

AMERICAN KESTREL BREEDING HABITAT: THE IMPORTANCE OF PATCH SIZE

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ABSTRACT.—Previous studies have examined vegetative cover and land use immediately surrounding American Kestrel (*Falco sparverius*) nest sites. However, the relationship of landscape-level habitat structure to nest-site selection has received little attention. Between 1995 and 2007, we erected nest boxes in pastures and meadows in northwestern New Jersey. The number of breeding pairs in boxes ranged from 2 in 1995 to 59 in 2002. We used a Geographic Information System to model habitats used by kestrels (open areas dominated by herbaceous vegetation) and delineated patches of contiguous suitable habitat within the study area and statewide. Nest boxes available in large (>1000 ha) patches of suitable habitat were occupied by kestrels at rates significantly higher than those in medium (250–1000 ha) or small (<250 ha) patches. Large patches exhibited relatively high occupancy rates every year, medium patches were most likely to be occupied during years when kestrels were abundant in the study area, and small patches were used infrequently, regardless of how many breeding pairs were present in the study area. That kestrels disproportionately select nest sites in contiguous patches sufficiently large to include many breeding territories has important implications for conservation strategies. We currently are using information on patch size to implement a statewide nest-box program for kestrels in New Jersey.

KEY WORDS: *American Kestrel; Falco sparverius; breeding habitat; patch size.*

HÁBITAT DE CRÍA DE *FALCO SPARVERIUS*: IMPORTANCIA DEL TAMAÑO DE PARCHE

RESUMEN.—Estudios previos han examinado la cobertura de la vegetación y el uso del suelo en las inmediaciones de los sitios de anidación de *Falco sparverius*. Sin embargo, la relación entre la estructura del hábitat a nivel de paisaje y la selección de sitios de anidación no ha sido estudiada en detalle. Entre 1995 y 2007, establecimos cajas de anidación en pasturas y prados en el noroeste de Nueva Jersey. El número de parejas criando en cajas de anidación varió entre 2 en 1995 y 59 en 2002. Usamos un Sistema de Información Geográfica para modelar el uso del hábitat de *F. sparverius* (áreas abiertas dominadas por vegetación herbácea) y definimos parches continuos de hábitat apropiado en el área de estudio y en todo el estado. Las cajas de anidación disponibles en parches grandes de hábitat apropiado (>1000 ha) estuvieron ocupadas por *F. sparverius* a tasas significativamente más altas que las cajas en parches medianos (250–1000 ha) o pequeños (<250 ha). Los parches grandes mostraron tasas de ocupación relativamente altas cada año y los parches medianos tuvieron mayor probabilidad de ser ocupados durante los años en que *F. sparverius* fue abundante en el área de estudio. Los parches pequeños fueron usados de modo infrecuente e independientemente de cuántas parejas estaban criando en el área de estudio. La selección desproporcionada de sitios de anidación en parches continuos suficientemente grandes para incluir varios territorios reproductivos tiene implicancias importantes para las estrategias de conservación. Actualmente, estamos usando información del tamaño del parche para implementar un programa de cajas de anidación para *F. sparverius* en todo el estado de Nueva Jersey.

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The American Kestrel (*Falco sparverius*) is a small, cavity-nesting falcon that breeds in a variety of open to semiopen habitats covered by short ground vegetation, including meadows, grasslands, pastures, agricultural fields, orchards, early old field successional communities, and some urban or suburban areas (Smallwood and Bird 2002). Although kestrel breeding habitat has been described qualitatively (e.g., Bird and Palmer 1988), fewer quantitative data are available. Smallwood and Wargo (1997) measured the vegetation structure and land-use characteristics of kestrel nest sites using 1-ha circular plots (56.4-m radius) centered on nest boxes erected for kestrels in New Jersey, and found that lack of woody canopy was the best predictor of a site's use by kestrels. Rohrbaugh and Yahner (1997) measured vegetation and land-use characteristics within 25 m of nest boxes in Pennsylvania, and found that frequently used nest boxes were characterized by high ambient light intensity and other factors associated with open habitats.

Although descriptions of the habitat immediately surrounding the nesting cavity provide insight into how kestrels select nest sites, such a focus on fine-scale attributes does not address how kestrels choose an entire breeding territory, which may be quite large. Craighead and Craighead (1956) reported that the mean size of kestrel breeding ranges (including the defended nesting territory and sometimes an inconsistently defended peripheral area of use; Smallwood and Bird 2002) were 129 ha in southern Michigan, and 194 ha in Wyoming. Thus, a plot of 1 ha or less likely does not adequately describe the landscape within which kestrels select breeding territories.

Understanding the habitat requirements of a species at appropriate spatial scales is prerequisite to developing effective conservation or management strategies. The objectives of this study were to analyze kestrel breeding habitat at two spatial scales (i.e., the territory and the surrounding landscape), and to examine the relationship between the size of patches of suitable breeding habitat and occupancy by kestrels.

METHODS

Study Area. The study area was located in rural northwestern New Jersey, bordered to the north and west by the Kittatinny Ridge and Delaware River, and to the east and south by residential and commercial development. The predominant land use was mixed agriculture, including corn, hay,

and cattle production, and forestland in the Ridge and Valley Physiographic Region (Sauer et al. 1997). Beginning in 1995, we erected a total of 194 wooden nest boxes (internal dimensions: 20 × 23 cm floor, about 34 cm in height) in habitats apparently suitable for kestrels; i.e., open areas covered by short herbaceous vegetation, in Sussex County (centered approximately 41°11'N, 74°38'W) and Warren County (approximately 40°47'N, 75°04'W). Most (141) nest boxes were erected between 1995 and 1997, with additional nest boxes erected in subsequent years. We also lost some nest boxes each year due to removal of the support structure (e.g., tree or barn), loss of access when the property changed ownership, or other reasons. Thus, the same nest boxes were not available every year.

Kestrel Monitoring. Nest boxes were checked at 21- to 28-d intervals, March through July, which encompassed the egg-laying period; most clutches are initiated in April and May in this study area (J. Smallwood unpubl. data). Kestrels typically produce 4- or 5-egg clutches, laying one egg every other day, and incubation lasts about 30 d, beginning with the penultimate egg (Smallwood and Bird 2002). Thus, our monitoring protocol ensured that kestrel breeding attempts would be discovered during the laying or incubation periods. We considered a nest box occupied by kestrels if at least one kestrel egg was laid in it. It is possible for a clutch to be laid by a kestrel and then removed by a predator between two successive monitoring checks of that nest box. Because kestrels do not build nests but instead lay eggs directly on the substrate that covers the floor of the cavity (we add a layer of wood shavings), there may be no reliable evidence that a breeding attempt had taken place and failed. Thus, our estimate of number of breeding pairs occupying the nest boxes is conservative, but because the sampling effort was consistent, estimates are comparable among years.

Habitat Analysis. By the end of the 2005 breeding season, 106 nest boxes were known to be occupied at least once by kestrels, and 88 nest boxes were not. However, most of the 88 unoccupied nest boxes had not been either available to kestrels or accessible to us for much of the study; 35 of these nest boxes had been available for at least three consecutive years so that there was a reasonable opportunity for them to have been selected by kestrels. We excluded from further analysis unoccupied nest boxes that may have been within the territory of kestrels using a nearby (<564 m; see habitat sampling methods below) nest box. In the case of two nearby nest boxes

that were used in alternate years, perhaps by the same pair of kestrels, we randomly selected one nest box for exclusion. We then compared the habitat surrounding the remaining 96 nest boxes occupied at least once by kestrels and 29 available nest boxes that had never been occupied by kestrels.

Using a Geographic Information System (ArcGIS version 9.2; Environmental Research Systems Institute, Inc. 2006) and a land-use/land-cover dataset (New Jersey Department of Environmental Protection 2000), we analyzed the habitat surrounding nest boxes at two spatial scales: one approximating a kestrel breeding territory (a 1-km² circular plot) and the other at a landscape scale (patches of uniform habitat, up to 29.2 km² in size). The land-use/land-cover polygon shapefile was developed using computer interactive interpretive techniques of color infrared aerial photography (1-m resolution, March 1995 and March 1997) and assigned one of 66 classes using a modified Anderson level III and IV classification system (Anderson et al. 1976, New Jersey Department of Environmental Protection 2001). We created 564-m radius buffers at each of the 125 nest-box sites, resulting in a 1-km² circular plot centered on each of the nest boxes. We quantified each plot with respect to the percent coverage by each of 46 land-use/land-cover categories present within our samples. Eleven of these land-use/land-cover categories describe open areas dominated by herbaceous ground vegetation that are suitable for foraging by kestrels (Smallwood 1987): cropland and pastureland, agricultural wetlands, herbaceous wetlands, old field with <25% brush, other agriculture, recreational land, orchards/vineyards/nurseries/horticultural areas, school athletic fields, managed wetlands within lawns, confined feeding operations, and modified wetland rights-of-way. These 11 land-use/land-cover categories were pooled to form a single category, "suitable habitat."

We then used the land-cover data to identify suitable habitat throughout the state. We dissolved these polygons to delineate patches of contiguous suitable habitat. The boundaries of patches that included at least one of the 125 nest boxes were verified in the field, and in several instances separate patches identified by the GIS were combined because they were separated by only a single row of trees. Because we were interested in the relationship of patch size to the number of kestrel territories they might support, we then calculated the area of each of the resulting patches and arbitrarily catego-

rized them as either large (>1000 ha, roughly corresponding in size to ≥ 10 territories), medium (250–1000 ha, about 2–10 territories), or small (<250 ha, perhaps only one or two territories).

Statistical Analyses. All data subjected to statistical analysis were tested for normality. We used nonparametric statistical treatments for those variables with distributions that differed significantly from normal: percent coverage of a sample plot by individual land-use/land-cover categories. The pooled variable (i.e., suitable habitat) and the mean occupancy rates for large, medium, and small patches met the criteria for parametric statistical treatments, normality, and homogeneity of variance. All statistical tests were two-tailed and performed using JMP version 5 (SAS Institute, Inc. 2004). Values presented with a measure of variability in the results section are means \pm SE.

RESULTS

Nest-box Use. Kestrels began using the nest boxes in 1995, the first breeding season in which nest boxes were available. The number of pairs of kestrels that bred in nest boxes increased from 2 in 1995 to a maximum of 59 in 2002, and generally was decreasing through 2007.

Breeding Habitat. Of the land use/land cover surrounding nest boxes, the most extensive category was cropland and pastureland, covering a mean of $47 \pm 1.9\%$ (range: 0.7–94.1%) of the 1-km² sample plots (Table 1). Nest boxes occupied by kestrels were associated with significantly greater coverage by cropland and pastureland than nest boxes not occupied by kestrels. The next most extensive coverage was by closed deciduous forest (mean = 15%). Nest boxes occupied by kestrels were associated with significantly less closed deciduous forest than nest boxes not occupied by kestrels. The ten most common land-use/land-cover categories together covered a mean of 90% of the sample plots (Table 1).

The five land-use/land-cover categories that represented open areas dominated by herbaceous vegetation accounted for a mean coverage of 62% of the sample plots (Table 1). The mean coverage by the pooled category, suitable habitat, of 1-km² plots surrounding nest boxes occupied by kestrels was $65.9 \pm 1.6\%$ (range: 25.2–98.0%) and was significantly greater than that of nest boxes not occupied by kestrels ($50.8 \pm 3.1\%$, range: 16.4–86.3%; $t_{123} = 4.4$, $P < 0.001$, Bonferroni adjusted).

Table 1. Land use/land cover surrounding nest boxes erected for American Kestrels in northwestern New Jersey, 1995–2005. Data are from 1-km² circular plots centered on 96 nest boxes that were occupied by kestrels in at least one year, and 29 that were available for at least three years but were not occupied by kestrels.

LAND USE/LAND COVER	MEAN PERCENT COVERAGE		WILCOXON RANK SUMS TEST	
	OCCUPIED	NOT OCCUPIED	Z	P
Cropland and pastureland ^a	51.6	35.4	3.7	<0.001
Closed deciduous forest	12.9	21.4	-3.2	0.002
Agricultural wetlands ^a	6.4	5.2	1.9	0.054
Rural residential	5.6	7.6	-2.4	0.018
Deciduous wooded wetlands	3.8	6.4	-1.6	0.105
Herbaceous wetlands ^a	2.9	3.9	-0.1	0.893
Old field (<25% brush) ^a	2.6	3.6	-0.1	0.930
Other agriculture ^a	1.7	2.1	-1.0	0.328
Deciduous brush/shrublands	1.6	1.6	-0.0	0.977
Deciduous forest (10–50% closed)	1.0	2.1	-1.8	0.072

^a Open areas dominated by herbaceous vegetation.

Patch Size. The statewide distribution of large, medium, and small patches of suitable habitat is presented in Fig. 1. In our study area, nest boxes were situated in 5 large, 11 medium, and 23 small patches of suitable habitat. The total number of nest boxes available in large patches varied from 3 in 1995 to 53 in 2001 (41.8 ± 4.8 per yr). There were totals of 5 (1995) to 40 (1999) nest boxes (30.5 ± 2.7 per yr) available in medium patches and 5 (1995) to 32 (1997 and 1999) nest boxes (24.0 ± 2.2 per yr) available in small patches.

Kestrels disproportionately occupied nest boxes in the largest patches of suitable habitat (Fig. 2). Between 1995 and 2007, the mean occupancy rate for nest boxes in large patches was 43% (range: 29–56%), which was significantly greater than that of medium patches (30%, range: 0–58; paired *t*-test: $t_{12} = 5.4$, $P < 0.001$, Bonferroni adjusted). Small patches had the lowest mean occupancy rate (17%, range: 4–35%) and differed significantly from those of large and medium patches ($t_{12} = 9.3$, $P < 0.001$, and $t_{12} = 3.2$, $P = 0.024$, respectively; Bonferroni adjusted).

The annual occupancy rates in large patches were positively correlated with the overall abundance of kestrels throughout the study area, (regression analysis: occupancy rate = $0.47 \times$ number of breeding pairs + 28, $r^2 = 0.89$, $P < 0.001$). There was an even steeper positive relationship in medium patches (occupancy rate = $0.82 \times$ number of breeding pairs + 3, $r^2 = 0.83$, $P < 0.001$). However, in small patches, there was no significant relationship between occupancy rate and overall kestrel abundance ($r^2 = 0.13$, $P = 0.23$).

DISCUSSION

Because American Kestrel populations tend to be nest-site-limited, the introduction of nest boxes typically results in a rapid increase in the number of pairs that breed in these boxes (Hamerstrom et al. 1973, Bloom and Hawks 1983, Toland and Elder 1987, Smallwood and Collopy 2009). Such an increase was evident in our study area. However, after reaching a peak in 2002, the nest-box occupancy rate has been declining. The decline that we observed in our local population apparently is widespread across North America (Smallwood et al. 2009). The reason, or reasons, for this decline currently are under investigation.

Kestrels generally locate their prey, arthropods and small vertebrates (for review see Sherrod 1978), from a perch and capture them on the ground by pouncing upon them (Bildstein and Collopy 1987, Smallwood and Bird 2002). Thus, two principal features of suitable foraging habitat are the lack of woody canopy cover, which would obstruct the bird's view, and a ground cover of short grasses and weedy forbs (Smallwood 1987). The vegetation structure of locations used by foraging kestrels has been well studied (Smallwood 1987, Bird and Palmer 1988, Rohrbaugh and Yahner 1997). We considered all land-use/land-cover categories that were open (mostly free of woody canopy) and covered by herbaceous ground vegetation to be suitable habitat for kestrels.

Kestrels occupied nest boxes located within the largest patches of suitable habitat at rates greater than expected by chance. The rate at which medi-

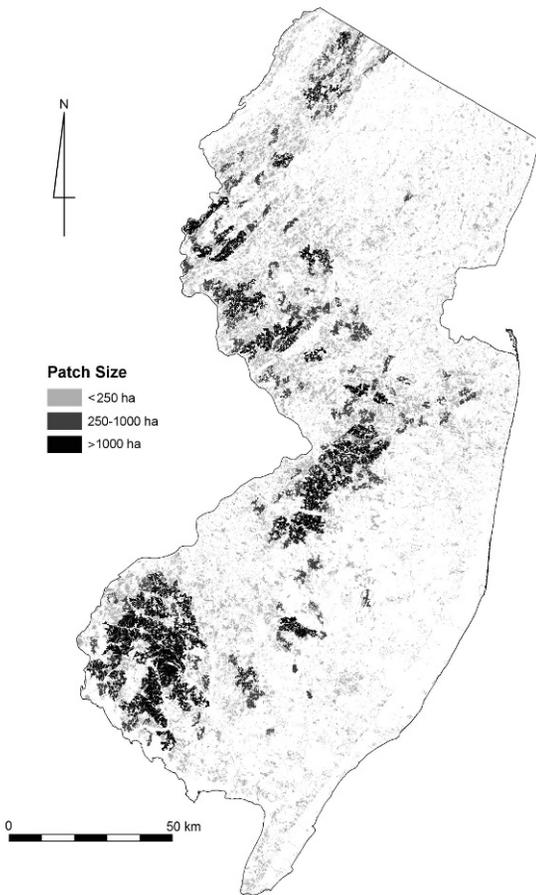


Figure 1. Patches of suitable breeding habitat, open areas covered by herbaceous ground vegetation, for American Kestrels in New Jersey.

um patches were occupied was positively related to the overall abundance of kestrels in the study area, and the rate at which small patches were occupied was low, regardless of the overall number of local breeding pairs. This pattern suggests that kestrels preferentially establish breeding territories in the largest available patches.

It is difficult to precisely estimate how many kestrel territories may be supported by a patch of a given size. There is surprisingly little information on the size of kestrel breeding territories; few studies have determined the boundaries of kestrel territories, and have instead reported the density of kestrels in a particular area (Smallwood and Bird 2002). These densities vary widely, and typically range from 0.11–1.74 pairs/km², but may be as high

as 24.7 pairs/km² (see review by Bird and Palmer 1988).

Kestrel territories vary with respect to the percent coverage by suitable hunting substrate. Some of the highest reported concentrations of kestrels were observed during winter in south-central Florida, where migrant kestrels establish solitary feeding territories (Smallwood 1988). In that study area, there were very large (several km²) “improved pastures” (those kept free of woody vegetation by periodic burning) that were essentially completely covered by suitable hunting substrate. Roadside utility poles and the lines they supported provided the only available hunting perches for kestrels (J. Smallwood unpubl. data), and the highest linear abundance observed was 15 kestrels along a 3.86-km stretch of road (Smallwood and Bird 2002). Food resources within the suitable hunting substrate also can be highly variable. If kestrels are able to accurately assess the distribution of food resources in an area, we would expect that territory size, and boundaries, would reflect that assessment.

The largest patch of suitable habitat in our study area was 2924 ha, and contained a maximum of 20 nest boxes per year and up to 10 pairs of kestrels breeding simultaneously. These nest boxes were clustered in the southern end of the patch, so it is reasonable to assume that this particular patch was sufficiently large to contain perhaps 20 or more kestrel breeding territories. Similarly, the second largest patch, at 2628 ha, included up to 13 nest boxes and 9 breeding pairs per year. Thus, kestrels select nest sites in patches that not only appear to have prey resources sufficient for a successful breeding attempt (i.e., can support a single kestrel territory), but also select suitable patches large enough for many kestrel territories.

It is unlikely that large patches are simply larger targets that are easier to detect, such that randomly moving kestrels settled within them without encountering smaller patches. Kestrels that breed at this latitude are partially migratory, with juveniles more likely than adults to overwinter south of the region (Bird and Palmer 1988, Smallwood and Bird 2002). Birds banded as nestlings in our study area were recaptured in southern Georgia and Florida during their first winter (J. Smallwood unpubl. data). However, even before juveniles begin fall migration, they apparently wander for some time after gaining independence. Varland et al. (1993) reported that the mean time for dispersal from natal areas for young radiotagged kestrels in Iowa was 22.7 d after fledging, but that the birds remained in the general vicinity

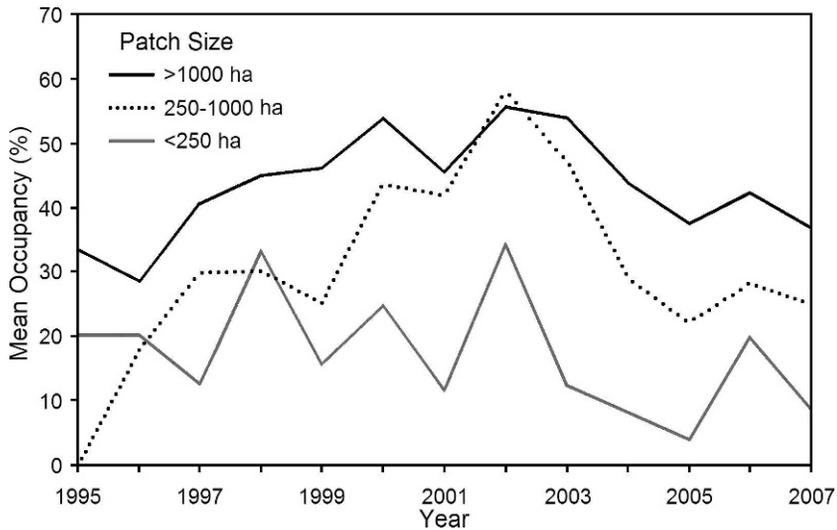


Figure 2. American Kestrels disproportionately breed in nest boxes located in the largest contiguous patches of suitable habitat in northwestern New Jersey.

(i.e., were still in radio contact) for a mean of six more days. Thus, young kestrels probably encounter many patches of various sizes during their dispersal.

It is possible that kestrels are drawn to large patches of suitable habitat for the opportunity to interact with other kestrels. Early in the breeding season as territories are being established or re-established, kestrels often are observed engaging in promiscuous behavior, especially among females with the nearest neighboring males (Cade 1955, Balgooyen 1976, Bird and Palmer 1988). Extra-pair copulation throughout the fertile period apparently is common. Extra-pair fertilization was detected by DNA analysis in 2 of 20 broods in southwestern Quebec (Villarroel et al. 1998), and the frequency of intrapair copulations, a mean of 454 per clutch laid (Villarroel et al. 1998) to as high as 690 per season (Balgooyen 1976) may be interpreted as a sperm competition strategy by the male.

Juvenile kestrels also may benefit from interacting with neighboring conspecifics. Varland et al. (1991) examined the development of foraging skills in kestrels during the first five weeks after fledging, and found that young kestrels hunted socially not only with their parents and siblings, but also with unrelated kestrels, from which they apparently learned foraging behaviors through imitation.

That kestrels preferentially establish breeding territories in large patches of suitable habitat has important conservation implications. The American

Kestrel currently is listed as a “species of special concern” in New Jersey (New Jersey Department of Environmental Protection 2008). We applied our designation of suitable habitat to the state land-use/land-cover map in order to identify high-value locations for nest boxes, large patches of such habitat. We currently are implementing a state-wide nest-box program based on this information. We recommend that those who develop conservation strategies for kestrels in other regions also consider the importance of patch size.

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