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POPULATION AND MORPHOLOGICAL CHANGES IN AMERICAN KESTRELS THROUGH SPACE AND TIME

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POPULATION AND MORPHOLOGICAL CHANGES IN AMERICAN KESTRELS THROUGH SPACE AND TIME

by

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POPULATION AND MORPHOLOGICAL CHANGES IN AMERICAN KESTRELS THROUGH SPACE AND TIME

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A once common raptor, the American kestrel (*Falco sparverius*) has experienced population declines in the last two decades throughout North America. Many hypotheses exist about the decline, including mortality from West Nile virus, rodenticide poisoning, climate change, an increase in predators, and core habitat loss or degradation, which could influence food availability. Food availability is key to raptor survival and reproduction, and changes in food availability throughout the year can have lifelong effects on size and body condition. Here we examine how morphology, specifically mass and wing chord, has changed at seven migration sites throughout North America as kestrel populations have declined. We hypothesized that if kestrel populations were declining due to lower food availability, there would also be declines in body size. Our results show a decrease in kestrel populations at all sites and a decline in mass and wing chord at five and four sites, respectively. We examined fat scores at two intermountain region migration sites and found that fat scores increased at one site and decreased at another. These results implicate a role for food availability in driving declines in kestrel populations, most likely during the breeding season. We also found differences in body mass and wing chord among migration sites. Despite being correlated within sites, variation in body mass and wing chord across sites differed, giving rise to variation in sexual size dimorphism and wing loading across sites. This variation may be due to

selective forces acting on traits, though random divergence due to low gene flow may be driving variation in wing chord. For body mass, regional variation in males and females could be a response to ecological processes. Overall, we can conclude that lower food availability is affecting some sites and not others, and that kestrels show regional morphological variation.

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TABLE OF CONTENTS

CHAPTER 1: Morphological Changes in American Kestrels (*Falco sparverius*) Suggest Multiple Causes Contribute to Widespread Population Declines.

CHAPTER 2: Geographic Variation in Morphology of the American Kestrel (*Falco sparverius*) Across North America.

Multimedia Objects

Chapter 1: Morphological Changes in American Kestrels (*Falco sparverius*) Suggest Multiple Causes Contribute to Widespread Population Declines.

ABSTRACT

Many American kestrel (*Falco sparverius*) populations are declining across North America. Potential causes include mortality from West Nile Virus, anticoagulant rodenticide exposure, climate change, an increase in avian predators, habitat degradation, and reduction in food availability. We analyzed American kestrel count and banding data from seven raptor migration sites throughout North America with at least 20 years of migration data. We used count data to determine the year at which the kestrel population began a significant decline and then used banding records to determine whether body mass and wing chord declined after this point. We found reductions in mass at five sites and wing chord at four sites. We also assessed wing pit fat for two sites, and this metric of energy reserves declined at one site and increased at another site. Our results indicate declines in body size at the majority of sites are consistent with the hypotheses that food availability, change in climate, predation risk, or increases in the use of anticoagulant rodenticides are causing population declines. In contrast, the sites that do not show significant trends in body size could indicate that West Nile virus is contributing to population declines.

INTRODUCTION

Raptors are top predators that are vulnerable to environmental change because they often occur at low densities, have low reproductive rates, and establish large home ranges (Bildstein 2001; Hoffman & Smith 2003). In addition, direct threats from humans include habitat loss, shooting, poisoning, electrocution, and collisions with wind turbines, vehicles and windows (DeLong 2000). Not surprisingly populations of many raptor species are declining and subsequently are of conservation concern, including Peregrine falcons (*Falco peregrinus*), Bald eagles (*Haliaeetus leucocephalus*), Swainson's hawks (*Buteo swainsoni*), and Osprey (*Pandion haliaetus*) during the last half-century (Cade *et al.* 1988; Bednarz *et al.* 1990; Hoffman & Smith 2003; McCarty & Bildstein 2005; Farmer & Smith 2009). Although some declining species have recovered due to intensive reintroduction programs, habitat protection, and efforts to limit direct threats, other species, including the American kestrel (*Falco sparverius*), are showing more recent declines (Farmer & Smith 2009).

American kestrels (hereafter referred to as kestrels) are the smallest North American falcon and are widely distributed across North America. Kestrels forage on a wide variety of small prey, including insects, lizards, birds, and mammals (Smallwood & Bird 2002). To take advantage of seasonal prey abundances, most kestrel populations migrate south of their breeding range for the winter (Smallwood & Bird 2002). Migration is an energetically expensive undertaking, and raptors frequently use thermals and orographic lift along prominent ridges and coastlines to save energy, generating concentration points where many raptors pass through particular sites each year (Kerlinger 1989; Bohrer *et al.* 2012).

Count sites and banding stations have been established at migration concentration points throughout North America to allow long-term monitoring of migratory raptors (Bildstein 2001; Hoffman & Smith 2003; McCarty & Bildstein 2005). The data collected from these sites provide inexpensive censuses of raptor populations critical to understanding and monitoring raptor populations at a broad scale. Such count data reflected Bald eagle and Peregrine falcon declines caused by DDT-induced egg shell thinning, as well as subsequent population recoveries after DDT was restricted from use in North America (Bednarz *et al.* 1990). Raptor banding at these sites also provides morphometric and health (fat stores) information about birds, along with longevity, survivorship and movement data when a banded bird is recaptured or recovered (Hoffman *et al.* 2002; DeLong & Hoffman 2004).

Fall migration counts and Breeding Bird Surveys (BBSs) show substantial and widespread declines in kestrel populations throughout North America (Farmer & Smith 2009; Sauer *et al*. 2014). We pooled two to four decades of banding data from seven sites across the continent to test for long-term changes in body size and energy stores that might accompany observed population declines. Our objective was to compare observed patterns of body size change with patterns of body size change that should be seen given potential sources of population declines (Table 1). Where observed patterns do not match the predicted patterns, we can infer that those potential causes of decline are not likely the main source of decline for kestrels.

Potential causes for kestrel declines include mortality from West Nile virus (WNV), anticoagulant rodenticide exposure (hereafter referred to as rodenticides), changes in climate, an increase in avian predators, loss of habitat, and decline in food availability (Table 1; Smallwood *et al.* 2009). Although numerous bird species have been affected by WNV since 1999 throughout North America, it is unlikely to be causing long-term kestrel declines because northeastern kestrel populations began to decline prior to the arrival of WNV (Farmer & Smith 2009). There is currently little evidence that WNV affects smaller or larger kestrels more severely, and thus if WNV is causing population declines in kestrels, there should not be a concomitant decline in body size.

Anticoagulant rodenticides negatively effects populations of raptors that forage on small mammals (Murray 2011; Rattner *et al.* 2011; Stansley *et al.* 2014). There is little information about how rodenticides influence body size, but Barn owl (*Tyto alba*) nestlings in areas where rodenticides were deployed grew to smaller sizes and had shorter wing chords than nestlings in control areas (Naim *et al.* 2010). Thus, sublethal rodenticide poisoning could potentially affect the size of kestrels as well, generating a parallel decrease in body size as populations decline.

In North America, wing lengths have been getting larger on the West coast but smaller in the East (Van Buskirk *et al.* 2010; Goodman *et al.* 2011). The link between wing length and climate in these studies is correlational, but overall this suggests that no consistent pattern of body size change should arise if climate is the direct cause of population declines. It is also unclear how population declines in kestrels would be linked directly to climate, such that effects of temperature per se, might be inconsistent as well. Indirectly, changes in climate could alter the availability of prey (see below).

Avian predators such as Cooper's hawks (*Accipiter cooperii*) and Peregrine falcons could have a negative impact on kestrel populations and have an effect on kestrel body size. Cooper's hawk populations have been steadily increasing in urban environments in the last decade (Fish 2003; Stout & Rosenfield 2010). After the ban of DDT use and successful large-scale reintroduction programs, Peregrine falcon populations began to steadily increase throughout North America (Cade *et al.*1988; Bildstein 2001). Cooper's hawks and Peregrine falcons will feed on a variety of prey, but birds make up a majority of their diets (Storer 1966; White *et al.* 2002; Ellis *et al.* 2004; Curtis *et al.* 2006). Few studies have analyzed prey remains in Cooper's hawk and Peregrine falcon nests, and very few kestrels have been taken as prey (Storer 1966; Ellis *et al.* 2004). However, an increase in avian predators may put stress on kestrel populations, causing body size selection (Scharf *et al.* 2000). Selecting for body size could drive kestrel body size to increase or decrease over time.

Shortages of food would generate both a decline in populations and a decline in body size through time. Food availability is important in all aspects of the kestrel life cycle, from reproduction, nestling growth, fledgling success and into adult life. Survival during migration depends on acquiring sufficient food during different periods of the year (Figure 1; Sillett & Holmes 2002; DeLong & Hoffman 2004). Food shortages during reproduction and development would lead to smaller eggs, and nestlings or fledglings that have a lower mass (Martin 1987). Food shortages during migration would not likely generate a decline in body size along with declines in abundance because kestrels are fully grown during migration. Instead, shortages of food during migration might be reflected in lowered fat stores, which reflect more short-term variation in foraging (King 1972; Blem 1980). Thus, if food availability during migration were a causal factor in generating population declines, we would expect to see lowered fat stores through time.

It is not clear which, if any, of these forces are causing kestrel declines. Here we investigate if changes in populations are accompanied by changes in morphology using long-term continent-wide data collected from fall migration banding stations. If kestrels are not declining in body size, this would suggest that rodenticides and changes in food are not the cause, but WNV, predators, and climate effects could still be at play. If kestrels are increasing in body size, this would only be consistent with predators and climate effects as causes of the declines. If kestrels are declining in body size, this would be consistent with rodenticide use and food shortages, but could also be seen if predators and climate effects are the cause of declines. Thus, although there are no clear-cut contrasts that can firmly rule out all of the potential causes, changes in morphology can help narrow the field of potential causes. If we can narrow the focus of reasons affecting population decline, we can begin to help kestrel populations recover.

MATERIALS AND METHODS

Study Sites

We collected migration count and morphometric data for kestrels observed and banded at seven raptor fall migration sites across North America over a 20-40 year period (Figure 2). The sites represent most of the different flyways that occur across North America, including the Atlantic, Mississippi, Southern Rocky Mountain, Intermountain, and Pacific flyways (Figure 2). Migration data were collected at sites run by Cape May Raptor Banding Project at Cape May Point, New Jersey (39°56′N, 74°57′W; Farmer & Smith 2009), Hawk Mountain Sanctuary near Kempton, Pennsylvania (40°40′N, 75°55′W; Viverette *et al.*1996), Hawk Ridge Bird Observatory in Duluth, Minnesota

(46°51´N, 92°02´W; Evans *et al.* 2012), HawkWatch International at the Manzano Mountains in central New Mexico (34°42´N, 106°25´W; DeLong 2006) and the Goshute Mountains in eastern Nevada (40°25´N, 114°16´W; (DeLong & Hoffman 1999), Intermountain Bird Observatory at Lucky Peak near Boise, Idaho (43°36´N, 116°04´W, Farmer & Smith 2009), and the Golden Gate Raptor Observatory (GGRO) in the Marin Headlands, California (37°49´N, 122°29´W; Hull *et al.* 2010).

Data collection

We used raptors per hour (RpH; the total number of birds counted divided by the total observation hours each year) to assess kestrel population trends through time. Although the data collection procedures vary slightly between sites, procedures are standardized within each site giving a robust index of kestrel population sizes each year (Hoffman & Smith 2003; Farmer *et al.* 2007; Hull *et al.* 2010; Evans *et al.* 2012).

Kestrels were trapped at the different sites using similar trapping procedures. A combination of bow nets, mist nets, or dho-gaza nets were used to capture raptors, and non-native avian species such as rock pigeons (*Columba livia*), Eurasian collared doves (*Streptopelia* decaocto), house sparrows (*Passer domesticus*), and European starlings (*Sturnus vulgaris*) were used as lures. Kestrels were fitted with a uniquely numbered, U.S. Geological Survey aluminum leg band (Hoffman *et al.* 2002).

Kestrels were sexed and aged by plumage (Smallwood 1989; Clark & Wheeler 2001). Males have slate-blue wings and females have reddish brown wings. Females can be aged by the size of the subterminal band on their tail. The adult female subterminal band is ~1.75 times wider than the next dark band on their feathers, whereas the juvenile subterminal bands are less than 1.75 times the next dark band on their feathers

(Smallwood 1989). Hatching-year females were termed “juvenile” and AHY (After hatching-year), SY (Second year) and ASY (After second year) females were grouped together as “adult”. Due to difficulties and inconsistences in aging males during migration, all males were assigned as “unknown” age for this analysis. We used a combined age/sex category that included juvenile females, adult females, and males. At Lucky Peak and Hawk Mountain Sanctuary, however, the majority of female kestrels that were captured were of unknown age so all females were assigned “unknown” at these sites.

Birds were weighed to the nearest gram and a standard ruler was used to measure wing chord to the nearest millimeter. Body mass and wing chord are both measures of overall body size, but wing chord is relatively fixed after feather growth ceases, except for minor wear, while body mass can vary through time to a greater extent. In addition to genetic effects, wing chord reflects energetic conditions of a bird while the feather is growing, while body mass reflects energetic conditions during nestling growth and through time after the bird stops growing. Kestrels that had food in their crops equivalent to being about half full or fuller, were not included in the analysis (approximately 300) because the crop contains undigested material such as bones, feathers, and fur, which would cause overestimation of the mass of the bird. If individuals were recaptured at the original banding location within the same banding season, we only used the initial mass and wing chord measurements in the analysis. Distributions of mass and wing chord were analyzed to identify and remove major errors in measurements of mass and wing chord. Birds with mass and wing chord measurements greater than 3 standard deviations (SD) of the mean mass and wing chord for each sex were excluded from the analysis due to the high likelihood that these measurements were incorrectly recorded, and eliminated approximately 250 individuals out of a sample size of about 16,300.

Wing pit fat is a good proxy for total body fat in raptors (DeLong & Gessaman 2001). At the Manzano Mountain and Goshute Mountain sites, wing pit fat scores were assigned with a 4-point scoring technique (DeLong and Hoffman 2004). A score of 0 was for kestrels with no visible fat, 1 for birds with a shallow streak of fat, 2 for birds with fat that was approximately flush with surrounding muscle tissue, and 3 for birds with fat that exceeded the depth of the surrounding muscle tissue.

Statistical Analysis

Data were analyzed by site due to regional differences in kestrel body size and wing chord (Table S1). We used a breakpoint regression for RpH against year to identify when populations switched from a period of stable or increasing population size to a statistically significant decline. Once the breakpoint year was determined, we subset the data into "before" and "after" datasets, with the before dataset covering the initial period of stable or increasing population size and the "after" dataset covering the period of recent population decline (Table S2).

We then used linear regression to determine whether the mass and wing chord length of the kestrels changed over time after declines began. A global model was developed for each site for the periods before and after the breakpoint year, or the whole time-period if there was no breakpoint. Predictor variables included year, Julian date (JD), a combined age/sex class (SA), and all two-way interactions. SA was included because kestrels differ by sex in size and morphology. We included Julian date in the analyses because later migrating raptors may have higher fat and protein reserves than earlier migrating birds (Gessaman 1979; DeLong 2006). We used backward model selection with the 'drop' function to remove non-significant predictor variables and obtain a minimum model. We carried out all statistical analyses in R version 3.1.2 (R Core Development Team 2014) and package 'Segmented' for the breakpoint regressions (Muggeo 2003; Muggeo 2008).

We used linear regression to assess changes in wing pit fat scores through time for the Goshute Mountains and the Manzano Mountains sites. These data were available for shorter periods of time, from 1993 to 2013 in the Manzano Mountains and 1992 to 2014 in the Goshute Mountains. As before, we developed a global model for each period before and after the breakpoint year. The response variable was wing pit fat and the predictor variables were year, SA, JD, and two-way interactions between year and SA, and JD and SA. We used the same breakpoint year described earlier to subset the data and then used backward model selection to drop non-significant terms.

RESULTS

Population declines

The rate of raptor passage (RpH) significantly declined at all seven migration sites during the last decade, with some sites showing declines for much longer periods (Table 2; Figure 3). Declines in RpH ranged across sites from 12.6% to 42.7 % per ten years (Table 2). Cape May, Hawk Mountain, and Lucky Peak did not show a breakpoint in their population trends, with declines evident during the entire period analyzed.

Mass

During the periods when RpH declined significantly, mass also declined significantly at most sites (Table 3a). In some cases, mass declined significantly for all age and sex groups, and in other cases only certain classes declined. The mass of juvenile females, adult females and males declined significantly at Cape May, Hawk Mountain, Goshute Mountains and Lucky Peak. The declines in kestrel mass over a period of 10 years ranged from 0.7% to 2.4% of their average mass, which corresponds to 1 g to 2.7 g decrease in mass (Table 3a). Juvenile females had a significant decrease in mass at Goshute Mountains and GGRO. Juvenile female kestrels at the Goshute Mountains lost 1.3% of their mass or 1.5 g whereas juvenile female kestrels at GGRO lost 0.89% of their mass or 1 g during a ten-year period (Table 3b).

Wing Chord

At Hawk Ridge, Manzano Mountains, Goshute Mountains, and Lucky Peak, wing chord declined from 0.2% to 0.7%, or 0.4-1.2 mm, per ten years across sites (Table 3a). At Cape May, wing chord did not decline significantly overall but juvenile female wing chords showed a decline of 0.52% of wing chord, or ~1 mm per ten years.

Wing Pit Fat

At Manzano Mountains, there was a non-significant increasing trend in fat scores before the breakpoint, and after the breakpoint year, wing pit fat increased significantly (Table 4). At the Goshute Mountains, wing pit fat showed a non-significant decreasing trend before the breakpoint and a significant decline after the breakpoint, at a rate 5-6% per ten years (Table 4).

DISCUSSION

Migration counts and breeding bird surveys have documented declines in kestrel populations beginning in the mid 1990s (Sauer *et al.* 2014; Farmer & Smith 2009). Our results show that in addition to population declines, kestrels are showing declines in body size and wing morphology at the majority of migration sites we analyzed. Kestrel mass has systematically been decreasing by about a gram or more per decade at five of the seven migration sites across North America, and wing chord has been decreasing by 0.4 mm to 1 mm per decade at four of seven migration sites.

Birds undergo significant changes in body mass, and both fat and non-fat tissue, throughout their annual life cycle (Lindström & Piersma 1993). The ability to accumulate pre-migratory fat reserves is important for migrating birds because it allows them to store energy needed while on migration when foraging might be limited (King 1972; Blem 1980; DeLong & Gessaman 2001; Delong & Hoffman 2004). We observed a decrease in wing pit fat over time in kestrels migrating through the Goshute Mountains, whereas fat stores increased for kestrels moving through the Manzano Mountains. These results suggest that it is not primarily migration-season food availability driving wide-spread declines, although declines in energy stores may play a role in survival or migration strategies for birds migrating through the Goshute Mountains.

The kestrel population at Hawk Ridge Bird Observatory and the Manzano Mountains did not show significant changes in the trends of mass throughout time. Our first hypothesis, that kestrel decline was due to mortality from West Nile virus, could explain the population decline at Hawk Ridge. From our population analysis, we determined that kestrel populations declined in 2002 at Hawk Ridge, which is consistent with when WNV entered North America (Reisen 2013). In contrast, our results from Manzano Mountains do not support the WNV hypothesis. From our breakpoint analysis, we determined the population began declining in 1996, which is well before the arrival of WNV in North America.

Rodenticide poisoning, climate change, avian predators, food availability and loss of habitat, cannot be ruled out as possible causes for kestrel decline at the Cape May, Hawk Mountain, Manzano Mountains, Goshute Mountains, Lucky Peak, and Golden Gate Raptor Observatory sites. These factors would have a negative effect on kestrel populations as well as an effect on body size. The secondary effects of rodenticide poisoning have recently gained more attention and further studies are needed to understand their sublethal effects. Raptors are relatively sensitive to anticoagulants, and can die from secondary poisoning (Rattner *et al.* 2011), and body size is stunted when young are exposed to rodenticides (Naim *et al.* 2010). However, further research is needed to determine if the nestlings that survive exposure to rodenticides (if any), and go on to produce smaller young.

Other factors that affect body size, such as climate change, food availability, and changes in habitat, are related and we analyzed the changes in size likely as a result of a combination of these hypotheses. We specifically focused on how food availability could be the main driver of decline. Changes in morphology can be expected if food availability is contributing to the declines, as resource availability affects clutch number, egg size and quality, nestling growth rate, fledgling success and survival, and the effects would be reflected in an overall decrease in body size over time (Martin 1987; Lindström 1999). Declines in food availability could affect kestrels during any time of the year (Figure 1, Segment A; Dawson & Bortolotti 2000). During egg production, energy and nutrients are required for the female to produce eggs and provision them with energy. The larger the caloric density of the eggs, the larger and more well-developed a young kestrel will be when it hatches (Martin 1987). Incubation of the young can be energetically costly because the more time a female spends on a nest, the less time she has to forage. A heavier and better-fed female should be able to sustain the loss of more weight during incubation, which would allow her to spend more time on the nest and increase nestling survival (Martin 1987). Kestrel clutches hatch asynchronously, creating a size difference among nestlings resulting in the last nestling being the smallest in size. When food is limited, the last hatched bird may not survive, reducing the brood size; this may however free up resources for the remaining young, potentially allowing the remaining nestlings to survive. Nestling growth depends on food provisioning (Dawson & Bortolotti 2000), and young birds reach their full structural size about a month after hatching. Better-fed fledglings will be larger, stronger, and more successful at hunting and preparing for fall migration, enabling higher survival (Dawson & Bortolotti 2000). In short, because food availability during the breeding season influences both growth and survivorship, declines in population size that are caused by lower food availability would likely be accompanied by declines in body size and we see this at the majority of study sites.

Factors such as climate and land-use change could cause decreases in food availability. Drought has been prevalent in the interior west of North America during a substantial portion of the kestrel declines (Hoffman & Smith 2003; Farmer & Smith 2009). Hoffman and Smith (2003) suggested that as drought has increased, raptor hunger levels and mortality have also increased in these regions. Changes in land-use also may be affecting the habitat structure in areas where kestrels hunt. Many northeastern farmlands have been reforested or developed, replacing open foraging habitats with forests or suburban land cover (Farmer & Smith 2009). Changes in landscape provide fewer nesting sites and foraging locations and potentially fewer opportunities for migration stopovers (Farmer & Smith 2009). Thus, changes in climate and land-use could be the cause of decreased resource supply, impacting kestrel growth and survival. Alternatively, behavioral changes in response to warming or change in precipitation could alter access to food resources. For kestrels, variation in weather may affect food availability and parental provisioning behavior (Dawson & Bortolotti 2000). In one study, young kestrels that were exposed to inclement weather were smaller, lighter, and less likely to survive to fledgling stage than those that were raised in better weather conditions (Dawson & Bortolotti 2000). The results suggest it may not be food abundance per se driving lower food intake, but potentially also food availability or behavioral changes that limit provisioning rates.

Other studies in Europe and North America have shown long-term changes in body size for other birds and have attributed these changes to changes in climate and food availability. The body size of Danish goshawks (*Accipiter gentilis*) was examined in museum specimens collected between 1854 and 1941 and between 1979 and 1998. In these birds wing chord, tarsi length and bill size decreased over time and the trends were linked to changes in diet because the decrease in body size was not uniform across age and sex class and immature birds were more affected than adults. Similarly, a study of passerines in western Pennsylvania from 1961 to 2006 showed that fat-free mass and wing chord were steadily decreasing over time (Van Buskirk *et al.* 2010). In contrast, wing chord and mass for a wide variety of passerine species at two sites in central California over 3-4 decades steadily increased over time, although not all changes were significant for all species (Goodman *et al.* 2011). Studies by Goodman *et al.* (2011) and Van Buskirk *et al.* (2010) both show changes in body size of a similar magnitude but in different directions. Changes in body size in both studies have been attributed to a changing climate, but Goodman *et al.* (2011) note that different biomes will respond differently to climate change because warming and changes in precipitation in mesic and arid environments may have different effects on body size. Our analysis is continental in scope, and we see changes in morphology at sites in different directions, which could suggest that the breeding areas from which migrants originate are responding differently to climate change, and also suggests different factors are driving population declines.

Although migration counts have clearly documented population declines in migratory raptors in the past, current declines and body size changes also could reflect shifting migratory patterns or migratory short stopping – when birds migrate shorter distances when conditions are good. Migratory short stopping could contribute to the pattern of fewer birds being counted at migration sites. For example, population declines were recorded in sharp-shinned hawks (*Accipiter striatus*) in the 1980s and 1990s in eastern North American, at Cape May Point and Hawk Mountain Sanctuary (Viverette *et al.* 1996). Band recovery data and CBS data indicate, however, that there was a significant increase in the number of birds observed north of the two sites over time, suggesting that sharp-shinned hawks in eastern North America may not be migrating as far as they once did. Food availability is known to influence migration distances (McClelland *et al.* 1994), altering distances or changing patterns and flyways. So, changes in food resources could be altering how far kestrels migrate. However, evidence for kestrel declines also comes from Breeding Bird Surveys (Sauer *et al.* 2014) and Christmas Bird Counts (Sauer *et al.* 1996b), indicating that short-stopping is an unlikely cause of reduced numbers of kestrels seen at migration sites.

Declines in kestrel body size do not necessarily imply a maladaptive change in phenotype. Indeed, body size is highly plastic and subject to rapid evolution, and theory suggests that body size may shift as an adaptive response to resource supply (DeLong 2012). For example, smaller animals require less food than larger animals and thus may be able to survive longer at lower food densities (Kooijman 1986). Smaller size may also make migratory travel less costly. Falcons predominately use flapping flight instead of soaring behavior during migration (Fuller *et al.* 1998; Dunne *et al.* 2012). Falcons will forage while flying and if they are able to do so during migration, they may be able to migrate faster because they do not have to stop to refuel. In general, flapping flight performance improves as body size decreases, suggesting that smaller birds would not have to feed agration and could migrate to wintering or spring grounds more quickly than larger birds (Hedenstrom & Alerstam 1998; La Sorte *et al.* 2013).

In addition to changing how far they migrate, kestrels could be migrating earlier or later. For example, in 2011 at Manzano Mountains, the average median passage date for all raptor species was 10 days later than the median passage date from 1985-2010 (Mika *et al*. 2011). Changes in the growing season could be driving shifts in seasonal food and resource availability. Such changes could influence the mass of kestrels during migration because kestrels migrating later would be heavier, so banding stations would be catching heavier and older birds. We accounted for this possible variation by including

Julian date in our analysis, such that any shift in migration timing would not influence our results.

The American kestrel might be the next canary in the coalmine, reflecting widespread changes in climate and habitat quality that may affect many avian species. Analyzing regional climate data during the fall migration season would be able to give us a better understanding of how temperature change might affect migration patterns and food availability. More research on West Nile virus is needed in the region around the Great Lakes, where Hawk Ridge Bird Observatory is located, to understand the impacts on kestrels specifically. More research is needed on the impacts of increasing populations of Cooper's hawks and Peregrine falcons in regions where there is overlap with kestrel populations. Also, there has not been a comprehensive study on prey remains in Cooper's hawk nests and this research could provide insight into why kestrel populations are declining. We suggest that efforts to understand how kestrel breeding and foraging behaviors change in response to climate and land-use changes are crucial to understand the mechanisms of kestrel declines, and how and whether we need to take steps to ensure that kestrels remain common.

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Table 1. List of potential causes of American kestrel declines and the effect each potential cause could have on population and body size. Up and down arrows indicate positive and negative effects, respectively. Circle indicates no effect, and question mark indicates that effect is unknown.

Potential cause for decline	Effect on population	Effect on body size
West Nile Virus	↓	⦸
Rodenticide poison	↓	↓
Climate	?	↓↑
Predators	↓	↓↑
Food/habitat decrease	↓	↓

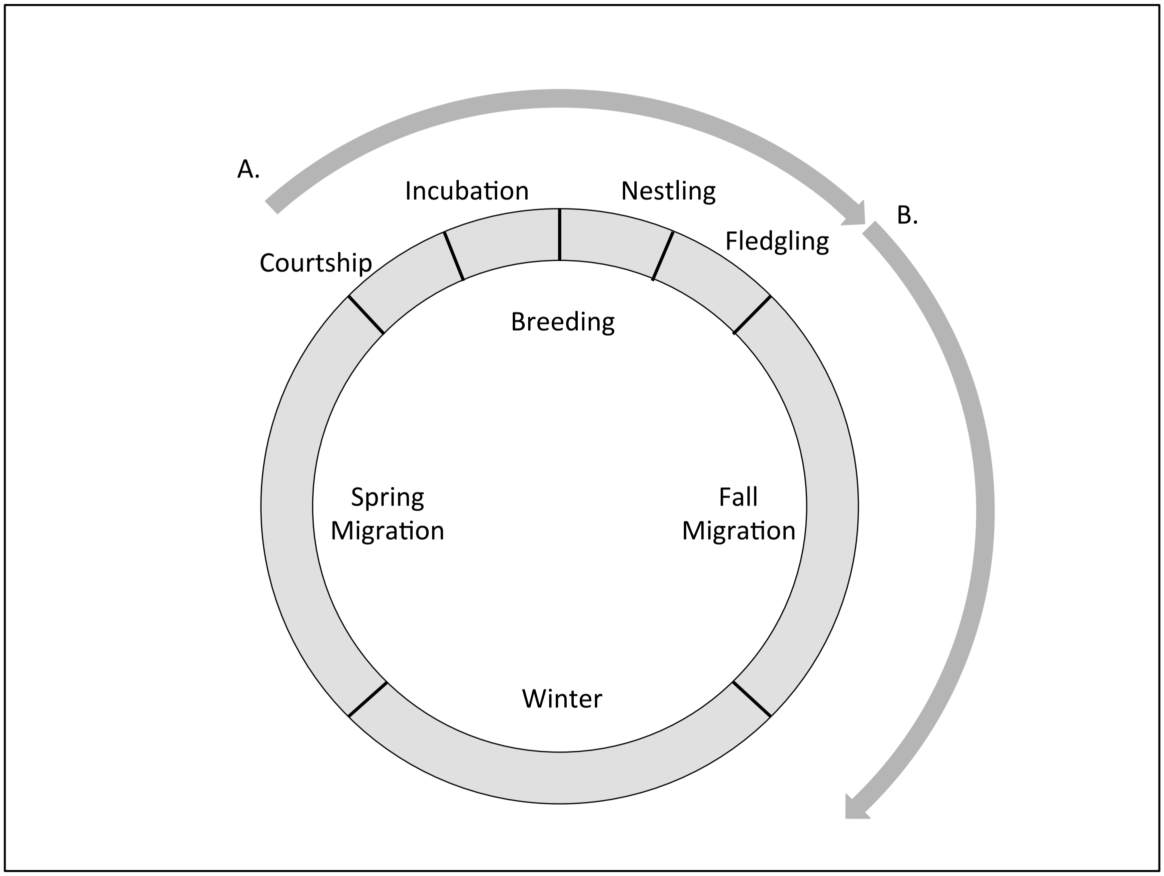

Figure 1. A. Food needed during breeding season affects the number of eggs in a clutch, the growth of nestlings, and fledgling success. B. Available food during fall migration influences fat reserves, mass, and survival during spring migration.

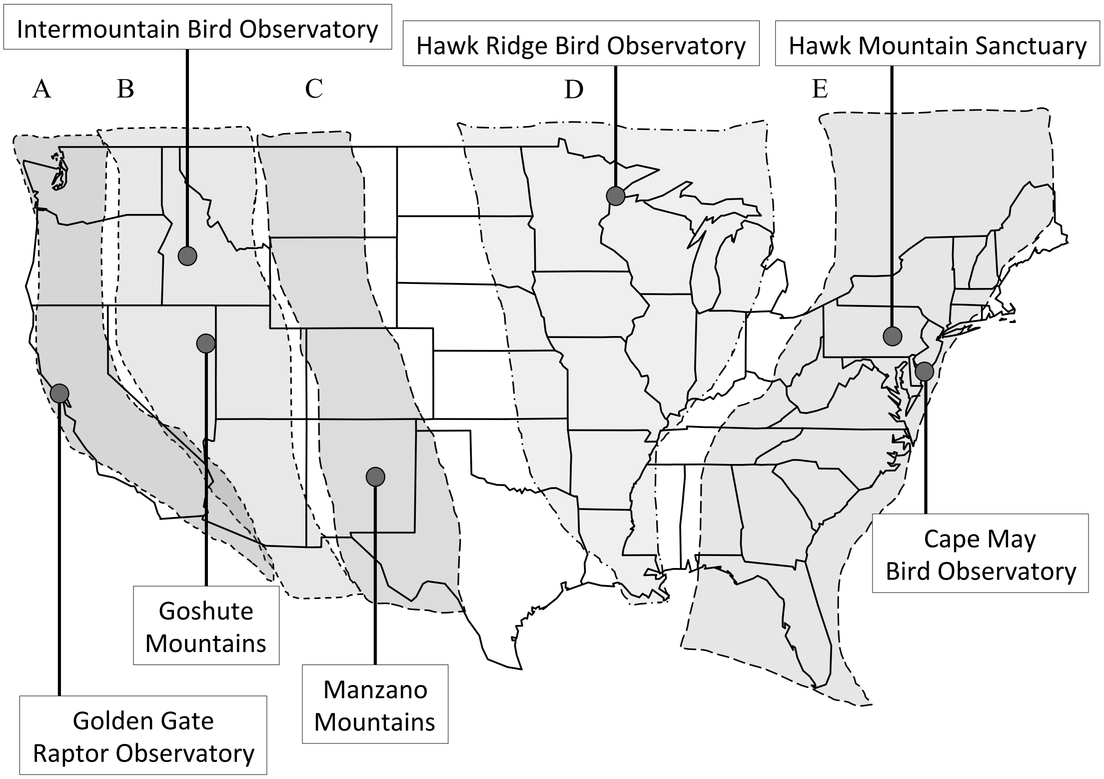

Figure 2. Fall migration station locations (black dots). The major raptor flyways from west to east (shaded areas): A. Pacific Coast, B. Intermountain, C. Southern Rocky Mountain, D. Mississippi, E. Atlantic Coast.

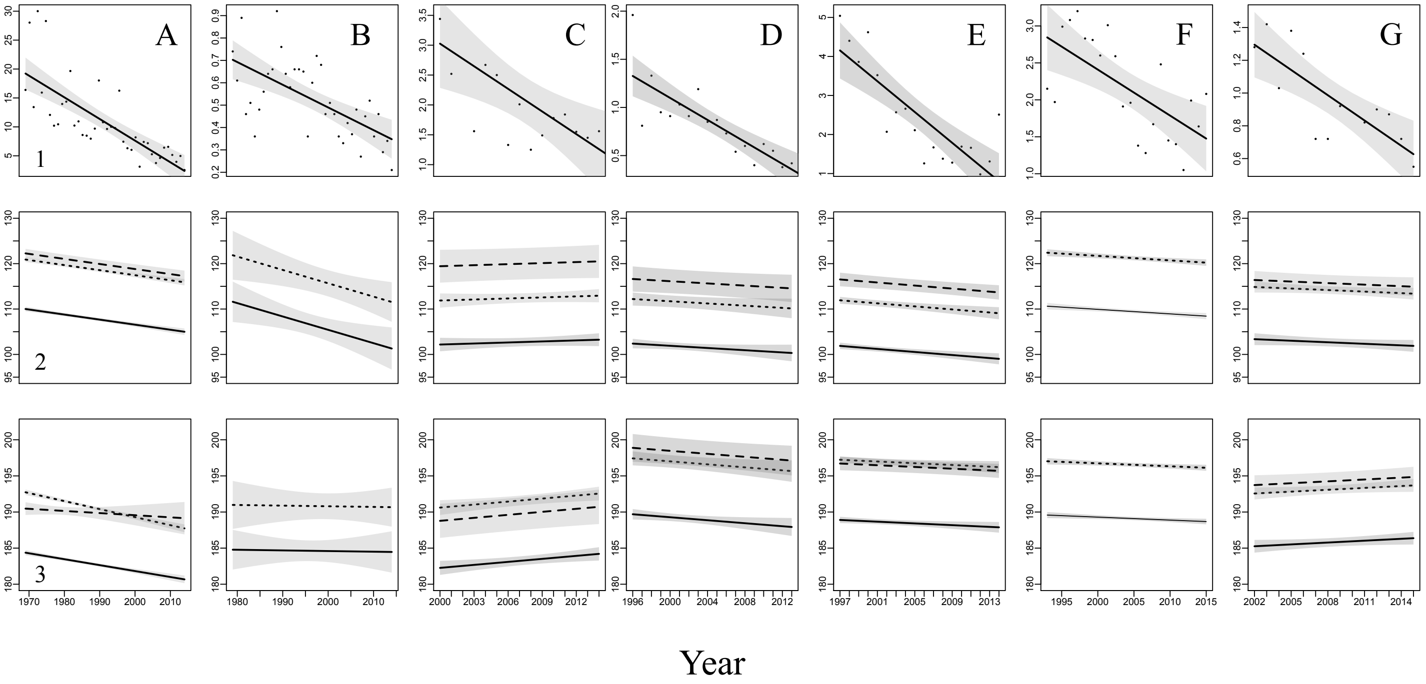

Figure 3. RpH (row 1), mass (row 2), and wing chord (row 3) graphs during period of population decline with 95% confidence intervals. Columns A-E are sites as follows: A: Cape May Raptor Banding Project, NJ. B: Hawk Mountain Sanctuary, PA. C: Hawk Ridge Bird Observatory, MN. D: Manzano Mountains, NM. E: Goshute Mountains, NV. F: Lucky Peak, ID. G: Golden Gate Raptor Observatory, CA. Row 1: RpH, 2: Mass (g), 3: Wing Chord (mm). Unknown males represented by a solid line, juvenile females represented by a dotted line, adult females represented by a dotted line with 95% confidence intervals.

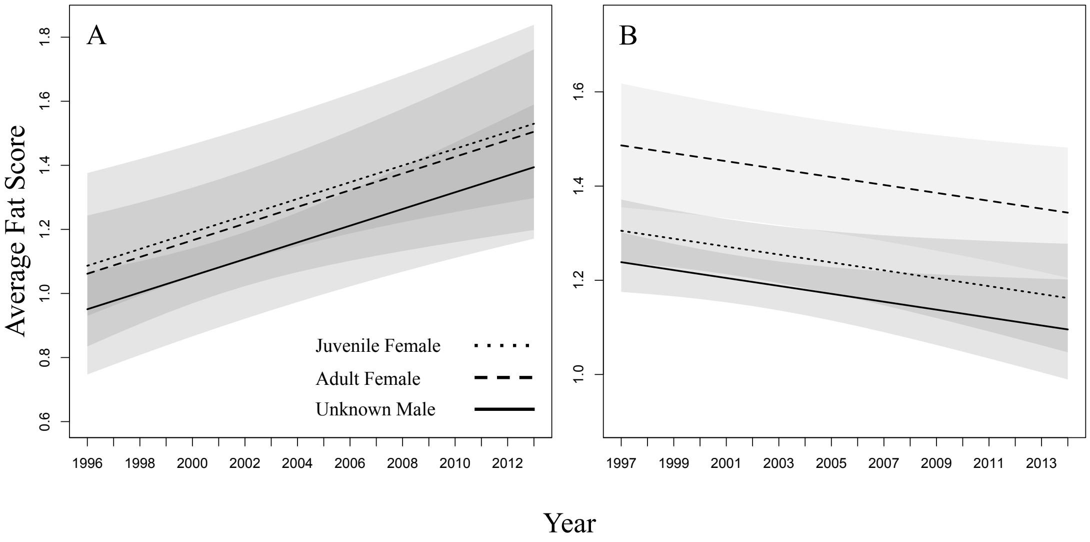

Figure 4. Change in average wing pit fat score at the (A) Manzano Mountains and (B) Goshute Mountains with 95% confidence intervals.

Table 2: Summary of sites, years available, and declines for seven sites across North America. Years refer to the span of time for which both banding and count data were available. Year declines detected are the beginning of the data window, if declines were apparent the entire time or the beginning of the decline as detected by breakpoint regression (see text).

Site	Years	Year declines detected	Decline % per 10 yrs	Decline p-value
Cape May	1976-2015	1976	20.2%	**<0.001**
Hawk Mountain	1979-2015	1979	12.6%	**<0.001**
Hawk Ridge	1972-2015	2000	37.5%	**<0.006**
Manzano Mountains	1985-2014	1996	38.7%	**<0.001**
Goshute Mountains	1983-2014	1997	42.7%	**<0.001**
Lucky Peak	1994-2015	1994	20.6%	**0.001**
Golden Gate Raptor Observatory	1989-2015	2002	35.7%	**0.001**

Table 3a. Summary of changes in mass (g) and wing chord (mm) from seven sites, during periods of decline determined by the breakpoint regression. (*) indicates that the model included a two way interaction. See Table 3b. for output tables.

		Mass changes per 10 years				Wing chord changes per 10 years			
Site	Years	Slope g/yr	%	Gram	p-val	Slope mm/yr	%	mm	p-val
Cape May	1969-2014	-0.11	0.8% - 0.9%	1 g	**<0.001**	-0.03	0.1% - 0.4%	0.3 - 0.7 mm	0.4*
Hawk Mt.	1979-2014	-0.3	2.2% - 2.4%	2.7 g	**0.01**	-0.01	0.04%	0.08 mm	0.9
Hawk Ridge	2000-2014	0.08	0.6% - 0.7%	0.7 g	0.34	0.14	0.7%	1.2 mm	**0.009**
Manzano Mts.	1996-2014	-0.12	0.9% -1%	1.1 g	0.09	-0.09	0.5%	0.9mm	**0.04**
Goshute Mts.	1997-2014	-0.17	1.3% - 1.5%	1.5 g	**<0.0002***	-0.06	0.3%	0.5 mm	**0.03**
Lucky Peak	1994-2015	-0.10	0.7% - 0.8%	.9 g	**0.0002**	-0.04	0.2%	0.4 mm	**0.008**
GGRO	2002-2015	-0.11	0.9% - 1%	1 g	0.12*	0.09	0.4%	0.8mm	0.09

Table 3b. Summary of changes in mass or wing chord from models with a two way interaction after the breakpoint regression with change in size as percent and measurement.

Site	Mass or WC	Interaction	Slope	%	Size change	p-val
Cape May	Wing Chord	Year: J F	-0.08 mm/yr	0.52	1 mm	**0.02**
Goshute Mts.	Mass	J F: Julian Date	-0.18 g/yr	1.3	1.5 g	**0.006**
GGRO	Mass	J F: Julian Date	-0.13 g/yr	0.89	1 g	**0.02**

Table 4. Summary of changes in wing pit fat output table after the determined breakpoint with slope, p-value and the change in score per 10 year interval.

Site	Years	Slope	Score Change	p-val
Manzano Mts.	1996-2013	0.03	0.23	**0.0008**
Goshute Mts.	1997-2014	-0.008	0.08	**0.03**

Table 5. Model used for each site for RpH, mass, wing chord, and wing pit fat (Manzano Mountains and Goshute Mountains only) during the period of decline.

Site	Response	After
Cape May	RpH	lm(RpH ~ Year)
	Mass	lm(Mass ~ Year + Age + Julian Date)
	Wing Chord	lm(Wing Chord ~ Year + Age + Year*Age + Julian Date)
Hawk Mt.	RpH	lm(RpH ~ Year)
	Mass	lm(Mass ~ Year + Sex)
	Wing Chord	lm(Wing Chord ~ Year + Sex)
Hawk Rd	RpH	lm(RpH ~ Year)
	Mass	lm(Mass ~ Year + Age)
	Wing Chord	lm(Wing Chord ~ Year + Age)
Manzano Mts.	RpH	lm(RpH ~ Year)
	Mass	lm(Mass ~ Year + Age + Julian Date)
	Wing Chord	lm(Wing Chord ~ Year + Age)
	Fat	lm(Wing Fat ~ Year + Age + Julian Date)
Goshute Mts.	RpH	lm(RpH ~ Year)
	Mass	lm(Mass ~ Year + Age + Julian Date + Age*Julian Date)
	WC	lm(Wing Chord ~ Year + Age)
	Fat	lm(Wing Fat ~ Year + Age + Julian Date)
Lucky Peak	RpH	lm(RpH ~ Year)
	Mass	lm(Mass ~ Year + Sex)
	WC	lm(Wing Chord ~ Year + Sex + Julian Date)
GGRO	RpH	lm(RpH ~ Year)
	Mass	lm(Mass ~ Year + Age + Julian Date + Age*Julian Date)
	WC	lm(Wing Chord ~ Year + Age + Julian Date)

Appendix (Supporting Information)

Table S1: Size parameters for each site using 3 SD from the mean mass, mean wing chord, Julian dates, and sample size for each migration season.

		Mass		Wing Chord		
Site	Julian Date	Male	Female	Male	Female	n
Cape May	226-302	80-140	88-147	163-200	170-207	5194
Hawk Mt.	243-301	80-135	85-140	170-210	172-210	101
Hawk Ridge	227-319	80-135	85-140	170-210	175-213	1750
Manzano Mts.	227-319	85-125	90-137	175-200	180-210	616
Goshute Mts.	227-319	80-130	82-142	170-210	175-213	3201
Lucky Peak	226-302	80-130	90-155	163-210	175-215	3012
GGRO	213-344	80-135	90-140	170-200	175-217	1265

Table S2. Slope of RpH before and after determined breakpoint with standard errors, t-values, upper and lower 95% confidence intervals for Hawk Ridge, Manzano Mountains, Goshute Mountains, Golden Gate Raptor Observatory.

Site	Breakpoint	Estimate	SE	t-value	CI 95 Lower	CI 95 Upper
Hawk Ridge						
	Before 2000	0.077	0.015	5.07	0.046	0.11
	After 2000	-0.13	0.035	-3.59	-0.2	-0.055
Manzano Mts.						
	Before 1996	0.012	0.024	0.48	-0.038	0.062
	After 1996	-0.049	0.011	-4.61	-0.071	-0.027
Goshute Mts.						
	Before 1997	0.22	0.05	4.44	0.12	0.32
	After 1997	-0.2	0.034	-5.78	-0.27	-0.13
GGRO						
	Before 2000	0.032	0.015	2.14	0.00091	0.063
	After 2000	-0.052	0.017	-3.1	-0.087	-0.017

Table S3 A - G. Output tables from models with response variables RpH, Mass, Wing chord, estimates, standard errors, t and p values, F-statistic, multiple R-squared, adjusted r-squared, f-statics and p-values for each model. Significant p-values are in bold.

A. Cape May Point, NJ.

	Term	Estimate	SE	t-value	p -value
RpH	(Intercept) RpH	872.6	120.0	7.3	**<0.0001**
	Year	-0.4	0.1	-7.2	**<0.0001**
	F-statistic:	51.62 on 1 and 38 DF			
	Multiple R-squared:	0.576			
	Adjusted R-squared:	0.5648			
	F-statistic:	51.62 on 1 and 38 DF			
	p-value:	1.386e-08			
Mass	(Intercept) Adult Female	312.1	22.0	14.2	**<0.0001**
	Year	-0.1	0.0	-10.1	**<0.0001**
	Juvenile Female	-1.4	0.5	-2.5	**0.01**
	Male	-12.3	0.5	-23.5	**<0.0001**
	Julian Date	0.1	0.0	11.7	**<0.0001**
	Residual standard error:	9.015 on 5173 degrees of freedom			
	Multiple R-squared:	0.2769			
	Adjusted R-squared:	0.2764			
	F-statistic:	495.3 on 4 and 5173 DF			
	p-value:	< 2.2e-16			
Wing Chord	(Intercept) Adult Female	252.8	64.4	3.9	**0.00009**
	Year	0.0	0.0	-0.9	0.36
	Juvenile Female	162.8	67.0	2.4	**0.015**
	Male	97.6	66.8	1.5	0.14
	Julian Date	0.0	0.0	-3.0	**0.003**
	Year: Juvenile Female	-0.1	0.0	-2.4	**0.016**
	Year: Male	-0.1	0.0	-1.6	0.12
	Residual standard error:	5.163 on 5171 degrees of freedom			
	Multiple R-squared:	0.3859			
	Adjusted R-squared:	0.3852			
	F-statistic:	541.5 on 6 and 5171 DF			
	p-value:	< 2.2e-16			

B. Hawk Mountain Sanctuary, PA.

	Term	Estimate	SE	t-value	p -value
RpH	(Intercept) RpH	20.21	4.09	4.94	**0.0000**
	Year	-0.01	0.00	-4.81	**0.0000**
	Residual standard error:	0.133 on 35 degrees of freedom			
	Multiple R-squared:	0.3982			
	Adjusted R-squared:	0.381			
	F-statistic:	23.16 on 1 and 35 DF			
	p-value:	2.823e-05			
Mass	(Intercept) Female	704.27	225.39	3.12	0.0023
	Year	-0.29	0.11	-2.61	**0.0104**
	Male	-10.25	1.90	-5.38	0.0000
	Residual standard error:	9.206 on 99 degrees of freedom			
	Multiple R-squared:	0.2415			
	Adjusted R-squared:	0.2261			
	F-statistic:	15.76 on 2 and 99 DF			
	p-value:	1.145e-06			
Wing Chord	(Intercept) Female	208.67	139.16	1.50	0.137
	Year	-0.01	0.07	-0.13	0.898
	Male	-6.20	1.18	-5.28	0.000
	Residual standard error:	5.684 on 99 degrees of freedom			
	Multiple R-squared:	0.2246			
	Adjusted R-squared:	0.2089			
	F-statistic:	14.34 on 2 and 99 DF			
	p-value:	3.4e-06			

C. Hawk Ridge Bird Observatory, MN.

	Term	Estimate	SE	t-vale	p-value
RpH	(Intercept) RpH	3.03	0.35	8.76	**<0.0001**
	Year	-0.13	0.04	-3.22	**0.0062**
	Residual standard error:	0.7232 on 14 degrees of freedom			
	Multiple R-squared:	0.4252			
	Adjusted R-squared:	0.3842			
	F-statistic:	10.36 on 1 and 14 DF			
	p-value:	0.006191			
Mass	(Intercept) Adult Female	119.43	1.84	64.85	**<0.0001**
	Year	0.08	0.08	0.95	0.34
	Juvenile Female	-7.56	1.84	-4.11	**0.00005**
	Male	-17.25	1.83	-9.45	**0.0000**
	Residual standard error:	7.262 on 432 degrees of freedom			
	Multiple R-squared:	0.3546			
	Adjusted R-squared:	0.3501			
	F-statistic:	79.1 on 3 and 432 DF			
	p-value:	< 2.2e-16			
Wing Chord	(Intercept) Adult Female	188.78	1.20	156.92	**0.0000**
	Year	0.14	0.05	2.64	**0.009**
	Juvenile Female	1.84	1.20	1.53	0.13
	Male	-6.51	1.19	-5.46	**0.0000**
	Residual standard error:	4.743 on 432 degrees of freedom			
	Multiple R-squared:	0.4372			
	Adjusted R-squared:	0.4333			
	F-statistic:	111.8 on 3 and 432 DF			
	p-value:	< 2.2e-16			

D. Manzano Mountains, NM.

	Term	Estimate	SE	t-value	p-value
RpH	(Intercept) RpH	1.33	0.10	13.26	**<0.0001**
	Year	-0.06	0.01	-6.01	**0.00001**
	Residual standard error:	0.2268 on 17 degrees of freedom			
	Multiple R-squared:	0.6799			
	Adjusted R-squared:	0.6611			
	F-statistic:	36.11 on 1 and 17 DF			
	p-value:	1.409e-05			
Mass	(Intercept) Adult Female	63.70	8.74	7.29	**<0.0001**
	Year	-0.12	0.07	-1.69	0.09
	Juvenile Female	-4.42	1.50	-2.95	**0.003**
	Male	-14.23	1.39	-10.25	**<0.0001**
	Julian Date	0.20	0.03	6.16	**<0.0001**
	Residual standard error:	6.914 on 469 degrees of freedom			
	Multiple R-squared:	0.3517			
	Adjusted R-squared:	0.3462			
	F-statistic:	63.6 on 4 and 469 DF			
	p-value:	< 2.2e-16			
Wing Chord	(Intercept) Adult Female	198.88	0.98	203.84	**<0.0001**
	Year	-0.10	0.05	-2.11	**0.036**
	Juvenile Female	-1.46	1.02	-1.42	0.16
	Male	-9.19	0.96	-9.60	**<0.0001**
	Residual standard error:	4.769 on 470 degrees of freedom			
	Multiple R-squared:	0.383			
	Adjusted R-squared:	0.379			
	F-statistic:	97.24 on 3 and 470 DF			
	p-value:	< 2.2e-16			

E. Goshute Mountains, NV.

	Term	Estimate	SE	t-value	p-value
RpH	(Intercept) RpH	4.15	0.34	12.23	**<0.0001**
	Year	-0.20	0.03	-5.78	**0.00003**
	Residual standard error:	0.7505 on 16 degrees of freedom			
	Multiple R-squared:	0.6765			
	Adjusted R-squared:	0.6563			
	F-statistic:	33.47 on 1 and 16 DF			
	p-value:	2.79e-05			
Mass	(Intercept) Adult Female	40.68	13.72	2.96	**0.003**
	Year	-0.17	0.04	-3.77	**0.00017**
	Juvenile Female	41.36	16.62	2.49	**0.01**
	Male	-13.87	14.92	-0.93	0.35
	Julian Date	0.30	0.05	5.57	**<0.0001**
	Juvenile Female : Julian Date	-0.18	0.07	-2.77	**0.006**
	Male : Julian Date	0.00	0.06	-0.05	0.96
	Residual standard error:	8.049 on 1521 degrees of freedom			
	Multiple R-squared:	0.3472			
	Adjusted R-squared:	0.3446			
	F-statistic:	134.8 on 6 and 1521 DF			
	p-value:	< 2.2e-16			
Wing Chord	(Intercept) Adult Female	196.72	0.48	413.44	**<0.0001**
	Year	-0.06	0.03	-2.16	**0.03**
	Juvenile Female	0.52	0.49	1.07	0.29
	Male	-7.81	0.47	-16.74	**<0.0001**
	Residual standard error:	5.041 on 1524 degrees of freedom			
	Multiple R-squared:	0.402			
	Adjusted R-squared:	0.4008			
	F-statistic:	341.5 on 3 and 1524 DF			
	p-value:	< 2.2e-16			

F. Lucky Peak, ID.

	Term	Estimate	SE	t-value	p-value
RpH	(Intercept) RpH	132.87	34.70	3.83	**0.001**
	Year	-0.07	0.02	-3.77	**0.0012**
	Residual standard error:	0.5152 on 20 degrees of freedom			
	Multiple R-squared:	0.415			
	Adjusted R-squared:	0.3857			
	F-statistic:	14.19 on 1 and 20 DF			
	p-value:	0.001214			
Mass	(Intercept) Female	320.50	53.70	5.97	**<0.0001**
	Year	-0.10	0.03	-3.71	**0.0002**
	Male	-11.78	0.31	-37.64	**<0.0001**
	Residual standard error:	8.705 on 3184 degrees of freedom			
	Multiple R-squared:	0.3092			
	Adjusted R-squared:	0.3088			
	F-statistic:	712.6 on 2 and 3184 DF			
	p-value:	< 2.2e-16			
Wing Chord	(Intercept) Female	283.58	31.31	9.06	**<0.0001**
	Year	-0.04	0.02	-2.65	**0.0080**
	Male	-7.45	0.18	-41.23	**<0.0001**
	Julian Date	-0.02	0.01	-2.63	**0.009**
	Residual standard error:	4.942 on 3183 degrees of freedom			
	Multiple R-squared:	0.362			
	Adjusted R-squared:	0.3614			
	F-statistic:	602.1 on 3 and 3183 DF			
	p-value:	< 2.2e-16			

G: Golden Gate Raptor Observatory, CA.

	Term	Estimate	SE	t-value	p-value
RpH	(Intercept) RpH	1.30	0.09	14.26	**<0.0001**
	Year	-0.05	0.01	-4.32	**0.0012**
	Residual standard error:	0.1788 on 11 degrees of freedom			
	Multiple R-squared:	0.6286			
	Adjusted R-squared:	0.5949			
	F-statistic:	18.62 on 1 and 11 DF			
	p-value:	0.001225			
Mass	(Intercept) Adult Female	86.13	12.89	6.68	**<0.0001**
	Year	-0.11	0.07	-1.54	0.12
	Juvenile Female	30.65	13.88	2.21	**0.03**
	Male	6.24	13.60	0.46	0.65
	Julian Date	0.12	0.05	2.34	**0.02**
	Juvenile Female : Julian Date	-0.13	0.05	-2.31	**0.02**
	Male : Julian Date	-0.08	0.05	-1.42	0.16
	Residual standard error:	7.982 on 792 degrees of freedom			
	Multiple R-squared:	0.341			
	Adjusted R-squared:	0.336			
	F-statistic:	68.29 on 6 and 792 DF			
	p-value:	< 2.2e-16			
Wing Chord	(Intercept) Adult Female	203.38	2.23	91.04	**<0.0001**
	Year	0.09	0.05	1.70	0.09
	Juvenile Female	-1.16	0.69	-1.68	0.09
	Male	-8.47	0.70	-12.14	**<0.0001**
	Julian Date	-0.04	0.01	-4.50	**<0.0001**
	Residual standard error:	5.482 on 794 degrees of freedom			
	Multiple R-squared:	0.3545			
	Adjusted R-squared:	0.3512			
	F-statistic:	109 on 4 and 794 DF			
	p-value:	< 2.2e-16			

CHAPTER 2: Geographic Variation in Morphology of the American Kestrel (*Falco sparverius*) Across North America.

ABSTRACT

We assessed geographical variation in American kestrel mass, wing chord, sexual size dimorphism, and wing loading index across seven fall migration sites. Although previous research suggested that eastern kestrels are larger than western kestrels, our results suggest a more complex pattern of variation. To address the potential for limited east-west gene flow to influence patterns of variation, we tested whether the magnitude of longitudinal distance between sites was related to the magnitude of differences in kestrel morphology between sites. Wing chord differed between sites to a greater extent when sites were farther apart, but there was no effect of longitudinal distance between sites on differences in body mass. This differential pattern suggests that wing chord and body mass vary across North America in response to different processes, even though wing chord and body mass are generally correlated with each other. Selective forces may drive variation in body size, and thus sexual size dimorphism and wing loading, across sites, while variation in wing chord may also be linked to genetic drift.

INTRODUCTION

Geographic variation in body size and morphology could reflect variation in the ecological and evolutionary processes that determine these traits (Mitchell-Olds *et al.* 2007). For example, species from more distant or isolated geographic regions may exhibit greater longitudinal divergence in body size resulting from reduced gene flow between populations (Chakraborty & Nei 1982; Storz 2002; González *et al.* 2011). Alternatively, regional variation in selective pressures may drive variation in morphology between regions (Johansson *et al.* 1998; Edelaar *et al.* 2008). Given the importance of body size in determining ecological and evolutionary processes (Calder 1984; Peters 1986), understanding geographic variation in size and morphology can inform our understanding of variation in ecological processes in different regions. Variation in body size and morphology is expected to periodically undergo selection and is generally assumed to represent adaptation to local environments, but the degree to which this variation occurs is still poorly understood (Wigginton & Dobson 1999; Stillwell & Fox 2009).

Evolutionary pressures influencing body size are now changing as the climate responds to greenhouse gas inputs (IPCC 2001). Although some species are able to cope with changing environments by moving to new locations (Parmesan *et al.*1999), others may display flexibility in traits that enable them to maintain fitness in the face of change (Bell & Gonzalez 2009). In particular, changes in body size and morphology are becoming a common response to climate change, specifically warming temperatures (Ozgul *et al.* 2010; Goodman *et al.* 2011; Sheridan & Bickford 2011; DeLong 2012). Developing a clear baseline about current geographic variation in size could facilitate understanding future changes in body size of widespread species.

Many avian species with widespread geographic distributions show morphological variation, including raptors such as sharp-shinned hawks (*Accipiter striatus*), cooper's hawks (*Accipiter cooperii*), northern goshawks (*Accipiter gentilis*), red-tailed hawks (*Buteo jamaicensis*) (Johansson 1998 ; Hull *et al.* 2008; Smith *et al.* 2013), great horned owls (*Bubo virginianus*), flammulated owls (*Otus flammeolus*)

(McGillivray 1989; Smith *et al.* 2011), passeriformes (Gardner *et al.* 2014), and Anseriformes (Larsson & Forslund 1991). There are some general patterns in this geographic variation. For example, raptors in the western parts of North America often show significantly longer wings and tails than conspecifics from eastern flyways (Pearlstine & Thompson 2004), and inland migrants tend to have lower flight-surface loading compared to coastal conspecifics (Smith *et al.* 1990).

American kestrels (*Falco sparverius*) are the smallest North American falcon and can be found in many habitats throughout North America south of the arctic tree line (Clark & Wheeler 2001). Kestrels show geographic variation in morphology, including body mass (Pearlstine & Thompson 2004). Previous studies have focused on data collected at only a few migration flyways such as Cape May Point, Goshute Mountains, Manzano Mountains, and have not included kestrel populations from the west coast or mid-west in their analysis. Furthermore, kestrel populations have been declining since the mid-1990s, and kestrels have shown concomitant changes in body mass and wing chord in most locations across North America (Ely *et al.* (*in prep.*), Chapter 1).

Here we use a continental-scale, multi-decadal database on kestrels captured during fall migration to evaluate regional patterns of body size, wing chord, sexual size dimorphism, and wing loading in kestrels. We also test the hypothesis that differences in size across the continent might have arisen through random divergence, which would be supported by a negative correlation between distance in space and difference in size.

MATERIALS AND METHODS

Study Sites

Kestrel banding data came from the study sites described in Chapter l (Figure 2; Ely *et al.* 2016) and include Golden Gate Raptor Observatory, Intermountain Bird Observatory, HawkWatch International, Hawk Ridge Bird Observatory, Hawk Mountain Sanctuary, and Cape May Raptor Banding Project (Viverette *et al.* 1996; Farmer & Smith 2009; Hull *et al.* 2010; Evans *et al.* 2012). Kestrels pass through these sites during fall migration from northern breeding areas to southern wintering grounds. Thus, birds from the different sampling sites vary in their longitudinal origin, though the latitudinal origin of the birds is unknown. We analyzed all data available over the entire period.

Data collection

Kestrels were trapped, banded, and measured using the methods described in Ely Chapter 1. The data were cleaned by removing birds with a crop score above ½ and birds where wing chord and body mass measurements were greater than 3 SD of the mean mass and wing chord measurements for each sex (Table 2). Only the first encounter measurements of an individual during a season were used in analysis. We report the mean mass and wing chord differences between males and females at each site (Table 2). Although adult kestrels tend to be heavier than juveniles, HY (Hatch year), AHY (After hatch year), SY (Second year), and ASY (After second year) were grouped together for this study because we were interested in the regional patterns rather than how they differ between ages. Male and female kestrels were sexed by wing and tail color (Clark & Wheeler 2001).

Data analysis

We used two-way analysis of variance (ANOVA) to test for differences in the mass and wing chord of kestrels among sites and sex (Table 1). We then used a post-hoc Tukey HSD (honest significant difference) test to determine significant differences between all pair-wise site and sex combinations (Table 3 and 4). The differences in longitude between each site were calculated by subtracting the longitudinal minutes, with the more western site subtracted from the eastern site so that the difference was negative (Table 3).

We then used linear regression to assess whether wing chord and mass differed to a greater extent when longitudinal differences were greater, suggesting random divergence in size across kestrel populations. The response variable was mass or wing chord and the predictor variable was longitudinal difference (Table 5).

The degree of sexual size dimorphism (SSD) for each site was calculated as the within-site ratio of the average male and female mass and wing chord. Standard errors were computed with the pooled standard error for males and females as follows (Figure 1; Ku 1966): $\sqrt{(\frac{SE_F}{F})^2 + (\frac{SE_M}{M})^2}$.

Wing loading is the ratio of total wing and tail area to body mass. In the absence of measurements of total wing area and tail, we used the wing loading index of Temple (1972), which is strongly correlated with wing loading. We calculated the wing loading index by dividing the cube root of body mass by wing chord. We used ANOVA (Table 1) to test for differences between sites and used a post-hoc Tukey HSD test to identify significant differences between all pair-wise site and sex combinations.

RESULTS

Kestrel mass differed significantly among sites, sexes, and the interaction between site and sex, as seen in Table 1. The female kestrels at Lucky Peak were 8% to 9% larger, and males were 6% larger than those of the same sex at Hawk Ridge, Manzano Mountain, and the Goshute Mountain sites. Female birds from Lucky Peak and Cape May Point were 5% and 3% larger, and, males were 3% larger than the birds found at Hawk Mountain and Golden Gate Raptor Observatory (Figure 1).

Wing chord also differed between sites and sexes (Table 1, Figure 1), but the interaction of site and sex was not significant. Female and male wing chords at the Manzano Mountains were approximately 1% longer than those at Lucky Peak and the Goshute Mountains. Wing chords in the Manzano Mountain were approximately 2% longer than those at Golden Gate, and approximately 3% longer than for birds at Hawk Ridge, Hawk Mountain, and Cape May.

Wing loading index differed between sites and sexes (Table 1; Figure 4). Wing loading index was higher in females than males across sites (p <0.0001). Overall, kestrels at Cape May Point and Lucky Peak had the highest wing loading index (p <0.0001), while kestrels in the Manzano and Goshute Mountains had the lowest wing loading index (p < 0.0001) (Table 6).

As a result of variation in male and female wing chord and body size across sites, sexual size dimorphism (SSD) also varied across sites (Figure 1), but the pattern of spatial variation in SSD was not the same for wing chord and body mass. SSD for mass was greatest in the two western most sites, Golden Gate Raptor Observatory and Luck Peak. The other five states had lower but similar SSD for mass. Wing chord SSD was similar for all seven sites (Figure 1). Variation in body mass was not associated with how far apart sampling locations were from each other (Table 5; Figure 2). In contrast, differences in wing chord across sites were larger the farther the sites were from each other (Table 5; Figure 2).

DISCUSSION

American kestrels showed variation in mass, wing chord, sexual size dimorphism, and wing loading index across flyways in North America. Patterns of variation across sites, however, were different for mass and wing chord. This variation in morphological traits could be linked to different climates, food resources, or migration strategies used across North America (Kerlinger 1989; Smith *et al.* 1990; DeLong *et al.* 2005; Hull et al. 2008). Alternatively, phenotypic variation across large spatial scales could arise through random divergence, where the farther apart populations are, the less chance there is for gene flow and the greater the resulting differences (Mitchell-Olds *et al.* 2007). We tested for such a relationship between longitudinal distance and the difference in mass or wing chords between sites and found that more spatially separated populations of kestrels showed greater divergence in wing chord but not body mass. As both wing chord and body mass are highly heritable (Brown & Brown 2013), this result suggests that wing chord variation arises in part due to genetic drift, while body size may be under more regional selection. However, because both wing chord and body size respond to variation in energetic conditions during growth, the differences might also reflect phenotypically plastic responses to conditions across longitude.

Body size may evolve in response to temperature, resource availability, and predation risk (Goodman *et al.* 2011; Lima 1986; Yom-Tov & Yom-Tov 2006). Unfortunately, migration sites sample migrating birds originating to the north of the sites, so the latitudinal origin of these kestrels is unknown. As such, breeding areas of the kestrels used in our study are unknown, and it is difficult to assess how any of these factors actually affect body mass variation across sites. However, it is possible to use differential wing loading, which is correlated with body mass, to infer something about different kestrel populations.

Wing loading is especially important for raptors that spend substantial time in the air and capture prey in flight (Mueller *et al.* 2002), and travel long migratory distances. Birds that use coastal flyways have different flight strategies than birds that use flyways through inland regions (Mueller *et al.* 1981; Smith *et al.* 1990; Mueller *et al.* 2002). The kestrels found moving along coastal migration sites, Cape May, N.J., and Golden Gate Raptor Observatory, CA, are generally heavier and shorter winged, and have heavier wing loading. Birds with heavier wing loading have increased maneuverability (Mueller *et al.* 1981), which aids in flying through forested areas typical of these regions. Kestrels that migrate through the central North America or Great Basin region, such as the Goshute Mountains and Manzano Mountains, are typically longer winged, weigh less, and have lighter wing loading. Birds with light wing loading can glide more slowly and rise more rapidly with updrafts, which are common in the open, warm, and dry Intermountain West. We expect to see birds in the Intermountain and Southern Rockies flyways with light wing loading because regions with vast deserts lined by mountains should have increased updrafts and thermal patterns (Smith *et al.* 1990; Hoffman & Smith 2003).

Raptors generally show reversed sexual size dimorphism where the male is smaller than the female (Reynolds 1972). Our results show that kestrel variation in sexual size dimorphism across regions takes on different patterns for mass and wing chord. Kestrels at the two most western sites show greater dimorphism in mass than birds east of the Rocky Mountains, but the sexual size dimorphism in wing chord is similar across the sites, which may be consistent with the idea of random divergence in wing chord but selective forces operating on body mass. There are many hypotheses about the origin of reversed sexual size dimorphism (Reynolds 1972). For example, females may be under selection to be larger to prevent the occurrence of filicidal behavior by the male (Brown & Amadon 1968). Alternatively, sexual size dimorphism might have arisen as an adaptation that reduces intraspecific competition (Reynolds 1972). Although it is still not understood what drives SSD in general, our results indicate that the mechanisms may vary in magnitude regionally.

Our research provides a new perspective on the geographical variation of American kestrel mass and wing chord. Previous studies suggest that raptors found in eastern North America are generally larger than western birds, but we show some regions in the west have larger birds and birds with longer wing chord. Most importantly, the interacting forces acting on body mass and wing chord across the continent have generated a complex pattern of variation in sexual size dimorphism and wing loading that remains poorly understood.

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Table 1. Output of ANOVA of kestrel mass, wing chord and wing loading index. Degrees of freedom (df), sum of squares (sum of sq), and mean square (mean sq). Significant p-values (<0.05) are in bold.

Term	df	sum of sq	mean sq	p-value
Mass				
Site	6	236768	39461	**<0.0001**
Sex	1	445557	445557	**<0.0001**
Site:Sex	6	5025	838	**<0.0001**
Residuals	16207	1292569	80	NA
Wing chord				
Site	6	104073	17346	**<0.0001**
Sex	1	246552	246552	**<0.0001**
Site:Sex	1	193	32	0.24
Residuals	16207	437912	27	NA
Wing Loading Index				
Site	6	1.037	0.1728	**<0.0001**
Sex	1	0.437	0.4369	**<0.0001**
Site:Sex	6	0.014	0.0023	**<0.0001**
Residuals	16207	3.842	0.0002	NA

Table 2. Sample size (n), mean mass (g), and mean wing chord (mm) and standard error for female and male kestrels at seven migration sites.

Location	Sex	n	Mass	Wing Chord
GGRO, CA (GG)	M	623	103.3 ± 0.31	185.5 ± 0.23
	F	682	115.1 ± 0.34	193.5 ± 0.21
Lucky Peak, ID (LP)	M	1865	109.8 ± 0.2	189.2 ± 0.11
	F	1322	122.1 ± 0.28	196.7 ± 0.14
Goshute Mountains, NV (GO)	M	1844	102.1 ± 0.2	188.9 ± 0.12
	F	1692	111.3 ± 0.23	196.8 ± 0.13
Manzano Mountains, NM (MA)	M	415	102.1 ± 0.34	189.5 ± 0.24
	F	230	112.1 ± 0.53	197.1. ± 0.34
Hawk Ridge, MN (HR)	M	920	102.4 ± 0.23	183.6 ± 0.15
	F	844	112.1 ± 0.29	191.8 ± 0.17
Hawk Mountain, PA (HM)	M	62	106.6 ± 1.2	184.6 ± 0.7
	F	40	115.9 ± 1.5	190.8 ± 0.92
Cape May, NJ (CM)	M	2571	108.8 ± 0.17	182.9 ± 0.1
	F	2980	119.2 ± 0.18	190.8 ± 0.1

Table 3. Differences in mean mass (g) within sexes across different sites from the Tukey HSD test. L. Diff is the longitudinal difference between sites in minutes. Difference is the difference in observed means, Lwr is the lower end point of the interval, Upr is the upper end point of the interval and p –value is the value after adjustment for the multiple comparisons. Significant p-values (<0.05) are in bold. See Table 2 for site acronyms.

		Female				Male			
Site	L. Diff	Diff	Lwr	Upr	p-val	Diff	Lwr	Upr	p-val
LP-GG	-6	6.95	5.55	8.34	**<0.0001**	6.55	5.17	7.93	**<0.0001**
GO-LP	-2	-10.84	-11.92	-9.75	**<0.0001**	-7.76	-8.74	-6.78	**<0.0001**
GO-GG	-8	-3.89	-5.24	-2.54	**<0.0001**	-1.21	-2.59	0.18	0.17
MA-LP	-10	-10.01	-12.12	-7.89	**<0.0001**	-7.72	-9.31	-6.13	**<0.0001**
MA-GG	-16	-3.06	-5.32	-0.80	0.0005	-1.16	-3.03	0.71	0.71
MA-GO	-8	0.83	-1.26	2.91	0.99	0.04	-1.55	1.64	1.00
HR-LP	-24	-10.03	-11.34	-8.72	**<0.0001**	-7.40	-8.60	-6.19	**<0.0001**
HR-GG	-30	-3.08	-4.62	-1.55	**<0.0001**	-0.84	-2.39	0.71	0.87
HR-GO	-22	0.81	-0.46	2.07	0.67	0.37	-0.84	1.57	1.00
HR-MA	-14	-0.02	-2.23	2.19	1.00	0.32	-1.42	2.06	1.00
HM-LP	-41	-6.25	-11.05	-1.44	0.001	-3.25	-7.11	0.62	0.22
HM-GG	-47	0.70	-4.17	5.57	1.00	3.31	-0.68	7.29	0.23
HM-GO	-39	4.59	-0.20	9.38	0.08	4.51	0.65	8.38	0.007
HM-HR	-17	3.78	-1.06	8.63	0.33	4.15	0.22	8.08	0.027
HM-MA	-31	3.76	-1.36	8.88	0.44	4.47	0.40	8.54	0.016
CM-LP	-42	-2.90	-3.88	-1.93	**<0.0001**	-1.09	-2.00	-0.18	0.0044
CM-GG	-48	4.04	2.77	5.31	**<0.0001**	5.46	4.13	6.80	**<0.0001**
CM-GO	-40	7.93	7.02	8.84	**<0.0001**	6.67	5.76	7.59	**<0.0001**
CM-HM	-1	3.34	-1.43	8.11	0.52	2.16	-1.69	6.01	0.84
CM-HR	-18	7.13	5.96	8.29	**<0.0001**	6.31	5.16	7.45	**<0.0001**
CM-MA	-32	7.10	5.07	9.13	**<0.0001**	6.63	5.08	8.18	**<0.0001**

Table 4. Differences in mean wing chord (mm) within sexes across different sites from the Tukey HSD test. L. Diff is the longitudinal difference between sties in minutes. Diff is the difference in observed means between sites, Lwr is the lower end point of the interval, Upr is the upper end point of the interval and p –value is the value after adjustment for the multiple comparisons. Significant p-values (<0.05) are in bold. See Table 2 for site acronyms.

		Female				Male			
Site	L. Diff	Diff	Lwr	Upr	P-val	Diff	Lwr	Upr	p-val
LP-GG	-6	3.22	2.40	4.04	**<0.0001**	3.64	2.83	4.45	**<0.0001**
GO-LP	-2	0.05	-0.58	0.69	1.00	-0.29	-0.86	0.28	0.92
GO-GG	-8	3.27	2.48	4.07	**<0.0001**	3.35	2.54	4.16	**<0.0001**
MA-LP	-10	0.40	-0.83	1.64	1.00	0.36	-0.57	1.30	0.99
MA-GG	-16	3.62	2.30	4.95	**<0.0001**	4.00	2.91	5.10	**<0.0001**
MA-GO	-8	0.35	-0.87	1.57	1.00	0.65	-0.28	1.59	0.52
HR-LP	-24	-4.94	-5.70	-4.17	**<0.0001**	-5.52	-6.23	-4.82	**<0.0001**
HR-GG	-30	-1.72	-2.62	-0.82	**<0.0001**	-1.89	-2.79	-0.98	**<0.0001**
HR-GO	-22	-4.99	-5.73	-4.25	**<0.0001**	-5.24	-5.94	-4.53	**<0.0001**
HR-MA	-14	-5.34	-6.63	-4.05	**<0.0001**	-5.89	-6.91	-4.87	**<0.0001**
HM-LP	-41	-5.93	-8.74	-3.12	**<0.0001**	-4.54	-6.80	-2.27	**<0.0001**
HM-GG	-47	-2.71	-5.56	0.13	0.08	-0.90	-3.23	1.44	0.99
HM-GO	-39	-5.99	-8.79	-3.19	**<0.0001**	-4.25	-6.51	-1.98	**<0.0001**
HM-HR	-17	-1.00	-3.83	1.84	1.00	0.99	-1.31	3.29	0.98
HM-MA	-31	-6.34	-9.33	-3.34	**<0.0001**	-4.90	-7.28	-2.52	**<0.0001**
CM-LP	-42	-5.99	-6.56	-5.42	**<0.0001**	-6.32	-6.85	-5.79	**<0.0001**
CM-GG	-48	-2.77	-3.51	-2.03	**<0.0001**	-2.68	-3.46	-1.90	**<0.0001**
CM-GO	-40	-6.05	-6.58	-5.51	**<0.0001**	-6.03	-6.56	-5.49	**<0.0001**
CM-HM	-1	-0.06	-2.85	2.73	1.00	-1.78	-4.03	0.47	0.31
CM-HR	-18	-1.06	-1.74	-0.37	**<0.0001**	-0.79	-1.46	-0.12	0.006
CM-MA	-32	-6.39	-7.58	-5.21	**<0.0001**	-6.68	-7.59	-5.77	**<0.0001**

Table 5. Summary of wing chord (WC) and mass change with longitudinal differences (Long). Est is the estimate, SE is standard error, t-val is the t-value and p-val is p-value. Significant p-values (<0.05) are in bold.

Term	Male				Female			
	Est	SE	t-val	p-val	Est	SE	t-val	p-val
Intercept (Mass)	-1.37	1.88	-0.73	0.47	-1.97	2.41	-0.82	0.43
Long	-0.1	0.067	-1.48	-1.48	-0.08	0.086	-0.96	0.34
Intercept (WC)	0.95	1.19	0.8	0.44	1.28	1.05	1.22	0.24
Long	0.13	0.042	3.06	**0.007**	0.16	0.03	4.16	**0.0005**

Table 6. Significant differences in wing loading index within sexes across different sites from the Tukey HSD test. Diff is the difference in observed means between sites, Lwr is the lower end point of the interval, Upr is the upper end point of the interval and p –value is the value after adjustment for the multiple comparisons Significant p-values (<0.05) are in bold. See Table 2 for site acronyms.

	Female				Male			
Site	Diff	Lwr	Upr	p-val	Diff	Lwr	Upr	p-val
LP-GG	0.01	0.01	0.01	**<0.0001**	0.008	0.006	0.010	**<0.0001**
GO-LP	-0.02	-0.02	-0.02	**<0.0001**	-0.01341	-0.02	-0.012	**<0.0001**
GO-GG	-0.01	-0.01	-0.01	**<0.0001**	-0.00550	-0.01	-0.003	**<0.0001**
MA-LP	-0.02	-0.02	-0.01	**<0.0001**	-0.01394	-0.02	-0.011	**<0.0001**
MA-GG	-0.01	-0.01	0.00	**<0.0001**	-0.00603	-0.01	-0.003	**<0.0001**
MA-GO	0.00	0.00	0.00	1.00	-0.00053	-0.003	0.002	1.00
HR-LP	-0.01	-0.01	-0.01	**<0.0001**	-0.00760	-0.01	-0.006	**<0.0001**
HR-GG	0.00	-0.01	0.00	0.0003	0.00031	-0.002	0.003	1.00
HR-GO	0.01	0.00	0.01	**<0.0001**	0.00581	0.004	0.008	**<0.0001**
HR-MA	0.01	0.00	0.01	0.0004	0.00634	0.003	0.009	**<0.0001**
HM-LP	0.00	-0.01	0.00	0.91	-0.00107	-0.008	0.006	1.00
HM-GG	0.00	0.00	0.01	0.92	0.00684	<0.001	0.014	0.05
HM-GO	0.01	0.01	0.02	**<0.0001**	0.01233	0.006	0.019	**<0.0001**
HM-HR	0.01	0.00	0.02	0.086	0.00652	<0.001	0.013	0.07
HM-MA	0.01	0.00	0.02	0.0001	0.01287	0.006	0.020	**<0.0001**
CM-LP	0.00	0.00	0.00	0.20	0.00469	0.003	0.006	**<0.0001**
CM-GG	0.01	0.01	0.01	**<0.0001**	0.01260	0.01	0.015	**<0.0001**
CM-GO	0.02	0.02	0.02	**<0.0001**	0.01810	0.02	0.020	**<0.0001**
CM-HM	0.01	0.00	0.01	0.55	0.00577	-0.001	0.012	0.17
CM-HR	0.01	0.01	0.02	**<0.0001**	0.01229	0.01	0.014	**<0.0001**
CM-MA	0.02	0.02	0.02	**<0.0001**	0.01863	0.02	0.021	**<0.0001**

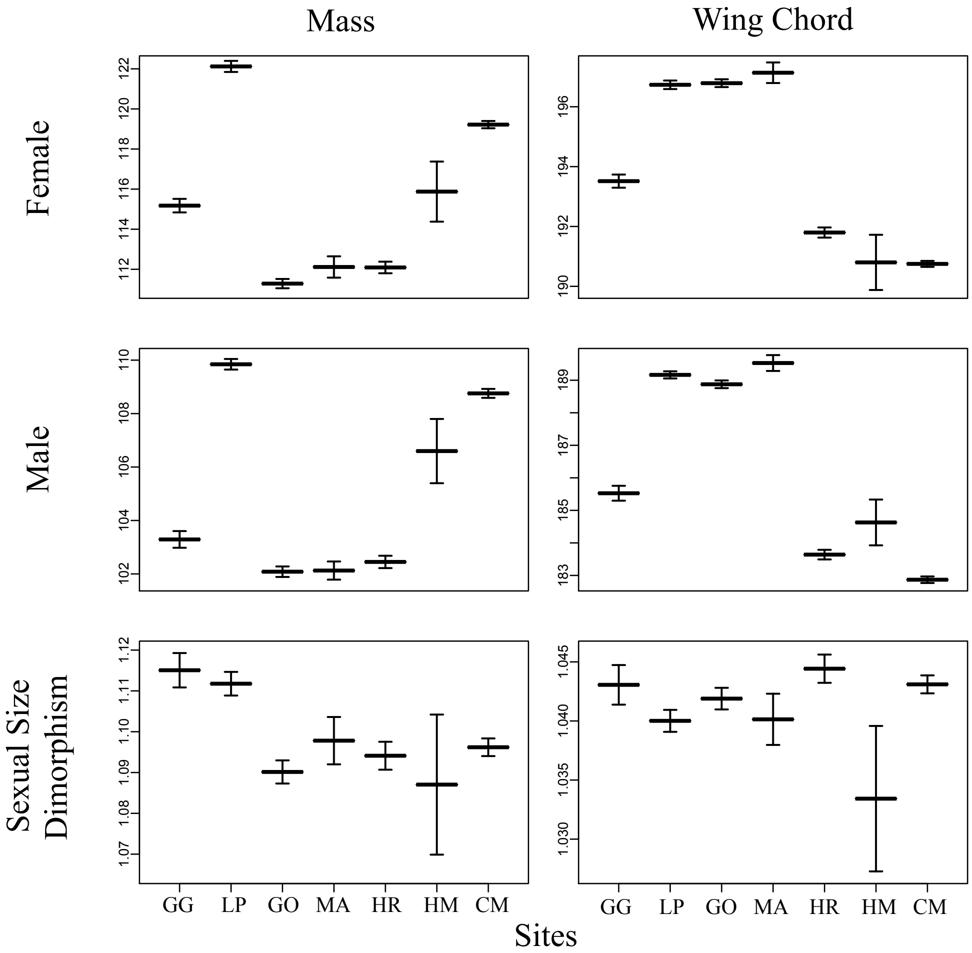

Figure 1. Average mass and wing chord for males and females with standard error bars, sexual size dimorphism for mass and wing chord with standard error bars for each site. Column and rows are as follows: Sites are as follows: GG: Golden Gate Raptor Observatory; LP: Lucky Peak; GO: Goshute Mountains; MA: Manzano Mountains; HR: Hawk Ridge; HM: Hawk Mountain; CM: Cape May.

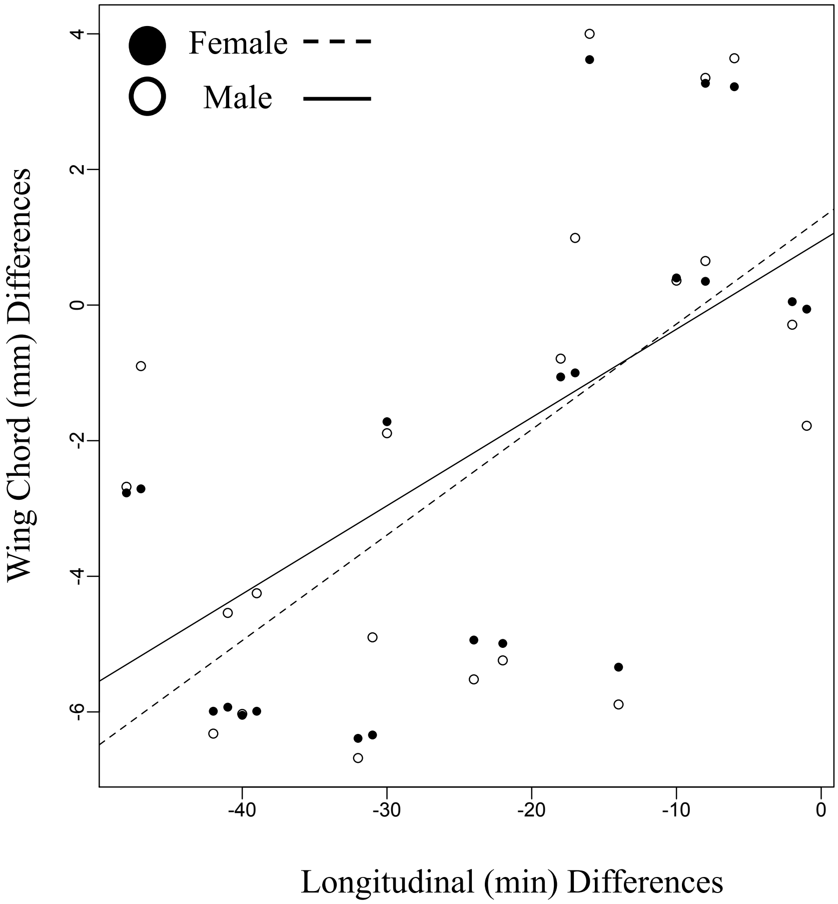

Figure 2. Difference in average wing chord (mm) by difference in longitudinal minutes with best-fit line. The dots represent the male and female pair-wise comparisons from Tukey HSD, see Table 4.

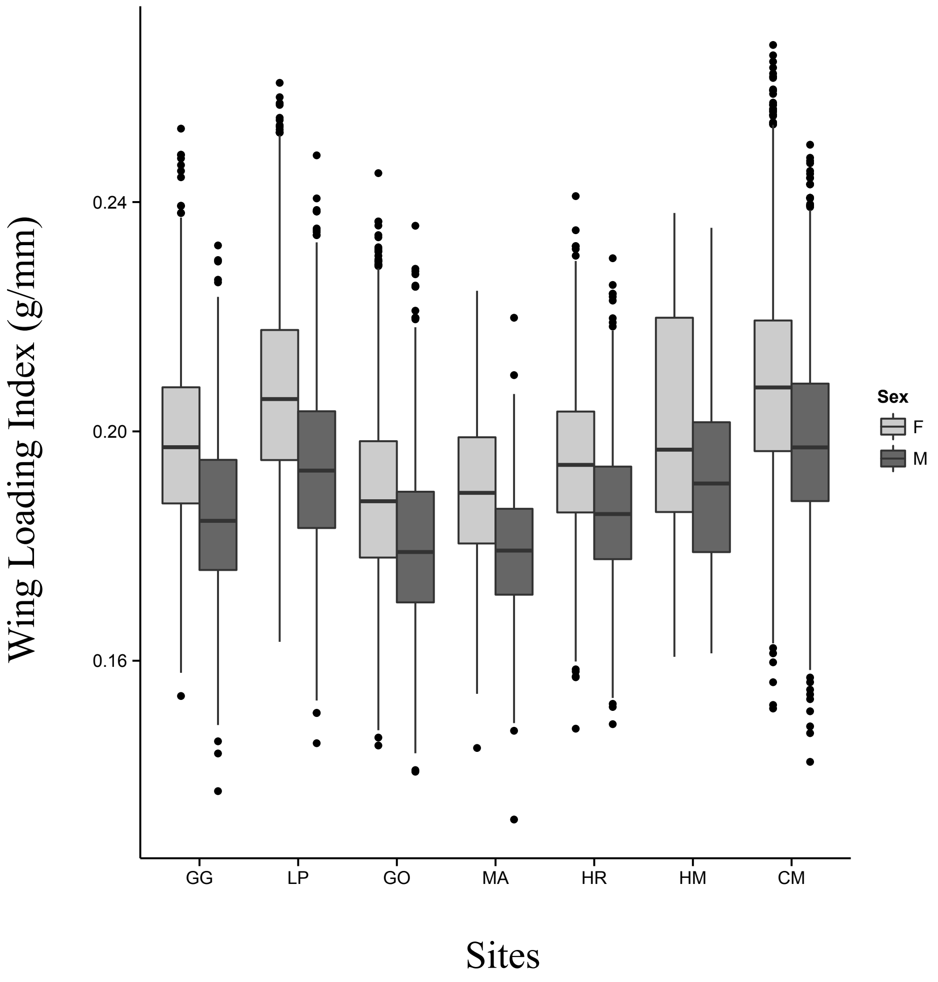

Figure 3. Wing loading index for female and male kestrel for each site with upper and lower hinges (similar to first and third quartile), whiskers extend +/-1.58 IQR (inter-quartile range) of the hinge. Data beyond the end of the whiskers are outliers.