AN ABSTRACT OF THE DISSERTATION OF

Michael D. Brawner for the degree of Doctor of Philosophy in Integrative Biology presented on September 15, 2021.

Title: Context and Scale Mediate the Impact of Climate on a Widespread Avian Predator.

Abstract approved:

Rebecca C. Terry

Anthropogenic climate change is threatening biodiversity as I currently understand it. There is now a large body of work highlighting species responses, globally, to this threat. Importantly, responses at the species level emerge from responses at lower levels of biological organization (individuals and populations) across a species' geographic range. For widespread species in particular, perturbations due to climate warming or other environmental changes in one part of a species' range may not have the same effect as in another part of that species' range. In fact, different populations within a species may show opposing trends in response to the same environmental stressor. Species level responses also have consequences for higher levels of biological organization (communities and ecosystems), depending on the rate and duration of the response. Integrating across

biological, spatial, and temporal scales is therefore critical to a deeper understanding of biotic responses to anthropogenic climate change.

My dissertation takes an integrative, multi-scale approach to better understand the role climate has played in shaping the distribution and dynamics of an iconic falcon in North America, the American kestrel. This species, a widespread generalist that is common across North America, is experiencing one of the most dramatic declines among all North American raptor species. Determining the degree to which anthropogenic climate change has played a role in this decline, or not, is an urgent area of inquiry. My second chapter addresses gaps in knowledge by presenting an analysis of whether the interactive effects of climate, the structure and composition of the landscape, and primary productivity of the breeding grounds have impacted nest success in a population of American kestrels in the high desert region of Central Oregon over a 7-year period and examining how the spatial and temporal grain of the data impacts results. I find that primary productivity has greater explanatory power than either climate or landscape variables. However, seasonal variables (nest initiation date, nest age and day-of-year) emerge as the most important predictors of variation in nest success regardless of primary production. These models also suggest that longer-term annual averages of environmental variables may not be as informative with respect to nest success as variables that capture within-season variation in the environment. In addition, I find no evidence of advancing phenology as has been found in other populations in similar habitats and at similar latitudes as this population.

Chapters 3 and 4 of my dissertation I turn to the relationship between body size and climate in the American kestrel. Evidence from bird species worldwide has shown reductions in mean body sizes over the past 50-100 years consistent with the notion of a response to climate warming. Body size has been shown to scale allometrically with many fundamental physiological, ecological, and evolutionary processes, raising concerns that asynchronous shifts in body size among species could lead to unexpected shifts in community and ecosystem dynamics. Yet previous studies of body size in birds vary with respect to how body size is measured. Measuring size is not a trivial matter, and the methods used can impact interpretation. In Chapter 3, I quantify size of kestrel sternums, a structural size element, via 3D geometric morphometrics to assess which standard non-structural (linear) morphological measurements that are typically applied to living birds or historical museum specimens (study skins) best capture the true structural size of a specimen. I find that single, commonly applied proxy measures of size in birds, such as mass, wing cord, or tarsus length, are poor representatives of structural size in the American kestrel, and that a combination of measurements from the wing, tail, leg and bill may be more appropriate for studies relating size to environmental parameters in this species.

In Chapter 4, I then use a combination of measurements from a data set of museum study skins to evaluate the degree to which American kestrels across North and Central America conform to Bergmann's Rule and Allen's rule, common ecogeographic rules relating body size and appendage length, respectively, to latitude. I use a spatial regression framework to examine patterns in size and appendage length across 60° of latitude and over a 112-year period. I then integrate climate models with satellite-derived data on primary productivity and a dataset of competitor richness and body sizes compiled from the literature to test common hypotheses about the mechanisms underlying these patterns. I find no evidence for a change in the average body size of kestrels through time when examined at the continental scale, although, at smaller spatial scales, many regions do show significant trends in morphology through time. I do find support for Bergmann's rule in American kestrels across the Northern hemisphere. In addition, the mechanism predicting size variation in American kestrels are found to be congruent across different spatial scales. I also find that bill size in American kestrels aligns with predictions from Allen's rule.

Taken as a whole, the studies presented in this dissertation add to the body of research currently underway to address the long-term declines in an iconic species of the American landscape. The research integrates insights across scales, from a single population in Central Oregon experiencing variability in climate and microhabitats over a sub-decadal period to multiple populations and subspecies arrayed across the entire North American continent that have been shaped by anthropogenic climate change over more than a century.   In doing so, this work also addresses logistical concerns in how size is measured in birds and addresses a long-standing debate over the multiple potential drivers of Bergmann’s Rule, a fundamental ecogeographical rule found in every ecology textbook.

Context and Scale Mediate the Impact of Climate on a Widespread Avian Predator

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Michael D. Brawner

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Michael D. Brawner, Author

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CONTRIBUTION OF AUTHORS

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DEDICATION

This dissertation is dedicated to Susan Weston who taught me the magic of birds and for encouraging my writing when I was an undergrad. And to all the educators changing lives daily.

Chapter 1: Introduction

Global temperatures over the past century have risen by an average of 0.85 °C, and the average global temperatures for each of the past four decades have been successively warmer than the last (Hansen *et al.*, 2006; IPCC, 2021). This warming has already contributed to major alterations of both terrestrial and marine ecosystems, and a predicted warming of 2 °C over the next century will exacerbate these changes (IPCC 2021). How Earth's biota has and will continue to respond to such changes in climate is an increasingly important concern. Among plants and animals, documented effects of climate change have included shifts in species' ranges (largely poleward and upward) (Chen *et al.*, 2011; Kelly & Goulden, 2008; Parmesan, 2006; Parmesan & Yohe, 2003), advances in phenology (e.g. earlier spring emergence, changes in migratory arrival and departure dates, reduced hibernation duration)(Cleland *et al.*, 2007; Inouye *et al.*, 2000; Marra *et al.*, 2005; Menzel *et al.*, 2006; Parmesan & Yohe, 2003; Visser & Both, 2005), population dynamic consequences (e.g. reduced fitness due to phenotypic mismatches with preferred prey, increased fitness as a result of longer growing seasons)(Both *et al.*, 2006; Gils *et al.*, 2016; Karell *et al.*, 2011; Ozgul *et al.*, 2010), and changes in behavior, morphology and physiology (Carleton, 2017; Gardner *et al.* 2011; Helmuth *et al.*, 2002; Kearney, Shine, & Porter, 2009; Pörtner & Knust, 2007; Scaven & Rafferty, 2013; Sheridan & Bickford, 2011; Tuomainen & Candolin, 2011). Of these responses, poleward (upward) range shifts and advances in spring phenology have been so well documented that they are now thought to represent a "universal fingerprint" of the impacts of climate change on plants and animals (Parmesan & Yohe, 2003; Walther *et al.*, 2002; although see Currie and Venne 2017). More recently, correlations between declining body size of animals and rising global and regional temperatures have become increasingly apparent, leading some researchers to suggest this phenomenon represents a "third universal response" to climate warming (Daufresne, Lengfellner, & Sommer, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011). The generality of the body size response to increasing temperatures and the mechanisms behind recent widespread declines in body size, however, remain unclear.

In addition to the assaults of climate change, animal populations are facing increasing threats from a host of other human-induced environmental changes: destruction of habitat, invasive species, toxic chemicals, pathogens, introduced predators, etc. Birds, in particular, have been especially hard hit (Inger *et al.*, 2015; Rosenberg *et al.*, 2019). Rosenberg *et al.* (2019) estimate that over 3 billion birds have been lost in North America since 1970, a nearly 30% loss. However, not all birds are equally impacted. While grassland birds have suffered extreme declines, wetland birds, for example, have increased in numbers as well as turkeys and grouse (Rosenberg *et al.*, 2019). Raptors are another group that has done well over the last several decades; Rosenberg *et al.* (2019) estimate that raptors have increased by up to 200%. Among this group are success stories like the bald eagle and peregrine falcon whose numbers were dangerously low just a few decades ago. But another raptor, the American kestrel, has not been as lucky. Since the late 1960's American kestrels have declined in numbers by approximately 54% (Sauer *et al.* 2019). A widespread, open country predator, the American kestrel is still ubiquitous in most regions of the continent. This cosmopolitan distribution, however, belies the astounding loss in numbers of this important predator, as a widespread distribution doesn't necessarily imply abundance. Reanalysis of data from Rosenberg *et al.* (2019) shows just how significant a loss kestrels have sustained relative to other raptors: of the seven diurnal species of raptors showing declines, American kestrels represent 82% by individuals. Despite their small size, they also make up 44% of the total biomass of raptors lost since 1970. This certainly offers cause for concern.

Like all common species, or perhaps historically common species, kestrels exert their greatest effects through their numerical abundance and play important roles in ecosystems (Sekercioglu, 2006). Raptors help to stabilize communities by exerting top-down control on food webs and aiding in nutrient and energy transfer. They help control pest populations, and serve as environmental clean-up crews thereby helping prevent the spread of disease (Donazar *et al.*, 2016, Whelan *et al.*, 2008). Small raptors like kestrels are particularly equipped in this regard: a 2008 study linking the increased incidence of Lyme disease to the disappearance of small to medium mammalian carnivores found significant upticks in the incidence of Lyme disease in the same regions that have experienced population declines in kestrels (Levi *et al.*, 2012, Smallwood *et al.*, 2009). Just four small rodent species are responsible for 80 to 90% of the transmission of Lyme disease to ticks, thus having an abundance of multiple predators on the landscape can help compensate for the predator loss and help to prevent the spread of disease.

Kestrels are also an economically important species. Studies into the use of nest boxes and perches installed in fruit orchards and on other agricultural production land have shown that birds and bats can provide multiple benefits to farmers and local economies (Jedlicka, 2011; Kross 2012; Maas *et al.*, 2015; Labuschange *et al.*, 2016). Kestrels will readily nest in artificial boxes, and their presence can act as a deterrence to crop pests. A study by Shave *et al.* (2018) found that the presence of kestrels in sweet cherry orchards reduced pest bird abundance and had the potential, if implemented state-wide, to provide a $2.2 million - $2.4 million increase in GDP for the state of Michigan over a 5-year period. It was estimated that the increase output in production would additionally result in the creation of approximately 50 jobs.

But American kestrels have been in decline since at least 1966 (Sauer *et al.*, 2019). Long-term monitoring efforts from breeding bird surveys and nest box populations have shown declines to be widespread and steady. Yet they went largely unnoticed until 2004 when the first symposium at a Raptor Research conference was convened to even discuss the possibility of kestrels in decline (Bird, 2009). It wasn't until another five years had passed that the first reports of population declines were published in the literature (Farmer and Smith, 2009; Smallwood *et al.* 2009). Thus, in terms of ecological research, kestrel decline is still a relatively new area of study. There is still little consensus on the causes of the decline, although many hypotheses have been debated (McClure *et al.* 2017a). It is clear however that not all populations are affected equally, and some populations are even increasing in numbers, suggesting that the causes may be localized and potentially multifaceted. New research into the American kestrel is being published at a fast pace and meetings, conferences, and symposia are bringing kestrel researchers from far and wide together. Unravelling the causes of declines in common species is becoming a priority.

Part of the new push in research on American kestrels is to understand how they will respond to and cope with climate change. Already some populations of kestrel have shown advances in spring phenology on the order of 3 weeks over a 20-year period (Heath *et al.*, 2012; Anderson *et al.*, 2016; Smith *et al.*, 2017). As with the kestrel declines though, this phenological shifts seems to be limited to a particular portion of the kestrel's range. Recent genetic work into American kestrel population structure suggests that there may be some role for genes in determine broad scale differentiation in response to environmental perturbations (Ruegg *et al.*, 2021). American kestrels may also be responding morphologically to warming global temperatures. A 2018 study by Ely *et al.* found significant declines in the mass and wing chord lengths of American kestrels across a network of raptor banding sites over a 20 to 30 year period. In light of the responses of species to climate change globally, American kestrels seem to be travelling a well-worn path. Studies focused on the impacts of climate and other environmental drivers on the behavior, physiology and morphology of American kestrels will therefore add both greater awareness of the particular assaults afflicting kestrel populations and a deeper understanding to the broader context of the impacts of climate change on animals.

The following dissertation tackles this challenge across different spatial and temporal scales and with observational and biogeographical approaches. In Chapter 2, I focus on a population of kestrels utilizing nest boxes in Central Oregon, collaborating with a group of community scientists who have monitored the boxes for over two decades. Using a detailed accounting of nest histories for each nest boxes, I assembled a seven-year observational data set to examine the impacts of climate, along with landscape composition and primary productivity, on the nest success of American kestrels in this population. Anecdotal evidence suggests Oregon represents an area of the country where kestrels may be doing better than other populations, yet they remain relatively understudied in this region. I apply statistical models to the nest history to find out. Specifically, I ask 1) how kestrels are influenced by different environmental factors, 2) whether they show response to climate warming similar to those seen in other populations in the Western US, and 3) how the spatial scale of analysis impacts the results of the study. New satellite derived methodologies for quantifying the landscape and environmental parameters could help save ecologist valuable time and money, but critically, only if they are able to capture the variation at a scale that is biologically relevant to the bird. In this study system, however, I find that variables indicating within-season environmental and ecological variation emerge as the more important predictors of variation in nest success than variables averaged over large spatial and temporal scales. Of these annual averages, primary production is the best predictor of variation in nest success, but models with only seasonal variables are just as competitive. I also investigate whether kestrels show advancing phenology in this population, and find that they do not, despite many similarities with other populations that do.

In chapter 3 I broaden the focus to ask how kestrels are responding to climate change at the scale of the species. Before I can do so, however, I first assess what it means to measure body size, as change in body size has been reported as a potential key response to climate warming. Body size is a term that lacks a clear definition. It is as often used to refer to the mass of an animal as it is to refer to length of some anatomical structure. Yet ideally, body size refers to structural size that is independent of nutrient reserves. In order to make the best use of the historical museum specimens I employ in chapter 4, I quantify structural size in American kestrels via 3D light scanning technology of kestrel sternums. I then use this measure of 3D size as a standard against which to compare different common linear measures of size to determine the best combination of measurements to use from museum study skins to represent structural size. I find support for previous findings that multiple measures of size from museum study skins are better than single measures in representing structural size of birds. Out of the single measures, however, tail length, not any of the traditional measures of size, is the best predictor of body size.

Having determined how best to characterize structural size from a museum study skin, I then examine a larger dataset spanning over 60° in latitude and 112 years to evaluate support for, or against, Bergmann's rule and Allen's rule in kestrels. Bergmann's rule and Allen's rule are two geographic rules relating body size and the shape and size of body structure to temperature, strictly speaking, and to environmental and ecological factors more broadly. I use spatial regression analysis to determine the degree to which structural size in kestrels through time and across space can be explained by temperature, aridity, primary productivity, and measures of the biotic community.

I conclude with a summary of the research within the broader context of climate change and outline directions for future work. I leave with some parting words about the potential for technology in population monitoring and museum research and need to keep common species common in a rapidly changing world.

Chapter 2: Environmental influences on the nest success of American kestrels in Central Oregon

Introduction

Nest success is a key parameter of population dynamics in birds (Brown *et al.* 2013). Understanding how nest success varies across space and time can provide critical information for predicting the resilience of species facing an increasing rate of environmental change in today's world. The factors that influence nest success, however, are legion, ranging from aspects of weather and climate to inter- and intra-specific interactions to the composition and configuration of the surrounding landscape, among others (Martin, 1993; Chalfoun *et al.*, 2002; Dreitz *et al.*, 2002; Rodewald, 2002; Greenwood and Dawson, 2011; McIntyre and Schmidt, 2012; Brown *et al.* 2014; Wallace *et al.*, 2016). Furthermore, these factors may interact in complex ways and across different spatial and temporal scales making accurate assessment of the factors driving success in reproduction challenging. Here I use remotely sensed data across multiple spatial scales to examine how aspects of the abiotic environment have impacted the nest success of a population of American kestrels in Central Oregon.

The American kestrel is a small falcon that is widespread in North America (Smallwood and Bird 2020). It is a generalist predator that is commonly associated with open country habitat. A secondary cavity nester, the American kestrel will readily breed in artificial nest boxes, and many nest-box programs have been established around the country to help supplement kestrel populations (Hamerstrom *et al.*, 1973; Stahlecker, 1979; Bloom and Hawks, 1983; Toland and Elder, 1987; Varland and Loughin, 1993; Katzner *et al.* 2005; Smallwood and Collopy 2009; Schulwitz *et al.*, 2021). Despite this effort, the American kestrel has shown a continuous steady decline in population size across their range since the 1960's based on Breeding Bird Surveys and monitoring of nest-box programs (Farmer *et al.* 2008, Farmer and Smith 2009, Smallwood *et al.* 2009, Paprocki *et al.* 2014, Sauer *et al.* 2019). The causes of American kestrel population declines remain unclear (McClure *et al.* 2017a). The most likely hypotheses include rodenticides (Rattner *et al.* 2015), endocrine disrupting chemicals (Carere *et al.* 2010), habitat destruction (Sullivan and Wood 2005; Farmer *et al.* 2009; Bolgiano *et al.* 2015), and climate change (Steenhof and Peterson 2009, Hoffman *et al.*, 2002). Some of these factors likely have varying effects on kestrel populations across their range (Wommack 2014; Ely *et al.* 2018; Powers *et al.* 2021).

What is clear is that no one single factor has emerged as a clear driver of declines across all kestrel populations (Smallwood *et al.* 2009; McClure *et al.* 2017a; Sauer *et al.* 2019). For instance, warmer winter temperatures and earlier spring green up, commonly associated with climate change, are driving shortened migration distances and phenological responses in western populations of American kestrels, but not in eastern populations (Heath *et al.* 2012; Smith *et al.* 2017; Powers *et al.* 2021; Ruegg *et al.* 2021). In addition, despite the continent-scale decline, many American kestrel populations in North America are holding steady or even increasing, especially in the Southeast, Midwest and Southwest regions of the United States (Sauer *et al.* 2019). Thus, documenting the extent and severity of declines at the population scale, and identifying populations that are perhaps more stable, remains an ecological imperative (McClure et al 2017a). A clearer understanding of the factors impacting reproductive success and survival of American kestrels is one piece of this puzzle (McClure *et al.* 2017a).

Here I focus on the effects of three aspects of the abiotic environment – climate, landscape, and primary productivity – on the reproductive success of an American kestrel population breeding in nest boxes in Central Oregon over an seven-year period. Aspects of each of these three categories are readily quantifiable from remote sensing data over a range of spatial and temporal scales. My goals were to 1) quantify reproductive parameters in this understudied population of American kestrels and compare with estimates from other populations across the North American range, 2) determine if spatial and temporal scales of analysis impact inferences, and 3) assess the degree to which different categories of the abiotic environment explain nest success in this population.

Methods

Study Area

Central Oregon consists of cold high desert habitats dominated by a mix of sagebrush and rabbitbrush steppe, ponderosa pine forests, and juniper and bitterbrush woodlands. It is a region with little to no published data on American kestrels. The data used in these analyses comes from nest boxes that were erected starting in 1999 by Jim Anderson and Don McCartney, local community scientists, and consists of over 160 nest boxes whose distribution covers approximately 2,900 km2. The study area encompasses the Deschutes River Valley, stretching north from Bend up into Jefferson County, and southeast to the town of Brothers, OR (Fig. 1). This area is dominated by sagebrush-grasslands, but also encompasses the eastern Cascade foothills where ponderosa pine, juniper and bitterbrush are common. The most common substrates for nest boxes are western juniper, followed by ponderosa pine with a few boxes on artificial structures. Box heights range between 138.5 cm and 420 cm (1st and 3rd quartiles 246.38cm and 362.96cm). A majority of nest boxes (54%) have a N, NE or NW orientation.

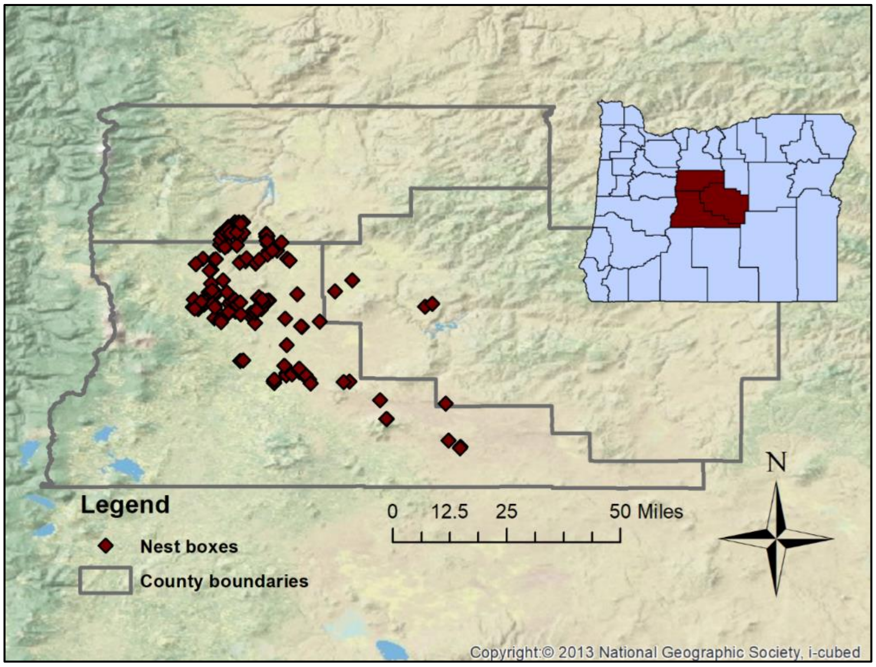

Figure 2.1: Locations of nest boxes across Central Oregon

Environmental Factors

I chose to evaluate the effects of three categories of environmental factors on the reproductive success of Central Oregon kestrels: climate, landscape, and primary productivity. These categories were determined based on the published literature documenting responses of birds to environmental change. For example, the effects of climate on reproductive success of birds are well documented. Aside from shifts in phenology and migration patterns, which can impact the timing of reproduction, climate can impact reproductive success through a variety of direct and indirect mechanisms. Temperature extremes can cause direct mortality of eggs and nestlings and impact the condition and foraging efficiency of adults (Bradley *et al.* 1997; du Pleiss *et al.* 2012; Cruz-McDonnell and Wolf 2015). Increased variability and severity of precipitation events can also impact success through delayed initiation of laying and decreased foraging efficiency and accessibility to prey (Olsen and Olsen 1992; Mearns and Newton 1988; Kostrzewa and Kostrzewa 1991; Steenhof *et al.* 1999; Dawson and Bortolotti 2000).

The composition and structure of the landscape, too, can influence nest success in a variety of ways. Microclimate of the nest site, which can affect egg viability, nestling growth and survival, and parental energy requirements (Wallace *et al.* 2016), is highly dependent on the localized vegetation type and the position of the nest within it. Fragmentation of the landscape can increase exposure to varying climatic regimes and a variety of predators or nest competitors in the area of the nest site. For example, more disturbance-tolerant species like European starlings may be able to outcompete native species for nest cavities in fragmented landscapes (Brown *et al.* 2014). Conversely, nest cavity predators associated with more continuous landscape composition, such as squirrels in more densely wooded areas, may have easier access to nest cavities where the habitat is less fragmented (Greenwood and Dawson 2011).

Climate and landscape both contribute to primary production, which itself can affect nest success of apex predators like raptors through complex ways. Recent work on small mammals, a critical food resource for many raptor species, suggests "bottom-up" influences on small mammal population dynamics through climate-induced variation in primary productivity may be stronger than previously thought (Fowerdew *et al.* 2017; Schmidt *et al.* 2018). These bottom-up influences could percolate up the food web over time. For example, a study in the Prairie Potholes region of North America found that lagged-increases in predator communities were implicated in the reduced nest success of ducks following years of high primary productivity (Walker *et al.* 2013; Ringelman *et al.* 2018). For consumers like American kestrels, time-lagged responses in food webs may drive reproductive success in subsequent seasons or years (Tornberg *et al.*, 2005).

Data Collection

Nest Data

In collaboration with the American Kestrel Partnership, standardized data collection on nest history for the nest boxes erected in 1999 began in 2012. Between 2012 and 2018, the total number of active boxes ranged from 49 – 63 per year. During the breeding season, nests were surveyed three times; first in late April/early May to establish nest initiation and clutch size. A box was deemed active upon the first appearance of an egg. The second survey occurred approximately 28 days later (the average incubation period for an American kestrel for this study site) to establish hatching. The last survey occurred 18 to 28 days post-hatching to band surviving nestlings. Nestlings were considered fledged when they reached 22 days post-hatching, 80% of the average age at which kestrel nestlings typically fledge (Steenhof and Newton, 2007, Steenhof and Peterson, 2009). Only nests deemed to have failed or that reached the 80% post-hatching time interval were used in these analyses. All other nests were assigned an undetermined fate and were excluded from the current analyses. I used a photographic aging guide available through the American Kestrel Partnership to estimate age of nestlings (Klucsarits and Rusbuldt 2007). The number of observations (i.e., each nest visit) per year used for analysis was as follows; 2012: 73, 2013: 40, 2014: 53, 2015: 71, 2016: 78, 2017: 70, 2018: 108.

Climate Data

I used 800m PRISM data to generate climate variables around each nest box at multiple spatial and temporal scales (PRISM Climate Group, 2019). Historical minimum, maximum, and average temperature climate layers for the years 2010-2018 were used to generate annual average, breeding season (April-July) maximum, and previous winter season (December-March) minimum raster layers. I then sampled these layers at a 1, 5, and 10km radius around each active nest box for the focal and two previous years to produce an average value for a given year and spatial scale for each nest. The same sampling process was repeated for PRISM precipitation layers to produce annual, breeding season, and previous winter season cumulative averages for a given year and spatial scale. This resulted in temperature and precipitation variables for 3 different years and 3 different spatial scales for each nest (Table 1, S1, and S2).

Table 2.1: Descriptive statistics for environmental variables at 1 km scale. *Variables also used in Brown *et al.*, 2014. §Units in mm. ‡Units in °C. ^Scale factor = 0.0001, units = kg C/m^2. Descriptive statistics for environmental variables at 5 and 10km scales in Tables S1 and S2.

Variable	Description	Mean	St. Dev.	Min	Pctl(25%)	Pctl(75%)	Max
ai*	Aggregation index: degree of aggregation of patch types accounting for diversity/eveness	79.68	7.69	57.61	75.31	84.29	100.12
area_cv*	Patch size coefficient of variation: degree of landscape dominance by large patches	554.47	194.01	0.00	422.22	694.69	1,034.63
frac_cv*	Fractal dimension coefficient of variation: variability in patch shape complexity	6.24	1.31	0.00	5.96	6.95	8.67
iji*	Itersperion/juxtaposition index: degree of intermixing of patch types	51.91	14.65	1.64	44.63	61.89	89.91
np	Number of patch types	124.97	71.02	1	69	176	442
pladj	Percentage of like adjacencies: degree of aggregation of patch types	78.41	8.07	56.26	73.48	83.54	99.67
shdi	Shannon's diversity index of patch types	1.00	0.36	-0.09	0.83	1.25	1.67
agriculture	% land in type	1.88	6.42	0.00	0.00	0.98	42.75
developed	% land in type	8.93	10.90	0.00	1.75	10.97	47.29
Grassland	% land in type	5.29	8.15	0.00	0.17	8.38	50.24
Shrubland	% land in type	47.39	25.04	2.21	27.62	65.53	100.00
Woodland	% land in type	32.52	22.07	0.00	11.84	47.63	83.07
ppt_y2§	Mean cumulative annual precip 2 years prior	310.04	80.49	126.47	255.19	372.24	501.49
ppt_y2b§	Mean cumulative breeding precip 2 years prior	71.10	21.84	24.98	52.76	87.65	115.88
ppt_y2w§	Mean cumulative winter precip 2 years prior	150.13	45.23	64.13	118.07	188.84	254.87
ppt_y1§	Mean cumulative precip 1 year prior	291.05	76.30	146.71	241.45	332.45	501.49
ppt_y1b§	Mean cumulative breeding precip 1 year prior	60.35	20.25	28.71	44.11	73.16	115.88

ppt_y1w§	Mean cumulative winter precip 1 year prior	172.71	51.18	59.30	133.85	205.98	295.55
ppt_y§	Mean cumulative precip current year	292.62	77.79	146.71	233.41	332.45	499.33
ppt_yb§	Mean cumulative breeding precip current year	63.02	20.63	27.77	49.63	73.97	115.88
ppt_yw§	Mean cumulative winter precip current year	149.53	58.12	53.77	98.99	190.37	295.55
tmean_y2‡	Mean annual temp 2 years prior	8.91	0.80	5.70	8.35	9.56	10.65
tmean_y1‡	Mean annual temp 1 year prior	8.87	0.81	5.70	8.38	9.43	10.56
tmean_y‡	Mean annual temp current year	9.06	0.67	6.36	8.61	9.56	10.56
tmax_y2b‡	Max breeding temp 2 years prior	17.29	1.90	12.16	15.95	18.80	20.80
tmax_y1b‡	Max breeding temp 1 year prior	17.34	1.89	12.16	16.34	18.45	20.90
tmax_yb‡	Max breeding temp current year	17.79	1.34	14.34	16.74	18.65	20.80
tmin_y2w‡	Min winter temp 2 years prior	-3.39	1.17	-7.08	-4.39	-2.50	-0.76
tmin_y1w‡	Max breeding temp 1 year prior	-3.87	1.42	-7.53	-4.78	-2.80	-0.78
tmin_yw‡	Max breeding temp current year	-3.82	1.33	-7.53	-4.63	-2.71	-0.96
gpp_y2^	Mean annual primary productivity 2 years prior	0.01	0.003	0.003	0.01	0.01	0.02
gpp_y1^	Mean annual primary productivity 1 year prior	0.01	0.003	0.003	0.01	0.01	0.02
gpp_y^	Mean annual primary productivity current year	0.01	0.003	0.003	0.01	0.01	0.02
gppb_y2^	Mean breeding primary productivity 2 years prior	0.02	0.01	0.01	0.01	0.02	0.04
gppb_y1^	Mean breeding primary productivity 1 year prior	0.02	0.01	0.01	0.01	0.02	0.03
gppb_y^	Mean breeding primary productivity current year	0.02	0.01	0.01	0.01	0.02	0.04

Landscape Data

Landscape covariates were derived from 30-m resolution LANDFIRE data products (LANDFIRE, 2016) Existing vegetation type (EVT) and existing vegetation height (EVH) layers were reclassified from 140 to 11 layers and 31 to 14 layers, respectively, that were considered more biologically meaningful for this study. I then used Fragstats software to produce class and landscape metrics describing the spatial structure and composition at a 1, 5 and 10km radius around each active nest box, resulting in landscape composition and structure variables for each nest at the same three spatial scales. I then selected landscape composition and structure variables that I thought, *a priori*, would have a significant effect on reproduction in American kestrels or that had been used in previous studies of American kestrels (Table 1, S1, and S2).

Primary Productivity Data

Primary productivity layers were sampled following the same routine as for the climate data resulting in the same three temporal and spatial scales for each nest site. The gross primary productivity index was derived from MODIS version 6 data (Running *et al.*, 2015). I used average annual GPP and created breeding season GPP raster layers from which to sample from for the primary productivity variables (Table 1, S1, and S2). I chose to use MODIS GPP data rather than NDVI because it has been shown to better represent primary productivity, especially where variation in vegetation cover is large (Phillips et al, 2008).

Seasonal Data

Nest initiation date, nest age, and day-of-year were used to determine within-season temporal effects on nest success, as all three of these within-season variables have been shown to have an effect on nesting success in birds more generally (Perrins, 1970; Newton, 1979; Verhulst *et al.*, 1995;

Dinsmore *et al.*, 2002; Shaffer, 2004; Grant *et al.*, 2005) (Table 2). Nest initiation date and day-of-year were measured as the distance from the beginning of the breeding season, in days, which I set as May 1 for this population (average nest initiation date was May 7 for the entire time period). Nest initiation date was recorded as the day of the breeding season that the first egg was laid in a nest box for that year. For nests that were first observed before clutch completion (*n* = 50 nests), I estimated nest initiation date by back-calculating two days for each additional egg beyond the first one, as kestrels typically lay one egg every other day (Porter and Wiemeyer, 1972). For nests that were first observed after completion of the clutch and for which nestling age could be determined (*n* = 157 nests), I back-calculated from the first observation when the age of the nestlings, post-hatching, could be determined using the 28-day average period of incubation for kestrels at this study site. If nestling ages could not be determined for nests that were first observed after clutch completion (i.e., they failed before any nestlings hatched; *n* = 29 nests) I estimated nest initiation date as per the first method. Nest age was estimated as the average of the age in days from the nest initiation date during the observation window (Shaffer, 2004). Day-of-year was determined as the average of the days of the breeding season over the observation period (Shaffer, 2004).

Table 2.2: Descriptive Statistics for seasonal variables

Variable	Description	Mean	St.Dev.	Min	Pctl(25)	Pctl(75)	Max
day-of-year	average of the days of the breeding season, relative to May 1, over the observation period	39.83	15.07	6	26.5	50.5	92
age	average of the nest age in days from the nest initiation date over the observation period	33.03	12.51	3.00	23.00	44.50	62.50
initiation date	day of the breeding season, relative to May 1, 1st egg was laid	6.43	11.44	-21	0	10	52

Statistical Analyses

Principal Components Analyses

Principal components analyses (PCA) were performed on the environmental covariates (Table 1) to reduce their dimensionality and avoid problems with collinearity among predictors. I performed separate PCAs for each spatial scale (1, 5 and 10 km) for all climate, landscape, and primary productivity variables together. I retained the principal components that cumulatively explained over 70% of the variation in each group (which was either 4 or 5 principal components depending on scale) to use as predictors of nest success.

Model Selection

Because nests were monitored infrequently and 1st observations of nests occurred at various stages of the nestling cycle, I accounted for survival bias of nests at later stages by modelling the daily survival rate (DSR) of nests (Dinsmore *et al.*, 2002; Stephens, 2003; Shaffer, 2004). DSR, defined as the probability of a nest surviving from day to day and first introduced by Mayfield (1961), accounts for the number of exposure days a nest is vulnerable to failure. Nest success can then be estimated by raising DSR to the number of days it would take to produce one or more fledglings. The "logistic-exposure" model introduced by Shaffer (2004) allows for assessment of continuous covariates on nest success by using a generalized linear model approach. In this model, DSR is modeled in terms of covariate(s), x, assuming a binomial response distribution,

$$DSR(x) = \frac{e^{\beta_0+\beta_1 x}}{1+e^{\beta_0+\beta_1 x}}. \tag{1}$$

A modified logit link function accounts for the number of exposure days in the model. Here θ = $[DSR(x)]^t$ such that the probability of surviving (DSR) the time interval (t) is

$$g(\theta) = log_e \frac{\theta^{\frac{1}{t}}}{1-\theta^{\frac{1}{t}}}. \tag{2}$$

In this framework, each nest's fate is assumed independent of that of all others and is modeled on the values of the covariates specific to that nest.

For each spatial scale, I built models with different linear combinations of all the retained principal components for that scale (28, 28 and 16 models respectively for 1, 5, and 10km scales). In each of these models I included all 3 seasonal variables. I also built models with different linear combinations of only the seasonal variables (6 models). All models were constructed as generalized linear mixed-effects models (GLMMs) using the *glmer* function in R package lme4 (Bates, Maechler, Bolker, & Walker, 2015) to incorporate both random and fixed effects. Random effects for all models included Nest ID and Year to account for repeat observations of the same nest box within the same year. I then perfromed multi-model selection using Akaike's information criterion (AIC_c) with the *mod.sel* function from the MuMIn package in R to compare models within each spatial scale (Burnham & Anderson, 2002; Barton, 2009). Models within $\Delta AIC_c < 2$ were considered competitive.

To examine the possible inclusion of uniformative covariates in the competitive model set, I calculated 85% confidence intervals (CI) for the β-coefficient of each additional covariate (Arnold, 2010). Covariates that had β-coefficients with 85% CI that did not cross zero were considered informative and were left in final models. I used the *predict* function in R to get model prediction estimates of DSR from top models, and results were translated into nest success probabilities, $n_{s(x)}$, following *Expression 3*, at t = 50 days (the average incubation period for American kestrels of 28 days plus 22 days to fledging),

$$n_{s(x)} = DSR(x)^t. \tag{3}$$

I also built several models to examine general patterns of reproductive parameters through time in this population. DSR was modeled on year using the logistic exposure method with a generalized linear model and year as a factor to compare population daily survival rates throughout the study period. I also performed a literature search to collect published data on nest success of other populations for comparison.

Initiation date was also modeled on year using simple linear regression to examine patterns of phenology in this population and I performed an ANOVA with a post hoc Tukey HSD test of nest initiation on year to determine if differences in nest initiation date existed throughout the study period. In the analysis of nest initiation dates, additional data was drawn upon, as there were many more nests for which I could confirm initiation dates but which were not followed long enough to confirm success or failure of the nests. Thus, the total number of observations for nest initiation models was 515.

Results

General Reproductive Patterns

Nest success ranged between 54.4% (2013, 95% CI, 29.2-74.0%) and 83.3% (2015; 95% CI, 64.6-92.7%) with an average of 74.7% (Fig. 2). Comparatively, this average is relatively high for American kestrel populations across North America (Table x). There was no trend in nest initiation date over the entire study period ($F(1,513) = 1.19$, $p = 0.276$) despite variation between years ($F(8, 506) = 4.19$, $p < 0.001$; Fig. 3). Initiation dates were earlier in 2015 compared to 2012, 2018, 2019, and 2020 ($p = 0.001$, 0.012, 0.002, and 0.012 for each pairwise comparison, respectively) Likewise, initiation dates where earlier in 2016 compared to 2012 ($p = 0.033$) and 2019 ($p = 0.055$)

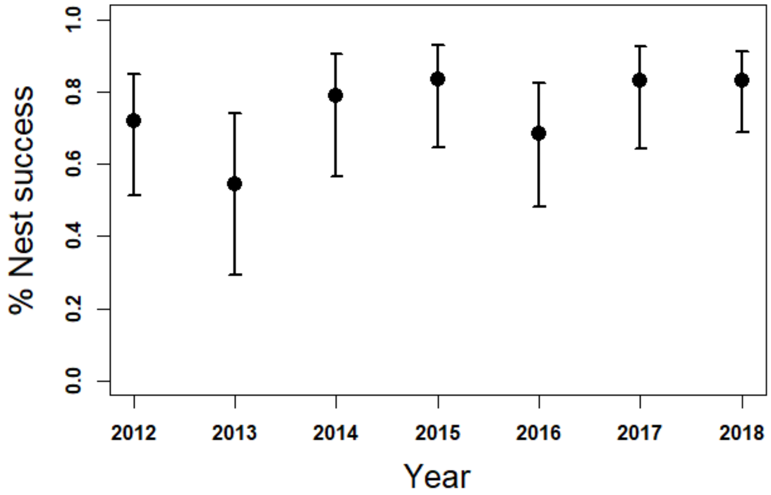

Figure 2.2. Average nest success by Year. Bars show 95% CI.

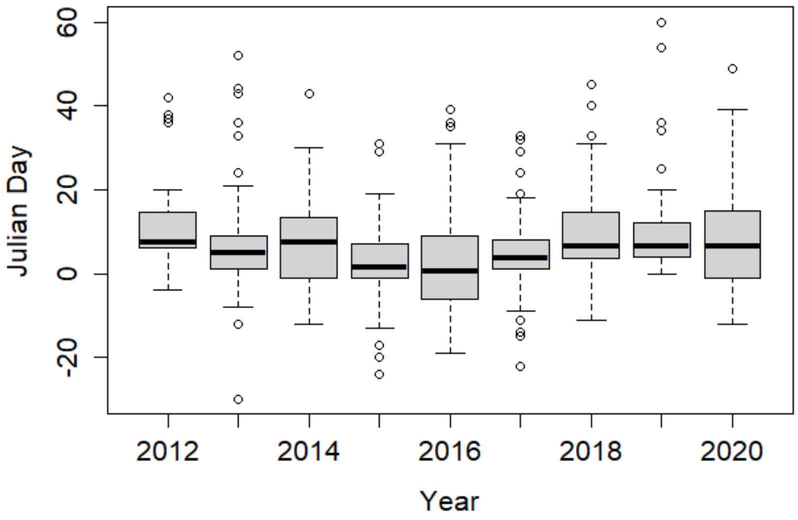

Figure 2.3. Initiation Date by Year. Bars show median dates relative to May 1.

Principal Components Analyses

The overall interpretation of the PCA for environmental variables suggested a differentiation between higher vs lower GPP, cooler and wetter years vs. warmer and dry ones, and a higher number of patch types vs. larger more continuous patches. The first 5 principal components explained 70.59% and 72.82% of the variation in environmental variables for the 1 and 5km spatial scales, respectively. Four principal components explained 71.87% of the variation at the 10km scale. Groupings of environmental variables and principal component loadings were similar across spatial scales (Table 3, S3 and S4). For instance, the 1st principal component (PC1), which explained between 26.24% and 27.35% for all spatial scales, had all 6 of the primary productivity variables loading negatively and with similar values. Variables describing maximum and mean temperature values for the two years prior to the breeding season were the strongest loadings for PC2 across all scales. PC3 primarily reflected the current year's temperature for all spatial scales. PC4 at the 5 and 10km scales and PC5 at the 1 km scale all shared the same pattern with winter precipitation one year prior loading most negatively and winter minimum temperatures one year prior loading most positively. Other notable variables that explained a large amount of variation along the principal component axes were the patch number (loading negatively along PC2) and variables describing precipitation in all years (loading positively along PC3 for the 1 and 5km scales). At the 10 km scale, PC3 differentiated between larger more contiguous patches vs. the number of patches, in addition to the aforementioned temperature of the current year.

Table 2.3. Principle components analysis for 1km scale

Summary Stats	PC1	PC2	PC3	PC4	PC5
Standard deviation	3.134	2.399	1.930	1.872	1.614
Proportion of variance	0.273	0.160	0.104	0.097	0.072
Cumulative proportion	0.273	0.433	0.536	0.634	0.710
Variable			Loadings		
ai	0.17	0.22	0.09	-0.19	0.21
area_cv	-0.01	-0.21	-0.16	0.07	-0.21
frac_cv	-0.14	0.05	-0.02	0.26	-0.26
iji	-0.17	-0.18	0.04	0.02	0.03
np	-0.12	-0.32	-0.12	0.09	-0.14
pladj	0.17	0.22	0.10	-0.20	0.22
shdi	-0.24	-0.16	-0.01	0.17	-0.12
agriculture	-0.13	-0.01	0.07	-0.14	0.17
developed	-0.17	-0.13	0.001	-0.07	0.09
grassland	-0.03	-0.18	-0.07	0.07	0.03

shrubland	0.24	-0.04	-0.17	-0.11	0.12
woodland	-0.12	0.20	0.20	0.16	-0.21
ppt_y2	0.08	-0.03	0.22	0.34	0.12
ppt_y2b	0.14	-0.21	0.24	0.11	-0.01
ppt_y2w	0.01	0.11	0.15	0.17	-0.15
ppt_y1	-0.03	0.07	-0.17	0.04	-0.20
ppt_y1b	0.07	-0.12	-0.01	0.18	0.22
ppt_y1w	0.03	0.09	0.13	-0.02	-0.44
ppt_y	0.08	-0.17	-0.04	0.33	0.12
ppt_yb	0.08	-0.19	-0.18	0.04	0.04
ppt_yw	0.02	0.01	0.08	0.41	0.22
tmean_y2	-0.14	0.30	0.07	0.18	0.04
tmean_y1	-0.18	0.23	-0.23	0.16	0.13
tmean_y	-0.15	0.12	-0.32	0.01	-0.11
tmax_y2b	-0.15	0.32	0.07	0.01	-0.04
tmax_y1b	-0.18	0.28	-0.11	0.08	0.17
tmax_yb	-0.18	0.18	-0.33	-0.06	-0.01
tmin_y2w	-0.02	0.19	0.28	0.10	-0.23
tmin_y1w	-0.05	0.09	-0.08	0.37	0.33
tmin_yw	-0.09	0.04	-0.43	0.02	-0.02
gpp_y2	-0.28	-0.08	0.13	-0.11	0.06
gpp_y1	-0.29	-0.09	0.11	-0.06	0.12
gpp_y	-0.29	-0.10	0.08	-0.09	0.09
gppb_y2	-0.28	-0.09	0.13	-0.13	0.07
gppb_y1	-0.28	-0.07	0.15	-0.10	0.09
gppb_y	-0.29	-0.07	0.12	-0.09	0.12

Model Selection

Model selection to evaluate nest success produced 9, 8, and 8 competitive models ($\Delta AIC_c < 2$) for the 1, 5 and 10 km spatial scales, respectively (Table 4). The three seasonal variables were present in all these models at all spatial scales. In each set of competitive models for each spatial scale, all retained principal components for that spatial scale were represented in varying combinations with other principal components or singly, but always with all three seasonal variables. Examination of model coefficients showed only PC1 had an 85% CI that did not cross zero. Therefore, I considered the seasonal only model (all three seasonal variables) and the model with all three seasonal variables plus PC1 to be the best models predicting DSR at all spatial scales in this study system, with other competitive models as nested subsets of these models with additional uninformative covariates (Arnold 2010). Here, I only report model results for the top model including PC1 at the 1km scale. However, top models at all scales had similar coefficients (Table 4).

Standard deviation for random effects of nest id was non-zero ($\sigma_{Nest\ ID}$ = 0.5003), suggesting that its inclusion in the model was warranted. The same did not hold for year as a random effect (σ_{Year} = 0.000), and it was subsequently dropped from the final models. There was a strong positive relationship of DSR with initiation date and the average age of nests ($\beta_{Initiate} = 0.1843, 85\%\ \mathrm{CI} = 0.0885$ to 0.2730; $\beta_{Age} = 0.1961, 85\%\ \mathrm{CI} = 0.1025$ to 0.2806; Figs. 4 and 5), while a strong negative relationship was found between the average day of the observation interval and DSR ($\beta_{Day} = -0.2013, 85\%\ \mathrm{CI} = -0.2829$ to -0.1075) (Fig 6). There was also a negative effect of PC1 on DSR ($\beta_{PC1} = -0.0755, 85\%\ \mathrm{CI} = -0.1425$ to -0.0070; Fig 7).

Table 2.4. Model selection results for 1 km scale. Each model includes random effects of nest ID and year.

Model	K	logLik	AICc	delta	weight
Initiate + AvgAge + AvgDay	6	-152.12	316.42	0	0.16
Initiate + AvgAge + AvgDay + PC1	7	-151.17	316.58	0.162	0.147
Initiate + AvgAge + AvgDay + PC3	7	-151.42	317.08	0.66	0.115
Initiate + AvgAge + AvgDay + PC4	7	-151.83	317.89	1.477	0.076
Initiate + AvgAge + AvgDay + PC1 + PC4	8	-150.85	318	1.585	0.072
Initiate + AvgAge + AvgDay + PC1 + PC2	8	-150.97	318.25	1.829	0.064
Initiate + AvgAge + AvgDay + PC2	7	-152.02	318.27	1.852	0.063
Initiate + AvgAge + AvgDay + PC5	7	-152.02	318.27	1.857	0.063
Initiate + AvgAge + AvgDay + PC1 + PC3	8	-151.02	318.34	1.921	0.061
Initiate + AvgAge + AvgDay + PC2	7	-152.07	318.38	1.958	0.06
Initiate + AvgAge + AvgDay + PC3	7	-152.08	318.39	1.971	0.06
Initiate + AvgAge + AvgDay + PC4	7	-152.09	318.42	1.998	0.059

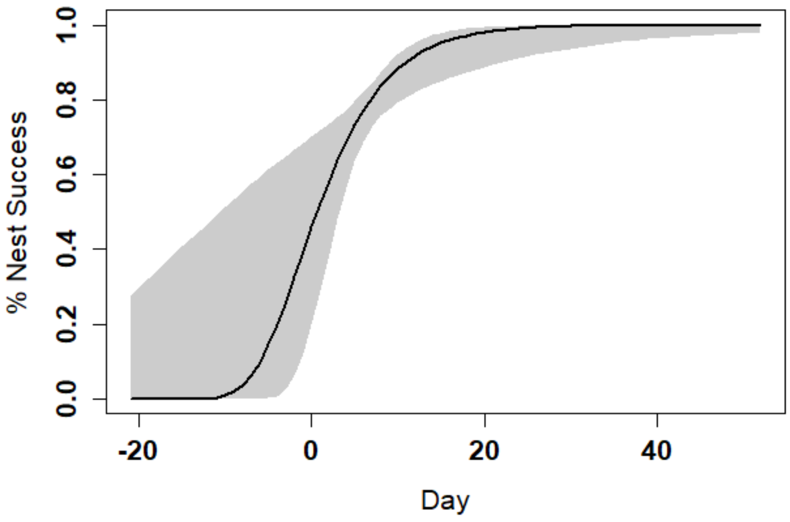

Figure 2.4. Nest success by initiation date. Gray shaded area shows 95% CI.

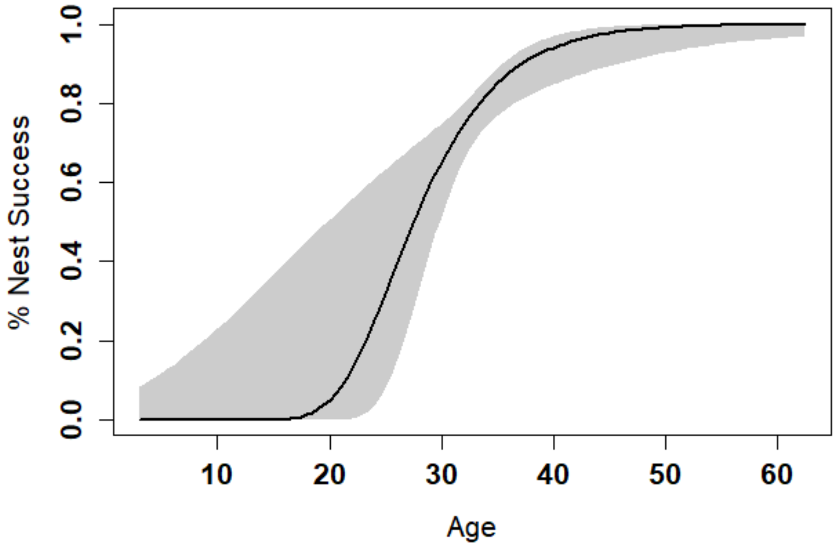

Figure 2.5. Nest success by age of nest. Gray shaded area shows 95% CI.

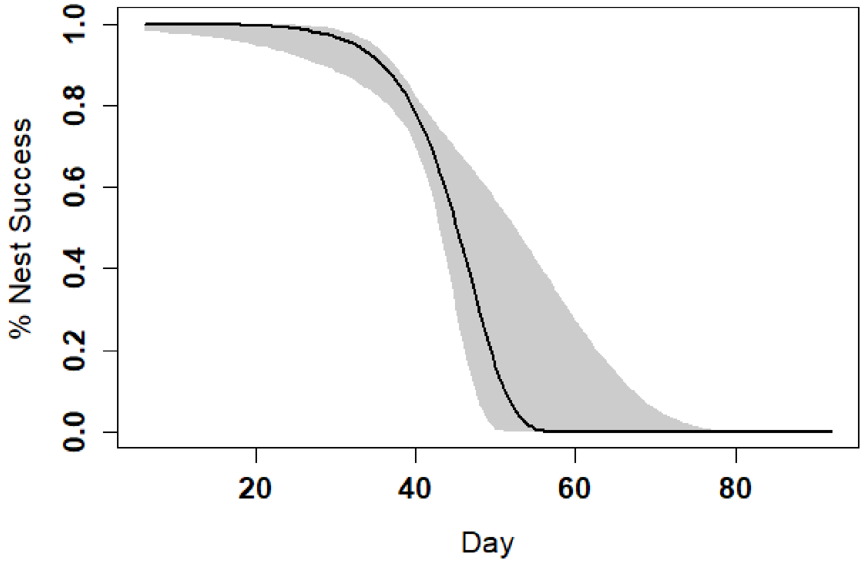

Figure 2.6. Nest success by day-of-year. Gray shaded area shows 95% CI.

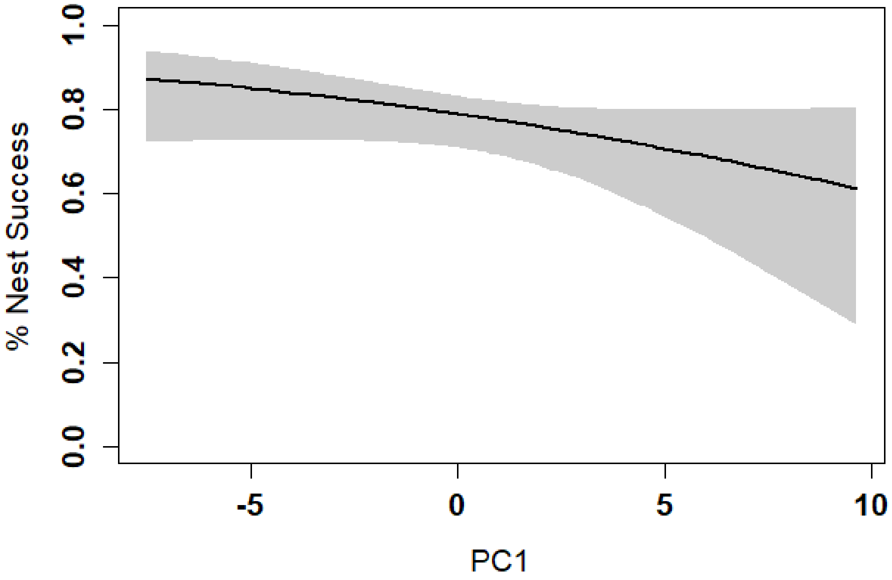

Figure 2.7. Nest success PC1. More negative values of PC1 represent increasing GPP. Gray shaded area shows 95% CI.

Discussion

Reports of American kestrel populations being in continual decades-long declines across North America have garnered increasing attention from the raptor research community (Farmer *et al.*, 2008; Farmer and Smith, 2009; Smallwood *et al.*, 2009; Paprocki *et al.*, 2014; Sauer *et al.*, 2014; McClure *et al.*, 2017a). Working with federal agencies, non-profit organizations, and community scientists monitoring American kestrels across their annual cycle, researchers are racing to identify the cause or causes of this decline (McClure *et al.* 2017a). Importantly, not all American kestrel populations are declining at an equal rate, nor are all populations declining; numbers are actually increasing in some regions of the continent (Sauer *et al.*, 2019). This suggests that the causes of decline might vary from region to region. I studied a population of American kestrels nesting in artificial nest boxes in Central Oregon, an understudied region for this species, to examine various reproductive parameters, how they compare with other populations, and to what degree successful reproduction is influenced by the abiotic environment.

Based on seven years of nesting history, I find that American kestrels in Central Oregon have a relatively high average rate of nesting success when compared with other populations around North America (Figure 1 and Table x). Moreover, the number of nests initiated each year has slightly increased over this time period, suggesting a stable or potentially increasing population (although see McClure *et al.*, 2017b). Recently published data from the Breeding Bird Survey (BBS) suggest that the decline in American kestrel populations for the Great Basin Bird Conservation Region (BCR), just to the southeast of Central Oregon is much lower than many other BCR's with significantly decreasing trends (Sauer *et al.*, 2019). Oregon, too, has a relatively low, albeit significan,t decreasing trend in the BBS data and Washington's trend is non-significant. The Great Basin BCR also has one of the highest relative abundances of American kestrels according to the BBS (Sauer *et al.*, 2019). It's likely that the Central Oregon high desert, which is similar to the Great Basin in that it is sparsely populated in many places with large tracts of open and semi-open sagebrush and grassland ecosystems, provides excellent habitat for American kestrels.

While these numbers are encouraging for American kestrel populations in the region, it should be noted that nest success and stable or increasing nest attempts do not necessarily signify a stable or increasing population. A long-term study of American kestrels breeding in Southwestern Idaho found steady rates of nest success across a 15-year period while at the same time the average number of breeding birds decreased in the region (Brown *et al.*, 2013; Sauer *et al.*, 2019). Work by McClure *et al.* (2021) examining population growth in four different American kestrel populations found that adult survival and immigration were the two most important vital rates describing population growth. Researchers also must be careful about interpreting data from kestrels nesting solely in boxes, as this may not reflect the entire regional population, and dynamics between kestrels nesting in boxes and kestrels nesting in natural cavities may be obscured by lack of information on the latter (McClure *et al.*, 2017b).

I did not find any trend in phenological shift in nest initiation over time (Fig 2). It is well documented that advances in spring phenology of nesting are increasingly common in birds as a result of a warming climate over the past several decades (Parmesan and Yohe, 2003; Visser *et al.*, 2003; Both *et al.*, 2004). Reports of American kestrels advancing nest initiation in Southwestern Idaho, at roughly the same latitude and within the same BCR and BBS stratum as Central Oregon, range from 15-21 days earlier since 1992. These shifts in phenology have been correlated with warmer winter temperatures, and in particular, advances in the start of the growing season in irrigated landscapes (Heath *et al.*, 2012; Anderson *et al.*, 2016; Smith *et al.*, 2017). While the data do not allow me to estimate the start of the growing season for each year, I did see significant warming in the average winter temperature across the sites through time. Why I don't see a concomitant change in nest initiation thus requires more investigation. One factor that might explain the disparity of responses is the roughly 700-800 ft elevation gain from the Southwestern Idaho study sites to the sites in Central Oregon. A recent analysis of spring arrival times for American kestrels across the Northern United States and Canada revealed that snow was a significant factor delaying spring arrival for American kestrels independent of latitude (Powers *et al.*, 2021). It is not uncommon for many of the nest sites to receive snow episodically into the spring months (personal observation) which could lead to prevention of advances in nest initiation. Powers *et al.* (2021) also note the general east/west divide in American kestrel phenological advances, with American kestrels in the Eastern U.S. showing little to no advancement. However, I show here that the variation in American kestrel phenology may be even more localized.

The abiotic environment can have wide-ranging direct and indirect effects on the nest success of birds (Dreitz *et al.*, 2002; Rodewald, 2002;

Greenwood and Dawson, 2011; McIntyre and Schmidt, 2012; Brown *et al.* 2014; Wallace *et al.*, 2016). However, I found that within-season variables (nest initiation date, age of nests, and day-of-year) had a stronger influence on the nest success of American kestrels in Central Oregon than any measured abiotic variables. While counterintuitive at first, two of these within-season variables, nest initiation date and day-of-year, likely reflect aspects of the abiotic environment, particularly changes in weather throughout the breeding season. The third variable, age of nests, is more likely to reflect chicks' abilities to maintain homeostasis and other physiological processes that promote survival as the chicks develop. Surprisingly, nest initiation dates were positively associated with nest success in this study, while for many bird species, including other populations of American kestrels, earlier initiation of nests have been shown to lead to higher probability of success and higher productivity of offspring (Perrins, 1970; Newton, 1979; Verhulst *et al.*, 1995; Dinsmore *et al.*, 2002; Shaffer, 2004; Grant *et al.*, 2005; Del Corso 2021). Predictions from the best supported model, however, seem to suggest that American kestrels at these study sites pay a high cost when initiating nests before the start of May 1 (Fig 3). I suspect that this may have to do with cooler spring temperatures and unpredictable late winter storms that can bring snowfall to the area, both of which may tip the scales towards survival in the trade-off between rearing a successful clutch and individual survival when resources suddenly become scarce or hard to acquire.

The one variable that that seemed to have a moderate effect on nest success was primary productivity (Fig 6). I found that higher measures of primary productivity conferred greater nest success to American kestrels no matter the scale. I was particularly interested in understanding if nest success showed a lagged response to primary productivity in previous years as this has been hypothesized for other systems (Walker *et al.*, 2013; Ringelman *et al.*, 2018). Primary productivity can lead to an increase in the prey base for American kestrels, thus one might expect there to be some sort of temporal lag between when an increase in primary productivity occurs, boosting the prey base, and when greater nest success is realized (Tornberg *et al.*, 2005; Polis *et al.*, 2004, Yang *et al.*, 2010). Based on the results of the PCA, however, I was unable to parse which years (prior or current years) or which measure of GPP (annual or breeding season) had the strongest effect on nest success because all variables loaded approximately equally on the 1st principal component axis at all spatial scales. It would therefore be useful to know how common diet items for kestrels at these study sites respond to pulses in productivity and on what time scale.

Other studies of kestrel nest box occupancy and nest success have found clear relationships with measures of landscape composition and structure, as well as measures of climate (Brown *et al.*, 2014; Dawson and

Bortolotti, 2000; Greenwood and Dawson 2011; Orozco and Grande, 2020). For example, an escalation in inclement weather in Alberta, defined by the authors as cooler, stronger winds and heavier rainfall, led to reduced development and higher mortality in American kestrel nestlings in artificial nest boxes (Dawson and Bortolotti, 2000). The authors interpreted variation in nest success in this Alberta population as an effect of food availability mediated through variation in weather. On the other side of the world, nest success of American kestrels in Argentina was negatively associated with increased maximum temperatures during the nestling period and increased rainfall in November, around the middle of the breeding season there (Orozco and Grande, 2020). Thus, I was surprised to find no other effects from the abiotic environment on the population of Central Oregon kestrels studied here.

One reason why I may not have found any effects of the abiotic environment beyond primary productivity could be the fact that the climate variables were averaged annually or seasonally (4 months). Such averaging could minimize important variation in weather patterns that might prove more influential in the analysis. The two studies highlighted previously averaged climatic variables over much shorter temporal spans (days to weeks). The fact that initiation date and day-of-year both had significant impacts on nest success at these sites also suggests that variables more indicative of weather rather than climate may be more useful predictors of nest success.

Another reason may be related to the methodological approach I take here, collapsing all of the environmental variables into a few principal component axes, rather than approaching the analysis via step-wise model building used in many other nest success studies. In the latter approach, variables are often separated along spatial or temporal scales or by some categorical ranking and subjected to separate analyses from which the significant covariates are carried forward and combined with a new grouping. Such analyses may fail to consider how the significant covariates from one grouping interact with the non-significant variables from another grouping and therefore preferentially select variables based on spurious conclusions. Such analyses also can fail to consider the correlation among predictor variables, leading to invalid results. While using the PCA approach I employ here allows me to avoid these issues, this method may mask important covariates that are overwhelmed by others in the PCA.

Conclusion

Overall, this study suggests that American kestrels in Central Oregon are not undergoing as dramatic declines, if any at all, as other populations across North America. Nest success appears to be relatively high and stable in this population, and there have yet to be clear shifts in phenology over the last 7 years as I have seen in other populations in similar ecosystems. Primary productivity and seasonal changes in the environment, likely driven by short-term variation in weather rather than longer-term variation in climate, best describe the variation in nest success. I note that this study was undertaken before some of the hottest summers on record and the widespread wildfires that occurred across the region in 2020. Therefore, continued study of this population might reveal new insights into various measures of population dynamics driven by changes in the environment due to these factors.

Chapter 3: Sizing up the rules: Evaluation of body size proxies for ecomorphological studies in birds

Introduction

The documented impacts of climate change on plants and animals have included a wide array of biological responses. The global coherence of certain responses suggests that a universal signal, or “fingerprint”, may be evidence of the role of climate change as a driver. Two of the most supported responses representing a climate change fingerprint are poleward (upward) range shifts, and advances in spring phenology (Parmesan and Yohe, 2003; Walther *et al.*, 2002; Parmesan 2006; Kelly 2008; Chen *et al.*, 2011; Cohen *et al.*, 2018; Kharouba *et al.*, 2018). A third universal response, declining body size, has also been suggested (Daufresne, Lengfellner, & Sommer, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011). Invoking Bergmann’s rule, the ecogeographic rule explaining patterns of clinal variation in the body size of endotherms as an adaptive mechanism for thermoregulation, some authors have argued that warming global temperatures may cause species to shift towards smaller body sizes (Millien *et al.*, 2006; Yoram Yom-Tov & Geffen, 2011; Daufresne, Lengfellner, & Sommer, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011). Documented correlations between warming temperatures and a decline in the average size of some species over decadal to millennial time spans lend support to this claim (Smith *et al.*, 1995; Yom-Tov, 2001; Yom-

Tov *et al.*, 2006; Van Buskirk *et al.*, 2010). However, results across taxa and regions have proved equivocal (Collins *et al.*, 2017; Goodman *et al.*, 2012; Meiri *et al.*, 2009; Salewski *et al.*, 2014; Teplitsky and Millien, 2014). Moreover, few researchers studying this phenomenon have provided a clear definition of body size, and many use single traits as proxies for body size that may or may not be germane to Bergmann's rule, *sensu stricto*, or thermoregulation more generally (Teplitsky & Millien, 2014; Yom-Tov & Geffen, 2011).

In order to assess whether body size is declining through time according to Bergmann's rule, or, more generally, to assess the role of environmental factors in driving body size variation within and among species, one must first obtain a reliable indicator of body size. This seemingly trite observation is not a trivial matter. Body size is multi-dimensional and there is no agreed upon definition of it in the literature; sometimes referenced using linear measurements, as in single dimensions of limb lengths, sometimes referenced in terms of volumes, as in mass. Indeed, researchers purporting to study the same phenomenon often use different dimensions of body size. This confusion of size and mass has led some to call for greater clarity in what is being measured (Piersma and Davidson, 1991; Pascual and Senar, 1996). Piersma and Davidson (1991) suggested the term structural size to describe the nutrient reserve-independent size of an organism and distinguish it from nutrient reserve mass, which is "the variable amounts of nutrients (chiefly fat and protein) that permit birds to exercise and survive periods of negative energy and nutrient balance." Structural size, therefore, is independent of nutritional status, and is the variable most appropriate in studies of geographic or temporal size variation (Piersma and Davidson, 1991). Below, I review the problems with the use of common body size proxies in the ornithological literature before arguing for a more reliable measure of structural size in birds. I then analyze which combination of external morphological traits easily measured from museum specimens or live birds best approximates this structural size measure.

A proxy for body size

Mass and wing chord are probably the two most common measurements used to describe body size in birds. Mass has a long history of use in the ecological literature because of its well-documented consistent scaling particularly with metabolic rate, but also with other life history characteristics and vital rates across many orders of magnitude (Kleiber, 1932; Calder, 1984; Peters, 1983; Schmidt-Nielsen, 1984; Brown *et al.*, 2004). When comparing the whole of life across twenty-plus orders of magnitude, mass may be seen as a reliable indicator of body size. However, in terms of structural size, especially when comparing size variation within a species, or closely related species, mass becomes a less reliable indicator. At this scale of analysis, the daily, seasonal and annually labile nature of mass within individuals has the potential to confound results. Depending on the time of year, whether a bird is migrating, molting, breeding, brooding, whether it's young or old, its genetic propensity, even the time of day, a bird's mass is likely to be in flux simply due to inherent natural cycles of fluctuation in metabolism. On top of the cyclical patterns of fluctuation in mass, conditions of the environment and the availability of resources create further variability. A single, instantaneous measure of mass, therefore, is an unreliable indicator of structural size, even when controlling for some of the above.

Wing chord on its own is not much better at describing structural size than mass. Wing chord is measured as the distance between the carpal joint of the wrist to the tip of the longest primary (Eck *et al.*, 2011; although see Stiles and Altshuler (2004) for discussion of terminology in regard to animal-flight research). As such, it is primarily a measure of feather length (Jenni and Winkler, 1989; Pascual and Senar, 1996). This measure has been in standard use in ornithological research for over a century and became a common proxy for body size following several studies that found a strong correlation between wing chord and mass, (Ridgeway, 1901; Baldwin *et al.*, 1931; Connell *et al.*, 1960, Svensson, 1970, Gosler *et al.* 1998; Winker 1998). However, similar to mass, feather length is a highly labile characteristic, prone to selection pressures on body condition, aerodynamics, foraging behavior, migration distance and predation pressure (Grubb, 1995; Norberg, 1981; Marchetti *et al.* 1995; Zink and Remsen, 1986; Telleria and Carbonell 1999; Leisler and Winkler, 2003; Gosler *et al.*, 1995; Lank, 2017). Age and time since molt can affect feather length and wear patterns independent of body size (Smith, 1992; Nilsson, 1992; Nielsen 1993; Rogers 1990). Sexual selection, too, imposes constraints on wing feathers (Bjorklund, 1990; Andersson and Andersson, 1994). All of these factors may be decoupled from thermoregulatory considerations, *sensu* Bergmann's rule.

The use of wing chord as a measure of body size no doubt stems in part from its practicality, ease of measurement, and the minimal training needed to perform the measurement without causing damage to museum specimens or live birds. However, its logic as a reliable indicator of structural size relies on its correlation with mass, itself an unreliable indicator of structural size among taxonomically close species for reasons I've just discussed. The evidence of the unreliability of these measures as indicators of structural size, one reliant on the other, is best shown when assessing changes in morphology through time. Several studies have found divergent trends in wing length and body mass within the same species (Collins *et al.*, 2017; Salewski *et al.*, 2014; Yoram Yom-Tov *et al.*, 2006). Whether this is evidence against Bergmann's rule, as claimed by some authors, or evidence of an unreliable indicator of size is unclear. Furthermore, Allen's rule, another well-known biogeographic rule that describes the inverse relationship between appendage length and temperature, predicts a trend for wing length that is opposite Bergmann's rule; that wing length should increase as temperatures warm (Teplitsky & Millien, 2014; Yom-Tov & Geffen, 2011). Studies using a decrease in wing length to suggest a declining trend in structural size therefore fail to meet the predictions of one biogeographic rule while supporting another.

Tarsus length is another commonly used proxy for body size. Essentially a measure of the tarsometatarsal bone (although see below), it is measured as the distance from the intertarsal joint to the joint between tarsus and toes (Eck *et al.*, 2011). It would seem to be more reliable given its direct correspondence to a skeletal element; such a character would presumably be less dependent on nutrient reserves or environmental conditions in adult vertebrates with determinant growth. Several authors have even suggested tarsus length as the best single measure approximating structural size in birds, although all authors subsequently advise against the use of a single linear measure to estimate structural size (Rising and Somers, 1989; Freeman and Jackson 1990; Senar and Pascual, 1997). In one study the external measure of tarsus length only explained 69% of the variation of the internal tarsometatarsus length, indicating significant influence from the epidermal and dermal layers of the skin, and only 46% of body size, as calculated from a principal components analysis (PCA, described below) (Senar and Pascual, 1997). Thus, none of these linear measures provide a reliable indicator of structural size in birds.

A path forward

Previous authors have argued that the first principal component of a PCA of linear measurements from multiple skeletal elements is a good representation of structural size (Ankney and Afton, 1988; Rising and Somers, 1989; Alisauskas and Ankney, 1990; Freeman and Jackson, 1990; Piersman and Davidson, 1991). Others have used dried and fat-free skeletal mass, or skeletal volume by water displacement (SV) (Wishart, 1979; Moser and Rusch, 1988). These methods are appropriate and robust, especially the latter two, when there is enough skeletal material to accurately assess variation among specimens. For species that are limited in geographic range, a few specimens with a full complement of skeletal material may be sufficient, however, for widespread species with potentially much higher morphological variation across their range, many more specimens may be required. This is problematic because most natural history collections do not prioritize the preservation and storage of more than a few reference skeletons per species, often only a few large skeletal elements are preserved, or skeletons are not paired with study skins (although see the Museum of Southwestern Biology at the University of New Mexico). This is largely a result of historical preference among ornithologists. The study skin emerged early on in the build-up of natural history collections of birds as the unit of comparison and largely remains so today (James, 2017).

More recently, photogrammetric, laser imaging and 3D computer modeling methods have been developed recreate body volumes from whole mounted skeletons. These methods use point clouds from 3D images to calculate convex hulls for the estimation of body volumes (Clauss *et al.*, 2017;

Brassey and Sellers, 2014; Bates *et al.*, 2009; Klein *et al.*, 2011; Gunga *et al.*, 2007; Sellers *et al.*, 2012). While more likely to accurately depict structural size than previous PCA methods, these methods, too, suffer from several drawbacks. If disarticulated skeletal elements stored in a small box in natural history collection cabinets are rare, fully articulated specimens are even more so. Research using these methods tends to focus on, and is probably more appropriate for, the paleontological record (Gunga *et al.*, 2007; Klein *et al.*, 2011; Bates *et al.*, 2009) or on a much broader taxonomic focus (Clauss *et al.*, 2017; Brassey and Sellers, 2014). Moreover, the quality of the articulated specimen is critical to obtaining accurate results, in particular the positioning and spacing of the ribs (Clauss *et al.*, 2017). Building off of previous research, I argue that a relatively simple method for 3D imaging the sternum of birds can circumvent these issues and provide a low-cost, easily obtainable, and reliable indicator of structural size.

Building off of previous research, I argue that a relatively simple, low cost method for 3D imaging of the sternum of birds can circumvent these issues and provide a reliable indicator of structural size. Sternums are a single skeletal element that convey a large degree of information about the structural size or volume of a specimen and are small enough to be stored in collections in amounts suitable to the study of intraspecific variation would eliminate some of the drawbacks of the above methods. In addition, Moser and Rusch (1988) lay out 4 other qualities that would make a desirable indicator of structural size, and I argue that the bird sternum fits them all: 1) relative constancy throughout a bird's adult life, 2) an inherent correlation between external structural measurements, 3) a standard of size against which correlations to external measurements can be tested, and 4) independence from nutrient reserves. I believe the bird sternum fits most of the qualities listed above.

The sternum is the largest and single most three-dimensional skeletal element in a bird (Zheng, 2012), providing the structure for the attachment of the single largest muscle in a bird, the pectoralis. In fact, for volant birds, the pectoral musculature is the largest organ in a bird's body, accounting for between 15-33% of the total body mass (Steen and Enger, 1957; Greenewalt, 1962; Calder and King, 1974; Dawson and Carey, 1976, Zheng 2012). The length, width, and camber of the lateral surface of the sternum, the *facies muscularis sterni*, along with the length of the ribs, helps to determine the volume of the body cavity. Longer, wider sternums with less camber, all else being equal, confer a trunk with larger volume. The length, height, and curvature of the keel of the sternum, the *carina sterni*, define the area of the muscle attachment for the pectoralis muscle. As these parameters increase, so too does the volume of the bird (Brassey and Sellers, 2014, Clauss *et al.* 2017).

Bird skeletal muscles, and in particular large muscles like the pectoralis, are a major source of heat generation and thermogenetic capacity in birds (Dawson and Carey, 1976; Block, 1994; Bicudo *et al.*, 2001). Unlike mammals which generate heat through non-shivering thermogenesis in brown adipose tissue, birds, lacking the thermogenetic mechanisms for these heat generating cells, rely on non-shivering and shivering thermogenesis in muscle cells (Duchamp and Barre, 1993; Rowland *et al.*, 2015; Nowack *et al.*, 2017). The larger the muscles, the greater the heat generating capability (Milbergue *et al.*, 2018; see Newman 2011 for the speculative role of muscle hyperplasia and thermogenesis in the evolution of flight). Thus, not only does the sternum convey information about the trunk volume of the individual, it also conveys information about the heat generating capacity of an individual via the area of muscle attachment. Volume and thermogenic capacity are two critical pieces of information in assessing ecogeographical rules such as Bergmann's rule (Bergmann, 1847).

In addition, the size of the sternum is fixed in the adult bird, and being a single skeletal element, is less likely to vary than the skeletal volume due to bone marrow loss post-mortem. Since the study of size variation often relies on the use of museum specimens, shrinkage of body elements during preparation can be a concern (Jenni and Winkler, 1989). Shrinkage due to museum specimen preparation is not common for the sternum and is equivocal for other skeletal elements (Winker, 1993, see also references in Jenni and Winkler, 1989), and most shrinkage through drying and study skin preparation appears to occur in external traits with significant soft tissue attachments (Winker, 1993). In fact, in a study of post-mortem shrinkage in falcons, no skeletal elements shrank (Eastham *et al.*, 2000). Thus, as with the entire skeleton, once cleaned, the sternum is independent of any nutrient reserves.

Below, we lay out a new method of quantifying structural size in birds based on the sternal element using a 3D geometric morphometric approach. With advances in and accessibility to 3D imaging technology increasing, I believe this method could provide a standard metric for structural size in birds. I then use this measure to determine which non-structural linear measurements on study skins best represent structural size. This will allow me to pursue more accurate studies of size variation in the subsequent chapter of this dissertation

Methods

Data collection

I focused this analysis on American kestrel specimens housed in museums for which I could find both study (round) skins and sternums registered in museum collection databases. I searched VertNet for records containing the words "*Falco sparverius*" and "skin" and "skeleton". Out of the 170 results returned from this search, I removed any records that indicated a full study skin was not available, e.g. "flat skin" or "partial skin" or "spread wing", or which I could not obtain all of the required measurements. For the remaining 118 records, I was able to obtain 29 specimens of which 24 were used in the analysis because they had both a full study skin (full complement of measurements) and an intact sternum for analysis (Table S1).

Measurements

For each study skin, I obtained measurements that are commonly used on avian museum specimens and on live birds in the field for the assessment of ecomorphological studies (Aldrich and James 1991; Winker *et al.* 1998; Eck *et al.*, 2011). These included, wing cord (WC), wing width (WW), tarsus length (TS), tail length (TL), bill length (BL), bill depth (BD), and bill width (BW) (see Table 1 for descriptions). A butted wing ruler was used to obtain WC, WW and TL to the nearest mm. I used digital calipers to obtain TS, BL, BD and BW to the nearest one hundredth of a mm (Fig 3.1c). All measurements were taken from the specimen's right side. All measurements were taken by a single observer (MDB) to reduce variation due to asymmetry and inter-operator error. I also recorded the mass for each specimen at the time of accession if it was provided in the records.

Table 3.1: Descriptive statistics of size variables. Mass in grams. All others in mm. WC=wing chord, WW=wing width, TL=tail length, TS=tarsus length, BL=bill length, BD=bill depth, BW=bill width, CS=centroid size.

Statistic	Description	N	Mean	St. Dev.	Min	Pctl(25)	Pctl(75)	Max
Mass	Recorded at time of accession	22	93.18	17.02	64.20	80.03	104.30	135.00
WC	From the carpal joint to the tip of the wing	24	189.42	11.32	167	182	196.5	206
WW	From the carpal joint and the tip of the longest secondary	24	109.96	6.40	100	104.5	115.2	120
TL	From the pygostyle felt below to the tip of the tail	24	124.00	6.09	111	120	129	139

TS	From the intertarsal joint to the joint between tarsus and toes	24	34.50	1.78	31.45	33.24	35.70	38.59
BL	From the distal edge of the nostrils to the tip of the bill.	24	12.16	0.68	10.60	11.65	12.78	13.25
BD	Depth of upper bill measured at the distal edge of the nostrils	24	7.27	0.61	6.06	6.83	7.58	8.39
BW	Width of upper bill measured at the distal edge of the nostrils	24	7.77	0.41	7.11	7.51	8.06	8.69
CS	Centroid size of sternum from geometric morphometric analysis (see text)	24	60.47	2.52	56.08	58.29	62.78	64.35

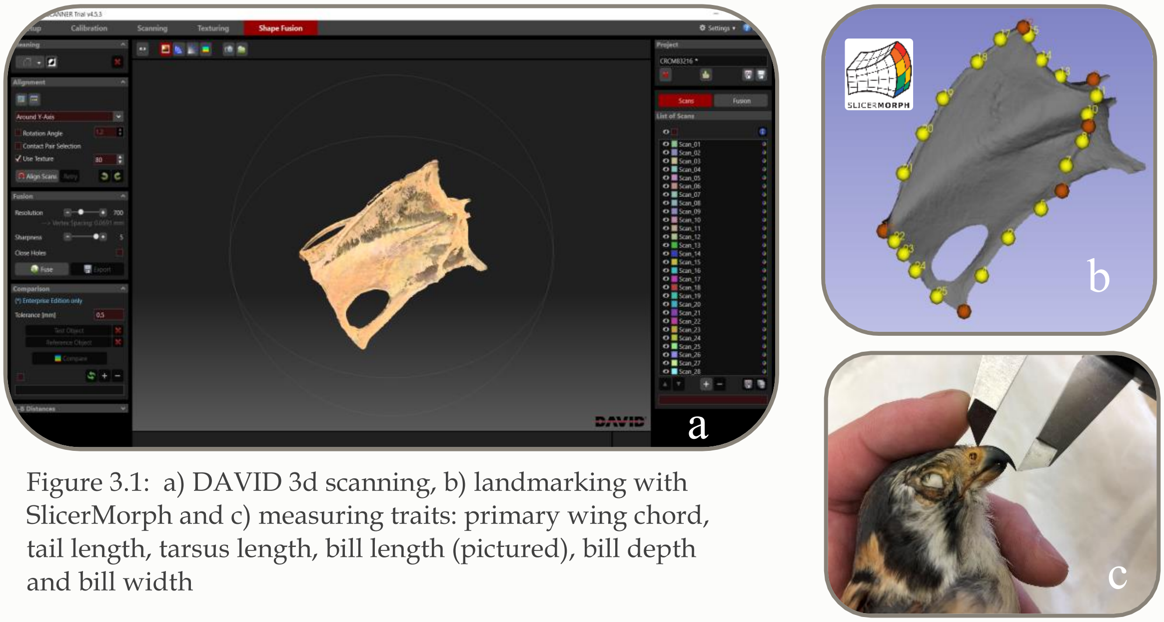

Figure 3.1: a) DAVID 3d scanning, b) landmarking with SlicerMorph and c) measuring traits: primary wing chord, tail length, tarsus length, bill length (pictured), bill depth and bill width

I used a 3D geometric morphometric approach to obtain a measure of structural size from each sternum which consisted of: imaging and landmarking followed by geometric morphometric analysis. The imaging was performed with a DAVID structured light scanning system and associated software (DAVID Vision Systems GMBH, Koblenz, Germany, version 3). Structured light scanning technology has been shown to be just as effective for imaging 3D surface structures as photogrammetry methods and represents a low-cost alternative to micro-CT scanning (Geng, 2011; Thomas *et al.*, 2016; Mate-Gonzalez *et al.*, 2017). The David system consist of camera and a LED projector (to project the structured light) mounted atop a tripod and interfaced with the specialized software, and a 3D calibration board for calibrating the software (Geng, 2011; McWhinnie and Parsons, 2019). Once calibrated, specimens were place approximately two feet in front of the tripod setup on a turntable in the field of view. An image was captured, and then the specimen rotated between 20 and 45 degrees at which point a second image was captured. This process was continued until all surfaces of the sternum had been successfully imaged. The number of images used to capture the full three-dimensional surface ranged between 8 and 21 (mean = 14). I then used the "Cleaning" and "Fusion" functions to isolate the sternum, removing all other skeletal elements and scanning artefacts (Fig 3.1a). Cleaned sternum images were then saved as a polygon file (.ply)

After imaging, all files were imported into the SlicerMorph software extension of 3D Slicer for landmarking (Rolfe *et al.*, 2021; Fedorov *et al.*, 2012; Buser *et al.*, 2020). SlicerMorph allows the user to generate landmark and semi-landmarks on 3D volumes, conduct geometric morphometric analyses, create animations, and export landmark files for analyses in other software (Rolfe *et al.*, 2021; Buser *et al.*, 2020). I used the "Markup" function in SlicerMorph to place 6 landmarks on the right side of the sternum outlining the area in contact with the pectoralis musculature (Chamberlain, 1943; Baumel, 1993; Pathak *et al.*, 2017; Kırbaş and Tacki, 2019) (see Table 2 for anatomical descriptions of landmarks; Fig 3.1b). I then used the "Curve Resample" function to create semi-landmark curves between landmarks along the 3D surface with semi-landmarks equidistant, resulting in 19 additional semi-landmarks (Fig 3.1b). All landmark data was saved and then imported into R statistical software for geometric morphometric analysis.

Table 3.2: Landmark numbers and their anatomical descriptions

Landmarks	Anatomical Description
1	Lateral caudal process/processus lateralis caudalis/trebecula lateralis
3	Caudal margin of the costal facets/incisura costales
6	Facet for articulation with corcoids bone/tuberculum labri externum
9	Sternal manubrium/manubrium sterni/sterni externus
12	Cranial process of the keel/apex carinae
16	Metasternum/trabecula mediana

I used package "Geomorph" in R to perform a Generalized Procrustes Analysis (GPA) on the set of saved landmarked points (Adams *et al.* 2004). GPA superimposes landmark configurations, scaling configurations to a common unit size and optimally rotating configurations to minimize the squared differences between corresponding landmarks (Bookstein 1986; Rohlf and Slice, 1990; Rohlf and Marcus, 1993; Adams *et al.*, 2004; Zelditch *et al.*, 2012). For this analysis, it is the scaling factor, the centroid size (CS) (the square root of the sum of squared distances of all landmarks from the centroid) that is the metric of interest. I extracted CS for each landmark configuration (i.e., each sternum) and used this measure as a measure of structural size (Cardini *et al.*, 2007; Tornberg *et al.*, 2014) (Table 1).

Statistical Analyses

All analyses were performed using Ordinary Least Squares regression (OLS) with CS as the independent variable. I constructed OLS models with all combinations of the seven size measurements from study skins as linear combinations of explanatory variables, resulting in 124 models. I also built an OLS model with mass as a single explanatory variable for n=*22* specimens that had an associated mass measurement in the specimen record. I then ran a several multi-model comparisons based on Akaike's information criterion (AIC_c) with the *mod.sel* function from the MuMIn package in R (Barton, 2009). Models within $\Delta AIC_c < 2$ of the top model were considered competitive (Burnham & Anderson, 2002). To examine the possible inclusion of uniformative covariates in the competitive model set, I calculated 85% confidence intervals (CI) for the β-coefficient of each additional covariate (Arnold, 2010). Covariates that had β-coefficients with 85% CI that did not cross zero were considered informative and left in final models. For the first model comparison, I restricted the analyses to only specimens that had mass measurements, n=*22*, and included all univariate models of study skin measurements, plus the model with mass as an explanatory variable. The second model comparison included all 124 models with linear combinations of study skin measurements.

Results

None of the most common single measurements used to describe the body size of birds in ecomorphological research, WC, TS and mass, were within $\Delta AIC_c < 2$ of the top model (Table 3). Mass explained the least amount of variation in CS in the dataset (R^2=0.058; *F(1,20) = 1.23; p = 0.28*), and neither tarsus nor wing chord explained more than approximately 16% of the variation in CS (R^2=0.161; *F(1,20) = 3.83; p = 0.064* and R^2=0.098; *F(1,20) = 2.16; p = 0.157*, respectively) (Fig 3.2a-c). Tail length explained the most variation in CS among univariate measures (R^2=0.365; *F(1,20) = 1.23; p = 0.003*) and was the only competitive model in the model comparison with all univariate measures of size (Table 3, Fig 3.2d).

Table 3.3: Model selection results for univariate size measures.

Model	**K**	**logLik**	**AICc**	**Δ AICc**	**weight**
TL*	3	-46.34	100.01	0	0.812
BL*	3	-48.41	104.15	4.147	0.102
TS	3	-49.4	106.14	6.131	0.038
WC	3	-50.2	107.74	7.732	0.017
Mass	3	-50.67	108.68	8.676	0.011
BD	3	-50.92	109.18	9.176	0.008
BW	3	-51.18	109.69	9.683	0.006
WW	3	-51.21	109.76	9.749	0.006

*Explantory variables with $p \leq 0.05$.

Comparison of models with all combinations of size measures resulted in a set of five competitive models (Table 4). Among these models, the β-coefficient for wing chord consistently crossed zero, and therefore, the final model set consisted of multivariate models without WC as a covariate. The final three models explained between approximately 45 – 62% of the variation in CS, with a linear combination of TL, TS, BL and BW explaining the most (R^2=0.615; *F(4,19) = 7.58; p = 0.0008*).

Table 3.4: Model selection results for multivariate size measures

Model	**K**	**logLik**	**AICc**	**Δ AICc**	**weight**
TL* + TS* + BL* + BW	7	-43.38	107.77	0	0.544
TL* + TS* + BL*	6	-45.59	108.12	0.356	0.456

*Explantory variables with p≤0.05. Bolded models represent final model set.

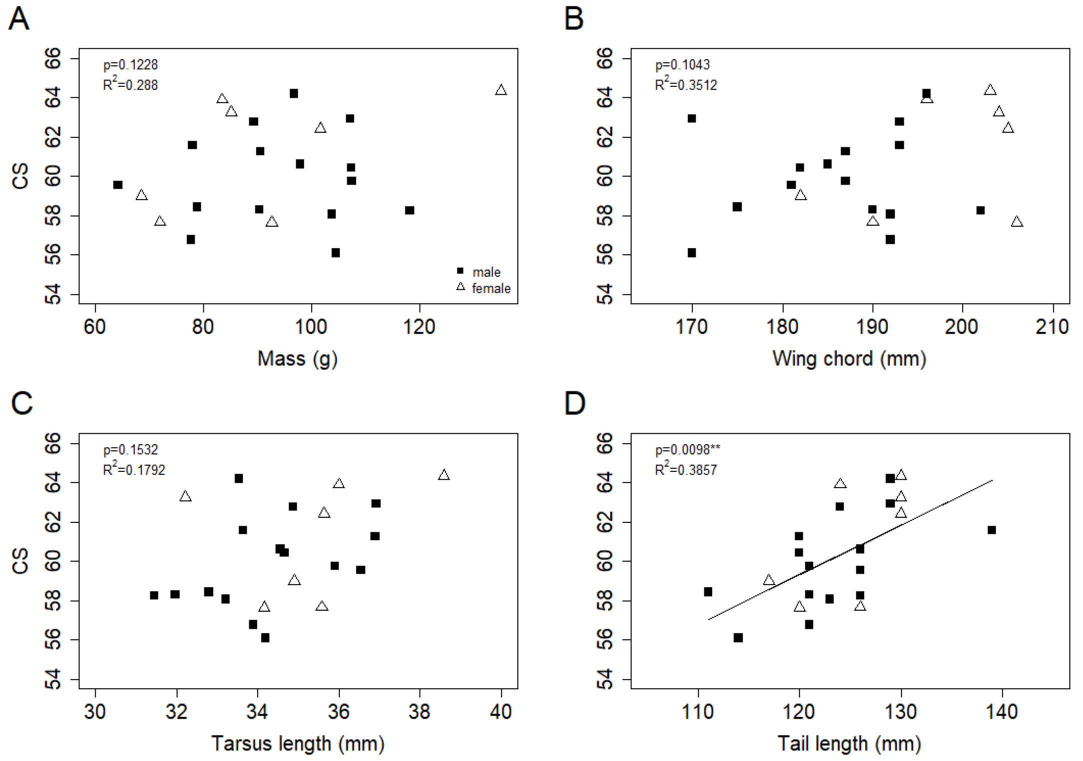

Figure 3.2. Centroid size (CS) regressed on univariate external measurements. Filled squares are male specimens, open triangles are females. P-values and R^2 value shown in top left corner. Lines show significant relationships between variables.

Discussion

This study provides support for an often-overlooked aspect of ecogeographic studies: single, external measurements are unreliable indicators of body size. I argue that structural size, based on nutrient reserve-independent characters rather than seasonally or annually labile characters, is most appropriate in studies of geographical size variation. I provide a low-cost method for quantifying structural size using 3D imaging of sternums and show that a combination of external linear measurements is a better approximation of this structural size metric than any single external measurement alone.

This study is not the first to raise concerns about the use of single external measurements of study skins or live birds as reliable indicators of structural size (see Winker *et al.*, 1998; Rising and Somers, 1989; Freeman and Jackson 1990; Piersma and Davidson, 1991; Pascual and Senar, 1996; Senar and Pascual, 1997; Moser and Rusch 1988). For example, Rising and Somers (1989) and Freeman and Jackson (1990) used the first principle component of a PCA of a large number (13-24) of skeletal elements to estimate structural body size, then asked to what degree univariate measures of size such as wing chord, mass or tarsus approximated the multivariate measure. The consensus was that wing chord was a poor measure of structural body size in all four species analyzed, and that if a single measure must be used, tarsus length provided the best choice. This analysis confirms these results of these results, albeit through a completely different method. I also found concordance in Freeman and Jackson's (1990) assessment that only between 40-60% of the variation in structural size could be explained by external measures. Contrary to the conclusions of both studies, however, this study indicated tarsus length was also a relatively poor predictor of structural body size, at least in American kestrels.

While I provide a "best" model (or models) for both univariate and multivariate approximations of structural size, I urge caution in the generalization of these results. First, the sample size for this study is quite small, only 24 specimens, and only 1/3 of these are female. American kestrels are highly sexually dimorphic in multiple dimensions of size and may, therefore, be under different selective pressures (Smallwood and Bird 2020, Newton 1979). The genetic coupling of traits combined with selection on body size can lead to complex morphological outcomes (Boag and Grant, 1981; Arnold and Wade, 1984). Differential selection among males and females of the same species could in theory produce differing associations between individual characters and body size. In addition, sexual selection often creates conditions of allometry between the sexes with respect to how traits scale with body size; bird tail lengths being a particularly notable example (Darwin, 1871; Andersson, 1982; Moller, 1988; Zuk *et al.*, 1990; Winquist and Lemon 1994). A larger sample size with equally distributed sex ratios could better determine if differences among sexes exist. We did not find any, but we also did not have the statistical power to do so.

Second, this study is limited to one species, as this study is part of a larger effort to catalogue the variation in body size of American kestrels across their North American range (see Chapter 4). Comparisons with similar studies show that the "best" combination of external traits is likely to be species specific (Piersma, 1988; Piersma and Davidson, 1991). For instance, Moser and Rusch (1988) found opposite patterns in how much variation was explained by wing chord and tail length, individually, in Canada geese than I found in American kestrels. Wing chord explained nearly 50% of the variation in skeletal volume (determined by water displacement) in Canada geese, whereas tail length explained only 0.5%. In this study of American kestrels, wing chord explained only 10% of variation in structural size and tail length 37%. Rising and Somers (1989) and Freeman and Jackson (1990) also show quite a bit of variation between species in the amount of variation in structural size explained by individual characteristics. Furthermore, most of the specimens come from only two localized regions in the Southwest United States. As there are differences in body size across a species' range, so to might there be differences in the relative association between body size and other traits. Future work should consider broader geographic and taxonomic sampling to examine how broadly results concur across populations, phylogenies and/or functional guilds.

Why tail length out of all the single size measures of structural size provided the best approximation is not clear. No other studies that I am aware of have suggested tail length as a reliable indicator of size in birds. Indeed, although it was the best supported single external metric in this study, it only explained 37% of the variation in structural size. Acknowledging the concerns above about difference in sex and sample sizes, the closer association of tail length to structural size than other external traits may be a consequence of the unique foraging strategy of hover hunting in American kestrels (Bowman *et al.*, 1987; Smallwood and Bird 2020). Hover hunting in American kestrels includes both flapping and non-flapping flight and is generally conducted in moderate wind speeds from 10-30 km/h (Bowman *et al.*, 1987). American kestrels have been reported to spend up to as much as 20% of active hunting periods hover hunting (Rudolf, 1982), although see Bowman *et al.* (1987) for limitations of associating motives to perched birds.

Recent research in hummingbirds and passerines suggests that the tail of birds may be more involved in lift, control and stability in low-speed hovering flight than previously thought (Thomas *et al.* 1997; Warrick *et al.*, 2002; Altshuler *et al.*, 2009; Tobalske *et al.*, 2009; Muijres *et al.*, 2012; Su *et al.*, 2012). By manipulating the tail lengths of zebra finches, Tobalske *et al.* (2009) found a significant relationship between length of tail and increasing lift:drag ratio. As much as a 42% increase in lift coefficients and only 19% increase in drag coefficients were observed when increasing the tail length 150%. Altshuler *et al.* (2009) further showed that the tail works in complex kinematic patterns with the wings to increase pitch stabilization (as proposed in Warrick *et al.*, 2002). In a study of pied flycatchers, Muijres *et al.* (2012) demonstrated that the tail is involved in an exceedingly high amount of lift during the upstroke of the wing beat compared to other birds and that this lift was greatest at low flight speeds; up to 23% of weight support was generated through the tail vortex system. These findings suggest that natural selection works to optimize tail length for flight performance in birds, particularly as it pertains to foraging (Balmford *et al.*, 1995). Due to the high metabolic cost of hover hunting, the length of American kestrel tails may be reflective of the support needed maintain lift and stability among individuals of different structural size.

Given the current lack of prioritization among many natural history collections for the preservation and storage of post cranial skeletons of birds, I suggest that the sternum, where available, can be used to obtain structural size estimates and act as a standard against which to determine the best combinations of linear measurements from study skins or live birds. Future research should work towards generalizing results across species and among the sexes. I believe that a more detailed accounting of structural size will lead to more robust results in studies of geographic and temporal size variation. Relatively low cost and easy to use 3D imaging systems are increasingly available that researchers can employ to investigate structural size. I encourage natural history collections to reevaluate the relevance of skeletal material in light of this new technology while recognizing the practical and financial limitations to the preservation and storage of additional specimens. Lastly, I encourage all ornithological researchers to be clear about what they are measuring when they use the term body size, and, as has been advised by many authors before me, avoid what Arnold and Wade (1984) termed single-trait myopia widespread among studies of avian morphology (Piersma and Davidson, 1991; Winker, 1998).

Chapter 4: Spatial and temporal size trends in a widespread avian predator

Introduction

Documented responses of animals to climate change are now common and widespread. Among the many responses, coherence between evolutionarily distinct organisms and geographically distinct habitats points toward a set of universal responses unfolding across the tree of life. Northward and upward shifts in species', ranges, and the advancement in spring phenology, for instance, are so widespread as to be commonly accepted as universal responses to climate change (Parmesan, 2006; Parmesan & Yohe, 2003; Walther *et al.*, 2002). Recent documentation of changes in animal body size with climate warming through time has led some researchers to posit thag declining body size may represent a third universal response to warming temperatures (Daufresne, Lengfellner, & Sommer, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011).

Bergmann's rule, and the related Allen's rule, are potential conceptual frameworks with which to understand these changes. Bergmann's rule, the ecogeographic rule explaining patterns of clinal variation in the body size of endotherms, is a commonly invoked mechanism to explain temporal trends in size (Bergmann 1847; James, 1970; Blackburn *et al.* 1999; Millien *et al.*, 2006; Yoram Yom-Tov & Geffen, 2011). Originally proposed to explain observed geographical patterns in body size, the rule states that larger individuals of the same, or closely related, species will occupy colder climates than smaller individuals due to an increased ability for reduced heat loss driven by a lower surface area to volume ratio (James, 1970; Watt *et al.*, 2010). Thus, on average, larger bodied organisms are found at higher latitudes and elevations than smaller bodied organisms. Over time, Bergmann's rule has become a common shorthand to represent a pattern of increasing size with increasing latitude, regardless of the specific mechanism, and in this sense, has been largely supported among endothermic animals with 76% of birds and 71% of mammals estimated to adhere to the pattern (Millien *et al.*, 2006; Watt *et al.*, 2010). Allen's rule, similarly, explains the observation of longer appendages in warmer climates and smaller appendages in colder climates as an adaptation to thermoregulatory demands (Ryding *et al.* 2021). Longer, thinner appendages allow for more efficient heat dissipation. There are many examples of both birds and mammals that adhere to this rule and new insights into the selective forces that drive appendage length or appendage surface area have emerged over recent decades (Symond and Tattersall, 2010).

Even though there is general support for both rules as they apply to geography, whether the rules are behind documented morphological changes in birds and mammals through the last century of rapid climate change remains equivocal. Part of the challenge lies in identifying a mechanism that could explain the patterns. This is not for lack of study, however. For example, Correll *et al.* (2015) recently documented some of the proposed mechanisms behind Bergmann's rule and Ryding *et al.* (2021) did as much for Allen's rule. Many others have discussed potential mechanisms elsewhere (see review in Blackburn *et al.* 1999). A major issue is the challenge of teasing apart the individual contributions from different explanatory variables, many of which covary with each other. In addition, the push and pull of different selective pressures on a particular trait could mean that one particular mechanism is only favored some of the time, or only under certain conditions (Danner and Greenberg, 2015). Clearly, assigning attribution from a single mechanism to an entire species or larger taxonomic order is challenging at best.

There is also the issue of how one measures size (Peirsma and Davidson, 1991; Pascual and Senar, 1996; Brawner 2021). In the case of birds this becomes particularly challenging as birds' feathers may mask important aspects of structural size, the nutrient reserve-independent size of an organism (Peirsma and Davidson, 1991). It is this trait that is the most likely recipient of selection on size *a la* Bergmann's rule, and it is also unfortunately the hardest to quantify. This latter quality often leads researchers to use body size proxies. In the case of birds, wing chord (WC) and tarsus length (TS) are two of the most common. Mass is also commonly used. But all three are inadequate as measures of structural size (see Chapter 3). Mass and wing chord (which have a particularly notable nutrient reserve-dependent component) are annually, seasonally and sometimes daily labile, and are often under the influence of selective pressures not germane to thermoregulation (Brawner 2021). Bailey *et al.* (2020) showed that the traits one uses to represent body size can strongly influence conclusions and other studies have shown opposing trends in traits that are both independently used to represent body size.

A third challenge lies in the scale at which a population or species is evaluated. For instance, several studies have used a single migration banding site to trap birds and compare their measurements through time (Collins *et al.*, 2017; Goodman *et al.*, 2012; McCoy, 2012; Salewski, Hochachka, & Fiedler, 2010; Van Buskirk *et al.*, 2010). While this method is key for controlling for certain ecological conditions over time, the potential for confounding effects due to the changing movement patterns as climates shift is high. Other studies that use a network of migration sites have done a better job at cataloguing among population variation in response, especially for widespread species (Ely *et al.*, 2018). However, this approach too, lacks critical information about the natal environment a bird was reared in or where it spends a solid portion of its annual cycle. Birds will likely only spend a few moments to a few weeks at migration stopover sites, and while they are crucial habitat in the annual cycle of a bird for its continued survival, the role this ephemeral habitat plays in influencing the thermoregulatory responses of birds is unclear. In contrast, the thermoregulatory environment of the nest has been shown to have profound impacts on the growth and final adult size of birds (James, 1983; Andrew *et al.*, 2017; Youtz *et al.*, 2020). Studies investigating the role of climate in shifting appendage length or structural size of species through time or across space must link the organism to the habitat most likely providing a selective pressure.

Here I investigate the degree to which American kestrels, small-bodied, generalist predators widespread across North America, conform to patterns of Bergmann's and Allen's rules. I then evaluate the relative contribution of climate, primary productivity, and competition to the observed patterns in order to tease apart potential underlying mechanisms. Specifically, I used a long-term dataset of historical museum specimens in order to examine multiple dimensions of morphological variation through time and across space. This data set covers ~60° of latitude across Central and North America and the Caribbean, 112 years, and incorporates 7 different subspecies of the American kestrel. I incorporate multiple types of ecological data to address the many abiotic and biotic factors proposed to influence Bergmann's and Allen's rules. This approach allows me to identify axes of ecological influence in explaining morphological variation rather than isolating single causes. I also compare and contrast several different size metrics to assess whether they shift in conjunction or independently from one another.

Methods

Data collection

Study species

The American kestrel is a small, widespread falcon that breeds throughout North and South America and is thought to comprise up to 17 subspecies throughout its range (Ferguson-Lees & Christie, 2001). All subspecies are secondary cavity nesters and considered dietary generalists, eating a variety of insect and small vertebrate prey. Evidence from breeding and winter surveys, and artificial nest box populations, suggest that several populations of American kestrels across North America have experienced steady declines for decades (Smallwood *et al.*, 2009; Farmer & Smith, 2009; Paprocki, Heath, & Novak, 2014). The ubiquity of these declines and the causes behind them, however, remain unresolved (McClure *et al.* 2017a). Observed responses to climate warming in this species include advances in spring phenology and shorter migration distances with increasing winter temperatures (Van Buskirk, 2012; Heath, Steenhof, & Foster, 2012; Smith *et al.*, 2017). Evidence from migration banding sites also suggest that several Northern and Western populations of American kestrels in North America have experienced reductions in mean body size over the past 20 – 40 years (Ely *et al.*, 2018), although the causes for declines have not been thoroughly examined. American kestrels are known to vary in mass and wing length geographically in patterns that are consistent with Bergmann's and Allen's rules (Ely *et al.*, 2018; Lane and Smith, 1992) suggesting the possibility that climate may play a role in shaping patterns of body size and/or appendage length through time as well as space. The large latitudinal range, variation in life history characteristics and population trends, and evidence for spatial and temporal body size clines, make the American kestrel a species well suited to explore mechanistic explanations underlying Bergmann's and Allen's rules.

Museum specimens

I searched the VertNet database for records containing the words "*Falco sparverius*" and "skin". I then limited these results to the dates 1901 – 2013, as this was the temporal span for which I could obtain climate records. All specimens labeled as immature were eliminated. Out of the 7 subspecies that I ended up with for analysis (Table 1), the *F. s. sparverius* subspecies data was further limited to the months from April to September. This decision was based on the fact that most *F. s. sparverius* subspecies are migratory or partially migratory (Smallwood and Bird, 2020, Reugg *et al.*, 2021). By restricting the analyses to specimens collected in the breeding season, or on the margins of it, I made the assumption that environmental records for those locations would be representative of their natal territory. Varland *et al.* (1993) were able to radio-track American kestrel fledglings on their natal territories to a mean age of 28.3 days and up to 39 days post fledging. Thus the assumption that American kestrels were at or near their natal territories when collected in the late spring or summer seems reasonable. The natal environment can have profound effects on growth patterns in birds, influencing their final attained adult size (James, 1983; Andrew *et al.*, 2017; Youtz *et al.*, 2020). The decision, therefore, to eliminate specimens collected in the fall and winter months for this subspecies was made because I could not control for natal environmental conditions. Because other subspecies are non-migratory, I included specimens collected throughout the year, again, assuming that the environmental conditions at the site of collection were representative of natal environmental conditions.

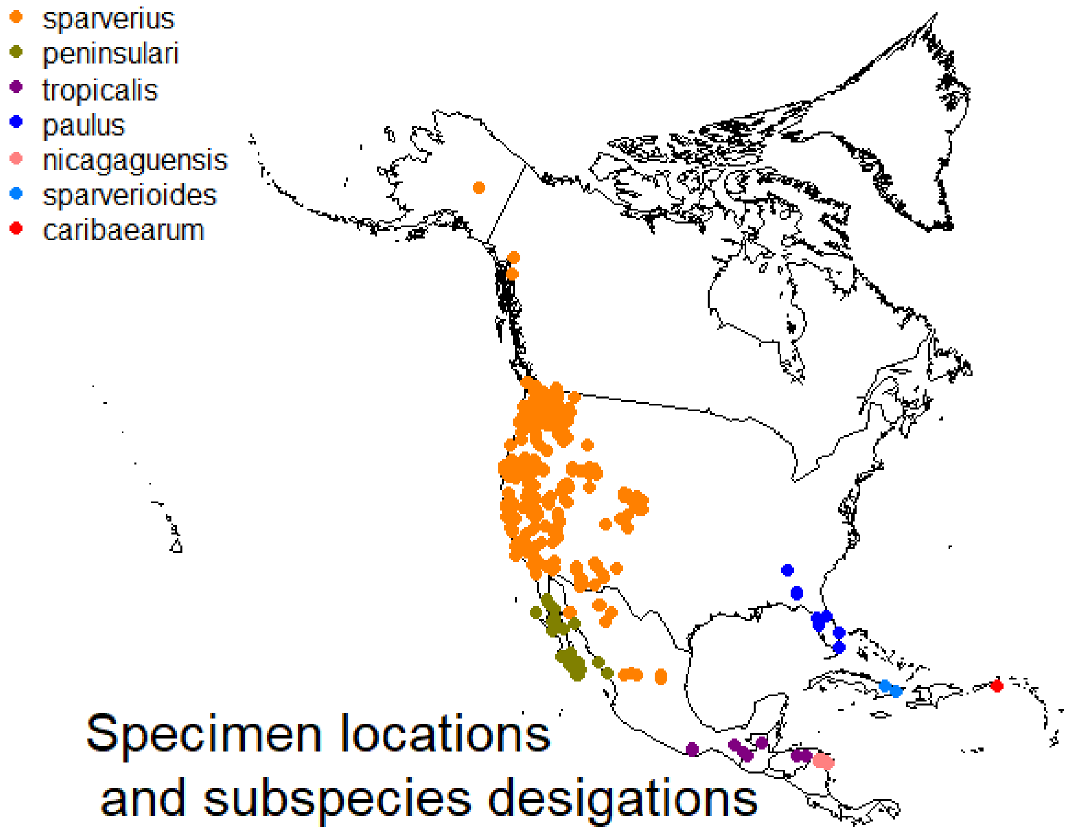

Figure 4.1. Locations of all specimens used in the analyses, color coded by subspecies.

Table 4.1: List of subspecies and range information

Subspecies	n	Location	Lat	Min Lat	Max Lat	Long	Min Long	Max Long
nicaraguensis	21	Nicauragua	14.376	14.116	14.55	-83.874	-84.233	-83.383
tropicalis	14	Honduras	15.678	15.17	16.917	-88.923	-97.100	-85.519
caribaearum	6	St. Croix, U.S. Virgin Islands	17.735	17.735	17.735	-64.741	-64.741	-64.741
sparverioides	3	Cuba	20.640	20.147	20.887	-75.910	-76.263	-75.206
peninsularis	53	Baja California and NW Mexico	25.002	22.883	29.750	-110.92	-115.541	-106.467
paulus	15	Florida and Southeastern US	28.327	25.540	33.466	-81.638	-85.205	-80.094
sparverius	450	Continental US and Canada	40.239	23.366	64.857	-117.136	-147.804	-100.581

From the list of 1258 specimens gathered through the search efforts, I measured 765 from 13 different natural history museum collections. Based on sample sizes from the collection efforts, I limited the geographic extent of analysis from Colorado west to the Pacific Ocean in the US and Canada; Florida and Georgia to include the *F. s. paulus* subspecies; Mexico; Honduras; Nicaragua and the Caribbean. The result was 590 specimens including seven subspecies ranging in latitude from approximately 14.117° N to 64.857° N (Fig 1). Recent genetic analyses support the separation of *F. s. paulus* and *F. s. sparverius* subspecies in the Continental US and indicate that the *sparverius* subspecies in the western US and Canada, excluding Alaska, represents a genetically coherent population; Alaska marking a geographically distinct population of its own (Ruegg et al, 2021). No literature exists that I know of for evidence of genetic structure in the other reported subspecies of American kestrel in the data. From the final specimen list, I eliminated a further 28 specimens based on molting, feather wear, missing or broken appendages or other anomalous features that impacted measurements, resulting in 562 specimens that were used for the analyses (Table S1).

Size measurements

For all specimens I took measurements of wing chord (WC), tail length (TL), tarsus length (TS), bill length (BL), bill width (BW), and bill depth (BD) (see Table 1 for descriptions). These measurements are commonly employed in the field on live birds and on avian museum specimens for the assessment of ecomorphological studies (Aldrich and James 1991; Winker *et al.* 1998; Eck *et al.*, 2011). A butted wing ruler was used to obtain WC, and TL to the nearest mm. I used digital calipers to obtain TS, BL, BD, and BW to the nearest one hundredth of a mm. All measurements were taken from the specimen's right side and all measurements were taken by a single observer (MDB).

Table 4.2: Descriptive statistics of size variables. BA in mm^2, all others in mm. WC=wing chord, TL=tail length, TS=tarsus length, BL=bill length, BD=bill depth, BW=bill width, BA=bill area.

Statistic	Description	Mean	St. Dev.	Min	Pctl(25)	Pctl(75)	Max
WC	from the carpal joint to the tip of the wing	186.15	10.37	157	180	194	209
TL	from the pygostyle felt below to the tip of the tail	120.02	7.85	96	115	125	140
TS	from the intertarsal joint to the joint between tarsus and toes	33.66	1.60	25.97	32.72	34.81	37.70
BL	from the distal edge of the nostrils to the tip of the bill.	12.23	0.67	9.37	11.80	12.68	14.58
BW	width of upper bill measured at the distal edge of the nostrils	7.72	0.56	5.96	7.39	8.06	9.66

BD	depth of upper bill measured at the distal edge of the nostrils	7.19	0.43	5.81	6.92	7.48	8.72
BA	bill area calculated using equation below	143.31	13.68	102.48	134.74	151.74	186.50

I used a Principal Components Analysis (PCA) to determine the structural size of American kestrel specimens. This method has been shown to be a more robust measure of structural size, the nutrient reserve-independent size of an animal than single external linear measurements (Rising and Somers, 1989; Freeman and Jackson, 1990; Piersma and Davidson, 1991; Winker 1998; Brawner, 2021). I argued in chapter 3, as have other authors, that structural size is the most appropriate measure to use in studies of geographic or temporal size variation, especially at the intraspecific level (Piersma and Davidson, 1991; Chapter 3). In chapter 3, I also demonstrated that a combination of external linear measurements including wing length, tail length, tarsus length, bill length, and bill width can be used as an indicator of structural size. To collapse this combination of measurements down to a single size metric that could be used as the dependent variable in this study, I used the first principal component (PC1_{size}) from this combination of traits in a PCA to represent structural size in the analyses.

I estimated bill surface area (BA) to analyze geographic and temporal patterns in bill structure. BA has been shown to vary with environmental conditions, especially temperature, in other bird species (Symonds and

Tattersall, 2010; Greenberg *et al.*, 2012, Larson *et al.*, 2018). I used the following formula, which has been empirically demonstrated to accurately represent bill surface area within species, to estimate BA (Subasinghe *et al.*, 2021);

$$BA = \left(\frac{BW+BD}{4}\right) x\, BL\, x\, \pi.$$

To account for potential allometry in geographical and temporal trends in structural size and appendage lengths, I corrected all appendage size measurements (WC, TS, and BA) by PC_{size} (Gould 1966; Mosimann, 1970; Klingenberg, 2008; Klingenberg, 2014). To do this, I regressed appendage size measurements on to PC_{size} and used the residuals from these regressions as a measures of size-corrected appendage length ($WC_{relative}$, $TS_{relative}$, $BA_{relative}$) (Monteiro *et al.*, 1999; Klingenberg, 2009). I were therefore able to represent trends in appendage length absent trends in structural size.

Environmental variables

Climate data was generated with the ClimateNA v6.40a and ClimateSA v1.0 software packages based on methodology described by Wang *et al.* (2016). Briefly, the software relies on PRISM (Daly, 2002) and ANUSPLIN (Hutchinson, 1989) climate databases to locally downscale historical and future monthly climate data layers to scale-free point estimates of climate values for a given set of input locations. I used specimen location data as an input file to the software and extracted time series for annual, seasonal and monthly climatic variables for each location for the years 1901 –

2013. I then limited the data to the specific year/location for which the specimens were collected. I retained seven variables to use in the analyses and created two more of my own (Table 3). These variables characterize annual and seasonal temperature (MAT, Tmax_sm) and precipitation (MAP, PPT_sp) at all specimen locations, as well as aridity (AHM, CMD) and temperature seasonality (TD). I calculated breeding season temperature and precipitation (brdngTavg, brdngPPT) by averaging or summing, respectively, the monthly temperature and precipitation values from April-August. Because the majority of this data set was restricted to the late spring and summer months, I did not use fall and winter variables to characterize the climate for the specimen locations. The unknown non-breeding locations for *sparverius* subspecies specimens makes it nearly impossible to even semi-accurately characterize the winter conditions experienced by these birds.

Table 4.3: Descriptive statistics of climatic variables

Statistic	Descriptoin	Mean	St. Dev.	Min	Pctl(25)	Pctl(75)	Max
Tmax_sm	summer max temperature (°C)	27.78	5.20	14.00	24.33	30.80	46.10
brdngTv	breeding season temperature (°C)	17.78	5.27	4.38	14.14	21.76	31.72
MAT	mean annual temperature (°C)	13.25	6.38	-2.20	8.90	17.30	25.90
PPT_sp	Spring precipitation (mm)	139.98	144.25	2	40	186	1,137
MAP	mean annual precipitation (mm)	685.74	699.96	31	260	870	3,438
brdnPPT	breeding season precipitation (mm)	212.75	300.44	4	52	245	1,619
AHM	annual heat-moisture index (MAT+10)/(MAP/1000))	86.74	134.93	3.50	25.02	90.20	1,092.90
TD	temperature difference between MWMT and MCMT, or continentality (°C),	17.18	8.04	2.30	10.20	23.70	35.50

CMD	Hargreaves climatic moisture deficit (mm)	796.61	402.34	10	529.2	991.5	1,803

I used gridded monthly primary productivity images produced by Nasa Earth Observations (NEO) using Terra/MODIS products (Running *et al.*, 2015), to generate annual (NPP_{annual}), breeding season ($NPP_{breeding}$), highest (NPP_{high}) and lowest (NPP_{low}) month and seasonal (the difference between the highest and lowest month, NPP_{diff}) primary productivity variables. Gridded images of global primary productivity in the year 2016 were downloaded at a 0.5° scale as GeoTIFF rasters. Because satellite generated data of primary productivity does not cover the entire temporal span of the data set, I opted to use a single year to represent variation in productivity with the assumption that general spatial patterns of productivity throughout the annual cycle (i.e., green up in the spring and diminishing productivity in fall and winter) are similar from year to year. I used R software to upload the GeoTIFF files as rasters and used package 'raster' to extract point samples for the variables above for all specimen locations (R Core Team, 2017; Hijmans, 2021).

Competition variables

In order to account for the potential effects of biotic interactions on the size of American kestrels (e.g., competition) I generated two variables to describe the competitor community a kestrel might experience at a specific location. I began by searching the Birds of the World database for species that overlap with American kestrels in geographic range, diet, and habitat for the range of latitudes and longitudes the data encompassed. I excluded any species that did not include vertebrates as part of its diet, even if they overlapped with American kestrels in other criteria (e.g., American Robin), since vertebrate prey is a large part of the American kestrel diet. I also eliminated obligate piscivores, obligate scavengers, and obligate forest species. For other species that shared a geographic range with American kestrels, I looked for overlap in two or more diet items (at least one a vertebrate species) and two or more habitat types. For the 66 species I found that met these criteria, I used the Birds of the World GeoDatabase to obtain range maps for each and recorded the average mass of each species from the literature. Next, I used the 'createSpeciesRaster' function in R package 'speciesRaster' to generate a species richness map of the competitor species that I could query (Fig 2). I extracted the "competitor community" for each specimen location using the 'speciesRasterToPhyloComm' function in the 'speciesRaster' package which generates a community matrix of species by location. The result was a presence/absence matrix for 54 species (Table 4).

Table 4.4: List of potential competitor species gathered from the literature. Mass in g.

Scientifc name	# of sites present	Average mass	Log(competitor mass/kestrel mass)
Accipiter cooperii	438	376.5	1.181647517
Accipiter gentilis	354	861.4	2.009288443
Accipiter striatus	268	139.45	0.188435584
Antigone canadensis	65	4670	3.699643821
Aquila chrysaetos	409	4383	3.63621817
Ardea alba	356	965.65	2.12353092
Ardea herodias	503	2295	2.989217593

Scientifc name	# of sites present	Average mass	Log(competitor mass/kestrel mass)
Asio flammeus	225	346.5	1.098612289
Asio otus	283	260	0.811411101
Athene cunicularia	373	151.2	0.269332934
Bubo virginianus	520	1505	2.567277647
Bubulcus ibis	506	365.8	1.152816206
Buteo albonotatus	70	757	1.880092723
Buteo brachyurus	46	453.5	1.36772474
Buteo jamaicensis	539	1126	2.277156279
Buteo lagopus	1	951	2.108243533
Buteo lineatus	116	606.9	1.659093503
Buteo plagiatus	47	528.2	1.52020447
Buteo platypterus	6	397	1.234665751
Buteo regalis	167	1469.5	2.543406956
Buteo swainsoni	290	958.5	2.116099033
Buteogallus anthracinus	60	746.1	1.86558911
Caracara cheriway	54	1168.35	2.314077246
Circus hudsonius	274	424.5	1.301641476
Coccyzus merlini	3	155.6	0.298018082
Corvus brachyrhynchos	379	399.7	1.241443736
Corvus corax	497	782.5	1.913223392
Corvus cryptoleucus	18	534	1.531125309
Elanoides forficatus	45	465	1.392766876
Elanus leucurus	177	333.9333333	1.061670842
Falco columbarius	149	211.2	0.603535022
Falco femoralis	28	351.5	1.112939181
Falco mexicanus	328	708.5	1.813879529
Falco peregrinus	335	814.5	1.953303898
Falco rusticolus	1	1325	2.439897208
Geococcyx californianus	182	302.71	0.963504722
Geococcyx velox	12	180	0.443686321
Geranoaetus albicaudatus	17	1057.5	2.214392381
Geranospiza caerulescens	31	417.125	1.284115407
Glaucidium brasilianum	44	140	0.192371893
Glaucidium siju	3	70.75	0.490117993
Haliaeetus leucocephalus	198	4790	3.72501516
Herpetotheres cachinnans	34	625	1.68848112
Ictinia mississippiensis	2	295	0.937704826
Lanius borealis	3	69.75	0.504353109
Lanius ludovicianus	413	47.7	0.884339132
Margarobyas lawrencii	3	95.2	0.193290588

Scientifc name	# of sites present	Average mass	Log(competitor mass/kestrel mass)
Micrathene whitneyi	61	44.5	0.953781341
Parabuteo unicinctus	71	863.2166667	2.011395192
Pica hudsonia	212	173.2	0.405176466
Pica nuttalli	43	154.05	0.288006695
Strix nebulosa	83	1078.75	2.234287712
Surnia ulula	3	320.5	1.020611746
Tyto alba	526	519.95	1.504462123

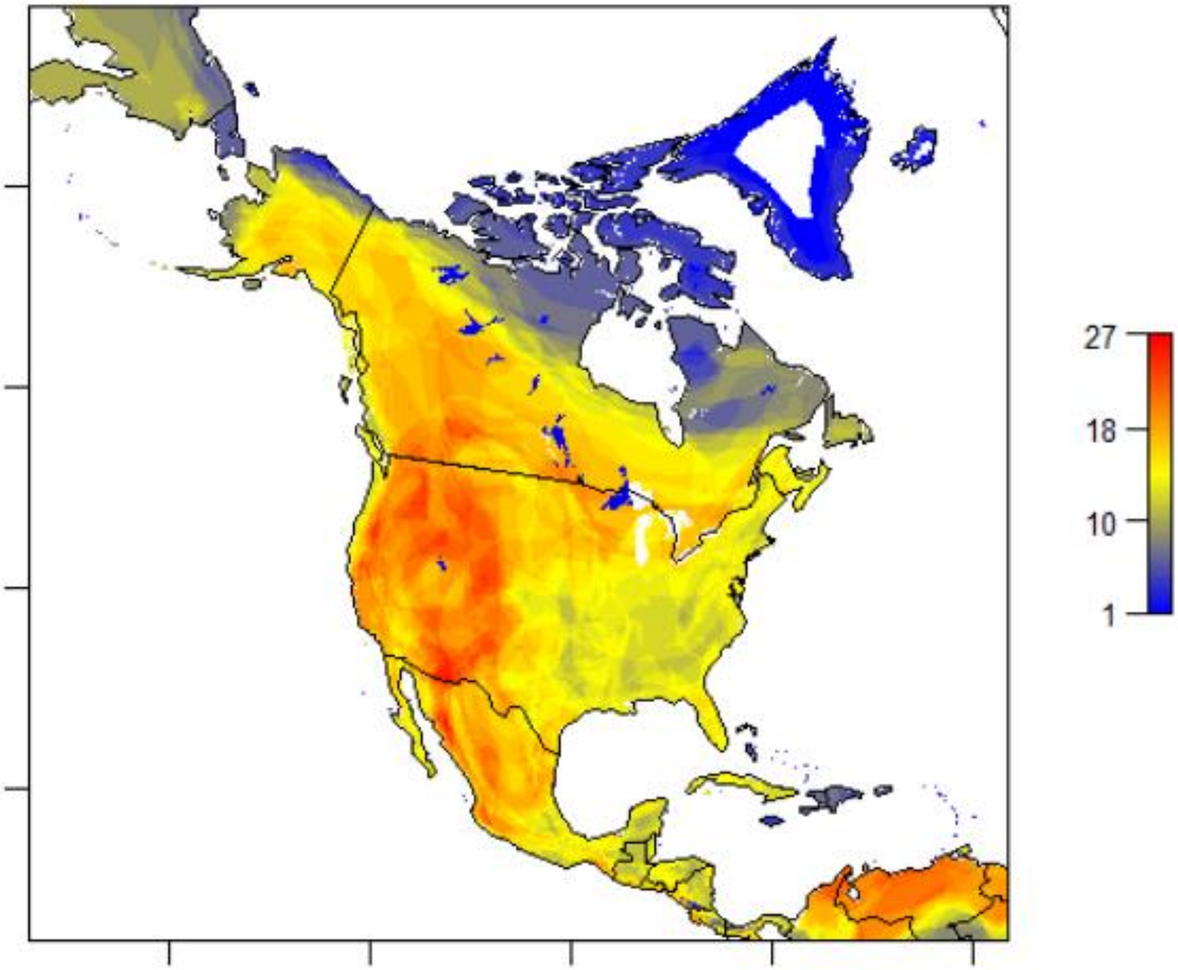

Figure 4.2. Competitor species richness map created with 'SpeciesRaster' Package. American kestrel specimen locations were overlayed on the map to extract competitor community data. The color scale represents number of species

The first measure of potential competition, richness of the competitor community, was a simple measure of species richness that I calculated using row sums for each specimen location. For the second measure, I used the log of the ratio of competitor mass to the average mass of kestrels for each competitor to build a distribution of differences in log mass for each site. I then calculated the skewness of each distribution using the 'moments' package in R (Komsta, 2015). The result was a measure of potential competition, $\text{Comp}_{skewness}$, that approximates a competitor community closer in mass to the average American kestrel (positive skew) vs. a competitor community increasingly larger in mass than the average American kestrel (negative skew). This allowed me to assess how both the number of potential competitors and a particular quality of competitor community, its relation in mass to American kestrels, affected the distribution of kestrel body sizes.

Statistical analyses

Collinearity among climate variables is common and must be eliminated prior to statistical analysis to avoid spurious results. Many authors studying the effects of multiple climate variables on geographic patterns in morphology will use pairwise correlation coefficients to avoid problems of collinearity in statistical models. The choice to drop an explanatory variable from a set of covariates because of a high correlation coefficient with another variable can often be arbitrary, as there is no standard practice for which variable among a pair to drop. Therefore, I used a PCA to avoid the pitfalls of collinearity among climate variables. All environmental variables described above were included in a PCA to reduce dimensionality and let important environmental variables emerge from the data via loadings instead of being imposed by myself via dropping collinear variables. The first three climate PCs explained a cumulative proportion of variance in the data > 82%, and each contributed over 12% to the proportion of variance explained individually, between 12.53% and 40.35%. I thus concluded that these three PCs ($PC1_{clim}$, $PC2_{clim}$, and $PC3_{clim}$) were sufficient to use as covariates in the models to represent the effects of the environment on the size variables. I did not include any competition variables in the PCA because it is unclear whether they routinely do or should, on conceptual grounds, covary with climate processes. I deal with potential collinearity of competition variables below.

Spatial dependence among data has the potential to confound results (reference, Bivand? Lengendre and Lengendre?). To account for this, I chose a spatial regression framework for the analyses using simultaneous autoregressive models (SAR) (Bivand *et al.*, 2008). SAR models assume a spatial autoregressive process in the error term, which can account for some or all of the spatial dependence. The error SAR model follows the form

$$\mathbf{Y}=\mathbf{X}\boldsymbol{\beta} + \boldsymbol{\mu}\,;$$

$$\boldsymbol{\mu} = \boldsymbol{\lambda}\mathbf{W}\boldsymbol{\mu} + \boldsymbol{\varepsilon}\,,$$

where $\mathbf{X}$ is the matrix of explanatory variables and $\boldsymbol{\beta}$ the vector of coefficients. The spatial dependence is built into the error term $\boldsymbol{\mu}$. Here, $\mathbf{W}$ is the spatial weights matrix, λ the spatial autoregression coefficient and ε are the spatially independent residual errors. Stronger positive spatial autocorrelation is indicated by λ values approaching 1.

For the weights matrix, I adopted a row standardized weighting scheme that assigned weights to neighbors based on the inverse of the distance between locations. I then tested different neighborhood distances to see how well they improved model fit and how quickly they reduced Moran's I between lagged distances. All models were fit using the function 'errorsarlm' within *R* package 'spdep' (Bivand and Gianfranco 2015). I fit SAR models with PC1_{size} regressed on latitude and longitude and squared terms for each with neighborhood distances ranging from 150-600km in increments of 50km. I then computed correlograms of Moran's I using the function 'sp.correlogram' within the 'spdep' package. Model fit was compared using Akaike's information criterion with a correction for finite sample sizes (AICc) calculated with the 'AICctab' function within R package 'bbmle' (Bolker, 2020; Burnham and Anderson, 2002) and correlograms visually inspected to determine the best neighborhood distance. I used 150km as a starting point as this is the approximate average natal dispersal distance of an American kestrels (30km) times their approximate average life span in the wild (5 years) (McCaslin *et al.* 2020, Smallwood and Bird, 2020). American kestrels have been shown to not infrequently disperse distances of several hundred km (McCaslin *et al.* 2020), thus this method incorporates biologically relevant lag distances over generational periods to account for average and potential long-distance dispersal influencing spatial autocorrelation. I chose a final neighborhood distance at 350km, as Moran's I approached zero the quickest at this scale and AICc was low relative compared to other models (Fig S1). This distance was used for all subsequent SAR models.

Using the neighborhood distance obtained from the procedure above, I first built models to examine geographic and spatial patterns in structural size, $WC_{relative}$, $TS_{relative}$ and $BA_{relative.}$ These models consisted of one of the four size variables as the dependent variable and latitude and/or year as the independent variable. To account for non-linear patterns in the size variables, I assessed if the inclusion of squared terms for latitude and/or year improved model fit using AICc, opting for the simpler model when ΔAICc was ≤ 2 between models (Burnham and Anderson, 2002). Because the American kestrel is a highly sexual dimorphic species and the potential for different selection pressures between males and females could influence patterns of size across the landscape or through time (Newton, 1979; Tornberg *et al.*, 1999; Ardia and Bildstein, 1997), I added a factor variable for sex into each model. As kestrels show genetic structure among subspecies and even populations (Reugg *et al.*, 2021, Miller *et al.*, 2012), to account for the potential of genetic influences in size, I also included subspecies as a factor variable where appropriate. I applied these models at the scale of the species (continental scale) and also at the small spatial scale of Bird Conservation Regions to investigate if different patterns emerged at regional scales.

To investigate which environmental or competition variables best explained the size variables, I built multiple models using different combinations of $PC1_{clim}$, $PC2_{clim}$, $PC3_{clim}$, Richness and $Comp_{skewness}$ for each dependent variable. First, I tested for collinearity between richness, $comp_{skewness}$, latitude and the three climate PCs using Spearman's rank correlation coefficient (r). Latitude and richness were both strongly correlated with $PC2_{clim}$ ($r \geq 0.68$). Because the focus was on the effects of climate on the size variables, and because I still retained one competition variable with low correlation to $PC2_{clim}$, $comp_{skewness}$, I therefore excluded latitude and richness from all models including $PC2_{clim}$. I subsequently built a set of models, exclusions permitting, with varying combinations of climate PCs, latitude, year, richness, $comp_{skewness}$, and sex and subspecies as factors. Squared terms for all quantitative variables were assessed as above and kept when they improved model fit. I applied the same procedure of model building for all dependent variables at the continental scale, and for dependent variables at regional scales only where geographic or temporal patterns were found.

Model assessment was performed using AICc, and all models with ΔAICc ≤ 2 were considered competitive. I further assessed models for possible uninformative covariates in the competitive model set following

Arnold (2010). Covariates with 85% confidence intervals (CI) of β-coefficients that did not cross zero were considered informative and left in the final models. Lastly, I checked for the influence of unaccounted-for spatial autocorrelation in the residuals of all SAR models using Moran's I. All statistical analyses were conducted using R software (R Core Team, 2017).

Results

Climate PCA

PC loadings of the climate variables delineated patterns in the data that help me to discern between support for or against the varied environmental hypotheses for the mechanisms behind Bergmann's and Allen's Rules (Table S2). The first principal component, for instance, delineated between high primary productivity environments on the negative end and hot, dry environments on the positive end. Negative loadings in $PC1_{clim}$ were driven by $NPP_{breeding}$ and NPP_{high}, and to a lesser extent, MAP and PPT_{spring}. CMD, $Tmax_{summer}$ and AHM all loaded heavily on the positive end (Table S3, Fig S2). I interpreted this as more humid and productive environments (e.g. the Pacific Northwest Forest region) on the negative side of the axis vs. drier hotter desert-like conditions (e.g. Sonoran or Chihuahuan Desert regions) on the positive side of the axis. $PC2_{clim}$ was split between highly seasonal, cooler environments (NPP_{diff}, TD) on the negative end and warmer environments with higher productivity in the least productive month

(MAT, $\text{Tavg}_{breeding}$, NPP_{low}) on the positive, the latter indicating more seasonally stable environments (Table S3, Fig S3). This axis is a little more difficult to interpret because the hotter climates with higher productivity in the lowest month could indicate more tropical regions or more desert like regions, both of which are equatorially located to the cooler, more seasonal environments. Given this finding and the strong correlation between latitude and PC2_{clim} that I found previously, I suggest that this axis likely recapitulates the large-scale latitudinal variation in environmental conditions. The third PC axis distinguished between variables that all loaded negatively on the first PC axis. NPP_{annual}, $\text{NPP}_{breeding}$, and NPP_{high} loaded positively on PC3_{clim}, this time in conjunction with, although to a lesser degree, AHM and CMD. These variables were distinguished from MAP, $\text{PPT}_{breeding}$, and PPT_{spring} on the negative end of PC3_{clim} (Table S3, Fig S3). $\text{PPT}_{breeding}$ had a particularly high loading relative to the other variables on this component axis. Because of the inclusion of AHM and CMD loading positively along this axis, I interpreted this as a humidity/aridity gradient, with higher humidity on the negative end, higher aridity on the positive.

General morphological trends

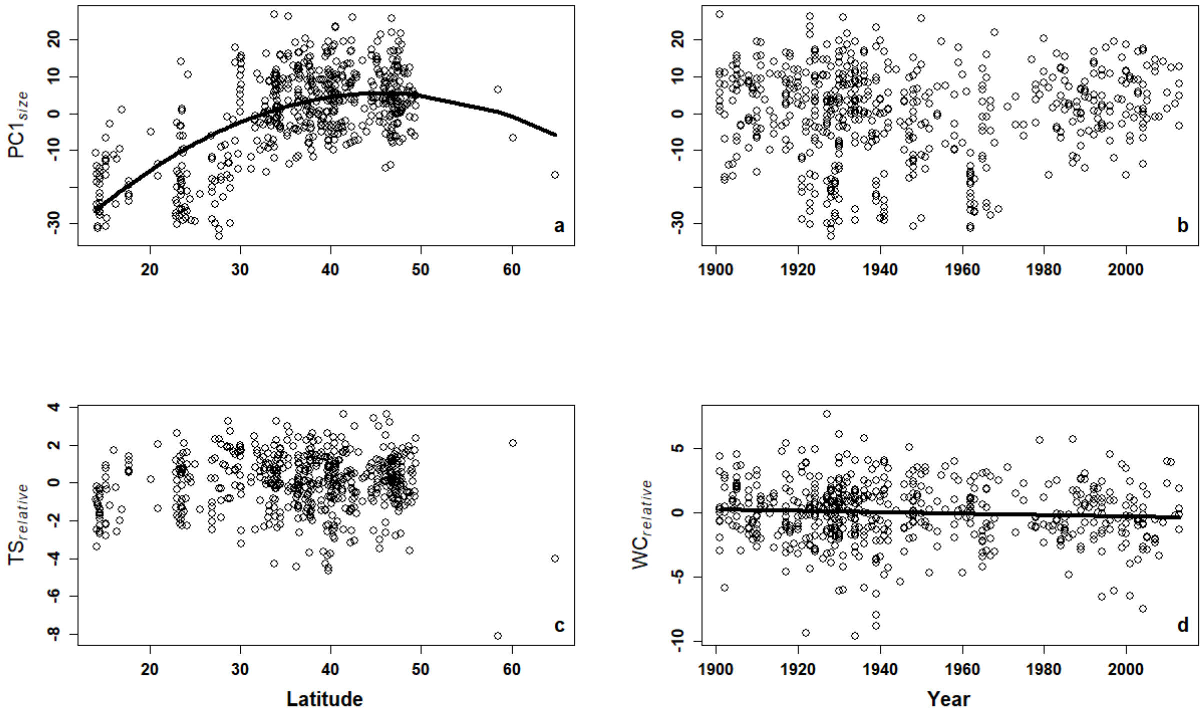

Figure 4.3. Temporal trends in size variables of American kestrels across their North American range: a) and b) structural size by latitude and year. c) Relative tarsus length by latitude, d) relative wing chord length by year. Lines show significant relationships between variables.

American kestrel specimens in the data set show significant morphological patterns across space and through time. For models exploring general patterns of structural size in American kestrels, the inclusion of squared terms for latitude and the factor variables sex and subspecies were supported by the improvement in AICc for each additional variable and the significance of β-coefficients at the 0.85% level (Table 5). The top supported model showed a non-linear effect of latitude on $\mathrm{PC1}_{size}$ accounting for sex and subspecies with size increasing to a peak around 40° latitude before decreasing again (Fig 4a). When accounting for latitude, sex, and subspecies I found no support for temporal trend in the structural size of American kestrels for the data as a whole (Fig 4b). Analysis of variance (ANOVA) showed sex, accounting for latitude and subspecies, unsurprisingly had a significant effect on size, males being smaller than females (*F*(1,553)=113.4, *p*<0.001). Subspecies also had a significant effect on size (*F*(6,553)=44.6, *p*<0.001; Fig 4a). Results from a Tukey HSD test showed *F. s. sparverius* was significantly larger than all other subspecies (*p*=0.011 for pairwise comparison of *F. s. sparverius* with *F. s. sparverioides*; *p*<0.001 for all other *F. s. sparverius* pairwise comparisons).

Table 4.5: SAR model results for geographic and temporal trends of size variables with year and latitude as covariates and factor variables for sex and subspecies. β-coefficients are shown for covariates with 85% confidence intervals in parentheses. Lambda values are reported with p-value in parentheses.

	Dependent variable:			
	PC1$_{size}$		TS$_{relative}$	WC$_{relative}$
Constant	-5.949	-5.987	1.364*	-5.307***
	(-12.520, 0.621)	(-12.550, 0.575)	(0.337, 2.390)	(-6.429, -4.184)
Year		-0.127		-0.200**
		(-0.615, 0.361)		(-0.329, -0.072)
lat	21.733***	21.656***	1.379*	
	(14.395, 29.072)	(14.321, 28.991)	(0.179, 2.579)	
lat2	-17.441***	-17.353***	-1.302*	
	(-23.590, -11.292)	(-23.502, -11.204)	(-2.313, -0.292)	
Sexm	-6.644***	-6.628***		-0.523***
	(-7.537, -5.751)	(-7.524, -5.732)		(-0.792, -0.254)
nicarauguensis	6.076	6.158	-2.016***	6.703***
	(0.210, 11.943)	(0.290, 12.025)	(-2.918, -1.115)	(5.429, 7.977)
paulus	-4.292	-4.279	-1.868**	6.966***

	(-11.211, 2.627)	(-11.189, 2.630)	(-2.942, -0.794)	(5.640, 8.291)
peninsularis	-3.770	-3.790	-1.105*	5.185***
	(-9.677, 2.138)	(-9.690, 2.110)	(-2.018, -0.192)	(4.003, 6.367)
sparverioides	8.142	8.009	-0.782	6.256***
	(-0.566, 16.850)	(-0.701, 16.720)	(-2.115, 0.550)	(4.310, 8.202)
sparverius	11.512**	11.548**	-1.360*	5.580***
	(4.422, 18.602)	(4.467, 18.630)	(-2.472, -0.248)	(4.452, 6.707)
tropicalis	13.677***	13.710***	-1.512**	5.816***
	(7.645, 19.709)	(7.686, 19.735)	(-2.436, -0.589)	(4.470, 7.163)
Observations	562	562	562	562
Lambda	0.13477 (0.0110)	0.13358 (0.0119)	-0.067841 (0.1736)	-0.1503 (0.0077)
Log Likelihood	-1,918.389	-1,918.319	-1,000.821	-1,239.886
sigma^{2}	53.700	53.692	2.055	4.795
Akaike Inf. Crit.	3,860.779	3,862.638	2,023.643	2,501.771
Wald Test (df = 1)	7.081***	6.949***	4.091**	8.136***
LR Test (df = 1)	6.469**	6.329**	4.511**	7.105***

*p=0.01****p0.05*****p<0.01

I did find support for a negative linear effect of year on WC$_{relative}$ when accounting for sex and subspecies (Fig 4d), although no trend in latitude was found. ANOVA for WC$_{relative}$ by subspecies showed *F. s. caribaearum* had significantly shorter WC$_{relative}$ than all other subspecies (*F*(6,555)=7.58, *p*<0.001; *p*≤0.001 for all pairwise *F. s. caribaearum* subspecies comparisons; Fig 4b). TS$_{relative}$ showed a similar effect of latitude as PC1$_{size}$ although the trend was non-significant when accounting for subspecies (Fig 4c). ANOVA of subspecies on TS$_{relative}$ revealed *F. s. nicarauguensis* had a significantly shorter TS$_{relative}$ than *F. s. caribaearum*, *F. s. peninsularis*, and *F. s. sparverius* (*F*(6,555)=10.58, *p*<0.001; *p*=0.013, *p*<0.001, and *p*<0.001, respectively for pairwise *F. s. nicarauguensis* subspecies comparisons, Fig 4c). I found no geographic or temporal trends in $BA_{relative}$. Contrary to results from $WC_{relative}$, however, *F. s. caribaearum* had a significantly larger $BA_{relative}$ than all other species except *F. s. sparverius* ($F(6,555)=6.61$, $p<0.001$; $p=0.006$ for all pairwise *F. s. caribaearum* subspecies comparisons, excluding *F. s. sparverius*; Fig 4d). Additionally, $BA_{relative}$ for *F. s. tropicalis* was significantly smaller than that of *F. s. peninsularis*, *F. s. paulus* and *F. s. sparverius* (p=0.003, p=0.02, and p=0.039, respectively; Fig 4d).

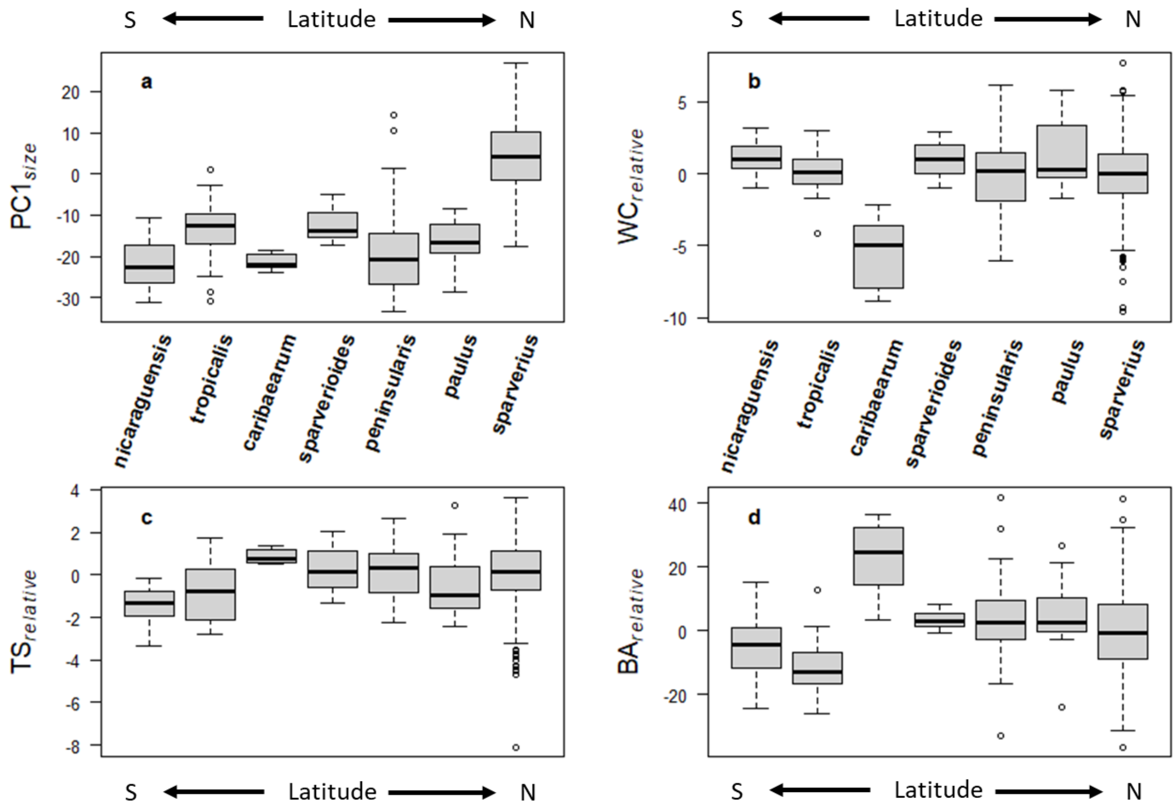

Figure 4.4. Comparison of different size measures among subspecies. Subspecies are arranged by average latitude of the specimen locations from left to right.

Table 4.6: SAR model results for regional temporal trends of size variables with year and latitude as covariates and a factor variable for sex. All specimens used for models were *F. s. sparverius*. β-coefficients are shown for covariates with 85% confidence intervals in parentheses. Lambda values are reported with p-value in parentheses.

	Dependent variable:					
	$PC1_{size}$		$WC_{relative}$		$BA_{relative}$	
	Columbia Plateau	Pacific Northwest Forest	Pacific Northwest Forest	Great Basin	Pacific Northwest Forest	Coastal California
Constant	3.842***	10.194***	0.622*	-0.063	9.541***	7.321***
	(2.166, 5.518)	(8.773, 11.615)	(0.153, 1.091)	(-0.383, 0.258)	(5.369, 13.714)	(4.905, 9.737)
Year	322.434***	1.363**	-0.529**	99.360**	-312.695**	2.452***
	(148.333, 496.535)	(0.381, 2.344)	(-0.836, -0.222)	(34.273, 164.448)	(-512.330, -113.061)	(1.095, 3.810)
Year2	-319.975***			-98.583**	313.396**	
	(-493.519, -146.431)			(-163.635, -33.530)	(114.305, 512.486)	
lat					-6.440**	
					(-10.276, -2.604)	
Sexm	-4.913***	-7.920***	-0.964*		-6.973***	-11.694***
	(-7.229, -2.597)	(-9.939, -5.901)	(-1.701, -0.226)		(-10.396, -3.550)	(-15.305, -8.082)
Observations	68	78	78	64	78	91
Lambda	-0.1242 (0.5117)	0.0016 (0.9916)	-0.2071 (0.1783)	-0.3687 (0.0352)	-0.4976 (0.0005)	-0.0710 (0.6488)
Log Likelihood	-223.228	-252.571	-172.848	-144.135	-290.997	-354.804
$sigma^2$	41.442	38.027	4.859	5.080	93.836	142.403
Akaike Inf. Crit.	458.456	515.142	355.697	298.269	595.994	719.608
Wald Test (df = 1)	0.472	0.0001	2.195	6.494**	20.148***	0.253
LR Test (df = 1)	0.431	0.0001	1.811	4.433**	11.814***	0.207

*p=0.01****p0.05*****p<0.01

After examining trends across the entire geographic extent of the data, I subsequently broke the data down to investigate potential regional temporal trends in size variables in regions that had adequate temporal coverage (Table 6). I used slightly modified Bird Conservation Regions (BCR) to categorize the data regionally (reference, Fig S4). Two regions showed a temporal trend in structural size, but with different dynamics (Fig 5a and 5b). A non-linear relationship between PC_{size} and Year was found in the Columbia Plateau region similar to that found between PC_{size} and latitude across the whole of the data, whereas a positive linear trend was found between the PC_{size} and Year in the Pacific Northwest Forest region. The Pacific Northwest Region also showed a trend in $WC_{relative}$ through time, although this time the relationship was negative. This was in contrast to the non-linear relationship between $WC_{relative}$ and Year in the Great Basin (Fig 5d). The final regional temporal trends I uncovered were in $BA_{relative}$ in the Pacific Northwest Forest region (Fig 5e) and in the Coastal California region (Fig 5f).

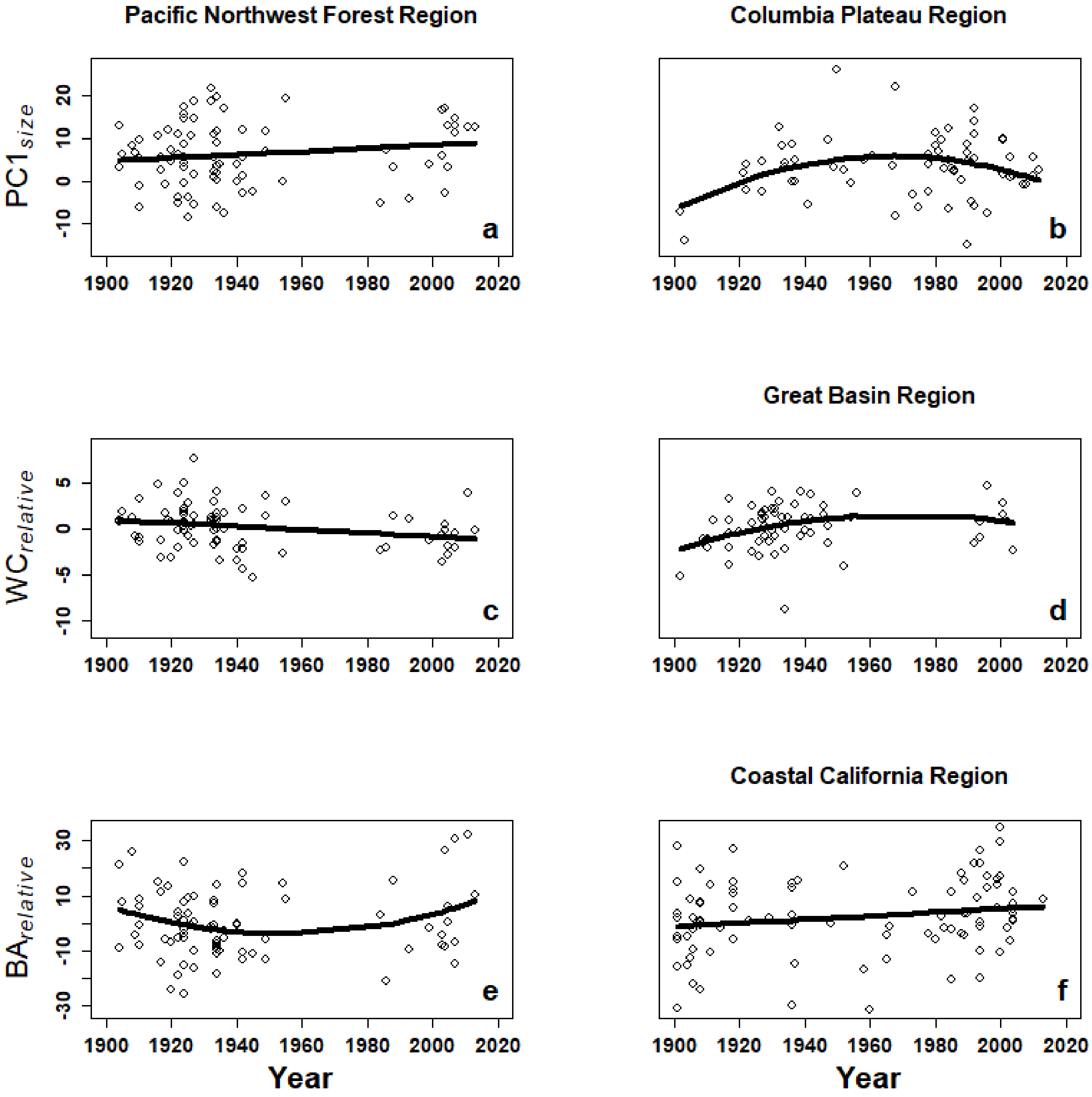

Figure 4.5. Regional temporal trends in size of American kestrels. All specimens in graphs are *F. s. sparverius* subspecies. Lines show significant relationships. Graphs a), c) and e) are all from the Pacific Northwest Forest Region.

Ecological Correlates of size

Environmental variables helped to explain all four measures of size at the continental scale. The best supported model for two of the size measures, PC1$_{size}$ and WC$_{relative}$, also included one of the competition variables, Comp$_{skewness}$ (Table 7). In both cases Comp$_{skewness}$ had a positive effect on the size measure. For PC$_{size}$, the largest effect by far was due to latitude, however the ecological factors improved model AICc by a large degree (ΔAICc=14.7). The addition of ecological covariates did not improve model AICc for WC$_{relative}$ by >2. The additional parameters were supported by the 85% CI interval criteria of Arnold (2010), however. Similarly, for the other two size measures, TA$_{relative}$ and BA$_{relative}$, the addition of environmental and competition variables improved model fit even less than for WC$_{relative}$, although in both cases the models were supported based on the 85% CI criteria.

Table 4.7: SAR model results for size variables at the continental scale with environmental and competition variables as covariates and factor variables for sex and subspecies. β-coefficients are shown for covariates with 85% confidence intervals in parentheses. Lambda values are reported with p-value in parentheses.

	Dependent variable:			
	pc1	WC_rel	TS_rel	BA_rel
Constant	-8.303^{*}	-5.129^{***}	1.440^{**}	23.367^{***}
	(-14.623, -1.984)	(-6.298, -3.960)	(0.406, 2.475)	(16.737, 29.998)
PC1$_{clim}$	-1.342^{***}		0.109	
	(-1.987, -0.697)		(0.006, 0.213)	
PC1$_{clim}^2$	-0.084^{**}			
	(-0.145, -0.022)			
climPC3$_{clim}$		0.142		
		(-0.005, 0.289)		
Comp$_{skewness}$	1.273	0.300		
	(0.107, 2.439)	(0.034, 0.565)		
Lat	20.144^{***}		1.344	
	(12.840, 27.447)		(0.140, 2.548)	

Lat^2	-17.200***		-1.205*	
	(-23.329, -11.071)		(-2.225, -0.184)	
Year		-0.212**		
		(-0.342, -0.083)		
PC2$_{clim}$				1.139
				(0.017, 2.260)
Sexm	-6.843***	-0.504***	0.247**	-8.868***
	(-7.725, -5.961)	(-0.773, -0.236)	(0.073, 0.422)	(-10.258, -7.479)
nicaraguensis	6.798*	7.550***	-1.995***	-24.723***
	(1.054, 12.542)	(6.161, 8.940)	(-2.900, -1.090)	(-31.841, -17.605)
paulus	-4.807	6.624***	-1.978***	-15.475***
	(-11.519, 1.905)	(5.188, 8.059)	(-3.055, -0.901)	(-22.899, -8.051)
peninsularis	0.989	5.456***	-1.338**	-17.067***
	(-4.898, 6.877)	(4.260, 6.652)	(-2.268, -0.409)	(-23.724, -10.409)
sparverioides	7.783	6.198***	-0.910	-15.671**
	(-0.529, 16.096)	(4.240, 8.155)	(-2.246, 0.427)	(-26.520, -4.823)
sparverius	13.992***	5.270***	-1.581**	-18.812***
	(7.151, 20.833)	(4.068, 6.472)	(-2.704, -0.459)	(-25.613, -12.011)
tropicalis	14.168***	6.309***	-1.562**	-28.531***
	(8.333, 20.002)	(4.930, 7.687)	(-2.493, -0.631)	(-36.049, -21.014)
Observations	562	562	562	562
Lambda	0.1053 (0.0493)	-0.15209 (0.0072)	-0.0997 (0.0497)	-0.064722 (0.2503)
Log Likelihood	-1,908.028	-1,237.403	-997.638	-2,162.251
sigma^2	51.872	4.752	2.033	128.468
Akaike Inf. Crit.	3,846.055	2,500.805	2,021.275	4,346.502
Wald Test (df = 1)	4.214**	8.337***	3.534*	1.484
LR Test (df = 1)	3.862**	7.215***	3.851**	1.321

*p=0.01****p0.05*****p<0.01

In regions where I found a significant temporal trend, the model criteria supported the inclusion of ecological covariates in 5 out of the 6 cases (Table 8). Interestingly, BA$_{relative}$ was the only size measure out of the 3 that showed regional temporal trends that did not include a competition variable in the model (Table 8). Best supported models for both PC1$_{size}$ and WC$_{relative}$ in all but one region contained a competition variable (Tables 9 and 10). Most striking was the coherence among regions and between the regional data and the continental data in the direction of the relationship of covariate effects (Figs 6-8).

Table 4.8: SAR model results for size variables at regional scales with environmental and competition variables as covariates and a factor variable for sex. β-coefficients are shown for covariates with 85% confidence intervals in parentheses. Lambda values are reported with p-value in parentheses.

	Dependent variable:					
	pc1		WC_rel		BA_rel	
	Pacific Northwest Forest	Columbia Plateau	Pacific Northwest Forest	Great Basin	Pacific Northwest Forest	Coastal California
Constant	10.194***	-1.698	-0.243	-0.905**	8.952***	11.466***
	(8.773, 11.615)	(-5.784, 2.389)	(-0.919, 0.433)	(-1.507, -0.302)	(4.576, 13.328)	(8.123, 14.810)
$PC2_{clim}$		-4.472*				-10.151**
		(-8.195, -0.749)				(-17.539, -2.764)
$PC3_{clim}$				-0.874*	-2.405**	5.763**
				(-1.554, -0.193)	(-4.097, -0.712)	(2.468, 9.059)
$PC3_{clim}^2$					-1.536**	-4.215***
					(-2.543, -0.529)	(-6.345, -2.085)
$Comp_{skewness}$		4.280*	1.140**			
		(0.674, 7.886)	(0.470, 1.811)			
Richness				0.849*		
				(0.219, 1.479)		
Year	1.363**	406.003***	-0.447**	91.155**	-540.472***	2.059**
	(0.381, 2.344)	(225.947, 586.058)	(-0.727, -0.167)	(31.015, 151.294)	(-766.517, -314.427)	(0.729, 3.389)
Year2		-402.895***		-90.282**	540.339***	
		(-582.284, -223.505)		(-150.389, -30.175)	(315.071, 765.607)	

Sexm	-7.920***	-5.488***	-1.059**			-11.391***
	(-9.939, -5.901)	(-7.733, -3.242)	(-1.772, -0.346)			(-14.911, -7.870)
lat					-7.577***	
					(-11.663, -3.491)	
Observations	78	68	78	64	78	91
Lambda	0.0016 (0.9916)	-0.2363 (0.2243)	-0.3187 (0.0443)	-0.4992 (0.0050)	-0.5614 (0.00005)	-0.1603 (0.3202)
Log Likelihood	-252.571	-221.063	-170.244	-141.835	-292.290	-350.949
sigma^2	38.027	38.539	4.462	4.554	94.532	130.107
Akaike Inf. Crit.	515.142	458.126	352.487	297.669	600.579	717.897
Wald Test (df = 1)	0.0001	1.853	5.813**	15.650***	31.150***	1.332
LR Test (df = 1)	0.0001	1.476	4.043**	7.861***	16.266***	0.988

*p=0.01****p0.05*****p<0.01

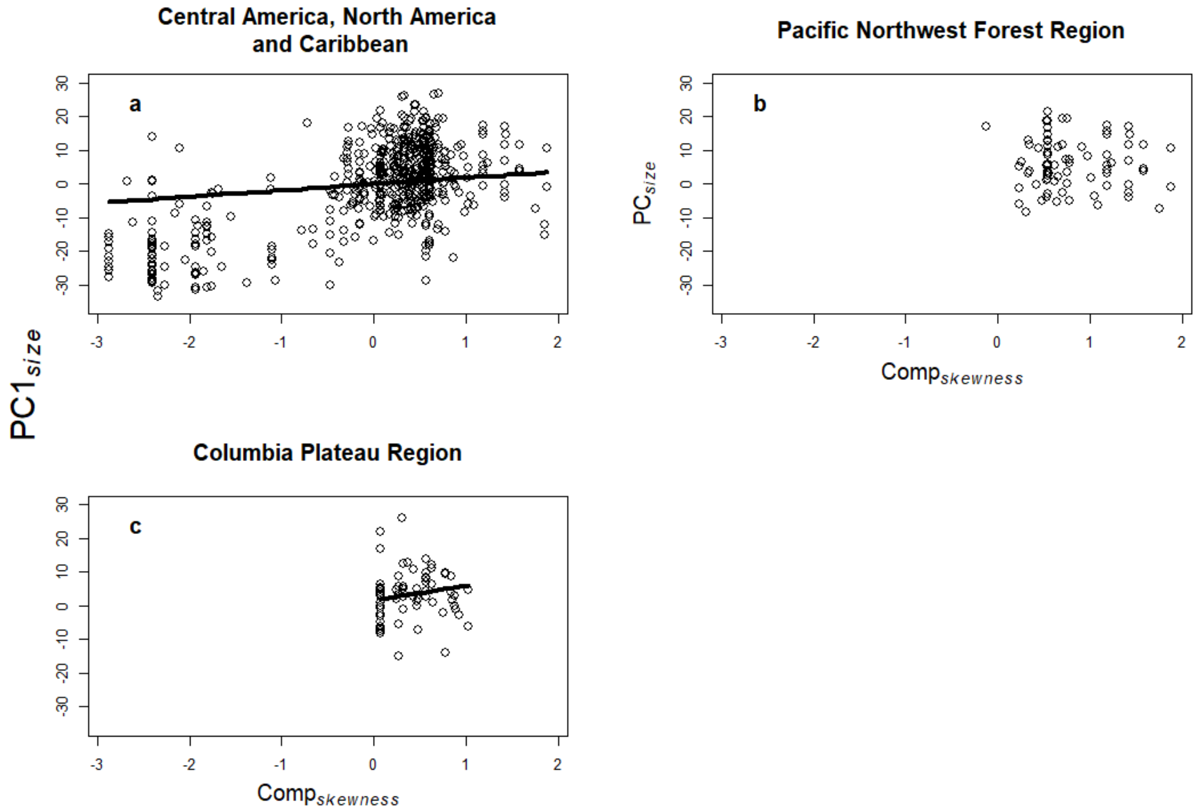

Figure 4.6. Coherence in the direction of effect of Comp$_{skewness}$ on PC1$_{size}$ between spatial scales: a) continental scale and c) Columbia Plateau. B) I did not find support for ecological covariates explaining variation in PC1size in the Pacific Northwest Forest region.

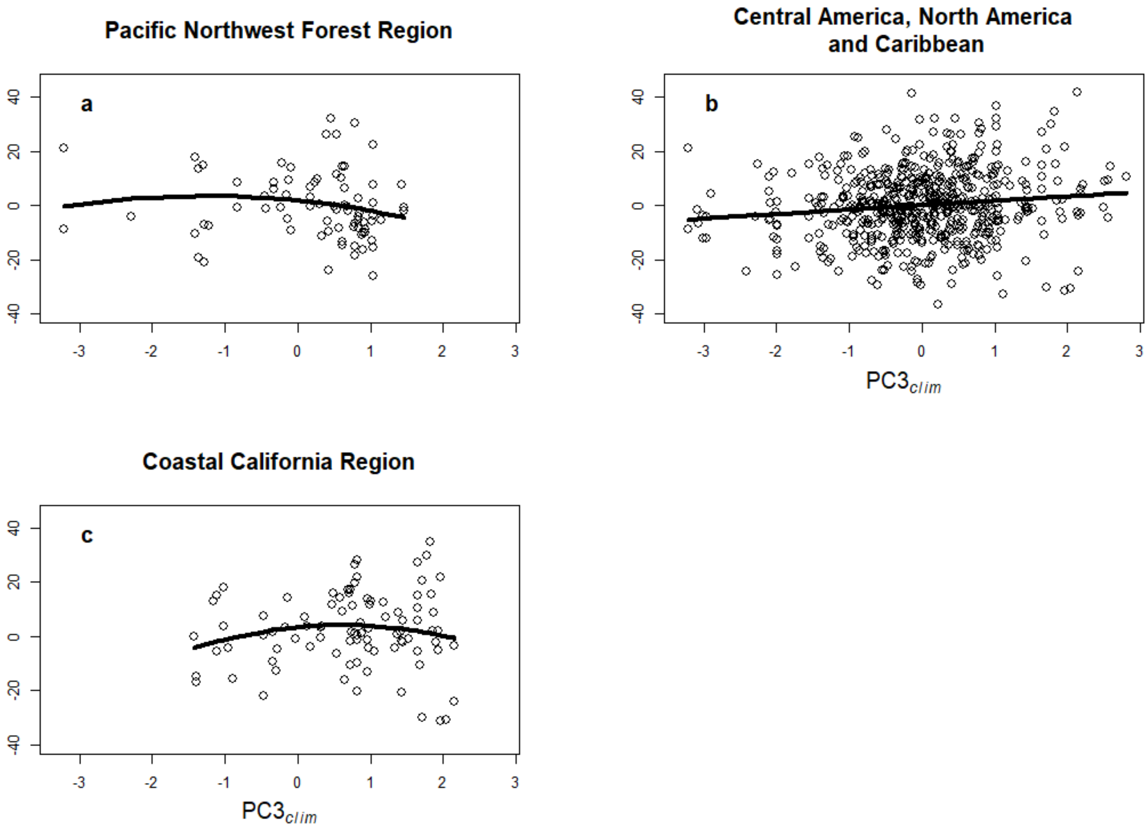

Figure 4.7. Coherence in the direction of effect of PC3$_{clim}$ on BA$_{relative}$ between regions and spatial scales: a) Pacific Northwest Forest and c) Coastal California similar patterns of response. b) the response at the continental scale was more linear.

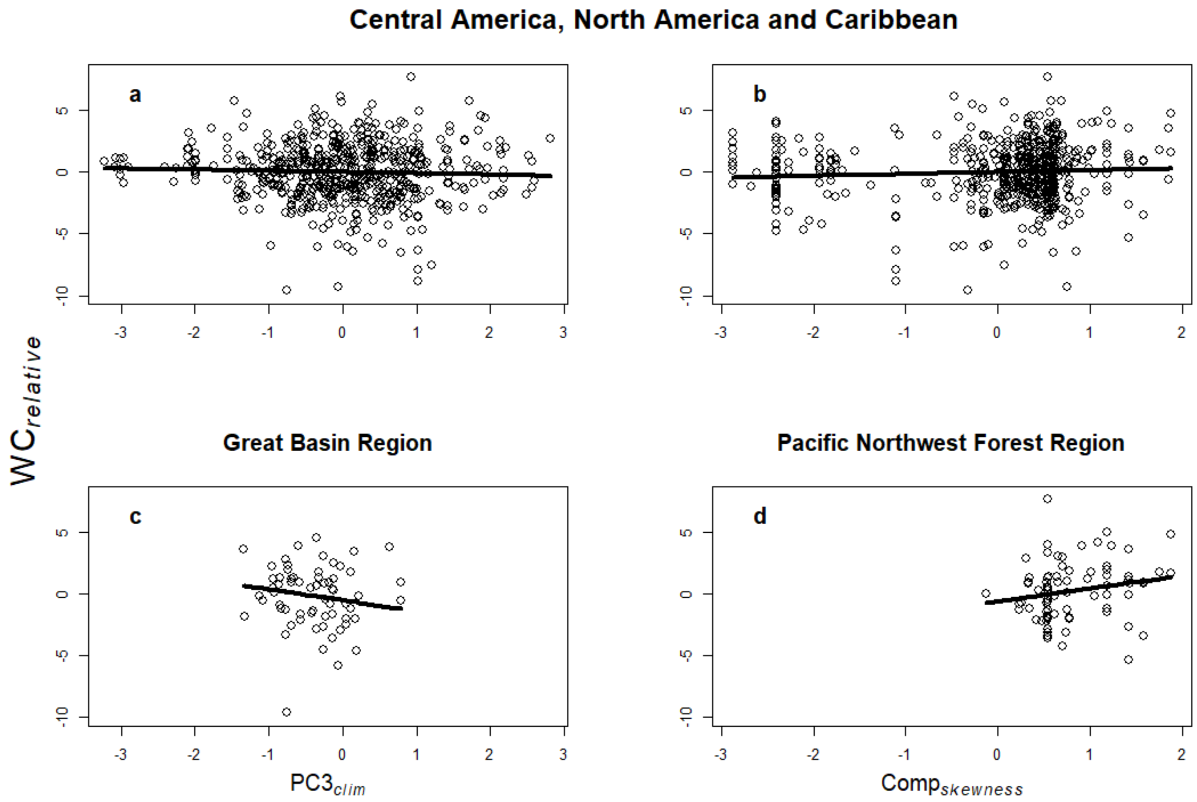

Figure 4.8. Coherence in the direction of effect of PC3$_{clim}$ and Comp$_{skewness}$ on WC$_{relative}$ between spatial scales: a) and b) continental scales show a much less pronounced effect than at the regional scales c) Great Basin and d) Pacific Northwest Forest.

Discussion

The findings highlight the multidimensional nature of the forces driving changes in morphology through time and across space. Despite this, I was still able to detect coherence in the underlying signals between regions and across spatial scales. These findings shed light on the complex nature of species' responses to climate change and the potential for other factors to interact or compete with these pressures. I find little support for a change in overall structural size through time, although I did find some interesting patterns within regions. While the support for Bergmann's rule through time was lacking, I did find strong support for the geographic expression of the rule as well as a role for Allen's rule in the temporal patterning of bill size of the American kestrel. In addition to climate, we detected a strong signal of ecological effects on structural size. I can't rule out the potential for genetic mechanisms at play as well, as there was a clear distinction between the most northerly and widespread subspecies, *F s. sparverius*, with subspecies from lower latitudes.

I found that structural size had a non-linear relationship with latitude. I did have a large latitudinal gap in the data at high latitudes and I only had three specimens above 50° N, so this could be a spurious result. However, recent analyses showed that Alaska supports a genetically distinct population of kestrels from the rest of the Western US and Canada (Ruegg *et al.*, 2021). This reversal toward a smaller size could reflect this population-level genetic differentiation. Geist (1986) argued that Bergmann's rule is invalid and used the reversal in body size (measured from wolf and cervid skulls) of large mammals at ~50° N to argue his point. Geist (1986) suggested that animal body size follows the primary productivity pulse that occurs along a north/south gradient which gradually increases before tapering off. Above a certain latitude animals can no longer sustain larger bodies because the resource pulse is too ephemeral. The data follow a similar trend, as limited as it may be.

This hypothesis also gains some support with the inclusion of $PC1_{clim}$ in the top model. American kestrels increased in structural size with increasing $NPP_{breeding}$ and NPP_{high}, accounting for other variables in the model. The variables define the high primary productivity pulses in the summer months. Both of these variables show a similar pattern with latitude as $PC1_{size}$, with the highest latitude values much lower than the mid to high latitude values. Huston and Wolverton (2011) have expanded on this idea, coining the term "eNPP", or ecologically and evolutionarily relevant NPP, that is, primary productivity available during the breeding (and growing) season. They claim that eNPP predicts the reversal in size at 60°N and also explains the lack of latitudinal variation in the tropics and is based on the availability of food resources, not temperature.

The fact that we detected a strong signal of size variation geographically in line with Bergmann's rule, begs the question why I did not detect a similar change temporally. For one, there may not have been enough change in temperature, assuming for the moment that is the driving force behind Bergmann's rule. Temperature change for the dataset over a 112-year period was, on average, approximately between 1° and 2° C for any given region. In comparison, the geographical variation in temperature for the data set was approximately 25° C. In addition, I show that competition and primary productivity may play just as important a role, if not more in determining size variation in this species. It should also be noted that size variation in kestrels subspecies was strongly patterned latitudinally (Fig 4), suggesting a genetic component to size variation in American kestrels. A strong pattern of inheritance in measures of size could result in stasis within subspecies through time, while still allowing for clinal geographical variation between species.

The inclusion of competition variables in so many of the models suggests that the biotic environment may play an equally important role in the geographic patterning of size. I characterized the competitive environment along two axes: richness of competitor species and their size distribution. In only one case did species richness end up in the final model. Richness had an approximately equal effect on relative wing lengths as $PC3_{clim}$, although in the opposing direction; richness was positively correlated with size. The skewness of the competitor distribution, on the other hand, had an effect on both structural size and relative wing chord, at both the regional and continental scale. It too had a positive association whereby more positive values of skewness, reflecting a competitor distribution closer in size to kestrels, increased kestrel structural size and relative wing chord. Again, I see the same pattern with latitude in skewness that I see with structural size. This may suggest that kestrels are somewhat limited in size by the inclusion of larger bodied (heavier) predators in the environment, a form of ecological release that peaks at the mid-high latitudes. McNab (1971) proposed a theory whereby Bergmann's rule was best explained by the interactions between a set of competing species. He suggested that the increase in size at higher latitudes of a smaller species in a set is the result of larger species stopping at a northern boundary while the smaller move beyond it and exploiting larger prey.

Why relative wing chord would vary with the size distribution of the competitor community is less clear. Shorter wings are associated with a higher degree of flight agility. Lank *et al.* (2017) suggested that the temporal trend of shortening wing lengths in semipalmated sandpipers was a response to reemergence of falcon populations after the crashes in the 1960's, noting that shorter wing lengths also resulted in rounder wings improving flight agility and hence predator evasion. However, hypotheses of kestrel declines related to Cooper's hawk predation have not been supported. Relative wing chord also declined with aridity; a somewhat surprising pattern given the associated metabolic costs of flying in hot arid environments.

Allen's rule was most noticeably supported in the analysis by association of BA to the humidity/aridity axis $PC3_{clim}$. The bird's bill has been shown to be an important thermoregulatory organ. Symonds and Tattersall (2010) found strong support for Allen's rule as applied to the bird bill across a wide phylogeny of bird species. In particular, they found that Australian parrots, along with penguins, Canadian galliforms and gulls, all had significant positive relationships with temperature. Greenberg *et al.* (2012), Greenberg and Danner (2012) and Danner and Greenberg (2015) show that bill size is highly influenced by coastal climate in song sparrows on the east and west coast, but the direction of influence depends on the critical season of stress. They provide evidence that the selection for smaller bills in song sparrows on the east coast is due to winter temperatures while selection for larger beaks in California is the result of selection acting to dissipate dry heat and retain water. Patterns of an association of bill size with climate have been noted elsewhere around the world too (Campbell -Tennant *et al.* 2015; Gardner *et al.* 2016).

I find that relative bill size responds non-linearly to a humidity/aridity gradient. The underlying response with this environmental variable manifests in the same pattern, despite the fact that the temporal dynamics between regions are different. In both cases at the regional scale, relative bill area decreases at both higher humidity and higher aridity. Greenberg and Danner (2012) found a convex pattern in relative bill area as they moved from the coast to the inland deserts in California. Both in the Coastal California Region and the Pacific Northwest Forest where I observe these patterns, the general trend is from more humid on the coast to more arid interiorly. These findings therefore seem to support, and are supported by, similar findings in the same regions. Given the highly specialized nature of the falcon bill, with its tomial tooth for severing the cervical vertebrae of prey, it would seem there would be strong selection for foraging on the bill. If kestrels do use the bill as a thermoregulatory organ, understanding how they balance the tradeoffs in foraging efficiency and heat dissipation would be an important area of future inquiry.

Conclusion

I find support for both Bergmann's rule and Allen's rule in the American kestrel. By examining multiple different measures of size, and correcting for shifts in structural size for appendages, I were able to detect significant temporal and geographic trends in several traits. Despite the variation in trends through time and space, I found a strong coherence to potential underlying mechanisms driving the variation. This suggests that just looking at temporal trends could be deceiving. The congruent patterns I see between regions and across spatial scales with ecological variables suggests multiple, and possibly opposing, forces acting on the morphology of American kestrels simultaneously. At the same time, they provide support for the same processes underlying different responses.

Chapter 5: Conclusion and future research directions

Summary of analysis chapters

In this dissertation, I looked at the effects of climate warming (among other environmental and ecological factors) on American kestrels at both a population level and at the scale of the species across 60° of latitude and 112 years. I show that context and scale are important factors in illuminating the degree to which climate or other factors influence an important population vital rate, nest success, and the morphology of this species. For instance, in Chapter 2 I highlight the importance of within-season variables that likely reflect more daily weather patterns, extreme weather events and/or biotic interactions that are not captured by annual or even seasonal averages of environmental parameters. I also show that a common response to climate warming among other populations was not found in This study population despite similarities in habitat, latitude and warming of the past several decades; local context likely attenuating the response.

In chapter 4 I show that spatial scale plays an important role in evaluating the impact of climate in shaping species morphology. Regional context here too likely plays an important role. Overall size or relative appendage lengths were found to have weak or no pattern with year at the continental scale but did show significant patterns at regional scales. This suggest that interpretations at regional scales may be insufficient to explain species wide patterns, especially when those species have a widespread distribution. However, I did find support for congruence in the underlying mechanisms of morphological change among regions and across spatial scales, both in overall size and in appendage lengths, despite differing patterns through time. Just because a spatial or temporal pattern is non-existent, or differs between populations, does not imply there is no response to environmental change or that the response is inconsistent.

In my approach to investigating morphological variation in American kestrels, I first asked a much more fundamental question: what do I mean by size in ecology in terms of ecogeographic rules? The literature is unclear on this and the measurement of size in birds, in particular, is inconsistent, hampering efforts to draw general conclusions from the multitude of specific cases (Rising and Somers, 1989; Freeman and Jackson 1990; Piersma and Davidson, 1991; Pascual and Senar, 1996; Senar and Pascual, 1997). In chapter 3, I repeat the call by other authors before me for a need to focus on structural size, independent of nutrient reserves, when investigating geographic and temporal variation in size, and argue that a 3-dimensional representation of the bird sternum represents a suitable standard for structural size in birds. I provide a method for quantifying a measure of structural size from the sternum, and then use this measure to determine which combination of traditional measurements performed on museum study skins and live birds is the best approximation of this. As discussed in more detail below, current technologies could allow for a similar approach with other species and provide a much-needed standardized basis for comparison.

Throughout these chapters, I tried to balance the specific with the general, the local with the global. The impacts of climate warming are global (IPCC 2021). The coherence in responses of disparate taxa in far flung regions of the globe confirm this (Parmesan, 2006; Parmesan & Yohe, 2003; Walther et al., 2002). These impacts, however, are also local. The localized direction and magnitude of warming and the interaction of warming with other environmental and ecological factors can drive divergent patterns between species and even populations of the same species as shown in this study of the American kestrels (Chapters 2 and 4). To fully understand the long-term impacts of climate on animal species, we will need to more fully integrate the global research with the local. Taking a common species approach is one pathway forward. The American kestrel is one example of a common species where research motivations for solving the proximate drivers of specific concerns could lead to more generalizable insights into species' responses to environmental and ecological perturbations at a range of spatial, temporal and biological scales.

Kestrels as a model system in ecology

There are many unanswered questions when it comes to population declines in American kestrels and their general ecology. Why are some populations declining and others increasing? Which vital rates are the most important for monitoring population health and does this hold for the whole species or just certain populations? Why do some populations show strong responses to climate warming and others do not? Should I expect a response to climate warming to manifest behaviorally, physiologically, morphologically or some combination of all three? How have migration patterns changed over time and what degree does the non-breeding ecology of kestrels play in their current declines. What is an appropriate baseline for American kestrel abundance? Are they declining in numbers from a historical baseline or returning to it from an elevated abundance due to human alteration of the landscape? To what degree does historical biogeography and genetics play a role in the distribution of kestrel subspecies and their associated phenotypes, and just how closely related are they to other kestrels of the world? For as much as American kestrels have been studied, there is still so much I do not know about them.

Fortunately, there is a currently a sense of priority and a widespread concerted effort among raptor researchers, community scientists, and federal and state agencies to learn more about the enigmatic decline of this species (McClure *et al.*, 2017). Just in the past few years, we have seen a continent-wide effort among these groups to put in practice standardized protocols and facilitate new understanding about some of the most pressing questions regarding kestrel populations (Mcclure *et al.*, 2021; Ruegg *et al.*, 2021;

Schulwitz *et al.*, 2021). New insights into population genetics, population dynamics, responses to climate change, and morphological trends are focusing future research questions (Smith *et al.*, 2017; Ely *et al.*, 2018; Mcclure *et al.*, 2021; Ruegg *et al.*, 2021). While this focus and energy will surely bring a much greater understanding of the specific cause or causes of American kestrel declines, it is important not to lose sight of the broader, more fundamental research questions that lie at the heart of Ecology as a scientific field. Both applied and basic ecological research approaches, focused population studies and species-wide studies, neontological and historical ecological perspectives are needed to tackle the mystery of vanishing American kestrels.

Beyond the specific problem of these population declines, American kestrels have the potential to become a model system for the field study of some of the most pressing ecological and environmental concerns of our time. Their willingness to nest in human made structures of known locations that can be easily monitored provides a readily available study subject. American kestrels are small and easily handled by non-experts which allows for a much greater participation of the non-scientific community to aid in efforts of data collection (Schulwitz *et al.*, 2021). Their latitudinal cosmopolitan distribution, seemingly catholic dietary preferences, and still relatively abundant (although declining) populations make for an ideal system for comparative studies. They can be found residing along a gradient of human habitation from urban to exurban to rural to wilderness (Smallwood and Bird, 2020). American kestrels are not just relegated to continental landmasses either. Distinct subspecies occur on oceanic islands spanning a range of sizes and distances from continental landmasses (Smallwood and Bird, 2020). There are a proposed 17 subspecies on the basis of phenotypes and likely even more genetically distinct populations (Smallwood and Bird, 2020; Ruegg *et al.*, 2021). The range of environmental and ecological factors these distinct populations and subspecies with different genotypes and phenotypes experience, and the degree to which they have been exposed to perturbations over the past two centuries provides a basis for understanding historical trajectories among them and insights into fundamental ecological processes that may be broadly applicable in their interpretation. While there is a pressing need to address American kestrels declines in the near term, the door to more fundamental questions of basic ecology using the American kestrel as a model system is wide open.

Directions for future research

Following on the research presented above, there are a few specific directions that future work might follow. A more detailed study of within season factors affecting nest success in the Central Oregon kestrel population is one. The results from the previous study point towards more daily or weekly patterns of variation in the environmental conditions or potential biotic factors (prey abundance and quality, predation, etc.) as more important in explaining the variation in nest success that I observe. In order to parse which factors are operating at this temporal scale, automated camera traps could be employed to monitor the population. This technology can provide local-scale field data collection at a coverage level not easily obtained with more traditional approaches. For example, unlike human observers, camera traps can maintain a continual presence that results in a highly robust, non-invasive means of monitoring behaviors such as foraging patterns, diet, and offspring provisioning and predation events (Rogers *et al.*, 2005; Garcia-Salgado *et al.*, 2015; Boal *et al.*, 2021). Machine learning strategies for analyzing the thousands of images are now readily available and vastly increase the efficiency of image classification techniques (Norouzzadeh *et al.*, 2018; Tabak *et al.*, 2019). Alternatively, online platforms such as Zooniverse (www.zooniverse.org) provide researchers a unique opportunity to engage communities in the scientific process by allowing internet users to review, tag, and classify images (Swanson *et al.*, 2016). When combined with other non-invasive technologies such as iButtons or other climate data loggers (Moore *et al.* 2010), image data from camera trap arrays could link American kestrel behavior to environmental conditions and ultimately to nest success at a high-resolution temporal scale.

A second avenue of future research regards the determination of structural size in museum study skins. In chapter 3 I provide a means of characterizing structural size in birds from the sternum and related a combination of measurements from study skins to this measure of size. This research was limited in scope in that the sample size and sample locations the paired sternums and study skins represented was small and quite limited. There is currently a dearth of avian skeletal elements in the world's natural history museums. The study skin has been the unit of choice for the comparison of variation in birds dating back to the late 19th century when natural history collections were being built up (James, 2017). Much less attention has paid to the skeletal anatomy in Ornithology throughout the generations. However, new technology in the form of 3D scanning and x-ray computed tomography (CT), magnetic resonance imaging (MRI), and optical surface imaging provides new opportunities various avenues of research into and using avian skeletal anatomy (James, 2017). In addition, software for geometric morphometric analysis of such skeletal elements has become much more available and user friendly (Buser *et al.*, 2020). In light of advances in and access to these new technologies and analytical tools, natural history collections should reevaluate the collection and storage of avian skeletal anatomy and make available these specimens for scientific research.

As new specimens become available, wider sampling and comparison of bird sternums to study skins could shed more light on the ability to accurately characterize structural size from museum study skins. Questions to be investigated might include: Does the same combination of traits from study skins predict structural size across a species range? Do males and females from sexually dimorphic species show the same link between study skin traits and structural size? Are there species-specific combinations of traits? Does the particular combination of traits relate to functional guilds or specific life-history categories? For instance, populations of American kestrels can be classified as migratory, partially migratory, or non-migratory. This data set was not extensive enough to allow a comparison between these different life history strategies in regards to which combination of traits from study skins best describes structural size. Future work in this area should take up these questions.

The widespread distribution, multiple subspecies and genetic differentiation of American kestrels across the Western hemisphere offers an enormous opportunity for comparative studies. Few other avian species are as cosmopolitan yet differ in life history characteristics as the American kestrel (Smallwood and Bird, 2020). A key aspect that remains unresolved and currently limits are abilities to accurately perform such research, however, is a robust phylogeny for American kestrel subspecies, or a clear understanding of American kestrels' place in the genera *Falco* for that matter (Groombridge *et al.*, 2002; Wink and Sauer-Gurth, 2004; Fuchs *et al.*, 2015; Ruegg *et al.*, 2021). A phylogeographic analysis of American kestrels across the whole of the Americas could provide a much greater understanding of the relationship between subspecies, their ancestral roots and the direction and timing of spread throughout the hemisphere. Such information could shed more light on the clinal nature of morphological variation in this species.

Finally, such an undertaking would certainly benefit from the use of natural history collections, but it would also offer an opportunity for American kestrel researchers from many nations across the Americas to build a collaborative network for future studies. A similar research project currently exists for swallows of the genus *Tachycineta* of the American continents, Golondrinas de las Americas (www.golondrinas.cornell.edu). This program has spurred many international and cross-cultural collaborations since its inception in 2007. Imagine how much knowledge could be generated if kestrel researchers across the Americas shared in a single goal to piece together the history of this species. How many future scientists, especially from underrepresented nations, ethnicities, or cultural backgrounds, might I inspire if I were to engage the general public through such an organization? What might those scientists from different cultural and environmental legacies bring to bear on the current status of American kestrel populations? Imagine a truly global perspective on the history and future of this species.

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