

Original Research Article

Morphological changes in American kestrels (*Falco sparverius*) at continental migration sites

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ABSTRACT

Many American kestrel (*Falco sparverius*) populations are declining across North America. Potential causes include mortality from reduction in food availability, a changing climate, habitat degradation, an increase in avian predators, disease, and toxins. 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 kestrel body mass at three sites and reductions in kestrel wing chord at five sites. Our results indicate declines in body size at the majority of sites are consistent with the hypotheses that food availability, impacts of a changing climate, or predation risk may be contributing to population declines.

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1. Introduction

Raptors are top predators that are vulnerable to environmental change because they often occur at low densities, establish large home ranges, and have low reproductive rates (Bildstein, 2001; Hoffman and Smith, 2003). In addition, raptors face direct threats from humans, including habitat loss, shooting, poisoning, electrocution, and collisions with anthropogenic structures (DeLong, 2000). As a result, populations of many raptor species have shown declines during the last half-century, including peregrine falcons (*Falco peregrinus*), bald eagles (*Haliaeetus leucocephalus*), and Swainson's hawks (*Buteo swainsoni*) (Cade et al., 1988; Bednarz et al., 1990; Hoffman and Smith, 2003; McCarty and Bildstein, 2005; Farmer and Smith, 2009). Although some declining raptors have recovered due to intensive reintroduction programs, habitat protection, the

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curtailment of environmental contaminants such as DDT, and efforts to limit direct threats, other species, such as the American kestrel (*Falco sparverius*), are showing ongoing declines (Farmer et al., 2008a). 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 and Bird, 2002). Most kestrel populations that breed at more northerly latitudes are migratory, migrating throughout late summer and fall (Smallwood and Bird, 2002).

Migration is an energetically expensive undertaking, and raptors frequently use thermals and orographic lift along prominent ridges and coastlines to save energy, resulting in concentration points where many raptors pass through particular sites each year (Kerlinger, 1989; Bohrer et al., 2012). Count sites and banding stations established at these migration concentration points throughout North America allow long-term monitoring of migratory raptor populations (Bildstein, 2001; Hoffman and Smith, 2003; McCarty and Bildstein, 2005). The data collected from these sites provide relatively inexpensive indices of regional raptor populations and are critical to understanding and monitoring raptor populations on a broad scale. Indeed, 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 use was restricted in North America (Bednarz et al., 1990; Bildstein, 2008; Hoffman and Smith, 2003). Banding operations at these sites also provide morphometric information about birds, along with longevity, survivorship and movement data when a banded bird is recaptured or recovered (Clark, 1985; Hoffman et al., 2002; DeLong and Hoffman, 2004).

Kestrel populations have been extensively monitored using fall migration counts (Farmer and Smith, 2009), Breeding Bird Surveys (BBS; Sauer et al., 2013), and National Audubon Society's Christmas Bird Counts (CBC; Sauer et al., 1996). These datasets provide evidence for widespread regional declines in kestrel populations throughout North America. However, the population trends are not clear in all regions and might conflict among datasets, making it difficult to determine drivers of decline (McClure et al., 2017). Previous studies suggest a number of factors that may be driving kestrel declines, such as a reduction in food availability, climate change, habitat loss (Smallwood et al., 2009), an increase in avian predators (Farmer and Smith, 2009), novel diseases (Smallwood et al., 2009), or toxins like anticoagulant rodenticides (Rattner et al., 2011; Gibbons et al., 2015). Despite these possibilities, it is still unclear what factors are causing declines in kestrel populations or how those causes may differ across geographic regions.

Increases in predation from larger raptor species, such as peregrine falcons or Cooper's hawks (*Accipiter cooperii*), could lead to kestrel declines through increased mortality rates. Therrien et al. (in review) have suggested increases in Cooper's hawk populations, in particular, might contribute to kestrel population declines. However, if these predators forage more on large or small individuals, or if they induced phenotypically plastic responses in growth or maturation in kestrels, then average kestrel body size could change as the populations decline. For example, Eurasian golden plovers (*Pluvialis apricaria*) and western sandpipers (*Calidris mauri*) have shown decreases in body mass at migration stopover sites when raptor predation increases (Piersma et al., 2003; Ydenberg et al., 2004).

Food limitation caused by climate or habitat change and declines in insect populations (Hallmann et al., 2014) and insectivorous prey (Nebel et al., 2010) also may be driving kestrel declines. If food availability is influencing kestrel populations, then we expect individuals would be in poorer body condition (i.e., have lower weight relative to body size), leading to both reduced reproduction and survival growth. During development, however, food limitations may result in decreased structural size, and thus, a decline in overall body size that accompanies population decline. For example, lesser snow geese (*Anser caerulescens caerulescens*) in poor nutritional condition grew slowly, that smaller goslings become smaller adults, and small goslings did not survive as long as the larger goslings (Cooch et al. 1991a, 1991b).

Thus, our aim is to evaluate patterns of morphological change in kestrels that occur along with kestrel declines. We hypothesize that factors driving declines can also result in morphological changes in kestrels, and that specific patterns in morphological change can be associated with potential stressors. We did this by first assessing regional population trends conducted at site-specific continental fall migration monitoring sites, and then examining for changes in body mass and wing chord through time.

2. Materials and methods

2.1. Study sites

We used migration count and morphometric data for kestrels observed and banded at seven fall raptor migration sites across North America over a 20–40 year period (Fig. 1). Migration data are from sites run by Golden Gate Raptor Observatory in the Marin Headlands, California (CA; 37°49'N, 122°29'W; Hull et al., 2010), Intermountain Bird Observatory at Lucky Peak and Boise Ridge near Boise, Idaho (ID; 43°36'N, 116°04'W; Farmer and Smith, 2009), HawkWatch International at the Manzano Mountains in central New Mexico (NM; 34°42'N, 106°25'W; DeLong, 2006) and the Goshute Mountains in eastern Nevada (NV; 40°25'N, 114°16'W; DeLong and Hoffman, 1999), and Hawk Ridge Bird Observatory in Duluth, Minnesota (MN; 46°51'N, 92°02'W; Evans et al., 2012). We used count data collected at Hawk Mountain Sanctuary near Kempton, Pennsylvania (PA; 40°40'N, 75°55'W; Viverette et al., 1996) and morphometric data from the Little Gap banding station (40°49'N, 75°31'W). We used count data from New Jersey Audubon's Cape May Bird Observatory and morphometric data collected at Cape May Raptor Banding Project at Cape May Point, New Jersey (NJ; 39°56'N, 74°57'W; Farmer and Smith, 2009).

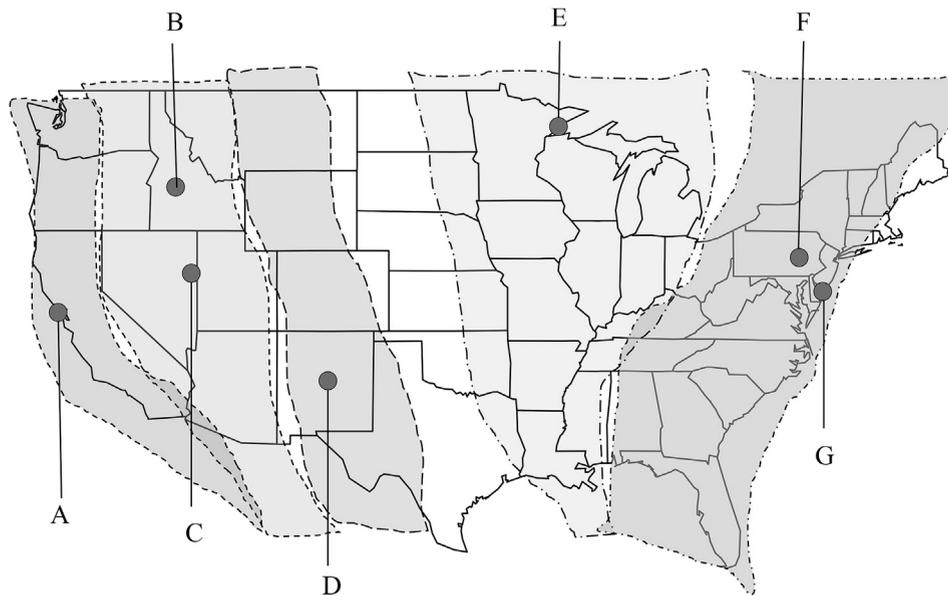


Fig. 1. Migration Station Locations. A. Golden Gate Raptor Observatory, CA; B. Intermountain Bird Observatory, Lucky Peak and Boise Ridge, ID; C. HawkWatch International, Goshute Mountains, NV; D. HawkWatch International, Manzano Mountains, NM; E. Hawk Ridge Bird Observatory, MN; F. Little Gap/Hawk Mountain Sanctuary, PA; G. Cape May Raptor Banding Project/ NJ Audubon's Cape May Bird Observatory, NJ. Migration Site "A" is located in the Pacific region; "B" and "C" are located in the Intermountain West region; "D" is located in the Southern Rocky Mountain region; "E" is located in the Central region; "F" and "G" are located in the Atlantic region (Hoffman and Smith, 2003; Goodrich and Smith, 2008).

2.2. 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 data collection procedures varied slightly between sites, protocols were standardized within each site, giving a robust index of kestrel population sizes each year (Hoffman and Smith, 2003; Farmer et al., 2007; Hull et al., 2010; Evans et al., 2012; Therrien et al., 2012).

Kestrels were trapped using a combination of bow nets, mist nets, and dho-gaza nets, and fitted each 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 and Wheeler, 2001). Females can be aged by the size of the subterminal band on their tail (Smallwood, 1989). We designated HY (hatch year) females as "juvenile". We combined SY (second year), AHY (after hatch year), and ASY (after second year) females as "adult". Due to difficulties and inconsistencies across sites in aging males during migration, we assigned all males as "unknown" age for this analysis. Therefore, we created three age/sex categories: juvenile females, adult females, and unknown males. At the ID and PA sites, however, the majority of female kestrels captured were of unknown age, so we designated all females at these sites as "unknown".

Birds were weighed to the nearest gram and we used a standard ruler to measure the unflattened wing (referred to as wing chord) to the nearest millimeter. Body mass and wing chord are both measures of overall body size. Body mass can vary through time, but wing chord is relatively fixed after feather growth ceases, except for minor wear. In addition to genetic effects, wing chord reflects the energetic conditions of a bird while the feather is growing, while body mass reflects the energetic conditions during nestling growth and through time after the bird's feathers stop growing.

We did not include kestrels with full or partial crops in the analysis (approximately 300 birds) because the crop contains undigested material such as bones, feathers, and fur that would cause overestimation of the mass of the bird. If an individual bird was recaptured at the original banding location within the same banding season, we used the initial mass and wing chord measurements in the analysis. We excluded birds with mass and wing chord measurements greater than 3 standard deviations (SD) of the mean mass and wing chord for each sex from the analysis due to the high likelihood that these measurements were recorded incorrectly. Migration sites at NJ, CA, NV, and NM record the age of female kestrels as HY, AHY, or unknown, when banding, and we did not include the "unknown" female birds in the analysis. Following these collective procedures, we eliminated 3538 individuals out of a sample size of 18, 848.

2.3. Statistical analysis

We analyzed data 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. A breakpoint is the year when a switch in the direction of a linear trend occurred (Muggeo,

2008). Once we determined the breakpoint year, we divided 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 during the decline period. We developed an initial model for each site for the after period or for the whole time-period if there was no breakpoint. Predictor variables included year, day of the year (DOY), the sex/age class (SA: juvenile females, adult females, all males), and all two-way interactions. SA was included because kestrels differ by sex in mass and morphology. We included DOY 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 final model, using AIC score to assess model fit (Table S3a; Table S3b). 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, 2008). We focused on the post-breakpoint because we were interested in patterns associated with the decline. These procedures further reduced the sample size of 15,310 by 3562 birds; the resulting sample size is 11,748.

3. Results

3.1. Population

Population size.—The rate of raptor passage (RpH) declined significantly at all seven migration sites during the last decade, with some sites showing declines for much longer periods (Table 1; Fig. 2). Declines in RpH ranged across sites from 12.6% to 42.7% per ten years (Table 1). The NJ, PA, and ID sites showed population declines during the entire period analyzed.

3.2. Morphometrics

Mass.—During the periods when RpH declined significantly, mass also declined significantly at sites (Table 2). In some cases, mass declined significantly for all age and sex groups, and in other cases only certain age/sex classes declined. The mass of juvenile females, adult females and males declined significantly at NJ, and PA (Table S4a.), but not significantly so in MN, NM, ID, and CA. The mass of juvenile females and males declined significantly at NV. The declines in kestrel mass over a period of 10 years ranged from 0.82% to 2.37% of their average mass, which corresponds to 1 g–2.65 g decrease in mass (Table 2). Juvenile females had a significant decrease in mass at the NJ (Table S4a.), and NV (Table S4c.) sites. Juvenile female kestrels from NJ lost 0.83% of their mass or 1 g, and NV lost 1.35% of their mass or 1.51 g, during a 10-year period (Table 2).

Wing Chord.—Sites in the Intermountain West – NM and ID – showed wing chord declines from 0.19% to 0.52%, or 0.37–1.03 mm, per 10 years across sites (Table 2). At NJ and NV, wing chord did not decline significantly overall, but juvenile female wing chords both showed a decline of 0.52%, or 1 mm at NJ and 1.03 mm at NV (Table 2). At MN, wing chord increased ($p = 0.012$, Table S4b.) 0.62%–0.65%, or 1.25 mm per 10 years, and at CA ($p = 0.090$) and PA ($p = \text{females: } 0.304$; males = 0.120), wing chord showed no significant change (Table S4a. and S4d.).

4. Discussion

Our analysis of continental site-specific fall migration counts showed regional declines in population trends, and similar to BBS and CBC counts, the magnitude of the declines varied between regions (Bednarz et al., 1990; Farmer and Smith, 2009; Paprocki et al., 2014; Sauer et al., 2013). In addition to population declines, we found changes in kestrel body mass and wing length at the majority of migration sites we analyzed, with individuals generally getting smaller and lighter. Mass decreased over the course of the study by about a gram or more per decade (1% per 10 years) at three of the seven migration sites, and wing chord decreased over the course of the study by about 1 mm or more per decade (about 0.5% per 10 years) at five of the seven migration sites included in this analysis. Two of the regional locations showed (e.g., NM/NV/ID and NJ/PA) similar trends in size and weight, and this suggests a common selective pressure for birds throughout a region.

Table 1

Summary of sites, years available, and percent declines of American kestrels (*Falco sparverius*) recorded at seven fall migration sites across North America. Years refer to the span of time for which both banding and count data were available. Estimated year the decline began represents the beginning of the data window as detected by breakpoint regression (see text).

Site	Years	Estimated year the decline began	% decline per 10 yr	<i>p</i>
NJ	1976–2015	1976	20.2%	<0.001
PA	1979–2015	1979	12.6%	<0.001
MN	1972–2015	2000	37.5%	<0.006
NM	1985–2014	1996	38.7%	<0.001
NV	1983–2014	1997	42.7%	<0.001
ID	1994–2015	1994	20.6%	0.001
CA	1989–2015	2002	35.7%	0.001

Bold indicates a significance *p*-value.

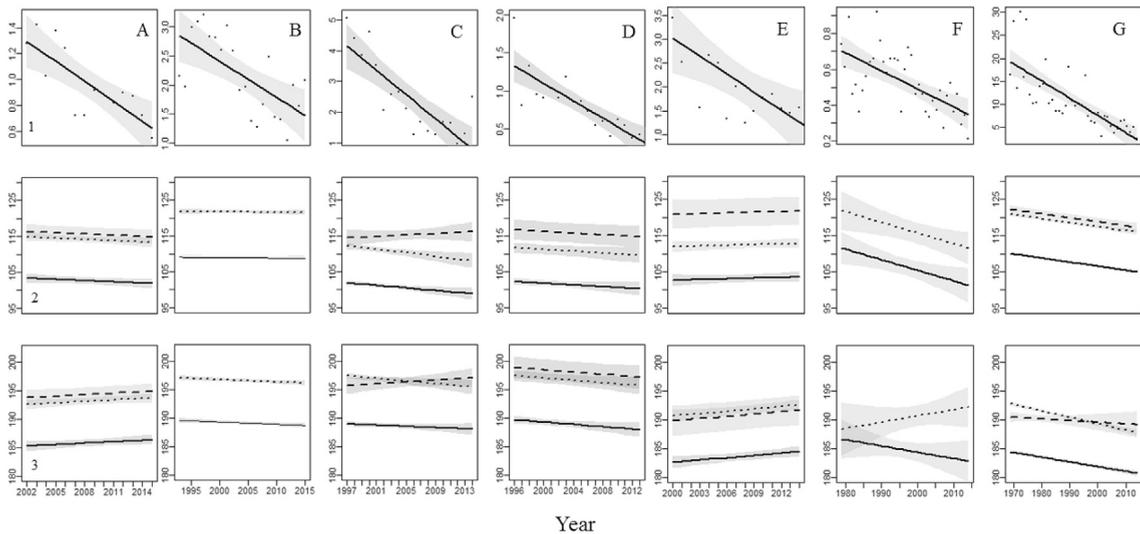


Fig. 2. Rph (row 1), mass (row 2), and wing chord (row 3) graphs during period of American kestrel (*Falco sparverius*) population decline with 95% confidence intervals. Columns A-G are sites as follows: A. Golden Gate Raptor Observatory, CA; B. Intermountain Bird Observatory, Lucky Peak and Boise Ridge, ID; C. HawkWatch International, Goshute Mountains, NV; D. HawkWatch International, Manzano Mountains, NM; E. Hawk Ridge Bird Observatory, MN; F. Little Gap/Hawk Mountain Sanctuary, PA; G. Cape May Raptor Banding Project/ NJ Audubon's Cape May Bird Observatory, NJ. Males represented by a solid line, juvenile females represented by a dotted line, adult females represented by a dashed line; Graphs B. and F. the males are represented by a solid line, females are represented by a dash, with 95% confidence intervals.

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 food availability caused by a dietary shift and climate. Northern goshawk (*Accipiter gentilis*) museum specimens collected in Denmark between 1854 and 1941 and between 1979 and 1998, showed decreases in wing length, tarsus length, and bill size by 1–4%, 0.5–5%, and 1–6% respectively per approximately 20 years. These trends were linked to changes in diet because the decrease in body size was not uniform across age and sex class, with immature birds more affected than adults (Yom-Tov and Yom-Tov, 2006).

Similarly, a study of passerines in western Pennsylvania from 1961 to 2006 showed that mass and wing chord steadily decreased over time (Van Buskirk et al., 2010). In contrast, wing chord and mass of passerine species at two sites in central California steadily increased over three to four decades, although not all changes were significant for all species (Goodman et al., 2011). The 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 are 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 was continental in scope, and results indicated that morphological changes in kestrels were occurring, but varied regionally. Kestrels were not declining in body size at all sites, and, in fact, they were increasing at the MN site, which could suggest that kestrels are experiencing different factors affecting body size in different breeding areas.

One study of migratory connectivity in red knots (*Calidris canutus canutus*), a long distant migrant, found a reduction in body sized coupled with decreased fitness and survival (van Gils et al., 2016). Red knot offspring hatched during summers with early snowmelts were smaller in body mass, bill, tarsus, and wing length. These shorter-billed individuals had reduced survival rates because they could not retrieve mollusk prey buried in intertidal sediments in their tropical wintering grounds (van Gils et al., 2016). We can expect changes in morphology 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 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. Thus, our observations for most sites, except for CA and MN, are consistent with a role for food shortage.

Other climatic factors could also cause morphological size and population to decrease together. Drought has been prevalent in the interior west of North America during a substantial portion of the kestrel declines (Hoffman and Smith, 2003; Farmer and Smith, 2009). Hoffman and Smith (2003) hypothesized that as drought increased, raptor hunger levels and mortality also increased in these regions. Alternatively, Dawson and Bortolotti (2000) showed that young kestrels exposed to inclement weather, such as increased precipitation, become smaller, lighter, and less likely to survive to fledgling stage compared to those raised in more optimal weather conditions. These climatic results suggest that it may not be food abundance driving lower food intake, but potentially behavioral changes that limit provisioning rates of parents to nestlings, as well as food availability.

Table 2

Summary of changes in migrating American kestrel (*Falco sparverius*) mass (g) and wing chord (mm) at seven fall migration monitoring sites across North America. Years represent periods of kestrel decline determined by breakpoint regression.

Site	Years	Age	Mass changes per 10 years				Wing chord changes per 10 yrs			
			Slope g/yr	%	grams	<i>p</i>	Slope mm/y	%	mm	<i>p</i>
NJ	1969–2014	Juv Fem	−0.11	0.83	1	<0.001	−0.08	0.52	1.00	0.016
		Ad Fem	−0.11	0.82	1	<0.001	−0.03	0.14	0.27	0.360
		Male	−0.11	0.91	1	<0.001	−0.05	0.40	0.74	0.119
PA	1979–2014	Female	−0.29	2.17	2.65	0.010	0.11	0.52	0.98	0.304
		Male	−0.29	2.37	2.65	0.010	−0.22	0.53	0.98	0.120
MN	2000–2014	Juv Fem	0.07	0.54	0.61	0.398	0.13	0.62	1.25	0.012
		Ad Fem	0.07	0.50	0.61	0.398	0.13	0.63	1.25	0.012
		Male	0.07	0.59	0.61	0.398	0.13	0.65	1.25	0.012
NM	1996–2014	Juv Fem	−0.11	0.96	1.07	0.099	−0.10	0.47	0.93	0.036
		Ad Fem	−0.11	0.91	1.07	0.099	−0.10	0.47	0.93	0.036
		Male	−0.11	1.04	1.07	0.099	−0.10	0.49	0.93	0.036
NV	1997–2015	Juv Fem	−0.34	1.35	1.51	0.020	−0.20	0.52	1.03	0.031
		Ad Fem	0.10	0.92	0.80	0.423	0.08	0.39	0.76	0.283
		Male	−0.28	1.60	1.63	0.045	−0.14	0.25	0.47	0.118
ID	1994–2015	Female	−0.02	0.12	0.14	0.534	−0.04	0.19	0.37	0.008
		Male	−0.02	0.13	0.14	0.534	−0.04	0.19	0.37	0.008
CA	2002–2015	Juv Fem	−0.11	0.89	1.02	0.120	0.09	0.40	0.76	0.090
		Ad Fem	−0.11	0.88	1.02	0.120	0.09	0.40	0.76	0.090
		Male	−0.11	0.99	1.02	0.120	0.09	0.42	0.76	0.090

Bold indicates a significance *p*-value.

Changes in land-use also may affect 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 and Smith, 2009). Such landscape changes might reduce nesting sites, foraging locations, and potentially reduce suitable locations for migratory stopover as well (Farmer and Smith, 2009). Thus, changes in land-use could be a cause of decreased resource supply, impacting kestrel growth and survival, and causing populations to decline, as well as their concurrent body size.

Predation also may play a role driving population and body size declines. Recent increases in avian predator populations, such as Cooper's hawks (Farmer et al., 2006) and peregrine falcons (Hoffman and Smith, 2003; Farmer et al., 2008b) could affect kestrel populations. This could be especially important where kestrels occur in low densities and where predation from Cooper's hawks, could cause further decline (Therrien et al. in review). Direct mortality from predation could not only drive populations down, but also create selection for large or small birds. However, many cases where predation drives changes in the body size of prey involve fairly strong predator-prey interactions (Brooks and Dodson, 1965; Osenberg and Mittelbach, 1989). Thus, more work needs to be done to understand whether predation is contributing to population and morphological changes in kestrels.

Although migration counts have documented population declines in migratory raptors in the past, current declines also could reflect shifting migratory patterns such as migratory short-stopping (i.e., when birds migrate shorter distances when environmental conditions and food levels are favorable at northern wintering sites) (McClelland et al., 1994; Viverette et al., 1996; Heath et al., 2012; Miller et al., 2015; Paprocki et al., 2017). Migratory short-stopping could contribute to the pattern of fewer birds being counted at migration sites, although it would not necessarily include decreases in size. Thus, short-stopping would be consistent with patterns at CA, NM, and ID, where population declines were not accompanied by decreasing body mass. Furthermore, evidence for kestrel declines also comes from BBS (Sauer et al., 2013) and CBC (Sauer et al., 1996) across North America, indicating that short-stopping is an unlikely cause of reduced numbers of kestrels seen in most locations, however further study is needed (McClure et al., 2017).

The concurrent declining trends of kestrel numbers and body size measurements may support the idea that food shortages or food stress may be responsible for the wide-spread continental declines of this species documented in recent decades. However, our results do not rule out the possible effects of life history shifts related to predation, or the influence of other factors such as West Nile Virus, direct mortality, and sub-lethal rodenticide poisoning. We suggest narrowing the field of potential factors further in three initial steps: 1) assess the breeding origins of migratory populations using genetic techniques to better understand the extent of each trend, 2) examine of long-term breeding population data to look for life history shifts such as clutch size or egg mass, and 3) a long-term examination of stress hormones to look for signals of enhanced predation risk, or other environmental stressors, between adult and juvenile individuals. Although some potential factors could be widespread, we advocate for considering different factors in different regions, but moreover, linking the magnitude of declines to the magnitude of potential threats across regions such as stress hormones in blood to elucidate food vs. enhanced predation risks to the magnitude of the decline.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.gecco.2018.e00400>.

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