grounds for Porcupine caribou will require additional sampling to determine an adequate buffer around drilling operations. Provisional policies should support wildlife buffers for areas that contain habitat of endangered species and increase non-surface operations (NSO) as an alternative to above-ground structures. Lastly, these provisions should reinstate recommended operating procedures (ROP) from the EIS and reinforce ROP with stronger protections for

wildlife recommended by the BLM in the original ROPs (BLM, 2020). Other stakeholders such as non-governmental organizations (NGOs), community groups, and concerned citizens should also play a role in advocating for the enforcement of these ROPs.

Research and Assessment

Lastly, in addition to forming tribal alliances and instituting environmental best practices for drilling, increased science initiatives focusing on understanding the effects of drilling on local ecosystems would benefit the community. ANWR is a pristine habitat and applying adaptive management by continuing research on drilling impacts will advance knowledge of the true effects of this practice. Adaptive management is often used in situations where the natural system is complex and uncertain, and where there is a need for ongoing learning and flexibility in management strategies. Research will promote transparency, inform communities directly impacted by development, and report long-term trends and effects of drilling impacts.

Furthermore, oil and energy development companies directly profiting from ANWR drilling should be required to fund proposals for research on renewable energy opportunities and monetization of ecosystem services in the refuge (e.g., carbon and wetland banking). A portion of lease fees should be set aside to fund these combined research efforts and provide students from Indigenous communities with scholarships. Communities impacted most directly by drilling in ANWR will benefit from such research initiatives that are focused on renewable energy development and understanding the impacts of oil drilling.

Conclusion

The potential economic and environmental impacts of drilling in the 1002 Area are subject to debate and uncertainty because they depend on a range of factors including the scale and intensity of oil and gas development in the area, the price of oil, and the regulatory and policy

frameworks governing the industry. Although drilling in the 1002 area has been long debated, it appears that it is inevitable since the Biden administration has greenlighted the Willow project in the National Petroleum Reserve—Alaska (NPRA) (Bureau of Land Management, 2022). How drilling proceeds is the only action we can control at this point. However, drilling can and should proceed in a way that minimizes impacts on the environment and Native communities while still offering economic benefits from resource development. Choosing practices that minimize disturbance to habitats and involving co-management by Indigenous groups whom drilling impacts the most is the best way to move ahead into ANWR's new chapter, impact, and legacy.

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