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

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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 causes 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 migra-

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tory 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. All eight populations underwent significant declines; the mean annual decline in nest-box occupancy rate was 3.0% and ranged from 0.6% in Pennsylvania to 4.7% in New Jersey. 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 principal 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 number of individuals available for replacing breeding birds that have died or dispersed.

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

¿POR QUÉ ESTÁN DISMINUYENDO LAS POBLACIONES DE *FALCO SPARVERIUS* EN NORTE AMÉRICA? EVIDENCIA DE PROGRAMAS DE CAJAS DE ANIDACIÓN

Resumen.—Existe amplia documentación de disminuciones en las poblaciones de *Falco sparverius* y los datos del censo de aves reproductivas (BBS, por sus siglas en inglés) sugieren que la población norteamericana disminuyó significativamente entre 1984 y 2007. Entre las causas potenciales se incluyen la difusión del Virus del Oeste del Nilo (VON), aumentos en las poblaciones de *Accipiter cooperii* y la pérdida de ambientes propicios para la especie. Examinamos las tendencias en el número de individuos entre 1984 y 2007 de poblaciones migratorias y residentes que utilizan cajas de anidación en ocho áreas de estudio en Florida, Georgia, Virginia y Maryland, Nueva Jersey, Massachusetts, Pennsylvania, Saskatchewan y el territorio Yukon. Las ocho poblaciones sufrieron disminuciones significativas. La disminución promedio anual en la tasa de ocupación de las cajas de anidación fue del 3.0%, y varió entre el 0.6% en Pennsylvania y el 4.7% en Nueva Jersey. Con excepción del programa de cajas de anidación más reciente, el cual fue establecido en 1995 y muestra señales de disminución desde 2002, todas las poblaciones que anidan en cajas empezaron a experimentar disminuciones antes del arribo del VON a Norte América en 1999. Para probar si los cambios en las densidades poblacionales de *F. sparverius* se asocian generalmente con la tendencia opuesta en *A. cooperii*, examinamos las 42 regiones fisiográficas del BBS para las cuales existían datos de tendencias para ambas especies. No se detectaron correlaciones significativas para el período de 1966 a 2007 ni para el de 1980 a 2007, el cual es más cercanamente coincidente con el de nuestros datos de cajas de anidación. Los datos de los conteos navideños de aves realizados entre 1959 y 1988 tampoco demostraron una correlación significativa. Finalmente, el hábitat dentro de nuestras áreas de estudio aún parece propicio y los individuos restantes parecen estar sanos y presentan un éxito reproductivo alto. Por lo tanto, la principal causa de las disminuciones poblacionales se encuentra probablemente en otra parte, quizás en las áreas de invernada o a lo largo de las rutas de migración. Además, tanto para las poblaciones migratorias como para las residentes, la disminución en la ocupación de las cajas de anidación podría reflejar disminuciones regionales, lo que reduciría el número de individuos disponibles para reemplazar a las aves reproductivas que han muerto o se han dispersado.

[Traducción del equipo editorial]

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 to increase the availability of nest sites in habitats suitable for foraging, open areas covered by short ground vegetation (Smallwood 1987). 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, Smallwood and Collopy 2009); 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 U.S. Geological Survey (USGS) Breeding Bird Survey (Sauer et al. 1997) and the National Audubon Society Christmas Bird Counts (Sauer et al. 1996). A number of possible explanations have been suggested, including negative effects of the West Nile virus (Nemeth et al. 2006), predation by increasing numbers of Cooper's Hawks (*Accipiter cooperii*; Farmer et al. 2008b), climate change (Steenhof and Peterson 2009), pesticides (L. Goodrich pers. comm.), and habitat degradation and loss (Farmer et al. 2008b).

Several long-term nest-box programs that have been established and maintained in various locations across North America represent an underutilized source of information for population trends in kestrels. The objective of this study was to examine the trends in numbers of kestrels breeding in nest boxes, and to explore three of the possible causes of the widespread decline: West Nile virus, predation by Cooper's Hawks, and habitat degradation and loss.

METHODS

Study Areas. We have been directing nest-box programs for American Kestrels in eight locations in Canada and the eastern U.S. 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) was 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 north-central 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. Smallwood 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 × 100%) are comparable among years and among nest-box programs. Except for the Pennsylvania program, which is a continuation of one that 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). Although transformed values were used in tests of significance, the untransformed slopes are presented in the results.

Survey Data. We obtained data on trends in kestrel sightings from the USGS Breeding Bird Survey (BBS), available online (http://www.mbr-pwrc.usgs.gov/bbs/trend/tf07.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 (USFWS) administrative regions and Canada. The analysis available online is linear regression on the selected dataset.

If increasing Cooper's Hawk density were responsible for the decline in kestrels, we would expect trends in Cooper's Hawk populations to be generally inversely related to trends in kestrel populations. To test this hypothesis, we obtained BBS data for both species, by physiographic region, for 1966–2007, the longest period available in the BBS 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 used 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, 1959–88, which were categorized by U.S. state and Canadian province (Sauer et al. 1996). 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 BBS data from 1984 to 2007 revealed significant declines for kestrel populations in Canada and four of the seven USFWS administrative regions (Fig. 2). The trend was negative in each Canadian province for which data were available, and significant annual declines were detected in Ontario (2.69%, $P = 0.050$), Manitoba (5.10%, $P = 0.008$), and British Columbia (3.39%, $P < 0.001$). For all BBS survey routes in Canada combined, the annual decline was 3.20% ($P < 0.001$); for all routes in the United States, 0.76% ($P = 0.026$); and for all North American routes, 1.27% ($P < 0.001$).

Population trends for both American Kestrels and Cooper's Hawks were detected in 42 of the physiographic regions used to categorize BBS locations from 1966 to 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 Christmas Bird Counts locations from 1959 to 1988. The weak positive cor-

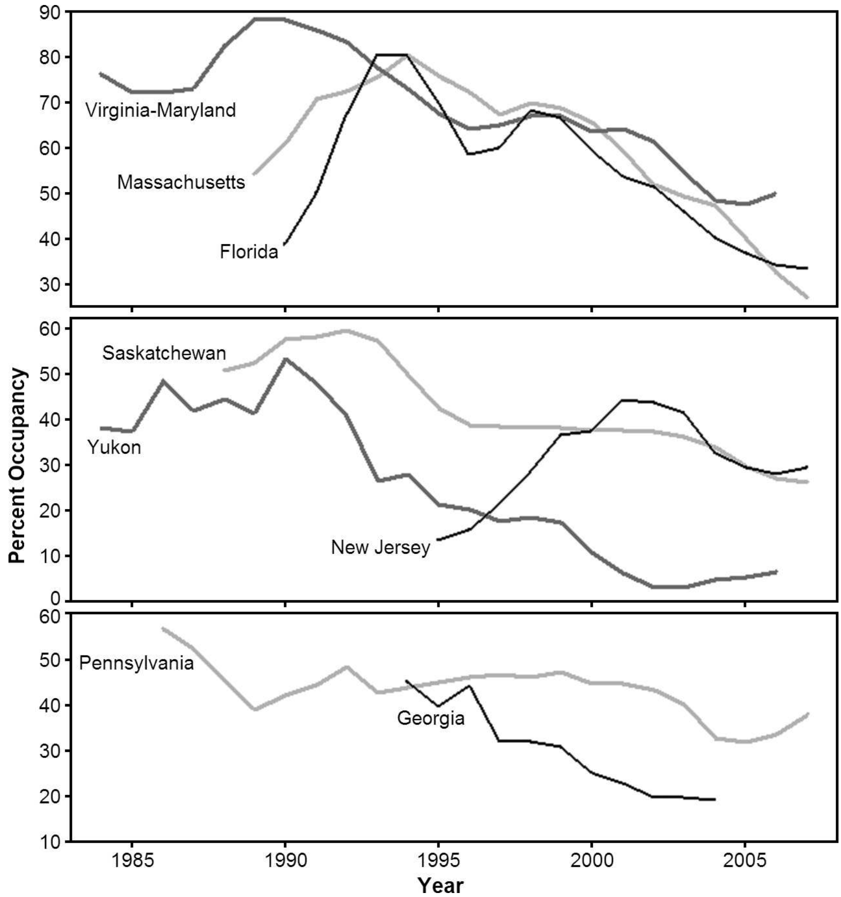

Figure 1. Populations of American Kestrels breeding in nest boxes have been declining in recent years. Percent occupancy is the number of nest boxes in which kestrels bred/number of nest boxes available × 100%. Data are presented as 3-yr running means. Except for the nest-box program in Pennsylvania,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

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 × 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 Program Established	Peak Occupancy Year	Linear Regression			
			N	Slope	F	P
Pennsylvania	–	1986[a]	22	−0.6	7.1	0.015
Yukon	1984	1987	22	−2.7	61.2	<0.001
Virginia/Maryland	1984	1989	18	−2.4	80.4	<0.001
Saskatchewan	1988	1992	16	−1.9	28.8	<0.001
Massachusetts	1989	1994	12	−3.8	40.7	<0.001
Florida	1990	1994	14	−3.6	27.1	<0.001
Georgia	1994	1995	10	−4.0	29.3	<0.001
New Jersey	1995	2002	6	−4.7	9.6	0.036

[a] First year of available occupancy data; program established during the 1960s.

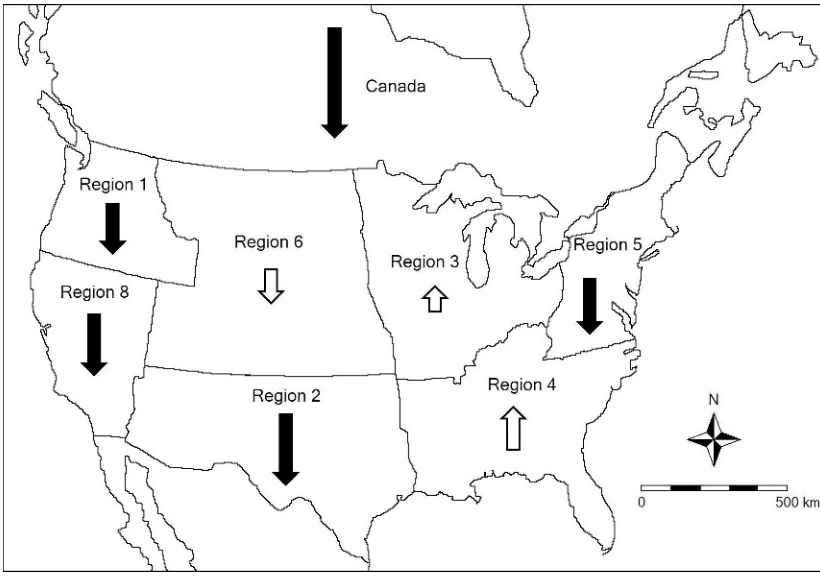

Figure 2. American Kestrel populations have been declining in North America. Data are from the U.S. Geological Survey Breeding Bird Survey, 1984–2007. Direction of arrow indicates increase or decrease, and length of arrow is proportional to the magnitude of the annual change. Black arrows indicate significant changes (Canada, −3.20%, $P < 0.001$; Region 1, −1.47%, $P = 0.011$; Region 2, −2.08%, $P = 0.051$; 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, $P = 0.11$).

relation 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, an apparent lack of nest cavities often provides the rationale for establishing a nest-box program. Compared with 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, Smallwood and Collopy 2009). 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, 1984–2007, also support the conclusion that there has been a widespread, although not uniform, decline in North American kestrel populations. Population trends were negative for all Canadian provinces for which data were available and for four of the seven USFWS regions. However, all significant population changes were negative, resulting in a highly significant negative trend survey-wide. Most of the nest-box programs were in Region 5 (northeastern U.S.) and Canada, where overall declines were highly significant (Fig. 2). The mean 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 to 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 2009). Since its first appearance in North America in 1999, WNV has been detected in >250 species of wild birds, including American Kestrels (CDC 2009). Thus, there was a possibility that the decline in kestrel populations could be related to the spread of WNV. However, data from our nest-box programs demonstrated that declines began 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, 2003–05 (D. 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). Although most birds infected with WNV survive and acquire life-long immunity (CDC 2009), corvids are particularly prone to become ill or die (Eidson et al. 2001). Some raptors also may have heightened vulnerability. Nemeth et al. (2006) suggested that wild kestrels would be at greater risk of mortality, even though the kestrels they experimentally infected with WNV survived. Nevertheless, the WNV-exposed kestrels in Quebec bred normally (D. 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 were 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 (Smallwood and Collopy 2009). 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 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 ''trapline'' (i.e., forage along an established route; Stiles 1995) nest boxes for recently fledged kestrels (B. Millsap unpubl. data). The BBS data suggest that Cooper's Hawk populations increased significantly in the United States from 1984 to 2007 (5.30% annually, $N = 568$ routes, $P < 0.001$; 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 Hawks 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 were 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 Christmas Bird Count data gave 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 areas, 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. Smallwood 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 the mean nesting success (attempts resulting in at least one chick surviving to banding age, generally 18–22 d) was 84.0% during the decline (J. Smallwood unpubl. data), which compares favorably with other kestrel populations (Smallwood and Bird 2002). Although the habitat in the study area appears suitable and the kestrels appear healthy and have high reproductive success, there simply are fewer kestrels using the nest boxes. Although these analyses are subjective, we nonetheless believe they indicate that the main cause of decline likely is operating somewhere beyond the immediate vicinity of these nest boxes.

Declines in breeding populations may be associated with an increase in mortality during the nonbreeding season, perhaps related to habitat change on the wintering grounds or along migration routes. However, not all the kestrels we studied in our nest-box programs 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 resident Southeastern American Kestrels (*F. s. paulus*; Howell 1932). Thus, our study populations span the range of entirely migratory to entirely nonmigratory, and all are declining.

Migratory kestrels 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 substantial turnover of adults from year to year (J. Smallwood 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 was corroborated by patterns of nest-box occupancy by both migratory and resident populations of kestrels. Because the decline in kestrels breeding in nest boxes 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 were associated with the decreasing trends in kestrels. Although 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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LITERATURE CITED

BIRD, D.M. AND R.S. PALMER. 1988. American Kestrel. Pages 253–290 *in* R.S. Palmer [ED.], Handbook of North American birds. Vol. 5, Diurnal raptors. Part 2. Yale Univ. Press, New Haven, CT U.S.A.

BLOOM, P.H. AND S.J. HAWKS. 1983. Nest box use and reproductive biology of the American Kestrel in Lassen County, California. *Raptor Res.* 17:9–14.

BORTOLOTTI, G.R. 1994. Effect of nest-box size on nest-site preference and reproduction in American Kestrels. *J. Raptor Res.* 28:127–133.

BREEN, T.F. AND J.W. PARRISH, JR. 1997. American Kestrel distribution and use of nest boxes in the coastal plains of Georgia. *Fla. Field Nat.* 25:128–137.

BROWN, L. AND D. AMADON. 1968. Eagles, hawks, and falcons of the world. McGraw-Hill, New York, NY U.S.A.

CADE, T.J. 1982. The falcons of the world. Cornell Univ. Press, Ithaca, NY U.S.A.

CDC. 2009. Vertebrate ecology. Centers for Disease Control and Prevention, Atlanta, GA U.S.A. http://www.cdc.gov/ncidod/dvbid/westnile/birds&mammals.htm (last accessed 30 July 2009).

CROSBIE, S.P., W.D. KOENIG, W.K. REISEN, V.L. KRAMER, L. MARCUS, R. CARNEY, E. PANDOLFINO, G.M. BOLEN, L.R. CROSBIE, D.A. BELL, AND H.B. ERNEST. 2008. Early impact of West Nile virus on the Yellow-billed Magpie (*Pica nuttalli*). *Auk* 125:542–550.

EIDSON, M., N. KOMAR, F. SORHAGE, R. NELSON, T. TALBOT, F. MOSTASHARI, R. MCLEAN, AND WEST NILE VIRUS AVIAN MORTALITY SURVEILLANCE GROUP. 2001. Crow deaths as a sentinel surveillance system for West Nile virus in the northeastern United States, 1999. *Emerg. Infect. Dis.* 7:615–620.

FARMER, C.J., R.J. BELL, B. DROLET, L.J. GOODRICH, E. GREENSTONE, D. GROVE, D.J.T. HUSSELL, D. MIZRAHI, F.J. NICOLETTI, AND J. SODERGREN. 2008a. Trends in autumn counts of migratory raptors in northeastern North America, 1974–2004. Pages 179–215 *in* K.L. Bildstein, J.P. Smith, E. Ruelas Inzunza, and R.R. Veit [EDS.], State of America's birds of prey. Nuttall Ornithological Club, Cambridge, MA U.S.A. and The American Ornithologists' Union, Washington, DC U.S.A.

———, L.J. GOODRICH, E. RUELAS INZUNZA, AND J.P. SMITH. 2008b. Conservation status of North America's birds of prey. Pages 303–419 *in* K.L. Bildstein, J.P. Smith, E. Ruelas Inzunza, and R.R. Veit [EDS.], State of America's birds of prey. Nuttall Ornithological Club, Cambridge, MA U.S.A. and The American Ornithologists' Union, Washington, DC U.S.A.

FITZPATRICK, J.W. 2004. Bird conservation. Pages 10·1–10·116 *in* Handbook of bird biology, Second Ed. Princeton Univ. Press, Princeton, NJ U.S.A.

GERRARD, J.M., G.R. BORTOLOTTI, AND K.L. WIEBE. 1996. Birds of the Besnard Lake area, north-central Saskatchewan, 1968–94. Nature Saskatchewan, Regina, SK Canada.

HAMERSTROM, F., F.N. HAMERSTROM, AND J. HART. 1973. Nest boxes: an effective management tool for kestrels. *J. Wildl. Manage.* 37:400–403.

HOWELL, A.H. 1932. Florida bird life. Coward-McCann, Inc., New York, NY U.S.A.

KATZNER, T., S. ROBERTSON, B. ROBERTSON, J. KLUCSARITS, K. MCCARTY, AND K.L. BILDSTEIN. 2005. Results from a long-term nest-box program for American Kestrels: implications for improved population monitoring and conservation. *J. Field Ornithol.* 76:217–226.

KLUCSARITS, J.R., B. ROBERTSON, AND S. ROBERTSON. 1997. Breeding success in American Kestrels nesting in boxes in eastern Pennsylvania. *Penn. Birds* 11:138–140.

MEDICA, D.L., R. CLAUSER, AND K. BILDSTEIN. 2007. Prevalence of West Nile virus antibodies in a breeding population of American Kestrels (*Falco sparverius*) in Pennsylvania. *J. Wildl. Dis.* 43:538–541.

MILLER, K.E. AND J.A. SMALLWOOD. 1997. Natal dispersal and philopatry of Southeastern American Kestrels in Florida. *Wilson Bull.* 109:226–232.

NAGY, A.C. 1963. Population density of sparrow hawks in eastern Pennsylvania. *Wilson Bull.* 75:93.

NEMETH, N., D. GOULD, R. BOWEN, AND N. KOMAR. 2006. Natural and experimental West Nile virus infection in five raptor species. *J. Wildl. Dis.* 42:1–13.

NIST/SEMATECH. 2006. e-Handbook of statistical methods. National Institute of Standards and Technology, Gaithersburg, MD U.S.A. http:\www.itl.nist.gov/div898/handbook/eda/section3/boxcoxno.htm (last accessed 30 July 2009).

ROSENFIELD, R.N. AND J. BIELEFELDT. 1993. Cooper's Hawk (*Accipiter cooperii*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 75. The Academy of Natural Sciences, Philadelphia, PA U.S.A. and The American Ornithologists' Union, Washington, DC U.S.A.

SAS INSTITUTE. 2004. JMP computer program and user's manual. SAS Institute, Inc., Cary, NC U.S.A.

SAUER, J.R., J.E. HINES, AND J. FALLON. 2008. The North American Breeding Bird Survey, results and analysis 1966–2007, Version 5.15.2008. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, MD U.S.A. http://www.mbr-pwrc.usgs.gov/bbs/trend/tf07.html (last accessed 30 July 2009).

———, ———, G. GOUGH, I. THOMAS, AND B.G. PETERJOHN. 1997. The Breeding Bird Survey results and analysis, Version 96.3. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, MD U.S.A.

———, S. SCHWARTZ, AND B. HOOVER. 1996. The Christmas Bird Count home page, Version 95.1. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, MD U.S.A. http://www.mbr-pwrc.usgs.gov/bbs/cbc.html (last accessed 30 July 2009).

SMALLWOOD, J.A. 1987. Sexual segregation by habitat in American Kestrels (*Falco sparverius*) wintering in south-central Florida: vegetative structure and responses to differential prey availability. *Condor* 89:842–849.

——— AND D.M. BIRD. 2002. American Kestrel (*Falco sparverius*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 602. The Academy of Natural Sciences, Philadelphia PA and the American Ornithologists' Union, Washington, DC U.S.A.

——— AND M.W. COLLOPY. 2009. Southeastern American Kestrels respond to an increase in the availability of nest cavities in north-central Florida. *J. Raptor Res.* 43:291–300.

———, V. DUDAJEK, S. GILCHRIST, AND M.A. SMALLWOOD. 2003. Vocal development in American Kestrel (*Falco sparverius*) nestlings. *J. Raptor Res.* 37:37–43.

——— AND P.J. WARGO. 1997. Nest site habitat structure of American Kestrels in northwestern New Jersey. *Bull. N. J. Acad. Sci.* 42:7–10.

STAHLECKER, D.W. AND H.J. GRIESE. 1979. Raptor use of nest boxes and platforms on transmission towers. *Wildl. Soc. Bull.* 7:59–62.

STEENHOF, K. AND B.E. PETERSON. 2009. American Kestrel reproduction in southwestern Idaho: annual variation and long-term trends. *J. Raptor Res.* 43:283–290.

STILES, F.G. 1995. Behavioral, ecological, and morphological correlates of foraging for arthropods by the hummingbirds of a tropical wet forest. *Condor* 97:853–878.

TOLAND, B.R. AND W.H. ELDER. 1987. Influence of nest-box placement and density on abundance and productivity of American Kestrels in central Missouri. *Wilson Bull.* 99:712–717.

WILMERS, T.J. 1983. Kestrel use of nest boxes on reclaimed surface mines in West Virginia and Pennsylvania (abstract). *Raptor Res.* 17:30–31.

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