We appreciate comments made on earlier drafts of this paper by C. D. Ankney, K. L. Bildstein, P. A. Gowaty, H. Mayfield, and J. L. Zimmerman.

The National Engineering and Science Research Council of Canada and the Ontario Research Council provided financial support for our broader studies of catbirds and cardinals.

LITERATURE CITED

- ANDERSON, T. R. 1979. Experimental synchronization of sparrow reproduction. Wilson Bull. 91:317–319.
- BARRY, T. W. 1962. Effect of late seasons on Atlantic Brant reproduction. J. Wildl. Manage. 26:19–26.
- CHANCE, E. P. 1940. The truth about the cuckoo. Country Life Ltd., London, England.
- DARLEY, J. A., D. M. SCOTT, AND N. K. TAYLOR. 1971. Territorial fidelity of catbirds. Can. J. Zool. 49:1465–1478.
- DELIUS, J. D. 1965. A population study of skylarks Alauda arvensis. Ibis 107:466-492.
- FINCH, D. M. 1984. Some factors affecting productivity in Abert's Towhee. Wilson Bull. 96:701–705.
- GILBERT, A. B. AND D. G. M. WOOD-GUSH. 1971. Ovulatory and ovipository cycles. Pp. 1353–1378 in Physiology and biochemistry of domestic fowl. Vol. 3 (D. J. Bell and B. M. Freedman, eds.). Academic Press, New York, New York.
- KREMENTZ, D. G. AND C. D. ANKNEY. 1986. Bioenergetics of egg production by female House Sparrows. Auk 103:299–305.
- LEINONEN, M. 1973. On the breeding biology of the White Wagtail *Motacilla alba* in Central Finland. Ornis Fenn. 50:53-82.
- MOUSLEY, H. 1917. A study of subsequent nestings after the loss of the first. Auk 34:381–393.
- NOLAN, V. JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. Ornithol. Monogr. 26.
- PAYNE, R. B. 1969. Breeding seasons and reproductive physiology of Tricolored Blackbirds and Redwinged Blackbirds. U. Calif. Publ. Zool. 90.
- RICKLEFS, R. E. 1973. Fecundity, mortality, and avian demography. Pp. 366-435 in Breeding biology of birds (D. S. Farner, ed.). Natl. Acad. Sci., Washington, D.C.
- Scort, D. M. 1963. Changes in the reproductive activity of the Brown-headed Cowbird within the breeding season. Wilson Bull. 75:123–129.
- AND C. D. ANKNEY. 1980. Fecundity of the Brown-headed Cowbird in southern Ontario. Auk 97:677–683.

SOKAL, R. R. AND F. J. ROHLF. 1981. Biometry, 2nd ed. Freeman, San Francisco, California.

DAVID M. SCOTT, ROBERT E. LEMON, AND JAMES A. DARLEY, Dept. Zoology, Univ. Western Ontario, London, Ontario N6A 5B7, Canada. (Present address of REL: Dept. Biology, McGill Univ., Montreal, Quebec, H3A 1B1, Canada; JAD: Dept. Psychology, St. Mary's Univ., Halifax, Nova Scotia B3H 3C3, Canada.) Received 4 Dec. 1986, accepted 23 Mar. 1987.

Wilson Bull., 99(4), 1987, pp. 712-717

Influence of nest-box placement and density on abundance and productivity of American Kestrels in central Missouri.—When extra nest sites are provided by man, an increase in raptor breeding densities often follows (Newton 1976, 1979). The scarcity of suitable cavities probably limits nesting populations of American Kestrels (*Falco sparverius*) (Cade 1982).

Nagy (1963) erected 9 nest boxes on his 130-ha farm in Pennsylvania, and, during a favorable prey year, 6 pairs of kestrels nested in boxes as close as 34 m apart. In Wisconsin, Hamerstrom et al. (1973) placed 50 nest boxes on a 20,243-ha study area where only 3 nests had been reported during the preceding 20 years; in 5 years kestrels nested 77 times. Craig and Trost (1979) erected 20 nest boxes in Idaho and reported a 30% increase in the number of kestrel nests found during the next 2 years. In British Columbia 24 of 137 nest boxes erected for Barrow's Goldeneye (*Bucephala islandica*) were occupied by kestrels (Savard 1982). Over a 3-year period in Colorado, Stahlecker and Griese (1979) increased the local breeding population of kestrels from 6 to 25 pairs after erecting 25 nest boxes. Between 1977 and 1980 Bloom and Hawks (1983) had kestrels in 31% of 247 available nest boxes in California. Similarly, Wilmers (1983) reported kestrels in 31% of 151 nest boxes during a 2-year study in Pennsylvania and West Virginia.

The objectives of the present study were (1) to determine how placement and density of boxes influence kestrel nesting density and nest-site fidelity, and (2) to compare productivity of kestrels using nest boxes with those using natural nest sites.

Study area. -A 194-km² area in Boone County, Missouri, was subdivided into (1) a 90-km² control area of farmland interspersed with woodlots, old fields, and meadows, and no nest boxes; (2) a similar 78-km² experimental area in which 30 nest boxes were placed in the first year and an additional 20 were placed in the second year; and (3) the city of Columbia, Missouri, and immediate suburbs, which consisted of 26 km² with no nest boxes.

Materials and methods.—Kestrels were captured with bal-chatri traps and marked with painted U.S. Fish and Wildlife Service bands and colored plastic jesses. We used a $30 \times$ spotting scope and $9 \times$ binoculars to observe kestrels for more than 1700 h from September 1981 through August 1984.

Population densities of kestrels were determined by driving a route approximately 120 km long at an average speed of 48 km/h. A lateral distance of 400–1600 m (depending on the physiography) on both sides of the route was covered by 1 or 2 observers. Because the areas were intersected at 1.6 km intervals by a network of highways, streets, and gravel roads, the route allowed complete surveillance of the entire study area. Each survey took about 3 h to complete and included stops at designated spots to obtain counts from areas difficult to observe. At least one survey was completed per week throughout the year during the 3 years of the study.

The possibility of counting the same bird twice was minimized by the number of colormarked kestrels (70 adults) and by keeping track of all birds flying out of an area being surveyed and into an area yet to be covered. Surveys were conducted between 10:00 and 14:00 h on days with conditions of good visibility and low wind velocity. Because of the area's open habitat and kestrel use of powerlines, power poles, snags, and fence posts as perches, we feel our surveys were thorough.

Wooden nest boxes had floors of 25-30.5 cm², were 38 cm deep, and had an entrance hole of 7.6 cm diameter near the top. Boxes were placed between 5 and 14 m above the ground. Nest-box sites included buildings, silos, utility poles, and live trees. Nests were visited briefly near the end of incubation to determine clutch size, and again before fledging to count and band the young.

The study area's 232 natural cavities with an estimated diameter of 6-10 cm were measured for depth and width, and subsequently monitored.

Nesting phenology. — There was no difference in date of nest initiation in natural cavities and nest boxes. In 1982, the mean laying, hatching, and fledging dates were 1 April, 6 May, and 6 June, respectively. Hatching and fledging averaged one week later in 1983, when the first nest was initiated more than 1 week earlier, and the latest nest nearly a month later than in 1982. Nesting was 2 weeks later in 1984 than in 1983. The time from earliest to latest initial nestings was just over 30 days during the first year, more than 75 days in the

Nesting Densities of American Kestrels in Central Missouri, 1982–84									
Study area	km²	1977-1981ª		1982		1983		1984	
Urban control	26	5	0.13	6	0.23	8	0.31	6	0.23
Rural control	90	2	0.02	4	0.04	5	0.06	3	0.03
Rural experimental ^b	78	4	0.05	12	0.15	26	0.33	25	0.32
Total	194	11	0.06	22	0.11	39	0.20	34	0.18

TADIE 1

* No nest boxes during this period.

^b Control areas had no nest boxes; the experimental area had 30 nest boxes in 1982, 50 in 1983, and 45 in 1984.

second, and about 45 days in the third. In 1983 the unusually warm spring-like weather during winter, coupled with winter weather during early spring, probably caused the prolonged nesting period (Roest 1957). In 1984 an exceptionally wet spring probably caused kestrels to begin nesting 15 days later. Kestrels began copulating and mutual perching in December or January each year. During March and April 1983, when mild weather was regularly interrupted by cold weather, kestrels stopped courting.

Population densities. - Prior to the erection of nest boxes, mean nesting density of kestrels was ca 0.06 pair per km² (1977-81) (Table 1). The number of nesting kestrels increased markedly in the area after the 50 nest boxes were in place in 1982 and 1983 (Table 1). Kestrels nested in 53% of the 125 boxes available during the 3 years of the study.

The notable increase in nesting kestrels between 1982 and 1983 may be due to the simultaneous increase in food abundance and nest availability, while the slight decline from 1983 to 1984 may be the result of a marked decrease in food supply. Although we did not quantify population densities of rodents, observations and interviews with farmers throughout our study area indicated a high vole (Microtus spp.) population in 1983 and a crash in 1984.

In the experimental area, densities of wintering kestrels increased from 0.22 birds/km² during winters preceding the study to 0.30 birds/km² during the first year (1982), 0.40 birds/ km² during the second year, and 0.42 birds/km² during the third year of the study. The difference between the years preceding and following erection of the boxes was significant $(\chi^2 = 5.34, df = 1, P < 0.05)$. During the winter of 1982–83 kestrels roosted in all 50 boxes. Mills (1975) mentioned the importance of winter roost availability as a factor limiting kestrel populations in Ohio. We also saw kestrels using the tops of nest boxes as feeding platforms during winter, and during several sleet storms kestrels hunted while perching in the nestbox hole.

Location of natural nests and nest-box sites. - Natural nest sites used by kestrels in the study area included buildings (84%), both abandoned and occupied, and cavities made by Northern Flickers (Colaptes auratus), Pileated Woodpeckers (Dryocopus pileatus) and Redheaded Woodpeckers (Melanerpes erythrocephalus) (16%). Two of the woodpecker cavities used by kestrels were in trees or snags; 3 were in power poles.

Kestrels seemed to prefer to nest in nest boxes even when there was an abundance of suitable natural cavities nearby (see also Hamerstrom et. al 1973). Nest boxes that were placed within 20 m of woodlots, however, were used by fox squirrels (Sciurus niger), which sometimes evicted kestrels. Wilmers (1983) reported that kestrels avoided nest boxes near the borders of woods.

Kestrels rarely used boxes on live trees, using both poles ($\chi^2 = 52.10$, df = 1, P < 0.01)

TABLE 2

NEST-BOX USE BY BREEDING AMERICAN KESTRELS IN BOONE COUNTY, MISSOURI, 1982-84

Nest-box location	No. available	% of available used	% nesting success ^a	
Utility poles	61	79	78	
Building and silos	22	68	64	
Live trees	42	7	33	
All sites	125	53	73	

* A successful nest was one that fledged young.

and buildings ($\chi^2 = 28.05$, df = 1, P < 0.01) significantly more often. Stahlecker and Griese (1979), working in Colorado, also reported a high occupancy rate (73%) in boxes on power poles.

Nesting success. — In 14 instances nest boxes were used by kestrels but no eggs were laid. Eggs were laid but nests failed in 8 cases, 3 of these clutches were destroyed by raccoons, 3 had broken eggs, and at 2 sites the eggs failed to hatch.

Young fledged from 52 broods in 46 boxes involving 43 pairs (including second broods) (Toland 1985). Thus, at least one young fledged from 70% (46 of 66) of the boxes used. Nesting success (total young fledged divided by total eggs laid) of kestrels in pole-mounted and building-mounted boxes was 78% and 64%, respectively (excluding a box where a yearling pair hatched 1 of 13 eggs laid). Pairs nesting in boxes on trees had a nesting success of 33% (Table 2). The nest success rate in pole-mounted boxes was significantly higher than in boxes on trees ($\chi^2 = 11.76$, df = 1, P < 0.01), but the difference between building-mounted boxes was not statistically significant ($\chi^2 = 3.78$, df = 1, P > 0.05).

Physical characteristics of natural and nest-box sites were similar. The average height of nest boxes was 7.2 m; that of natural sites averaged 9.8 m ($\chi^2 = 0.40$, df = 1, P > 0.05). Kestrels used 72% of the 7-m or higher nest boxes, but only 36% of the 6-m or lower boxes ($\chi^2 = 11.60$, df = 1, P < 0.01). The average diameter of the nest hole was 7.6 cm in nest boxes and 9.4 cm in natural cavities ($\chi^2 = 0.20$, df = 1, P > 0.05). The average distance from the nest to the favorite plucking post was 20.5 m from boxes and 30.0 m from natural sites ($\chi^2 = 2.0$, df = 1, P > 0.05). Kestrels nesting in natural sites seemed to prefer southerly or easterly openings (68%), even though there may have been more available cavities facing north or west because buildings in the area deteriorate more severely from weathering on their north and west sides. Kestrels chose nest boxes with southerly or easterly openings (68%), as well as a preference for higher nest cavities (Brauning 1983). The former most likely protects birds from northerly storms and increases solar exposure, while the latter increases protection from ground predators (Balgooyen 1976, Brauning 1983).

Annual productivity. — During the first year, hatching success in boxes was less than half that found in natural cavities (Table 3). This is in part attributable to predation by raccoons (3 clutches) and other disturbances (4 clutches cracked). Although care was taken to simulate natural nest sites when placing nest boxes, some sites may have been more accessible to predators. After moving 3 tree boxes that suffered predation in 1982 to new sites less accessible to mammalian predators, no predation occurred in these boxes during the following 2 years. The sudden availability of nest sites after placement of the boxes may have allowed inexperienced yearlings and adult nonbreeders to nest (Newton 1976, 1979). Two

BOONE COUNTY, MISSOURI, 1982–84								
Site	No. pairs	Total no. eggs	No. nesting attempts	% hatching success	No. fledged	% fledging success ^b	Produc- tivity ^c	% overall nesting success
Nest boxes								
1982	6	44 (4.8) ^a	15	34	15	100	2.5	34.1
1983	23	172 (5.3)	124	72	123	98	5.4	71.5
1984	17	81 (4.8)	72	89	69	96	4.06	85.2
All years	46	297 (5.0)	211	71	207	98	4.5	70.0
Natural cav	ities ^a							
1982	11	63 (5.0)	57	90	54	95	5.0	85.7
1983	13	80 (5.2)	71	. 89	71	100	5.46	88.8
1984	4	19 (4.8)	15	79	14	93	3.5	73.7
All years	28	162 (5.1)	143	88	139	97	5.0	86.0

TABLE 3

SUCCESS OF AMERICAN KESTREL NESTS IN BOYES VERSUS THOSE IN NATURAL CAUTTER DI

* Mean size of initial clutches shown in parentheses.

^b Number fledged divided by number hatched.

° No. fledglings/nest.

^d Includes woodpecker cavities and holes in buildings.

kestrels produced in boxes in 1982 subsequently nested as yearlings in boxes in 1983. One was a yearling female paired with a color-marked male yearling that produced one fledgling from 13 eggs. The other was a color-marked yearling male mated with an adult female where 5 eggs were infertile.

Reuse of nest-sites. - Successive use of the same territory for at least 2 years occurred in 70% of the color-marked nesting pairs. Consecutive use of the same nest sites occurred in 62% of these pairs.

Six boxes used in 1982 were reoccupied in 1983, and 18 boxes used in 1983 were reused in 1984. One nesting site on a building was occupied for at least 6 successive years (J. Peters, pers. comm.), and another was used for at least 5 years. A natural cavity was occupied by kestrels during 4 consecutive years, and 4 other cavities were used for at least 3 years each. Craighead and Craighead (1956) reported a kestrel pair using the same nest for 6 consecutive years, and Balgooyen (1976) reported that 61% of the nesting territories he studied were reoccupied.

Summary.-Both nesting and wintering populations of kestrels increased significantly after implementation of nest boxes. More "natural" nests were in buildings than in tree cavities. Similarly, kestrels nested in nest boxes mounted on buildings and utility poles significantly more often than they nested in tree-mounted nest boxes. Nesting success was significantly higher in boxes mounted on man-made structures than on trees. Physical characteristics of nest sites, including nest height, orientation, cavity-hole diameter, and distance from plucking perch, were similar for boxes and natural cavities. Although nesting success of kestrels using nest boxes was lower than in natural nest sites during the first 2 years of the study, the persistent nature of nesting kestrels (double broods, replacement clutches) enabled them to produce the same number of young per nest in nest boxes as in natural sites.

Acknowledgments.—We sincerely thank N. Thompson-Toland, T. Haithcoat, D. Scarbrough, and M. Miller who provided valuable assistance in the field. F. N. Hamerstrom and G. S. Mills made many helpful suggestions on an earlier draft of this paper. K. Bildstein, D. Bird, and P. Gowaty made editorial comments that improved the manuscript. W. Sanderson generously provided transportation, equipment and complete freedom to work on the University South Farms. The Natural History Section of the Missouri Department of Conservation funded this study.

LITERATURE CITED

- BALGOOYEN, T. G. 1976. Behavior and ecology of the American Kestrel (*Falco sparverius*) in the Sierra Nevada of California. Univ. California Publ. Zool. 103.
- 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.
- BRAUNING, D. 1983. Nest site selection of the American Kestrel (Falco sparverius). Raptor Res. 17:122.
- CADE, T. J. 1982. The falcons of the world. Cornell Univ. Press, Ithaca, New York.
- CRAIG, T. 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.
- CRAIGHEAD, J. J. AND F. C. CRAIGHEAD. 1956. Hawks, owls and wildlife. Stackpole, Harrisburg, Pennsylvania.
- HAMERSTROM, F., F. N. HAMERSTROM, AND J. HART. 1973. Nest boxes: an effective management tool for kestrels. J. Wildl. Manage. 37:400-403.
- MCCOMB, W. C. AND R. NOBLE. 1981. Nest box and natural-cavity use in three mid-south forest habitats. J. Wildl. Manage. 45:93-101.
- MILLS, G. S. 1975. A winter study of the American Kestrel in central Ohio. Wilson Bull. 87:241–247.
- NAGY, A. C. 1963. Population density of Sparrow Hawks in eastern Pennsylvania. Wilson Bull. 75:93.
- NEWTON, I. 1976. Population limitation in diurnal raptors. Can. Field-Nat. 90:274-300.
- ------. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota.
- ROEST, A. I. 1957. Notes on the American Sparrow Hawk. Auk 74:1-19.
- SAVARD, J. P. L. 1982. Barrow's Goldeneye nest-box utilization in the Cariboo parkland, British Columbia: year 1. Canadian Wildl. Serv. Progress Notes No. 131:1–4.
- STAHLECKER, D. W. AND H. J. GRIESE. 1979. Raptor use of nest boxes and platforms on transmission towers. Wildl. Soc. Bull. 7:59-62.
- TOLAND, B. R. 1985. Double brooding by American Kestrels in central Missouri. Condor 87:434–436.
- WILMERS, T. J. 1983. Kestrel use of nest boxes on reclaimed surface mines in West Virginia and Pennsylvania. (Abstract) Raptor Res. 17:30–31.

BRIAN R. TOLAND AND WILLIAM H. ELDER. 112 Stephens Hall, School of Forestry, Fisheries, and Wildlife, Univ. Missouri, Columbia, Missouri 65211. (Present address of BRT: Florida Game and Fresh Water Fish Commission, P.O. Box 1840, Vero Beach, Florida 32961.) Received 21 Mar. 1986, accepted 30 Apr. 1987.