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EVIDENCE OF CONTINUING DOWNWARD TRENDS IN AMERICAN KESTREL POPULATIONS AND RECOMMENDATIONS FOR RESEARCH INTO CAUSAL FACTORS

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Abstract.—We analyzed long-term datasets from nest box programs, Breeding Bird Surveys run by the US Geological Survey, Christmas Bird Counts run by the National Audubon Society, and counts from two key fall migration watch sites, Hawk Mountain Sanctuary and Cape May Hawkwatch. We found that populations of American Kestrels (*Falco sparverius*) in North America are generally still declining, albeit with some caveats. Some populations are actually increasing, while others are remaining stable. Overall, the magnitude of annual change appears to be decreasing slightly during recent years. To understand potential causes of the decline, we recommend the following courses of action in no particular order: (1) determine whether the increase in Cooper's Hawk (*Accipiter cooperii*) populations is restricting kestrel distributions by the mere presence of the larger raptor; (2) study the effects of habitat loss and/or degradation on the falcon's wintering range; (3) further investigate on a broader spatial scale whether within-season habitat alterations are creating ecological traps for breeding kestrels; (4) determine the importance of arthropods in the diet of kestrels, especially the long-term population trends and timing of emergence of grasshoppers in relation to kestrel breeding chronology; (5) discover whether rodenticides pose a serious risk to American Kestrels across North America; (6) learn more about possible effects, both direct and indirect, that the use of neonicotinoids may have on kestrels; and (7) continue ongoing studies of the effect of climate change on these birds.

Key Words: *American Kestrel*; Falco sparverius; *arthropods*; *climate change*; *neonicotinoids*; *population decline*; *research recommendations*.

EVIDENCIA DE TENDENCIAS POBLACIONALES DECRECIENTES EN LAS POBLACIONES DE *FALCO SPARVERIUS* Y RECOMENDACIÓN PARA LA INVESTIGACIÓN DE LOS FACTORES CAUSALES

Resumen.—Analizamos conjuntos de datos de largo plazo provenientes de programas de cajas nido, censos de aves reproductoras realizados por el Servicio Geológico de EEUU, conteos navideños de aves realizados por la Sociedad Nacional Audubon y conteos de dos sitios clave de observación de la migración de otoño, el Hawk Mountain Sanctuary y el Cape May Hawkwatch. Encontramos que las poblaciones de *Falco sparverius* en América del Norte en general siguen disminuyendo, aunque con algunas salvedades. Algunas poblaciones en realidad están aumentando, mientras que otras se mantienen estables. En general, la magnitud del cambio anual parece estar disminuyendo ligeramente durante los últimos años. Para comprender las causas potenciales de la disminución, recomendamos los siguientes cursos de acción sin un orden en particular: (1) determinar si el aumento de las poblaciones de *Accipiter cooperii* está afectando las poblaciones de *F. sparverius* al restringir su distribución por su mera presencia; (2) estudiar los efectos de la pérdida y/o degradación del hábitat en el rango de invernada de *F. sparverius*; (3) seguir investigando en una escala espacial más amplia si las alteraciones del hábitat dentro de la temporada están creando trampas ecológicas para los individuos reproductivos de *F. sparverius*; (4) determinar la importancia de los artrópodos en la dieta de *F. sparverius*, especialmente las tendencias poblacionales a largo plazo y el momento de aparición de los saltamontes en relación con su cronología reproductiva; (5) descubrir si los rodenticidas plantean un riesgo grave para *F. sparverius* en América del Norte; (6) aprender más sobre los posibles efectos, tanto directos como indirectos,

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que el uso de neonicotinoides puede tener sobre esta especie; y (7) continuar los estudios en curso sobre el efecto del cambio climático en estas aves.

[Traducción del equipo editorial]

INTRODUCTION

The American Kestrel (*Falco sparverius*), once the most commonly seen raptor in some North American landscapes, has now been the subject of four symposia organized by the Raptor Research Foundation, Inc. (RRF). The first, published as a Raptor Research Report in the form of an edited proceedings by RRF in 1987 (Bird and Bowman 1987), focused mostly on general biology and management. The second symposium on this species was convened at the RRF meeting held in Fogelsville, Pennsylvania, in 2007, stimulated mostly by alarming reports of kestrel declines in various parts of North America. About half of the papers included in the special kestrel issue of the *Journal of Raptor Research* in 2009 mentioned population declines (e.g., Bird 2009, Farmer and Smith 2009, Smallwood et al. 2009a). Following that special issue were two key papers analyzing population trends in kestrels, discussing the possible reasons for the decline, and providing suggestions for ameliorating the downward trend (McClure et al. 2017, 2021). A third symposium, more limited, was held at the RRF meeting in Corpus Christi in 2014, but no proceedings were published.

In the fall of 2021, the fourth RRF symposium on the American Kestrel was held for four reasons: (1) to provide a forum for new research pertaining to the biology and conservation of the species; (2) to document any changes to the status of kestrel populations in the Americas; (3) to give an opportunity for the presentation of detailed populations analyses; and most important of all, (4) to create a forum for discussion about why the falcon's numbers are declining and what can be done about it. The proceedings of this fourth symposium delivered an opportunity for the presenters to contribute papers to this special issue of the *Journal of Raptor Research*.

The overall aim of this report is to update the status of American Kestrel populations based on analyzed results from nest box programs, Breeding Bird Surveys (BBS) run by the US Geological Survey (USGS), Christmas Bird Counts (CBC) run by the National Audubon Society, and counts from two key fall migration watch sites (Hawk Mountain Sanctuary and Cape May Hawkwatch). Each of these measures has proven over the last few decades to provide invaluable snapshots of the health of raptor populations in North America. Another useful monitoring tool is the Raptor Population Index, which is being featured in a separate article in this issue (Oleyar et al. 2023). The second objective of this report is to discuss possible reasons for the changes in American Kestrel populations in North America and to recommend future avenues for productive research on this topic.

METHODS

Nest Box Occupancy. Smallwood et al. (2009a) reported nest box occupancy rates from seven nest box programs in the United States and Canada that met the following criteria: (1) nest boxes were systematically monitored such that occupancy data were comparable each year; (2) data were available for at least 10 yr, including the first year of the program; and (3) the median number of nest boxes available to kestrels each year was at least 15. Those seven data sets spanned the years 1984 to 2007. Three of those nest box programs continued to operate through 2021, and a fourth through 2015; here we present data from these four nest box programs. The nest box programs were located in the (1) Yukon Territory, Canada, (2) Massachusetts, USA, (3) New Jersey, USA, and (4) a study area that included parts of northern Virginia and central Maryland, USA. The locations and descriptions of study areas and the monitoring protocols are given in Smallwood et al. (2009a).

For kestrel populations that are limited by the availabilty of nesting cavities, the expected response to an introduction of a significant number of nest boxes is an initial increase in the number of kestrel pairs occupying those nest boxes. That initial increase could mask a longer term population trend. Following the procedure of Smallwood et al. (2009a), we examined the relationship of occupancy rate (number of nest boxes in which at least one kestrel egg was observed/number of nest boxes available $\times$ 100%) to year, beginning with the year of initial peak occupancy. Because the curves did not appear linear, we used the Spearman correlation to determine whether the trends were significant.

Breeding Bird Survey. We obtained data on the trends in kestrel sightings from the BBS, which is available online (https://www.mbr–pwrc.usgs.gov/bbs/trend/tf19.html) for the years 1966 through 2019, the most extensive period available (Sauer et al. 2020). The online analysis uses hierarchical models to estimate temporal trends (Sauer and Link 2011), producing an index of relative abundance with 95% confidence intervals. The analysis also generates a regional credibility measure based on the number of routes and the abundance of the selected species (https://www.mbr-pwrc.usgs.gov/bbs/credhm09.html). We obtained the relative abundance values for the entire kestrel range in continental North America and population trends separately for each of the 26 terrestrial bird conservation regions (https://www.usgs.gov/media/images/terrestrial-bird-conservation-regions-north-america) for which kestrel population trend data were available, omitting an additional seven regions for which the credibility measure indicated that the data had an important deficiency. Using this online map as a template, we color-coded each of the 26 regions to indicate the direction and magnitude of the trend.

Christmas Bird Counts. We obtained CBC data from the National Audubon Society's website (https://www.audubon.org/conservation/science/christmas-bird-count). We pooled the summary data for Canada and the United States, from 1966 through 2015, the most recent year available. We used Spearman correlation to determine whether there was a significant trend over time in number of birds per party hour and we used linear regression to estimate the slope for significant trends.

Migration Counts. We obtained migration count data from the Hawk Migration Association of North America's Raptor Migration Database (http://hawkcount.org). We selected two hawkwatch sites (Hawk Mountain Sanctuary and Cape May Hawkwatch) to examine the trends of kestrels counted during fall migration. (1) Hawk Mountain Sanctuary, a ridge site in eastern Pennsylvania, is the oldest continuously operating watchsite in North America. We obtained annual kestrel counts from 1966 to 2020, comparable to the period covered by BBS data. (2) Cape May Hawkwatch, a coastal site in New Jersey, records the greatest number of migrating American Kestrels each fall. Cape May counts were available from 1976 to 2020. We used Spearman correlation to determine the existence of trends and whether they were significant and we used linear regression to estimate the slope.

All statistical procedures, except for the analyses obtained from the USGS BBS website, were performed with SAS 9.4 software for Windows operating systems (SAS Institute 2013).

RESULTS

Nest Box Occupancy. Each of the nest box programs experienced an initial increase in occupancy rate upon introduction of nest boxes into the study area (Fig. 1). The duration of the initial increase ranged from 4 yr in the Yukon to 8 yr in New Jersey. Following the initial increase, all four programs experienced significant declines (Table 1). The most severe decline occurred in the Yukon, where the occupancy rate decreased to 3.1% in 2001 and has remained low (mean = 4.2%, range = 0.0–7.8%). In contrast, the Virginia/Maryland program experienced an increase in occupancy during the final 11 yr of that program, 2005–2015.

Breeding Bird Survey. The number of kestrels observed on the USGS BBS (all North American routes pooled, $n = 3690$) declined over the entire duration of the survey, with a mean change of –1.45% per yr (Fig. 2). However, the magnitude of change appears to have decreased slightly. We divided the 54 yr of BBS data into three 18-yr periods: from 1966 through 1983 the annual change was –1.71%; from 1984 through 2001, –1.57%; and from 2002 through 2019, –1.39%. For all BBS survey routes in Canada combined ($n = 727$) the annual change from 1966 through 2019 was –2.1% ($P < 0.05$) and for all routes in the United States ($n = 2963$) the annual change from 1966 through 2019 was –1.1% ($P < 0.05$).

The BBS data revealed declines for kestrel populations in 23 of the 26 bird conservation regions for which credible trend data were available (Fig. 3). New England/mid-Atlantic Coasts experienced the greatest annual change (–4.2%) and eight other regions experienced annual declines of at least 2%. Population increases were found in only three bird conservation regions: Central Hardwoods, Chihuahuan Desert, and Mississippi Alluvial Valley, with annual changes of +0.2%, +0.4%, and +2.2%, respectively.

Christmas Bird Counts. The number of kestrels observed per party hour on CBCs, 1966–2015, ranged from 0.178 to 0.349 (Fig. 4). The mean decrease of 0.003 birds per party hour/yr represents a 44.5% decline over 49 yr.

Migration Counts. The number of kestrels counted at Hawk Mountain each year during fall

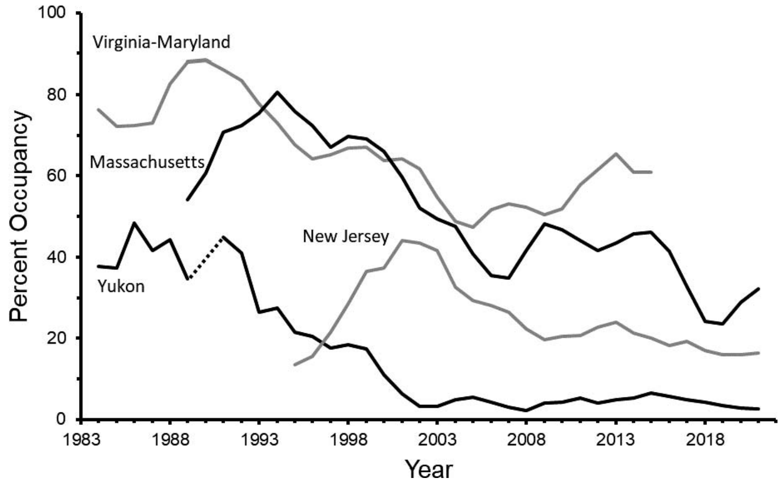

Figure 1. Populations of American Kestrels breeding in nest boxes have experienced various levels of decline in recent years. Percent occupancy is the number of nest boxes in which kestrels laid eggs/number of nest boxes available × 100%. Values are presented as 3-yr running means. Each curve begins the year the program was established and shows the initial response to the local increase in nest site availability. Data were not available for the Yukon program in 1990.

migration, 1966–2020, ranged from 218 to 839 (Fig. 5). Although counts varied considerably from year to year, over the study period the negative correlation was significant. The mean decrease of 2.7 birds/yr represents a 26.1% decline over 55 yr. The number of kestrels counted at Cape May each year during fall migration, 1976–2020, ranged from 2237 to 21,515 (Fig. 6). The decline was more uniform than that at Hawk Mountain, with a mean decrease of 219 birds/yr, representing a 75.7% decline over 45 yr.

DISCUSSION

Population Measures. Each of the four types of data we examined (nest box occupancy, Breeding Bird Survey, Christmas Bird Counts, and autumn hawk migration counts) have limitations as to how accurately they represent underlying population trends. Nest box occupancy rates, for example, may not accurately reflect changes in the local population during the first few years after nest boxes are installed. Simulations by McClure et al. (2017) demonstrate that for populations not limited by the availability of nest sites, the presence of unmonitored nesting sites can affect the occupancy rate of monitored nest boxes, and that it may take several years for the nest box occupancy rate to equilibrate with the true local population density. In contrast, for a Florida population of kestrels that was limited by nest site availability, the sharp initial rise in occupancy rates closely tracked population density estimates obtained by survey plots that controlled for nest box locations (Smallwood and

Table 1. After an initial increase in occupation rates associated with the establishment of nest box programs, the populations of American Kestrels that laid eggs in those nest boxes have experienced significant declines. Number of nest boxes is the median number of nest boxes available to kestrels each year, beginning with the year of peak occupancy. Correlation is between occupancy rate (number of nest boxes in which kestrels laid eggs/number of nest boxes available × 100%) and n is the number of years (peak year to most recent year).

Location	Median Number of Nest Boxes	Year Program Established	Year of Peak Occupancy	Last Year Included in Analysis	Spearman Correlation		
					n	r	P
Yukon	59	1984	1987	2021	34	−0.728	<0.0001
Virginia/Maryland	73	1984	1989	2015	27	−0.680	<0.0001
Massachusetts	38	1989	1994	2021	28	−0.821	<0.0001
New Jersey	100	1995	2002	2021	20	−0.784	<0.0001

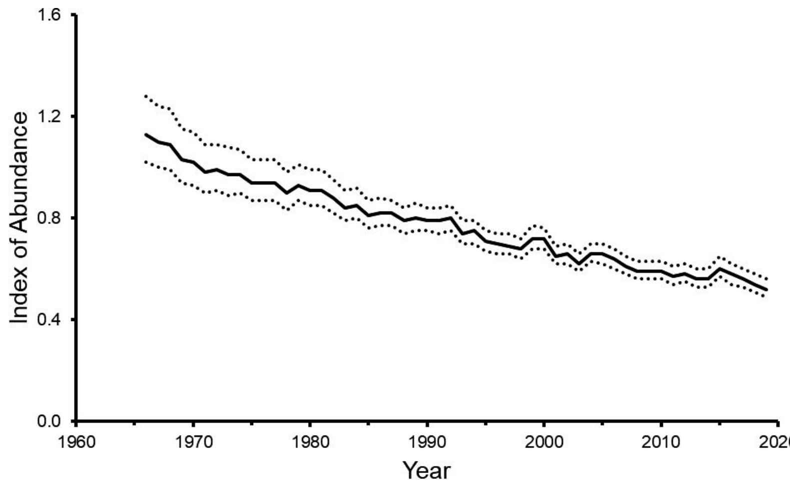

Figure 2. The number of American Kestrels observed on the USGS Breeding Bird Survey has been decreasing since the program began in 1966. Data are from all survey routes ($n = 3690$) in Canada and the USA, 1966–2019. Curves represent point estimates and 95% confidence intervals (Sauer et al. 2020).

Collopy 2009). In the present study, long-term declines in occupancy rates *after* the initial increase should reflect the true local population trend.

The trends from nest box studies, BBS and CBC data, and migration counts are notably similar, corroborating that kestrel populations across North America have decreased significantly over the past several decades. However, this decline is neither temporally nor spatially uniform. For example, the population that breeds in nest boxes in the Yukon Territory declined sharply after the initial response to the introduction of nest boxes, but more recently appears to have stabilized at a much lower density (Fig. 1). A similar pattern of occupancy was observed in New Jersey, i.e., a sharp decline followed by a less severe decline that continues to the present. In contrast, nest box occupancy rates in the Massachusetts study have shown a long-term decline, but with large annual variation, and the population breeding in the Virginia/Maryland study appears to have increased during the final decade of that program.

Temporal patterns of decline also are evident in data from the Breeding Bird Survey, which began in 1966. McClure et al. (2017; Fig. 1B) concluded that the trend in BBS data, 1966 through 2013, represented a steady decline (constant proportional annual decrease). The implicit consequence of an unchanging proportional loss over time is that the population level would eventually converge on zero, i.e., extinction. However, our analysis of BBS trends suggests that the magnitude of the decline may be decreasing, consistent with nest box data and migration counts. If such a trend (decreasing proportional loss) continues over time, kestrel population levels may instead stabilize at a new, lower level.

BBS data also show that the decline varies geographically, with particularly severe declines throughout the Canadian Boreal Softwood Shield, Prairie Potholes, the northeastern USA, the Piedmont, southern Rockies, and coastal California (Fig. 3). Population trends can be quite local, with one region experiencing a decline while an adjacent region experiences an increase (e.g., Southern Rockies/Colorado Plateau versus Chihuahuan Desert). On a finer spatial scale, the nest box program in Virginia and Maryland experienced an increase in occupancy rates from 2005 to 2015 while the surrounding bird conservation region (Piedmont) underwent an annual change of –2.37% (https://www.mbr-pwrc.usgs.gov/bbs/trend/tf19.html).

The number of kestrels counted during fall migration at Hawk Mountain varied considerably from year to year, with 8 of the 10 highest annual totals recorded between 1989 and 1999 (Fig. 5). However, there was a significant downward trend across all years examined. The trend in kestrels counted at Cape May during autumn (Fig. 6) appeared similar to that of the Breeding Bird Survey and two of the nest box studies, i.e., a severe decline followed by a milder decline or possible stabilization at a lower density. The Raptor Population Index,

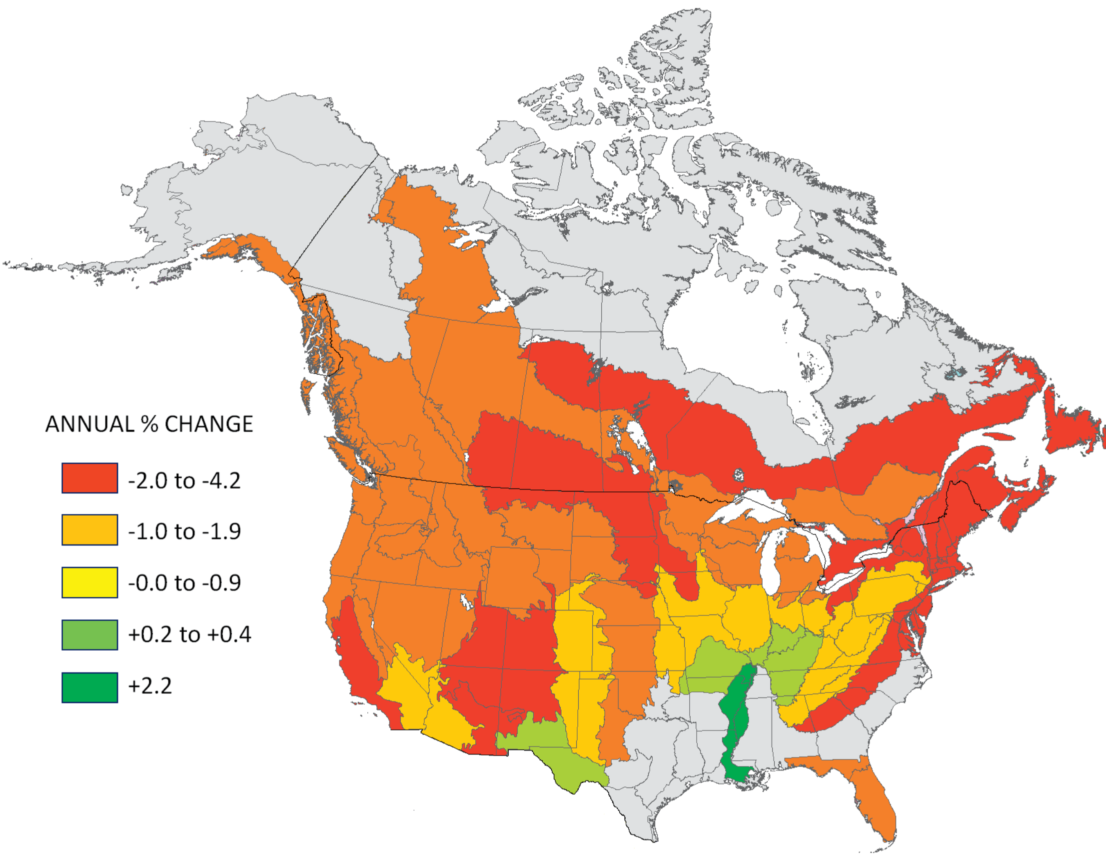

Figure 3. American Kestrels have been declining in 23 of 26 North American bird conservation regions (https://www.usgs.gov/media/images/terrestrial-bird-conservation-regions-north-america). Data are from the USGS Breeding Bird Survey, 1966–2019.

which is calculated from a compilation of autumn hawkwatch sites across North America, also indicates that the decline in American Kestrel populations has at least moderated in the last decade (Oleyar et al. 2023).

Possible Causes of Decline. So, despite some measures indicating stability but at a lower density, why are some American Kestrel populations still in a state of decline, and what might be the most productive avenues for research to determine the causes? To date, three main papers offer a general discussion of possible causes: Bird (2009), Smallwood et al. (2009a), and McClure et al. (2017). Bird (2009) provided an initial cursory overview of possible causes, while Smallwood et al. (2009a) employed a more analytical approach to at least three frequently mentioned potential hypotheses, i.e., West Nile Virus, Cooper's Hawk (*Accipiter cooperii*) predation, and habitat loss and/or degradation. McClure et al. (2017) took an important step further by adding more discussion and support (or lack thereof) for the various hypotheses and included recommendations for further research.

For a number of reasons discussed in the aforementioned papers, West Nile Virus and competition for nesting cavities by European Starlings (*Sturnus vulgaris*) are not worth any further discussion as major contributors to the decline of the American Kestrel. Smallwood et al. (2009a) presented evidence to suggest that Cooper's Hawks were not a primary cause of the decline, but see below. McClure et al. (2017) also argued against the habitat loss and degradation issue, citing instances of a decrease in the use of nest boxes by kestrels in areas with an abundance of appropriate habitat, e.g., New Jersey (Smallwood et al. 2009a). Below we offer some

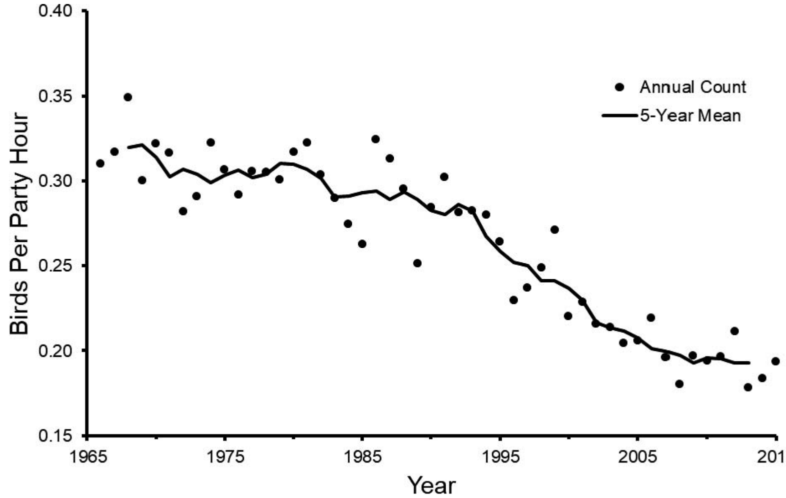

Figure 4. The number of American Kestrels observed on Christmas Bird Counts decreased significantly during recent decades ($n = 50$ yr, Spearman $r = -0.896$, $P < 0.001$). Data are pooled from all counts in Canada and the USA, 1966–2015.

thoughts on possible reasons for the decline that may or may not be worthy of further research and in no particular order.

Predation by larger raptors. The Cooper's Hawk hypothesis (Farmer et al. 2006) may well be worth revisiting, albeit with a different slant. Smallwood et al. (2009a) analyzed BBS and CBC data and suggested that predation on kestrels by the larger raptor (now experiencing a major population resurgence after the banning of organochlorines, more protection from persecution as vermin, and the species' widespread adoption of urban spaces) may not be in itself a major factor in kestrel decline. Perhaps there is another way of looking at this issue. Specifically, Ian Newton (2017) published a summary of his plenary talk on 50 yr of raptor research in which he discussed the role of "intra-guild predation" in the dynamics of raptor populations.

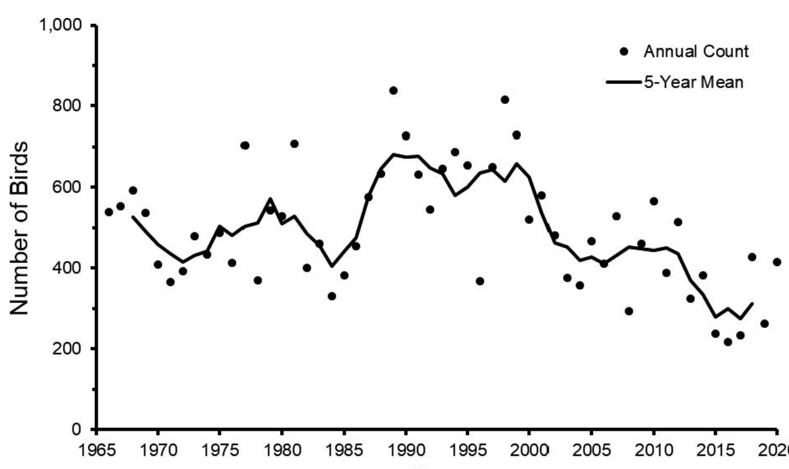

Figure 5. The number of American Kestrels counted at Hawk Mountain Sanctuary, eastern Pennsylvania, USA, during fall migration decreased significantly in recent decades (1966–2020, $n = 55$ yr, Spearman $r = -0.306$, $P = 0.023$). Data are from the Hawk Migration Association of North America's Raptor Migration Database (http://hawkcount.org).

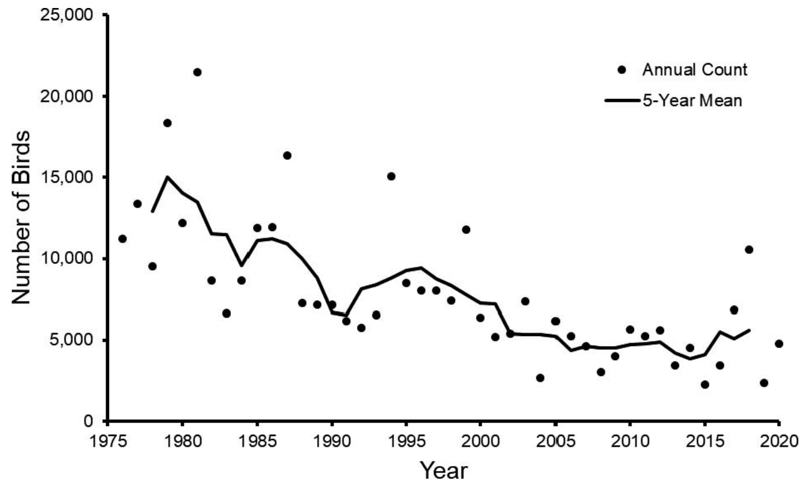

Figure 6. The number of American Kestrels counted at Cape May Hawkwatch, a coastal site in New Jersey, USA, during fall migration decreased significantly during recent decades (1976–2020, $n = 45$ yr, Spearman $r = -0.753$, $P < 0.001$). Data are from the Hawk Migration Association of North America's Raptor Migration Database (http://hawkcount.org).

Essentially, he clarified that it is not the actual predatory acts that are allowing large raptor species to control numbers of smaller raptors, but instead that "the bigger raptor limits the distribution of the smaller raptor to only some parts of the habitat it might otherwise occupy" (I. Newton pers. comm.). The end result is that we simply see fewer of the smaller raptors. This phenomenon is now well established in mainland Europe (Sergio and Hiraldo 2008; see the table in Newton 2017). Newton has now witnessed this very same phenomenon in a species that he studied for several decades in the UK. The Eurasian Sparrowhawk (*A. nisus*), once a very plentiful bird in forest habitat all over the UK, has now retreated to the densest parts of forest habitat to avoid being preyed upon by Northern Goshawks (*A. gentilis*), which have difficulty penetrating thick vegetation. The larger accipiters are even building their nests on vacated sparrowhawk nests (I. Newton pers. comm.). Goshawks have experienced a major reappearance in the UK not as a direct result of the organochlorine ban but almost solely due to the release, accidental or otherwise, of falconry birds (Kenward et al. 1981). Goshawks on the European mainland have had a similar impact upon several smaller raptor species there (Sergio and Hiraldo 2008). Likewise, Golden Eagles (*Aquila chrysaetos*) and Eurasian Eagle-Owls (*Bubo bubo*) are also affecting the populations of various smaller raptor species in parts of the world (Sergio and Hiraldo 2008). This phenomenon is also occurring in North America. As far back as 2006, growing populations of highly invasive Barred Owls (*Strix varia*) were having negative impacts upon numbers of the smaller Western Screech-Owls (*Megascops kennicottii*; Elliott 2006, Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2012), and possibly even Northern Saw-whet Owls (*Aegolius acadicus*; A. Nightingale pers. comm.) in British Columbia, Canada, and elsewhere in the Pacific Northwest (Acker 2012).

In other words, while Cooper's Hawks and American Kestrels, which hunt very different prey species, cannot be considered to be part of the same predator guild, mortality resulting from direct predation by the larger accipiter on the smaller falcon might not be the main or sole cause of the decline of the latter bird. However, it might instead be worth examining their relationship in terms of available habitat: could the increasing numbers of Cooper's Hawks somehow reduce the amount of breeding and foraging habitat available to American Kestrels, and thus reduce their abundance and distribution?

Habitat loss and degradation. As pointed out above, McClure et al. (2017) did not wholly support this issue as a major factor in the decline of the American Kestrel. They did point out that habitat loss and degradation is contributing significantly to the decline of many bird species throughout the world. Urban sprawl, modern farming practices, and growing interests in various monoculture crops (e.g., soybeans for biofuels or a source of protein to feed increasing human populations) are just some of the important contributors to habitat loss and degradation. Thus, although habitat loss should not be discarded as a major factor in the kestrel decline, one might argue that, with respect to American Kestrels specifically, declines in nest box occupancy have occurred in areas (e.g., New Jersey) where no local land use changes have been observed (Smallwood et al. 2009a). Furthermore, there has been no apparent change in their breeding success at sites of decline that might suggest some form of continuous degradation to their habitat quality (Smallwood et al. 2009a). On the other hand, Smallwood et al. (2009b) did demonstrate that habitat fragmentation can affect bird populations in subtle ways, such as the influence of patch size on American Kestrels. Thus, more in-depth studies exploring relationships between kestrel demography and different land cover and development types are needed.

Habitats do not always remain the same within a breeding season. Changes in habitat quality in terms of landscape composition within a breeding season can be critical to reproductive success as measured by the number of young successfully fledged to join the population as future breeders. For instance, American Kestrels favor extensive agricultural lands, especially fallow fields, for both foraging and nesting (Smallwood and Bird 2020). However, choosing such habitat in some locations might not always prove to be the best strategy in the end. For example, Touihri et al. (2019) suggested that in some cases, habitats that can change within a breeding season might create an ecological trap for American Kestrels, especially those populations at the northern extent of their range (e.g., south-central Quebec). They examined how the availability of six open habitat types (agricultural lands, open forests, alder swamps, young forests, regeneration, and wetlands) could affect the habitat selection process, as well as the hatching and fledging successes of American Kestrels breeding in these places. They hypothesized that natural open habitats are less disturbed by anthropogenic activities than extensive agricultural lands and thus represent higher quality habitats for kestrels. While the open agricultural land appeared to be initially more attractive to kestrel breeding pairs, such habitats were less stable throughout the nesting season due to unforeseen planting and harvesting practices leading to less available food, and resulting in a significantly lowered hatching and fledging success compared to birds nesting in the more stable open habitat types (Touihri et al. 2019). Whether their results can be applied to those regions further south and elsewhere with declining kestrel populations is not known.

Finally, few, if any of the papers that have focused on kestrel population declines have paid attention to the loss and degradation of wintering habitat. Although not all American Kestrels head south in the fall to seek out adequate wintering grounds, many of these small falcons do engage in this behavior (Smallwood and Bird 2020). While some wintering habitat (e.g., Baja Mexico; DMB unpubl. data) still appears to provide a wide variety of prey items, especially small lizards, other regions in the southern part of the USA (i.e., Florida to Texas to California) are undergoing massive anthropogenic changes. It would be worthwhile to acquire a measure of the scale of these negative trends in habitat quality in the southern parts of the kestrel's range and at the same time, undertake comparative counts of wintering American Kestrel populations.

Changes in available prey. Habitat quality also can be measured in terms of the food it can provide for any given wildlife species. Although American Kestrels consume a broad diet of various food items ranging from songbirds and small mammals to arthropods and even small fish (Smallwood and Bird 2020), there may well be some prey species that are crucial not only to their day-to-day survival but also to their overall nesting success.

Because American Kestrels are mostly insectivorous (Smallwood and Bird 2020), it is logical to think that our perpetual "war on insects" and recently documented declines in insect populations not only in selected countries where they have been studied, but all over the world (Sánchez-Bayo and Wyckhuys 2019) may be having some impact. For instance, Germany has lost three-quarters of its aerial insects since 1989 (Habel et al. 2016, Seibold et al. 2019) and various studies in the UK (e.g., Brooks et al. 2012, Fox et al. 2014) have also reported significant declines in certain insect populations. On a global basis, Dirzo et al. (2014) announced that in the world of invertebrates, "67% of monitored populations show a 45% mean abundance decline." However, to counter this rather dire report, and more importantly, to refer specifically to the North American continent inhabited by the American Kestrel, Crossley et al. (2020) analyzed a long-term data set collected at 68 different natural and managed areas across the USA to demonstrate no overall increase or decline in net abundance and biodiversity of insects and other arthropods. Though they stated that "the apparent robustness of US arthropod populations is reassuring," Crossley and his coinvestigators also called for the continued monitoring and suggested that there could exist subtler changes in species composition. On a broader but similar note, some ecologists are calling for some caution in interpreting results from studies showing large-scale insect declines (Simmons et al. 2019).

Although insects are widely regarded to be important to the diet of the American Kestrel, it is not known which insects and other arthropods (e.g., beetles, dragonflies, grasshoppers, etc.) might be critical to the overall survival of these small falcons and to the successful fledging of their young to survive to the next generation. For example, based upon the two reviews of prey selection by American Kestrels (Sherrod 1978, Smallwood and Bird 2020), grasshoppers of various species are clearly important to this falcon's diet. One cannot discount the possibility that kestrels might time their breeding to ensure that their young leaving the nest have large numbers of grasshoppers to feed upon while practicing their foraging skills to catch more difficult prey (e.g. mice, small birds, etc.). Should this food source no longer be available for a variety of reasons not mutually exclusive (e.g., pesticide applications, landscape changes, altered synchronicity caused by climate change), it could explain why fewer kestrels are surviving to breed in their first year. Even if the fledged birds do survive to migrate, the absence of grasshoppers in their diet during late summer could perhaps lead to lower body fat levels and decreased survival during migration. Although at least one recent study (Welti et al. 2020) has documented a decline in common grasshopper populations in one North American locale, M. Crossley (pers. comm.) remains skeptical about a widespread decline in numbers of grasshopper populations across North America, especially considering the time, money, and effort still being expended controlling them as agricultural pests by concerned rangeland managers (see Dakhel et al. 2020). Crossley (pers. comm.) further suggested that one might collect comparable data on grasshopper numbers in areas with and without kestrel declines during post-fledging stages, as well as consider undertaking molecular gut content analyses to confirm the importance of grasshoppers in kestrel diets, especially for young fledglings.

American Kestrels are dietary generalists, eating anything catchable, including birds up to their own size, a variety of small mammals, reptiles, amphibians, arthropods, and even trout fingerlings (Smallwood and Bird 2020). With such a wide variety of prey to choose from, it is not surprising that kestrels can engage in prey-switching by opportunistically taking what prey is most available. For example, JAS (unpubl. data) has observed an increasing frequency of avian and mammalian remains, and fewer insect parts, in nest boxes in New Jersey in recent years. Interestingly, another example of prey-switching may be occurring in kestrel populations on southeastern Vancouver Island in British Columbia. According to D. Fraser and A. Nightingale (unpubl. data), American Kestrel numbers appear to be showing signs of a resurgence, at least in some locations in that province. Their hypothesis for the upsurge is the recent rapid invasion of European wall lizards (*Podarcis muralis*) into habitat with mild climates (Engelstoft et al. 2020). This may not be surprising, considering that reptiles (e.g., lizards) play a major role in the diet of American Kestrels breeding and wintering in other regions (Frixione and Rodríguez-Estrella 2020, Smallwood and Bird 2020).

Whether certain arthropod species critical to American Kestrels are declining or not in North America and whether other suitable prey can be found as a substitute remains to be seen, but meanwhile, research into the importance of specific food items (i.e., grasshoppers, lizards) in the diet of this species during post-fledging and in certain locations on the continent should prove fruitful.

Pesticides and industrial chemicals. The use of pesticides and other types of chemicals has long affected birds of prey positioned near the top of the food chain and American Kestrels are no exception. It is highly unlikely that there exists in the environment a particular chemical (or suite of chemicals) that could precipitate a decline in kestrel populations on such a broad scale but not populations of other raptorial species. For example, polybrominated diphenyl ethers, a major component of flame retardant compounds, affect reproductive success in captive American Kestrels in various ways (e.g., Marteinson et al. 2012, Sullivan et al. 2013, Letcher et al. 2015); however no one has yet demonstrated that these compounds adversely affect wild kestrel populations so as to cause their decline on a continent-wide basis.

On the other hand, two classes of pesticides in current use are definitely worth considering as possible factors contributing to the decline of American Kestrel populations: rodenticides and neonicotinoids. Regarding the former, Radvanyi et al. (1988) initially demonstrated with the use of captive kestrels that these chemicals definitely have the potential of inflicting harm to birds of prey. Rodenticides thin the blood and cause a targeted animal (e.g., rodent) to slowly bleed to death. Even after the animal dies, its carcass contains enough chemical residue to be lethal for scavengers in the same manner. Moreover, secondary injuries, such as lacerations or cuts, to a raptor can become life-threatening because the blood cannot clot. In recent years, several studies have connected rodenticides to harmful effects on raptorial birds, particularly in Europe (e.g., Christensen et al. 2012, Ruiz-Suárez et al. 2014, Rattner and Harvey 2021), and their worldwide use in the control of commensal rodents will continue at least for the foreseeable future (Rattner and Harvey 2021). Whether these compounds pose a serious risk to American Kestrel populations is unclear. Although there is evidence that the American Kestrel is 15 to 20 times more sensitive to diphacinone than other avian species tested (Rattner et al. 2011) and that at least some rodenticides (e.g., brodifacoum) may have prolonged effects that increase the toxicity of subsequent exposure to anticoagulants, a definitive link to the decline of wild kestrel populations has not been found. For instance, the American Kestrel did not figure prominently in recent studies on the impact of rodenticides on raptors in British Columbia (J. Elliott pers. comm.). However, a more up-to-date assessment is provided by Buechley et al. (2023) in a separate article in this issue. For an excellent review of the potential impact of anticoagulant rodenticides on non-target wildlife species, see Rattner and Harvey (2021).

Our knowledge of the effect of neonicotinoids on American Kestrels on either an individual or population level is even more nebulous. First introduced in the USA in 1994, these neurotoxic compounds are found in hundreds of products including insect spray, veterinary ointments, tree injections, and more importantly, seed treatments. Neonicotinoids, or neonics, act systemically in plants; rather than just remaining on the surface of treated foliage, they permeate all tissues, including leaves, flowers, roots, and stems, as well as pollen and nectar. They are capable of exerting direct and indirect impacts on both terrestrial and aquatic wildlife (see review by Gibbons et al. 2015) and now are under serious scrutiny all over the world (e.g., Lennon et al. 2019, Rogers et al. 2019, Sabin and Mora 2022). Among raptors, neonicotinoid residues have been detected in insectivorous European Honey-Buzzards (*Pernis apivorus*; Byholm et al. 2018). In addition, field-realistic doses of imidacloprid administered during a migratory stopover caused a rapid reduction in food consumption, body mass, and body fat of White-crowned Sparrows (*Zonotrichia leucophrys*), which significantly affected their probability of departure (Eng et al. 2019). Neonicotinoid pesticides can exert metabolic effects on avian pollinators such as hummingbirds (English et al. 2021). Whether these compounds induce similar effects in insectivorous American Kestrels remains to be seen.

As an insectivorous, migratory bird species positioned near the top of the food chain, the American Kestrel has the potential to be significantly affected by these neurotoxic chemicals in at least three ways: direct toxicity and mortality, subtle indirect effects on migratory and foraging abilities, and loss of invertebrate food sources. Although it would be convenient to identify these compounds as the main cause of the decline of kestrels, it does not explain why some populations across North America are decreasing while others remain stable or are increasing.

Climate change. Global climate change is affecting myriad species of wildlife all over the world and in myriad ways (e.g., LeDee et al. 2021). The continent of North America is no exception (Schneider and Root 2013) and neither are birds in general (Dunn and Møller 2019) or raptors in particular (Martínez-Ruiz et al. 2023). The very fact that several papers have addressed the subject of the effect of global climate warming on American Kestrel populations in the last decade, starting with Heath et al. (2012) and more recently by Powers et al. (2021), and Callery et al. (2022a, 2022b), underscores the importance of including this phenomenon in any discussion of causal factors in kestrel population declines. It is a complex subject and can have multiple impacts, some subtle, on the welfare of kestrel populations. To our knowledge, there have been no reports of direct mortality to kestrels, whether breeding, migrating, and/or wintering, caused by severe weather systems associated with climate warming.

As for indirect impacts, climate warming might potentially affect kestrels by altering food resources along migration routes and on wintering grounds. Much research to date though has focused on the timing of reproduction. The timing of avian reproduction generally coincides with peak food availability to ensure adequate resources for self-maintenance and to raise offspring (Newton 1998). If the birds breed later or earlier, their health, productivity, and survival as a species can be altered. Climate-driven advances in spring can result in a phenological mismatch between brood rearing and prey availability and consequently cause decreased productivity in birds (Callery et al. 2022a). To complicate matters further, climate warming trends apparently can affect the timing of breeding in one part of a species' range and not in another (Callery et al. 2022b). For instance, nesting dates for kestrels are advancing in Idaho populations whereas they appear to be remaining static in New Jersey. Moreover, Callery et al. (2022b) reported a trade-off between reproduction and survival; in Idaho early nesters experienced higher adult survival while in New Jersey, where the nesting season is shorter, early-nesting birds had lower adult survival. This might partially explain why kestrels in the north-eastern part of North America are declining more severely than in some western regions such as the Great Basin and Northern Rockies (Fig. 3). Whether or not climate change can stand alone as the main causal factor behind kestrel population declines, it is certainly worth pursuing further as a research avenue.

Summary and Recommendations. Based on our data and records from North America, nest box programs almost always experience an initial bout of success followed by serious declines, some more severe than others depending on the location in the continent. According to our analyses of available data, Breeding Bird Surveys continue to reveal significant declines of American Kestrels across Canada and most of the USA. The fall counts of kestrels at two major raptor migration sites in the northeast, Hawk Mountain and Cape May, may still be decreasing. According to Christmas Bird counts conducted over five decades, kestrel numbers have almost been halved during that period.

However, there are encouraging signs for this species. Despite BBS showing declines in kestrel populations in Canada, at least one population on the southeastern part of Vancouver Island is showing a resurgence according to recent Christmas Bird Counts and observations by local birders (A. Nightingale unpubl. data). Moreover, concern for the American Kestrel does not appear to be serious enough for the COSEWIC to list them as a Species of Special Concern in Canada (M. Gabhauer pers. comm.). In the USA, although kestrel populations are declining in most regions, they appear to be increasing in the Mississippi Alluvial Valley, the Central Hardwoods, and the Chihuahuan Desert (Fig. 3). According to Oleyar et al. (2023), the Raptor Population Index indicates that the decline in American Kestrel populations has moderated in the last decade, but the species has shown no signs of rebounding as yet. However, this small falcon does show some capability for adaptation and resilience. For example, Oleyar et al. (2023) reported that kestrels in western regions are shifting migratory tendencies, with some short-stopping and others not migrating at all. Prey-switching behavior in kestrels as seen in a long-term nest box program in New Jersey (more mammals and birds; JAS unpubl. data) and in the southeastern part of Vancouver Island (more lizards; D. Fraser and A. Nightingale unpubl. data) provides some hope for future populations of American Kestrels.

As for determining the causal factors of the decline, we must use limited time and resources effectively and efficiently. We recommend the following courses of action and in no particular order of importance. First, it would be useful to settle the question of whether or not Cooper's Hawks are having an impact on kestrel populations, either by direct predation pressure or by their mere presence restricting kestrel distributions. Second, habitat loss and degradation on the wintering range of the American Kestrel has not been adequately studied. Third, within-season alterations in habitat quality that create ecological traps for breeding birds would be worth pursuing. Fourth, with respect to the diet of kestrels, the importance of arthropods, especially grasshoppers and their long-term population trend and the timing of their emergence in relation to kestrel breeding chronology should be explored. Similarly, the role of increases in lizard populations in the western regions such as Vancouver Island should prove rewarding. Fifth, while rodenticides have posed a serious risk to some raptor populations in the world, we need to determine whether they truly constitute a serious threat to kestrel populations across North America. Sixth, neonicotinoid pesticides are becoming more widely used by the agricultural sector and a growing number of studies are demonstrating both indirect and direct effects on insect-eating bird populations, including those species positioned near the top of the food chain. To date, we know very little as to how this suite of chemicals might affect American Kestrels. Finally, studies on the effect of climate change specifically on kestrels are fortunately underway, but there is still much to learn.

In the end, there might be no single causal factor in this puzzling decline of the American Kestrel, but instead some combination of all or some of the factors discussed in this paper, or perhaps something yet to be discovered. Perhaps kestrel numbers might never rebound but settle at some "new normal" in which they still exist in North America but at lower numbers than in the past. Quoting Ian Newton's exact words to DMB (pers. comm.) at the end of his plenary speech at the RRF meeting in Cape May in 2016, "We may just have to get used to seeing less of them."

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