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EFFECTS OF MACROHABITAT AND MICROHABITAT ON NEST-BOX USE AND NESTING SUCCESS OF AMERICAN KESTRELS

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ABSTRACT.—We studied the nesting ecology of American Kestrels (*Falco sparverius*) in Berks and Lehigh Counties, Pennsylvania, from 1987–1991. Kestrels used 99 (76%) of 130 nest boxes dispersed throughout a 1000-km^2 study area. A total of 259 nesting attempts was noted: 67, 53, 49, 35, and 55 in 1987, 1988, 1989, 1990, and 1991, respectively. Of the 259 nesting attempts, 124 (49%) successfully fledged at least one offspring. We measured five macrohabitat and 14 microhabitat variables at the 130 nest boxes. Ten (53%) variables were correlated to levels of nest-box use and nesting success. Kestrels most frequently used nest boxes with high nestling-light intensity ($P = 0.02$) and low nest-box concealment ($P = 0.05$). Frequently used boxes were associated with extremely open habitat dominated by herbaceous vegetation ($P < 0.005$). Nesting kestrels avoided using boxes associated with dense habitats, such as late-successional old fields. Frequently used nest boxes were farther from forested areas than unused boxes ($P = 0.05$). Nest boxes with southeast orientations were used more frequently than expected ($P < 0.025$), and all other orientations were used in proportion to availability. Kestrels had the greatest nesting success when using nest boxes with high selection-light intensities ($P = 0.05$). Received *12 Dec. 1996, accepted 25 Mar. 1997.*

Kestrels readily use nest boxes, suggesting that paucity of natural nest sites (i.e., tree cavities) may limit breeding populations (Brauning 1982, 1992; Dahmer et al. 1984; Wheeler 1992). In several cases, the number of breeding pairs of kestrels has been shown to increase locally following the installation of boxes (Hamerstrom et al. 1973, Toland and Elder 1987, Smallwood and Collopy 1993). Natural nest cavities located within suitable breeding territories may become more limiting as habitat area and quality decline because of intensive agricultural practices and residential and commercial development. Thus, installation of nest boxes in suitable habitats where nest cavities are limiting may be increasingly important to maintain stable populations of kestrels.

Bortolotti (1994) identified the need for research concerning the influence of nest-site parameters on the breeding biology of kestrels using nest boxes. Because of the paucity of research in this area, it is not known if nest-site parameters can have detrimental effects on kestrels by increasing rates of abandonment, predation, or adult mortality. Nest boxes should be placed in habitats that promote successful reproduction as well as box

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occupancy; however, quantitative management guidelines regarding the placement of nest boxes in such habitats have not been published.

Nest sites presumably are selected on the basis of habitat characteristics associated with the nest box and the immediate vicinity (Balgooyen 1976, 1990; Brauning 1982, 1983; Raphael 1985; Curley et al. 1987; Toland and Elder 1987). Previous studies have examined macrohabitat and microhabitat characteristics relative to nest-site selection in kestrels, but few have considered these characteristics simultaneously or related them to nesting success.

We evaluated macrohabitat and microhabitat characteristics associated with 130 nest boxes placed for American Kestrels and related these characteristics to nest-box use and nesting success. Our specific objectives were to (1) determine frequencies of nest-box use and rates of nesting success at nest boxes used by kestrels during a 5-year period, and (2) compare frequencies of nest-box use and rates of nesting success with macrohabitat and microhabitat characteristics associated with nest boxes used and unused by kestrels.

STUDY AREA AND METHODS

We conducted our study in eastern Pennsylvania, southeast of Hawk Mountain Sanctuary, in Berks and Lehigh Counties. The 1000-km^2 study area was dominated by agricultural land use and was interspersed with fencerows, woodlots, and riparian forests. Forested areas varied from early-successional to mature stands (>30 yr old) of harvestable timber. Natural vegetation was Appalachian oak (*Quercus* spp.) and oak-hickory (*Carya* spp.)-pine (*Pinus* spp.) associations (Kuchler 1964). Predominant agricultural species were corn (*Maze* spp.), soybeans (*Glycine max*), wheat (*Triticum* spp.), alfalfa (*Medicago* spp.), and mixed grasses (*Lolium* spp., *Festuca* spp., *Trifolium* spp., and *Phleum* spp.) for hay production.

Over the past 25 years, personnel from Hawk Mountain Sanctuary Association have installed 149 nest boxes for breeding kestrels throughout the study area (Heintzelman and Nagy 1968). These boxes were placed in suitable habitat based on qualitative information and unpublished records from Hawk Mountain Sanctuary Association. The mean distance between each nest box was 0.8 km. Kestrel territories probably only included one nest box because the average diameter of kestrel breeding territories in eastern North America is 0.5 km (Bowman and Bird 1986, Gard and Bird 1990). We conducted our research at 130 nest boxes that remained in the same locations for at least five breeding seasons (1987–1991). Most boxes were mounted on deciduous trees ($N = 127$), and three were mounted on utility poles. Height above ground of boxes ranged from 2.0–6.5 m. All nest boxes were constructed of untreated lumber and had the following internal dimensions: depth = 26 cm, width = 24 cm, and height = 33 cm. The entrance hole was 7.6 cm in diameter and was 26 cm above the floor of the box. Nest-box contents from the previous breeding season were removed from each box in February or early March of each year and replaced with 2.5–5.0 cm of wood chips. In addition, throughout the breeding season, a bed of wood chips was maintained inside nest boxes that were not actively used by kestrels.

Nest-box use and nesting success.—We visited nest boxes during incubation, early nestling, and late nestling periods to determine rates of nest-box use and nesting success. We inspected nest boxes twice during the incubation period and once each during the early nestling and late nestling periods. These visits were kept brief (<10 min) to minimize any observer-related effects on nesting success. During all three time periods, nests and eggs of European Starlings (*Sturnus vulgaris*) were removed and replaced with 2.5–5.0 cm of fresh wood chips. Nest boxes were inspected during the incubation period to determine breeding activity and clutch size. Nest boxes were not considered active until at least one kestrel egg or eggshell fragments was found inside the box. Each active nest box was considered a nesting attempt. We considered each nesting attempt to be an independent observation, as nest-box fidelity (i.e., reuse of nest boxes by the same individuals) was observed to be low (14%) for this kestrel population (Rohrbaugh 1994).

Nestlings were counted during the first 10 days of the nestling period (early-nestling period). We visited boxes again when nestlings were ≥22 days old (late-nestling period) in order to determine numbers of fledglings. Steenhof and Kockert (1982) recommended that nestlings of diurnal raptors be considered successfully fledged when they attain 80% of average age to fledging; this age is 22 days for kestrels.

Nest-box use was defined as the frequency of nest boxes used by breeding kestrels during a given year. For temporal comparisons, nesting success was calculated as the proportion of nesting pairs that successfully fledged at least one offspring during a given breeding season. For comparisons of nesting success with macrohabitat and microhabitat characteristics, nest boxes were categorized based on the number of years they housed a successful pair of breeding kestrels.

Macrohabitat and microhabitat.—We measured five macrohabitat and 14 microhabitat variables at each nest box in June and July of 1990 and 1991 (Table 1). Macrohabitat variables were distances to key ecological and human-related features in the landscape. Microhabitat variables were vegetative and physical characteristics within a 25-m radius of each nest box. Macrohabitat variables were measured in the field using a meter tape if ≤100 m from the nest box. If distances were >100 m, they were measured from 1:24,000 scale USGS topographic maps or 1:40,000 scale aerial photographs taken in 1987. Microhabitat variables were quantified within a 25-m radius (0.20 ha) circular plot centered on the nest tree at each of the 130 nest boxes.

We determined the percent of Anderson Level III and IV land-use types (PELU) within each plot based on 20, 1 × 1 m square grid samples taken at 5-m intervals along two perpendicular transects centered on the nest tree. We classified nest boxes into three categories based on the percent of "open" land-use types associated with each box. Open land-use types included cropland, pastureland, hayland, and herbaceous rangeland. Nest box locations containing ≥65% (≥13 of 20 grid samples) open land-use types were considered to be in open habitat; those with 30–60% (6–12 of 20 grid samples) open land-use types were considered to be in semi-open habitat; and those with ≤25% (≤5 of 20 grid samples) open land-use types were considered to be in dense habitat.

We measured selection-light intensity (SELT) and nestling-light intensity (NELT) inside each nest box. Selection-light intensity was measured from 5 to 11 March prior to "leaf-out," and at time when nest sites are presumably being selected by kestrels (Heintzelman and Nagy 1968, Stokes 1979). Nestling-light intensity was measured following the fledging of offspring (24 July–7 August). Selection- and nestling-light intensities were measured using a photometer (Curley et al. 1987). The photometer consisted of a cadmium-sulfide photoelectric cell (Tandy Corporation, Fort Worth, Texas, Archer Catalog No. 276-1657) attached to an energy meter. The photoelectric cell was placed inside the nest box through the entrance hole. The cell then was attached to a 10-cm tall wooden stand placed inside the nest box. The access door of the nest box was closed, and the light-intensity measurement was read in microamperes (ma) from the energy meter held outside the nest box (Curley et al. 1987). Light-intensity measurements were taken only between 11:00 and 13:00 h on clear days (≤30% cloud cover) to eliminate bias that may be created due to angle or intensity of the sun.

Statistical design and analyses.—Three levels of nest-box use were identified: unused boxes (used 0 of 5 years), occasionally used (used 1–2 years), and frequently used (used ≥3 years). We classified nest success as (1) low-nesting success (boxes that housed nesting kestrels, but failed to fledge offspring in 5 years), (2) average-nesting success (boxes that were successful 1 or 2 years), and (3) high-nesting success (boxes that were successful ≥3 years).

We compared macrohabitat and microhabitat variables among levels of nest-box use and nesting success using single-classification analyses-of-variance (ANOVA) (Sokal and Rohlf 1981). When necessary, variables were transformed (arcsin, natural log, or square-root) to meet the assumptions of normality and homogeneity of variance. If a variable differed significantly ($P \leq 0.05$) between levels, we used Student-Newman-Keuls multiple comparison tests to determine locations of the statistical differences (Sokal and Rohlf 1969).

We performed chi-square tests on categorical data using the same levels (categories) of nest-box use and nesting success as with continuous variables. The data were formatted into multi-way contingency tables, and tables with ≥20% of expected counts ≤5, or ≥1 expected count <1 were considered invalid. When a variable was found to be significant ($P \leq 0.05$), the table was collapsed to isolate the cell(s) of interest. These cells then were tested a posteriori using Chi-square tests-of-independence (Sokal and Rohlf 1981).

RESULTS

Nest-box use and nesting success.—Kestrels used 99 (76%) of 130 nest boxes during the 5-year period. The average number of nest boxes used per year was 52 (40%) (range = 35–67, SE = 5.14) (Table 2). There were 31 (24%) unused boxes, 52 (40%) occasionally used (used 1–2 years) boxes, and 47 (36%) frequently used (used ≥3 years) boxes. The mean number of years that a given nest box was used was 2.0 (N = 130, range = 0–5, SE = 0.14). The frequency of nest boxes used differed significantly among years ($\chi^2 = 17.1$, df = 4, $P < 0.005$). The number of nest boxes used during 1987 (N = 67) was significantly higher, and the number used during 1990 (N = 35) was significantly lower than the expected values for those years. In addition, the number of nest boxes used declined annually by an average of 19% from 1987–1990 and then increased by 57% in 1991 (Table 2).

We noted 259 nesting attempts during the five nesting seasons. The mean number of successful nests per year was 25 (49%) (range = 20–28, SE = 1.53) (Table 2). The mean proportion of nests that survived through the incubation period (1987–1991) was 30%. Of the 99 boxes used at least once during the five years, 29 (29%) never fledged young, 57 (58%) fledged young during one or two years, and 13 (13%) fledged young during at least three years. The mean number of years in which a nest box was successful was 1.3 (N = 99, range = 0–4, SE = 0.12).

Macrohabitat.—One (20%) macrohabitat variable differed significantly ($P \leq 0.05$) among levels of nest-box use. Distance to forest (DFOR) was

TABLE 1

MACROHABITAT AND MICROHABITAT VARIABLES MEASURED AT 130 NEST BOXES OF AMERICAN KESTRELS IN BERKS AND LEHIGH COUNTIES, PENNSYLVANIA, 1990–91

Variable	Description
Macrohabitat:	
Distance to human habitation (DHUM)	Distance (m) of nest box to nearest building as measured in the field or from topographic maps.
Distance to forest (DFOR)	Distance (m) of nest box to nearest forested area ≥0.5 ha as measured in the field or from aerial photographs.
Distance to active nest box (DBOX)	Mean distance (m) (1987–1991) of nest box to nearest active nest box as measured from topographic maps.
Distance to water (DWAT)	Distance (m) of nest box to nearest body of water, such as a creek, pond, or lake as measured in the field or from topographic maps.
Type of water (TWAT)	Type of closest water (intermittent stream, tributary stream, creek or river, pond or lake) as classified in the field or from topographic maps.
Microhabitat:	
Nest tree dbh (TDBH)	Diameter breast height (cm) of nest tree.
Nest tree health (NTHL)	Estimated health of nest tree based on categorized drawings of trees (Devereux and Mosher 1984).
Nest-box height (NBHT)	Height (m) from bottom of nest box to ground, measured with tape measure.
Nest-box concealment (NBCO)	Percent (%) of nest box concealed by vegetation, measured using a 30- × 380-cm visibility board (Curley et al. 1987).
Nest-box orientation (NBOR)	Compass azimuth in degrees of the entrance hole of the nest box (Balgooyen 1976, 1990, Brauning 1982, Raphael 1985).
Number of suitable perches (PERC)	Number of perches ≥1.5-m tall within the plot (snags, poles, etc.).
Percent land use (PELU)	Percent (%) of each Anderson Level III and IV land use types within each plot based on 20, 1- × 1-m square grid samples at 5-m intervals along two perpendicular transects centered on the nest tree (Anderson et al. 1976).
Shannon-Weiner index (SWIN)	Diversity of Anderson land-use types (levels III and IV) based on the Shannon-Weiner Index (H').

TABLE 1
CONTINUED

Variable	Description
Overstory density (OSHA)	Density (no. stems/ha) of overstory stems (≥10.5-cm dbh).
Understory density (USHA)	Density (no. stems/ha) of woody understory stems (2.5- to 10.5-cm dbh and <1.5-m tall) based on two, 1- × 50-m transects.
Tall shrub density (TSHA)	Density (no. stems/ha) of woody stems 1.5-m tall and <2.5-cm dbh based on two, 1- × 50-m transects.
Short shrub density (SSHA)	Density (no. stems/ha) of woody stems 0.5- to 1.5-m tall and <2.5-cm dbh based on two, 1- × 50-m transects.

TABLE 2

YEAR, NUMBER NEST BOXES USED, PERCENT NEST BOXES USED, AND PERCENT NESTING SUCCESS AT 130 AMERICAN KESTREL NEST BOXES IN BERKS AND LEHIGH COUNTIES, PENNSYLVANIA, 1987–91

Year	Number of boxes used	Percent of boxes used	Percent of nesting success
1987	67	52	42
1988	53	41	43
1989	49	38	51
1990	35	27	57
1991	55	42	51
Mean	52	40	49

greater ($P = 0.05$) for occasionally and frequently used nest boxes than for unused nest boxes (Table 3).

Microhabitat.—Nine (64%) microhabitat variables differed significantly ($P \leq 0.05$) among levels of nest-box use and nesting success: nest-box concealment (NBCO), overstory stems/ha (OSHA), understory stems/ha (USHA), tall shrubs/ha (TSHA), short shrubs/ha (SSHA), percent land use (PELU), nest-box orientation (NBOR), selection-light intensity (SELT), and nestling-light intensity (NELT).

Nest-box concealment, which was highly correlated with nestling-light intensity ($r = -0.47$, df = 106, $P < 0.05$), differed ($P = 0.05$) among levels of nest-box use, with frequently used nest boxes having the lowest percent concealment (Table 3).

Density of overstory stems ($P = 0.00$), understory stems ($P = 0.00$), tall shrubs ($P = 0.00$), and short shrubs ($P = 0.04$) differed among levels of nest-box use (Table 3). However, these variables were highly correlated ($P \leq 0.05$) with each other. Results from percent land use (PELU) measures indicated that kestrels most frequently used nest boxes associated with open habitats dominated by herbaceous vegetation ($\chi^2 = 16.8$, df = 4, $P < 0.005$) (Fig. 1). These open habitats frequently were bottomland pastures that lacked vertical structure.

Nest-box orientation differed among levels of nest-box use ($\chi^2 = 14.6$, df = 6, $P < 0.025$). Kestrels used nest boxes oriented southeast more frequently than expected ($\chi^2 = 13.35$, df = 2, $P < 0.005$) and avoided northwestern facing boxes ($\chi^2 = 6.2$, df = 2, $P < 0.05$). Boxes in all other orientations were used in proportion to their availability (Fig. 2). Twenty-six (90%) of 29 nest boxes oriented southeast were used at least one year during the 5-year period, and 18 (62%) were used ≥ 3 years.

TABLE 3

F-RATIOS, *P*-VALUES, AND MEANS (SE) OF EIGHT VARIABLES[a] MEASURED AT 130 AMERICAN KESTREL NEST BOXES IN BERKS AND LEHIGH COUNTIES, PENNSYLVANIA, 1990–91

				Mean (SE) for nest-box use levels		
Variable	Transformation	F	P	Unused	Occasionally used	Frequently used
NELT	UT[b]	4.11	0.018	5.09 (0.37)	5.86 (0.27)	6.39 (0.27)
NBCO[a]	UT	2.94	0.056	46.32 (6.32)	40.00 (4.97)	28.13 (4.59)
NBCO	AS[c]	3.02	0.052	0.58 (0.10)	0.48 (0.07)	0.32 (0.06)
OSHA	UT	8.52	0.000	67.32 (13.75)	29.67 (4.76)	23.81 (5.19)
USHA	UT	11.36	0.000	112.52 (23.50)	32.63 (7.60)	22.11 (11.76)
TSHA	UT	7.60	0.001	590.32 (182.89)	188.46 (48.09)	106.38 (33.92)
SSHA	UT	1.74	0.180	1435.16 (369.77)	726.92 (149.71)	1014.87 (280.59)
SSHA	LN[d]	3.18	0.045	5.26 (0.63)	3.15 (0.53)	3.48 (0.57)
DFOR	UT	3.03	0.052	221.93 (26.35)	390.68 (51.84)	343.39 (40.77)

[a] The variables were tested using ANOVA to examine differences among levels of nest-box use. Descriptions of variable acronyms are given in Table 1.
[b] Variable untransformed for final analyses.
[c] Variable transformed using arcsin for final analyses.
[d] Variable transformed using natural log for final analyses.

Furthermore, 36 (77%) of the 47 frequently used nest boxes faced eastward (0–180°).

Means for selection-light intensity and nestling-light intensity were 6.7 ma (range = 3.5–9.5, SE = 0.11) and 5.9 ma (range = 1.0–9.3, SE = 0.17), respectively. We did not observe a significant difference in selection-light intensity (F = 1.19; df = 2, 121; P = 0.31) among levels of nest-box use. However, selection-light intensity was significantly higher in the high nesting success level versus the low or average levels (F = 3.15; df = 2, 121; P = 0.047). Mean selection-light intensities were 6.66 (0.23), 6.67 (0.15), and 7.57 ma in the low, average, and high nesting success levels, respectively. Nestling-light intensity differed (P = 0.018) among levels of nest-box use, and was highest at frequently used boxes (Table 3).

DISCUSSION

Nesting success.—The mean rate of nesting success for kestrels in our study (49%) was intermediate to success rates observed elsewhere: Ken-

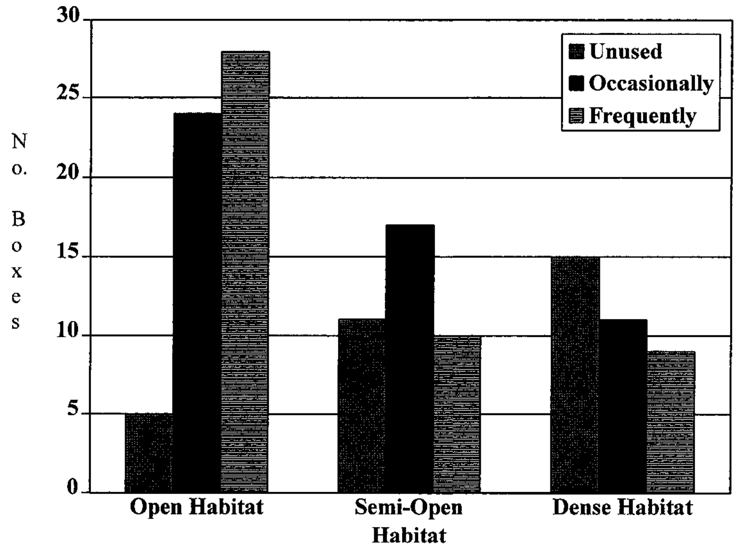

FIG. 1. Number of unused, occasionally used (used 1–2 of 5 years), and frequently used (used ≥3 of 5 years) American Kestrel nest boxes associated with open, semi-open, and dense habitats in Berks and Lehigh counties, Pennsylvania.

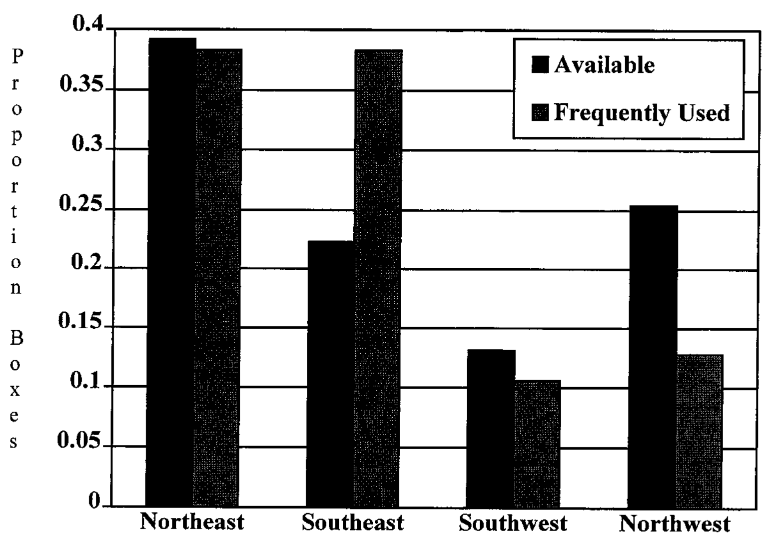

FIG. 2. Proportionate distributions of 130 nest boxes available for use by American Kestrels and 47 nest boxes that were frequently used (used ≥3 of 5 years) by kestrels within four compass azimuth orientations in Berks and Lehigh counties, Pennsylvania.

tucky—36% (Kellner and Ritchison 1988), Wisconsin—67% (Hamerstrom et al. 1973), Idaho—81% (Craig and Trost 1979), California—82% (Bloom and Hawks 1983), and Missouri—86% (Toland and Elder 1987). Apanius (1992) observed similar nesting success (44%) by kestrels in our study area. The low-to-intermediate rate of nesting success exhibited by kestrels in our study may have been a result of nest desertion during the incubation period, as 70% of nest failures occurred during this period. Subsequent to the commencement of incubation in early May, the habitat of the study area was altered extensively by agricultural practices (e.g., plowing, planting, and spraying, of agricultural fields). These habitat alterations and disturbances may influence rates of nest desertion in kestrels.

In recent years, mechanized farming coupled with the use of modern fertilizers and pesticides (i.e., herbicides and insecticides) have enabled farmers to harvest hay and grain crops earlier and more frequently (Castrale 1985, Best 1986, Rodenhouse et al. 1993, Warner 1994). Earlier and more frequent harvests may reduce diversity and biomass of prey species (i.e., insects and small vertebrates; Bollinger et al. 1990, Frawley and Best 1991, Gard et al. 1993). In our study area, some harvests are coincident with the latter stages of incubation in late May and early June. In addition, the rapid conversion of dormant agricultural fields to row crops in spring may substantially reduce prey availability and abundance during the incubation period. Moreover, land-use changes (i.e., residential and commercial development) have reduced the amount of alternate hunting habitats for kestrels. Although not documented in American Kestrels, nest desertion during the incubation period associated with low prey availability is the most prominent cause of nest failures in Eurasian Kestrels (*Falco tinnunculus*) (Village 1990).

Inter-specific competition.—In North America, starlings are frequently associated with agricultural and human-dominated landscapes. Starlings usurp nest boxes during the kestrel egg-laying stage, often causing kestrels to abandon a partial clutch of eggs before incubation commences (Hamerstrom et al. 1973, Wilmers 1987). In our study, eggs of usurped kestrel nests often were punctured, and starling nests were constructed on top of the kestrel eggs. Puncturing of kestrel eggs by starlings has not been documented, but starlings are known to puncture eggs of Wood Ducks (*Aix sponsa*) (Bellrose et al. 1964, Muncy and Burbank 1975). Starlings may have precluded the use of nest boxes and reduced nesting success of kestrels. We have accurate data on the use of nest boxes by starlings for the final year (1991) of our study. During this year, starlings used 57 (42%) nest boxes, and 17 (30%) of these also were used by kestrels at some time during the breeding season. Eleven (65%) of the 17 nesting attempts initiated by kestrels in boxes occupied by starlings were unsuccessful, whereas only 14 (37%) of 38 nesting attempts by kestrels in boxes unoccupied by starlings were unsuccessful.

Other nest-box competitors include, gray squirrels (*Sciurus carolinensis*) and white-footed mice (*Peromyscus leucopus*). Nest boxes situated <150 m from forested areas were often used by these two species. This may partially explain why occasionally and frequently used nest boxes were on average situated 145 m farther from forested areas than unused boxes.

Microhabitat relationships.—Curley et al. (1987) found that kestrels selected nest boxes with high-light intensities inside the box. Richards (1970) and Wilmers (1987) suggested that this preference for high-light environments was a consequence of recent evolutionary changes in nesting behavior of kestrels. Richards (1970) proposed that cavity nesting by kestrels was a relatively recent occurrence, which evolved subsequent to the use of open nests. Eggs of kestrels are heavily marked, unlike the pale eggs of most cavity-nesting birds, suggesting that kestrels evolved in high-light environments (i.e., open nests). Our observation that nest-box use increased with greater nestling-light intensity was perhaps a consequence of the amount of nest-box concealment and not differences in nestling-light intensity per se. Kestrels probably used nest boxes with high nestling-light intensities more frequently because these boxes also had low nest-box concealment.

Nest boxes with low concealment may attract kestrels because they are more visible than those with high concealment or because low nest-box concealment allows an unobstructed flight path into the box. An unobstructed flight path into the nest box may be important when kestrels deliver prey to mates and nestlings. Curley et al. (1987) reported that starlings have a preference for nest boxes with high nest-box concealment and low-interior light intensity. Hence, usurpation of kestrel nest boxes by starlings may be less frequent at boxes with low concealment and high nestling-light intensity. However, for the one year that we have starling data (1991), we found no relationship between use of nest boxes by starlings and nestling-light intensity ($F = 1.1$; df = 1, 125; $P = 0.30$).

We confirmed that kestrels have a preference for nest boxes (cavities) that are oriented southeast, which was similar to results obtained by Brauning (1982). He noted that these southeast-facing nests averaged higher morning temperatures and lower afternoon temperatures than cavities oriented in other directions. Balgooyen (1976, 1990) suggested that cavities facing eastward provide thermoregulatory advantages because of warmth of morning sun and protection from hot afternoon temperatures, thereby reducing thermoregulatory stress and theoretically increasing nesting success. We found that nesting success of kestrels using boxes oriented southeast or eastward did not differ from nesting success of kestrels using boxes with other orientations. However, high nest-box concealment may nullify the thermoregulatory effects of orientation by blocking sunlight, and this may explain why kestrels nesting in boxes with high selection-light intensity exhibited increased nesting success in our study. Increased selection-light intensity may result in higher temperatures and lower moisture inside the nest box during early morning and evening, which may be important during incubation when ambient temperatures are relatively low.

We noted that kestrels most frequently used boxes located in extremely open habitats dominated by herbaceous vegetation. Smallwood and Collopy (1991) noted a similar relationship between nest-box use and openness of habitat at 355 nest boxes erected in hardwood hammocks and longleaf pine (*Pinus palustris*)-turkey oak (*Quercus catesbaei*) sandhills in north-central Florida. Occupancy rates of nest boxes located in the more open sandhills were twice that of boxes located in hammocks, and percent nesting success was greater in sandhills (67%) than in hammocks (36%).

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LITERATURE CITED

ANDERSON, J. R., E. E. HARDY, J. T. ROACH, AND R. E. WITMER. 1976. A land use and land cover classifications system for use with remote sensor data. Geological Survey Professional Paper 964.

APANIUS, V. 1992. Blood parasitism, immunity, and reproduction in American Kestrels (*Falco sparverius*). Ph.D. diss., Univ. of Pennsylvania, Philadelphia, Pennsylvania.

BALGOOYEN, T. G. 1976. Behavior and ecology of the American Kestrel (*Falco sparverius*) in the Sierra Nevada of California. Univ. Calif. Publ. Zool. 103:1–83.

———. 1990. Orientation of American Kestrel nest cavities revisited. J. Raptor Res. 24: 27–28.

BELLROSE, F. C., K. L. JOHNSON, AND T. U. MEYERS. 1964. Relative value of natural cavities and nesting boxes for Wood Ducks. J. Wildl. Manage. 28:661–676.

BEST, L. B. 1986. Conservation tillage: ecological traps for nesting birds. Wildl. Soc. Bull. 14:308–317.

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

BOLLINGER, E. K., P. B. BOLLINGER, AND T. A. GAVIN. 1990. Effects of hay-cropping on eastern populations of the Bobolink. Wildl. Soc. Bull. 18:142–150.

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

BOWMAN, R. AND D. M. BIRD. 1986. Ecological correlates of mate replacement in the American Kestrel. Condor 88:440–445.

BRAUNING, D. W. 1982. The role of cavity availability and cavity temperatures in nest site selection of the American Kestrel. M.S. thesis, The Pennsylvania State Univ., University Park, Pennsylvania.

———. 1983. Cavity availability and nest site selection of the American Kestrel (*Falco sparverius*). J. Raptor Res. 17:122.

———. 1992. American Kestrel (*Falco sparverius*). Pp. 108–109 *in* Atlas of breeding birds in Pennsylvania (D. W. Brauning, ed.). Univ. of Pittsburgh Press, Pittsburgh, Pennsylvania.

CASTRALE, J. S. 1985. Responses of wildlife to various tillage conditions. Trans. of the North American Wildlife and Natural Resources Conf. 50:142–156.

CRAIG, T. H. AND C. H. TROST. 1979. The biology and nesting density of breeding American Kestrels and Long-eared Owls on the Big Lost River, southeastern Idaho. Wilson Bull. 91:50–61.

CURLEY, E. M., R. BOWMAN, AND D. M. BIRD. 1987. Nest site characteristics of boxes occupied by starling and kestrels. Pp. 160–164 *in* The Ancestral Kestrel (D. M. Bird and R. Bowman, eds.). Raptor Res. Foundation, Inc. and Macdonald Raptor Res. Centre of McGill Univ., Ste. Anne de Bellevue, Quebec, Ontario.

DAHMER, T. D., N. C. FORRESTER, J. M. LOCKHART, AND T. P. MCENEANEY. 1984. Nest box use by American Kestrels on and around western surfaced-mined lands. Pp. 210–213 *in* Proceedings of a Symposium on Issues and Technology in the Management of Impacted Western Wildlife. Technical Publication No. 14, Thorne Ecological Institute, Boulder, Colorado.

DEVEREUX, J. G. AND J. A. MOSHER. 1984. Breeding ecology of Barred Owls in the central Appalachians. J. Raptor Res. 18:49–58.

FRAWLEY, B. J. AND L. B. BEST. 1991. Effects of mowing on breeding bird abundance and species composition in alfalfa fields. Wildl. Soc. Bull. 19:135–142.

GARD, N. W. AND D. M. BIRD. 1990. Breeding behavior of American Kestrels raising manipulated brood sizes in years of varying prey abundance. Wilson Bull. 102:605–614.

———, M. J. HOOPER, AND R. S. BENNETT. 1993. Effects of pesticides and contaminants on Neotropical migrants. Pp. 310–314 *in* proceedings of Status and management of Neotropical migratory birds (D. M. Finch and P. W. Stangel, eds.). U.S. For. Serv. Gen. Tech. Rep. RM-229.

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

HEINTZELMAN, D. AND A. C. NAGY. 1968. Clutch sizes, hatchability rates, and sex ratios of Sparrow Hawks in eastern Pennsylvania. Wilson Bull. 80:306–310.

KELLNER, C. AND G. RITCHISON. 1988. Nesting success and incubation behavior of American Kestrels in central Kentucky. Wilson Bull. 110:317–319.

KUCHLER, A. W. 1964. Potential natural vegetation of the conterminous United States. Amer. Biol. Soc. Spec. Pub. 36. New York.

MUNCY, J. A. AND J. H. BURBANK. 1975. Comparative use of three types of Wood Duck nest boxes. Proc. Southeast Assoc. Game and Fish Comm. 29:493–500.

RAPHAEL, M. G. 1985. Orientation of American Kestrel nest cavities and nest trees. Condor 87:437–438.

RICHARDS, G. L. 1970. American Kestrel, *Falco sparverius*, exhibits relic nest building behavior. Condor 72:476.

RODENHOUSE, N. L., L. B. BEST, R. J. O'CONNOR, AND E. K. BOLLINGER. 1993. Effects of temperate agriculture on Neotropical migrant landbirds. Pp. 280–295 *in* proceedings of Status and management of Neotropical migratory birds (D. M. Finch and P. W. Stangel, eds.). U.S. For. Serv. Gen. Tech. Rep. RM-229.

ROHRBAUGH, R. W. 1994. Effects of macrohabitat, microhabitat, and microclimate on nest-box use and nesting success of American Kestrels in Eastern Pennsylvania. M.S. thesis, The Pennsylvania State Univ., University Park, Pennsylvania.

SMALLWOOD, J. A. AND M. W. COLLOPY. 1991. The responses of southeastern American Kestrels to increased availability of nesting sites in two habitats. J. Raptor Res. 25:160.

——— AND ———. 1993. Management of the threatened southeastern American Kestrel in Florida: population responses to a regional nest-box program. J. Raptor Res. 27:81.

SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, California.

——— AND ———. 1981. Biometry. W. H. Freeman and Co., San Francisco, California.

STEENHOF, K. AND M. N. KOCHERT. 1982. An evaluation of methods used to estimate raptor nesting success. J. Wildl. Manage. 46:885–893.

STOKES, B. W. 1979. A guide to bird behavior volume 1. Little Brown and Co., Boston, Massachusetts.

TOLAND, B. 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.

VILLAGE, A. 1990. The Kestrel. Poyser, London, England.

WARNER, R. E. 1994. Agricultural land use and grassland habitat in Illinois: Future shock for midwestern birds? Conserv. Biol. 8:147–156.

WHEELER, A. H. 1992. Reproductive parameters for free ranging American Kestrels (*Falco sparverius*) using nest boxes in Montana and Wyoming. J. Raptor Res. 26:6–9.

WILMERS, T. J. 1987. Competition between starlings and kestrels for nest boxes: A review. Pp. 156–159 *in* The Ancestral Kestrel (D. M. Bird and R. Bowman, eds.). Raptor Res. Foundation, Inc. and Macdonald Raptor Res. Centre of McGill Univ., Ste. Anne de Bellevue, Quebec, Ontario.