

WHY ARE AMERICAN KESTREL (*FALCO SPARVERIUS*) POPULATIONS DECLINING IN NORTH
AMERICA? EVIDENCE FROM NEST BOX PROGRAMS

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rrh: AMERICAN KESTREL POPULATION DECLINE

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ABSTRACT.---Declines in American Kestrel (*Falco sparverius*) populations are widely reported, and Breeding Bird Survey (BBS) data suggest that the North American population declined significantly from 1984 to 2007. Potential factors include the spread of West Nile Virus (WNV), increases in populations of Cooper's Hawks (*Accipiter cooperii*), and loss of suitable habitat. We examined trends in the numbers of both migratory and resident kestrel populations that use nest boxes in eight study areas in Florida, Georgia, Virginia and Maryland, New Jersey, Massachusetts, Pennsylvania, Saskatchewan, and the Yukon Territory, 1984-2007. Except for the most recent nest box program, established in 1995 and declining since 2002, all nest box populations began to experience declines before WNV arrived in North America in 1999. To test whether changes in kestrel population densities generally are associated with the opposite trend in Cooper's Hawks, we examined the 42 BBS physiographic regions for which trends for both species were available. No significant correlations were detected for the period 1966-2007, or for 1980--2007, more closely concurrent with our nest box data. Christmas Bird Count data from 1959 through 1988 also failed to demonstrate a significant correlation. Finally, the habitat within our study areas still appears suitable, and the remaining kestrels appear healthy and have high reproductive success. Thus, the principle cause of the decline probably lies elsewhere, perhaps on the wintering grounds or along migration routes. Further, for both migratory and resident populations, the decline in nest box occupancy may reflect regional declines, which would reduce the availability of individuals available for replacing nest box-breeding birds that have died or dispersed.

Key Words: *American Kestrel*; *Falco sparverius*; *population decline*; *nest boxes*.

The American Kestrel (*Falco sparverius*) is a small falcon that breeds across most of North America. It is a secondary cavity-nesting species, and many local populations apparently are nest site limited (Cade 1982, Smallwood and Bird 2002). Kestrels readily accept artificial nesting cavities, particularly wooden nest boxes (Bird and Palmer 1988). Nest boxes commonly are erected in habitats suitable for foraging, open areas covered by short ground vegetation (Smallwood 1987), in order to increase the availability of nest sites. Kestrels typically respond with rapid population increases (Nagy 1963, Hamerstrom et al. 1973, Stahlecker and Griese 1979, Bloom and Hawks 1983, Wilmers 1983, Toland and Elder 1987, J.A.S. and M.W Collopy unpubl. data [in review at JRR]); thus, nest box programs have been shown to be a valuable component in the conservation of this species.

Although kestrels have been considered the most numerous North American falconiform species (Smallwood and Bird 2002), there is concern that kestrel populations are now declining. Significant decreases since 1974 in the number of kestrels observed during autumn migration, particularly in the northeastern United States, have been reported (Farmer et al. 2008a). Other sources of data on kestrel population trends include the USGS Breeding Bird Survey (Sauer et al. 1997) and the National Audubon Society Christmas Bird Counts (Sauer et al. 1966).

Several long-term nest box programs that have been established and maintained in various locations across North America represent an under-utilized source of information for population trends in kestrels. The objective of this study was to examine the trends in nest box-breeding kestrels, and to explore some of the possible causes of the widespread decline, which include possible effects of West Nile Virus, predation by Cooper's Hawks (*Accipiter cooperii*), and habitat degradation and loss.

METHODS

Study Areas. We have been directing nest box programs for American Kestrels in eight locations across North America. In general, nest boxes were placed in habitats apparently suitable for kestrels, open areas such as meadows, hayfields, early oldfield successional communities, agricultural fields, and open parkland (Smallwood and Bird 2002). The nest boxes in the Yukon Territory (managed by DM) extended from near the southern border of the territory (approximately 60° N) almost to tree line (approximately 66° N), traversing open patches within the boreal forest. The study area in Saskatchewan (RDD and GRB) was in the vicinity of Besnard Lake, and was approximately centered on 55° 20' N, 106° 05' W; a detailed description has been published previously (Bortolotti 1994). The study area in Massachusetts (JM and MJM) was approximately centered on 41° 45' N, 70° 40' W, and habitats included commercial cranberry bogs. The New Jersey study area (JAS; centered on 41° 00' 36" N, 74° 50' 41" W) has been described previously (Smallwood and Wargo 1997). The Pennsylvania study area (JRK, BR, and SR) was in the vicinity of Hawk Mountain Sanctuary (40° 38' N, 75° 59' W; see Klucsarits et al. 1997). The nest boxes in northern Virginia and central Maryland (MFC) were centered on 39° 01' N, 77° 25' W. The Georgia study area (JWP, TFB, and KB) were in the vicinity of Ft. Gordon military base (32° 23' N, 82° 14' W; see Breen and Parrish 1997). The southernmost study area was in northcentral Florida (RJM and JAS), approximately centered on 30° 01' N, 82° 52' W, and was described by Miller and Smallwood (1997).

Nest Box Data. The number of nest boxes in each program tended to vary among years, and all increased during the first few years of each program. The median and maximum number of nest boxes available for each program was 15 and 64 in the Yukon, 308 and 388 in Saskatchewan, 64 and 69 in Massachusetts, 109 and 129 in New Jersey, 158 and 213 in Pennsylvania, 75 and 86 in Virginia and Maryland, 100 and 100 in Georgia, and 34 and 60 in Florida. The Florida

nest boxes reported here were monitored each year since 1990, and are part of a larger program (>600 nest boxes monitored intermittently since 1995; J.A.S. unpubl. data). For all eight nest box programs, the number of years of study range from 11 (Georgia) to 24 (Virginia/Maryland).

Each nest box program operated under its own protocol, so the number of monitoring visits to each box per season varied somewhat; e.g., each nest box in the Pennsylvania study area was visited 2–5 times each season, depending on occupancy (Katzner et al. 2005) while nest boxes in New Jersey were visited at intervals of 21–28 d (Smallwood et al. 2003). However, we believe that the monitoring effort was sufficient that the calculated occupancy rates (number of nest boxes in which at least one kestrel egg was observed/number of nest boxes available x 100%) are comparable among years and among nest box programs. Except for the Pennsylvania program, which is a continuation of one which began in the 1960s, all occupancy rates presented here begin with the year of program establishment, i.e., the first year that nest boxes were made available to the study population.

The introduction of nest boxes to a population that is nest site-limited is expected to result in an initial increase in the occupancy rate for those nest boxes. This initial increase might mask a longer term underlying population trend. Therefore, to test for the presence of an underlying trend, we omitted the first years of data from each nest box program if those years represented an initial increase. Trends were tested with regression analyses. Six of the eight data sets met the requirement of normality. The two that did not (Yukon and Georgia) were successfully normalized with the Box-Cox transformation method (λ -values of 0.1892 and -1.4789, respectively; NIST/SEMATECH 2006). While the transformed values were used in tests of significance, the untransformed slopes are presented in the results.

Survey Data. We obtained data on the trends in kestrel sightings from the USGS Breeding Bird Survey, available online (<http://www.mbr->

pwrc.usgs.gov/bbs/bbs.html) for the years corresponding to our nest box data, 1984–2007 (Sauer et al. 2008). Locations included the U.S. Fish and Wildlife Service administrative regions and Canada. The online analysis performs a linear regression on the selected dataset.

If increasing Cooper's Hawk density was responsible for the decline in kestrels, we would expect that trends in Cooper's Hawk populations generally are inversely related to trends in kestrel populations. To test this hypothesis, we obtained Breeding Bird Survey data for both species, by physiographic region, for the period 1966–2007, the longest period available in the Breeding Bird Survey dataset, and 1980–2007, the available period most closely concurrent with our nest box data (Sauer et al. 2008). Trends for both species co-occurred in 42 physiographic regions for the period 1966–2007, and in 41 regions for the period 1980–2007. Not all of these trends were significant, but their use in a meta-analysis should be unbiased with respect to the relationship between the two species. Because these data were not normal, we subjected them to nonparametric statistical treatments. Using region as the sampling unit, we tested the association between kestrel and Cooper's Hawk population trends in two ways. First, we compared the slopes of the population trends with Spearman's correlation coefficients. Second, we compared just the directions (increase or decrease) of the trends with Fisher's exact tests.

We also obtained population trends for both species based on National Audubon Society Christmas Bird Count data, 1959–1988, which was categorized by U.S. state and Canadian province (Sauer et al. 1966). Trends for kestrels and Cooper's Hawks co-occurred in 40 states and provinces. Using state or province as the sampling unit, we followed the same procedure as above to compare the slopes and directions of the population trends for the two species.

All statistical procedures, except those received from the USGS Breeding Bird Survey website, were performed with JMP software (SAS Institute 2004).

RESULTS

Of the seven nest box programs for which we have occupancy rates from the year of program establishment (all programs but Pennsylvania), each exhibited an initial increase in occupancy rate (Fig. 1). The shortest duration of the initial increase was 2 yr in Georgia (although not apparent in a 3-yr running mean, Fig. 1 bottom), and the longest was 8 yr in New Jersey; all other increases ranged from 4–6 yr. Following the initial increase, all seven programs have undergone significant declines, and the Pennsylvania program also had a significant decline during concurrent years (Table 1).

Our analysis of Breeding Bird Survey data from 1984–2007 revealed significant declines for kestrel populations in Canada and five of the seven USFWS regions (Fig. 2). For all BBS survey routes in Canada, the annual decline was 3.20% ($P < 0.0001$); for all routes in the United States, 0.76% ($P = 0.026$); and for all North American routes, 1.27% ($P < 0.0001$).

Population trends for both American Kestrels and Cooper's Hawks were detected in 42 of the physiographic regions used to categorize Breeding Bird Survey locations from 1966–2007. The correlation between the two trends was not significant (Spearman $r = -0.095$, $P = 0.55$), and there was no significant association between the directions of those trends (Fisher's exact test, $P = 0.76$). For the period 1980–2007 ($N = 41$ physiographic regions with trends for both species), there was no significant correlation between the trends (Spearman $r = 0.047$, $P = 0.77$) and there was no significant association between the directions of those trends (Fisher's exact test, $P = 0.48$).

Similarly, trends for both kestrels and Cooper's Hawks were detected in 40 U.S. states and Canadian provinces used to categorize locations for the National Audubon Society Christmas Bird Counts from 1959–1988. The weak

positive correlation was not significant (Spearman $r = 0.244$, $P = 0.13$), nor was there a significant association between the directions of those trends (Fisher's exact test, $P = 0.34$).

DISCUSSION

Population Trends. The initial increase in occupancy rates that followed the introduction of nest boxes was expected. Local kestrel populations commonly are nest site-limited (Cade 1982, Smallwood and Bird 2002); indeed, this apparent limitation often provides the rationale for establishing a nest box program. Compared to most larger falconiform species, kestrels have relatively high reproductive potentials (they mature quickly and lay large clutches; Brown and Amadon 1968) and once released from nest site limitation, populations can respond quickly (e.g., Toland and Elder 1987, J.A.S. and M.W. Collopy unpubl. data [in review at JRR]). Most of the nest box programs experienced an increase in occupancy rates for 4–6 yr after establishment. The Georgia program reached its peak occupancy rate in its second year, suggesting that there may have been a relatively large floater population in that study area.

All eight nest box programs exhibited significant declines following the initial response to the local increase in nest site availability. The similarity in the slopes of those declines is remarkable, considering the wide geographic range the various nest box programs represent. The results from these nest box programs strongly support the conclusion that a significant, widespread decline in kestrel populations has been occurring in recent years.

Results from the Breeding Bird Surveys also support this conclusion. Significant declines were detected for Canada, the United States, and survey-wide. Most of the nest box programs were located in Region 5 and Canada, where the overall declines were highly significant (Fig. 2). The annual

decline estimate from Canadian BBS data, 3.20%, was even greater than the annual decline experienced by nest box programs in the Yukon (2.7%) and in Saskatchewan (1.9%). The increase detected in USFWS Region 4, where the Georgia and Florida nest box programs are located, was not significant. BBS trends for kestrels from 1984–2007 in just Georgia and Florida also were not significant, but were based on small sample sizes, only 5 and 15 survey routes, respectively (Sauer et al. 2008).

Possible Causes. West Nile Virus (WNV) is transmitted between bird reservoir hosts by mosquito vectors (CDC 2007). Since its first appearance in North America in 1999, WNV has been detected in >250 species of wild birds, including American Kestrels (CDC 2007). Thus, there was the possibility that the decline in kestrel populations could be related to the spread of WNV. However, data from our nest box programs demonstrate that declines began occurring before WNV arrived on the continent. Occupancy rates for the nest boxes in Pennsylvania underwent a net decline for the entire period covered, 1986–2007, although there was an increase during the most recent two breeding seasons. Of the seven nest box programs for which we have occupancy data since establishment, six began their declines prior to the arrival of WNV. The only exception was New Jersey, which is the most recently established program. In general, the early-established programs have experienced the longest declines.

Kestrels appear to have had substantial exposure to WNV. In southern Quebec, WNV antibodies were detected in blood samples from 17 of 28 (61%) adult kestrels captured during the breeding season, 2003–2005 (D.M. Bird unpubl. data). In eastern Pennsylvania the exposure rate was even higher; during 2004, 21 of 22 (95%) wild-caught adults tested positive for WNV antibodies (Medica et al. 2007). While most avian species infected with WNV survive and acquire life-long immunity (CDC 2007), corvids are particularly prone to become ill or die (Eidson et al. 2001). Raptors also may have

heightened vulnerability; although the kestrels they experimentally infected with WNV survived, Nemeth et al. (2006) suggested that wild kestrels would be at greater risk of mortality. Nevertheless, the WNV-exposed kestrels in Quebec bred normally (D.M. Bird unpubl. data), and Medica et al. (2007) reported both normal reproduction and body weights for exposed kestrels in Pennsylvania.

If WNV or another pathogen was the principal agent of the decline, we would expect rapid selection, as the most vulnerable genotypes would be excluded from the population, leaving the most resistant genotypes. The subsequent recovery would likely be rapid; kestrel populations demonstrate this capability when released from nest site limitation. Thus, the expected population trend due to a serious pathogen would be a brief, marked decline (e.g., Crosbie et al. 2008) followed by a rapid recovery. In contrast, we have been observing a prolonged, steady declines.

Another possible cause of the decline in kestrels is an increase in predation by Cooper's Hawks. Cooper's Hawks are known to prey upon kestrels (Farmer et al. 2008b), and there is evidence that Cooper's Hawks may learn to "trap-line" nest boxes for recently fledged kestrels (B.A. Milsap, unpubl. data). BBS data suggest that Cooper's Hawk populations increased significantly in the United States during the period 1984–2007 (5.30%/yr, $N = 568$ routes, $P < 0.0001$; Sauer et al. 2008). However, no significant increases were found concurrently in Canada, perhaps due to small sample sizes ($N = 39$ routes, $P = 0.42$). Predation by Cooper's Hawks cannot explain the declines we observed in the two kestrel nest box programs in Canada; Cooper's Hawk do not occur in the Yukon Territory (Rosenfield and Bielefeldt 1993), and they are very uncommon in the Saskatchewan study area (Gerrard et al. 1996).

We expected that if an increase in Cooper's Hawk predation was an important factor in the decline of kestrels, then the population trends of the two species generally would have an inverse relationship. Our analysis of

both BBS data and NAS Christmas Count data found no evidence of such a relationship. It is possible, however, that kestrel populations could be negatively affected by dietary shifts in Cooper's Hawks, independent of the density of Cooper's Hawks.

Habitat loss or degradation has been considered the most important factor in the decline of avian populations (e.g., Fitzpatrick 2004), and may be involved in the observed decline in kestrels. However, in our study area the relationship between declining occupancy of our nest boxes and possible changes to the surrounding habitat is not clear. In New Jersey, for example, there was no obvious change in the land use immediately surrounding the nest boxes; 82% of the nest boxes that were vacant in 2007 had been occupied in one or more previous years (J.A.S. unpubl. data). There has been no evidence of the effects of reduced habitat quality, such as low prey availability, or problems with disease or toxic contamination; all kestrels appeared healthy, and during the decline the mean nesting success (attempts resulting in at least one chick surviving to banding age, generally 18-22 d) was 84.0% (J.A.S. unpubl. data), which compares favorably with other kestrel populations (Smallwood and Bird 2002). While the habitat in the study area appears suitable and the kestrels that are present appear healthy and have high reproductive success, there simply are fewer kestrels using the nest boxes. Therefore, the main cause of decline likely is operating somewhere beyond the immediate vicinity of the nest boxes.

This suggests that there may be an increase in mortality during the nonbreeding season, perhaps related to habitat change on the wintering grounds or along migration routes. However, not all of our nest box-breeding kestrels are migratory. In North America, the tendency to migrate decreases from north to south, and the northernmost breeding populations tend to winter in the southernmost wintering grounds (Smallwood and Bird 2002). Populations in the middle latitudes, approximately 44-36° N, are partially migratory and

appear to respond to local conditions, migrating short distances during relatively harsh winters (Bird and Palmer 1988). The populations in our study areas in Georgia and Florida are Southeastern American Kestrels (*F. s. paulus*), which are resident (Howell 1932). Thus, our study populations span the range of entirely migratory to entirely nonmigratory, and all are declining.

Those kestrels that do migrate are vulnerable to many mortality factors, including those related to habitat quality, along the routes and on the wintering grounds. Resident populations, however, also may wander to some extent outside the breeding season (Bird and Palmer 1988), and thus may be affected by habitat issues beyond the immediate vicinity of the nest boxes. Further, the decline in our nest box-breeding populations could reflect the respective regional declines. Although the numbers of marked adults in the Florida and New Jersey programs are small, there appears to be a substantial turn-over of adults from year to year (J.A.S. unpubl. data). Thus, regional declines might reduce the number of individuals from outside the study areas that replace nest box-breeding individuals that have either dispersed or died between breeding seasons.

Conclusions. The widespread decline in kestrel populations detected in the USGS Breeding Bird Surveys during recent decades is corroborated by patterns of nest box occupancy by both migratory and resident populations of kestrels. Because the decline in nest box breeding kestrels began before the arrival of WNV in North America, the virus clearly is not the primary cause of the decline. Further, we found no evidence that increasing trends in Cooper's Hawk populations are associated with the decreasing trends in kestrels. While habitat loss and degradation were not evident in the vicinity of the nest boxes, these factors may nevertheless be important, particularly in reducing the number of kestrels available for occupying nest boxes.

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Table 1. After increases in occupancy rates associated with the establishment of nest box programs, the populations of American Kestrels that breed in these nest boxes have undergone significant declines. Regression analysis models occupancy rate (number of nest boxes in which kestrels bred/number of nest boxes available x 100%) as a function of year, N is the number of years (peak year to most recent year), and slope is mean annual change in percent occupancy.

LOCATION	YEAR	PEAK	LINEAR REGRESSION			
	PROGRAM	OCCUPANCY	-----			
	ESTABLISHED	YEAR	N	SLOPE	F	P
Pennsylvania	--	1986 ^a	22	-0.6	7.1	0.0152
Virginia/Maryland	1984	1989	18	-2.4	80.4	0.0001
Saskatchewan	1988	1992	16	-1.9	28.8	0.0005
Massachusetts	1989	1995	12	-3.8	40.7	0.0001
Florida	1990	1994	14	-3.6	27.1	0.0002
Yukon	1994	1987	22	-2.7	61.2	0.0001
Georgia	1994	1995	10	-4.0	29.3	0.0006
New Jersey	1995	2002	6	-4.7	9.6	0.0362

^aFirst year of available occupancy data; program established during the 1960s.

Figure 1. Populations of American Kestrels breeding in nest boxes have been declining in recent years. Percent occupancy is the number of nest boxes in which kestrels bred/number of nest boxes available x 100%. Data are presented as 3-yr running means. Except for the nest box program in Pennsylvania, each curve begins the year the program was established.

Figure 2. American Kestrel populations have been declining in North America. Data are from the USGS Breeding Bird Survey, 1984–2007. Direction of arrow indicates increase or decrease, and length of arrow is proportional to the magnitude of the annual change. Black arrows indicate significant changes (Canada, -3.20%, $P < 0.0001$; Region 1, -1.47%, $P = 0.011$; Region 2, -2.08%, $P = 0.052$, Region 5, -1.65%, $P = 0.006$; Region 8, -1.78%, $P = 0.017$), and white arrows indicate nonsignificant changes (Region 3, $P = 0.37$; Region 4, $P = 0.15$, Region 6, $P = 0.11$).



