Wilson Bull., 105(3), 1993, pp. 465–474

REPRODUCTIVE SUCCESS OF AMERICAN KESTRELS NESTING ALONG AN INTERSTATE HIGHWAY IN CENTRAL IOWA

DANIEL E. VARLAND[1] AND THOMAS M. LOUGHIN[2]

ABSTRACT.—We studied the reproductive success of American Kestrels (*Falco sparverius*) nesting in nest boxes attached to the backs of highway signs along Interstate 35 (I-35) in central Iowa, 1988–1992. Nest box occupancy averaged 45.1%. All nest boxes faced either north or south, and there was no significant association between nest box occupancy and nest box orientation. European Starlings (*Sturnus vulgaris*) built nests in almost every nest box not occupied by kestrels. Apparent nesting success, the percentage of nests fledging at least one young, averaged 68.9%. There was no significant association between apparent nesting success and nest box orientation. Using the Mayfield method, we detected a significantly lower probability of survival during the incubation stage than during the brood-rearing stage. Clutch size averaged 4.8 over the five years of the study, and mean hatching success was 62.5%. Mean brood size was 3.1, and mean number of young in a brood to fledge was 2.9 (90.9% fledging success). The kestrels in this study had reproductive success similar to that of kestrels nesting in nest boxes in other areas of North America. *Received 10 Nov. 1992, accepted 22 Feb. 1993.*

American Kestrel (*Falco sparverius*) nesting in boxes was first reported in the 1930s (Kalmbach and McAtee 1930, Bent 1938), and since that time others have shown that providing nest boxes for kestrels can increase breeding densities (Hamerstrom et al. 1973, Stahlecker 1979, Bloom and Hawks 1983, Toland and Elder 1987). Boxes have been attached to trees (Bloom and Hawks 1983, Toland and Elder 1987), wooden posts (Wheeler 1992), utility poles (Stahlecker 1979, Toland and Elder 1987), and buildings (Hamerstrom et al. 1973, Toland and Elder 1987). In 1988, we began a study of kestrels nesting in nest boxes on signs along I-35 in central Iowa. In this paper, we describe the reproductive success of kestrels using these boxes. We also compare the reproductive success of kestrels nesting along the interstate highway with that of kestrels using nest boxes elsewhere in North America.

STUDY AREA AND METHODS

The nest boxes in this study were placed on both sides of the north-south highway at about 2-km intervals (Fig. 1). All nest boxes faced north or south. Land bordering the interstate is farmed intensively with row crops. Field work was conducted in central Iowa between 1988 and 1992. We monitored 50 nest boxes in 1988, 1991, and 1992 (Story and

[1] U.S. Fish and Wildlife Service, Iowa Cooperative Fish and Wildlife Research Unit, Science II, Iowa State Univ., Ames, Iowa 50011. (Present address: ITT Rayonier Inc., P.O. Box 200, Hoquiam, Washington 98550.)
[2] Dept. of Statistics, Snedecor Hall, Iowa State Univ., Ames, Iowa 50011. (Present address: Dept. of Statistics, Kansas State Univ., Manhattan, Kansas 66502.)

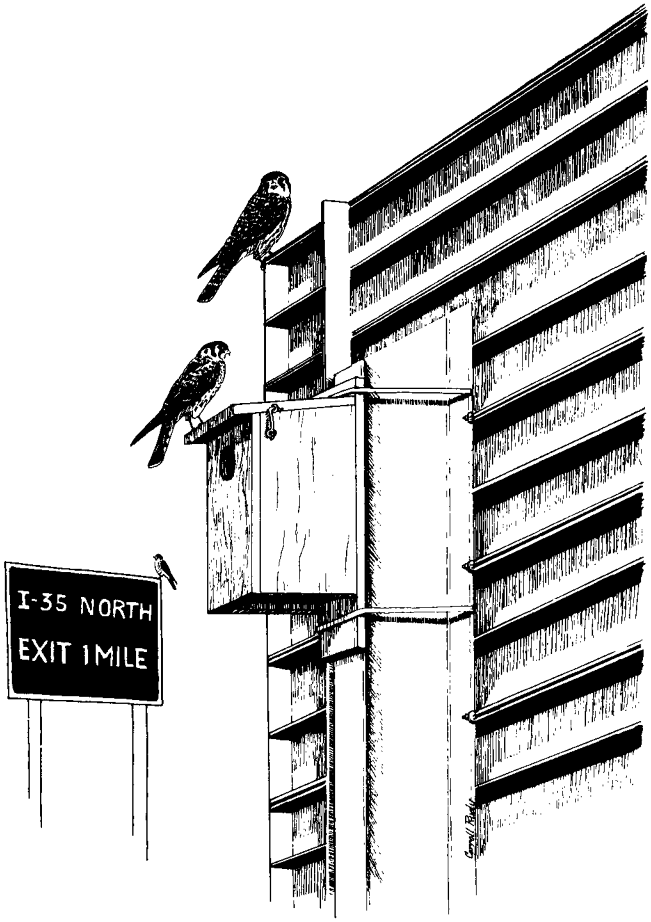

FIG. 1. American Kestrel nest box attached to an I-beam on the back of an interstate highway sign.

Hamilton counties); 72 in 1989 (Story, Hamilton, and Franklin counties); and 90 in 1990 (Story, Hamilton, Franklin, and Cerro Gordo counties). In late February or early March of each year, the nest boxes were repaired and about 8 cm of pine-wood shavings were placed in the bottom of each box. We monitored nesting activity at intervals of 1–10 days from early May through mid-August. When we found European Starling (*Sturnus vulgaris*) nests, which frequently contained eggs or young, we removed them and added wood shavings again. Starlings initiated nesting either by placing grass and other nesting materials in the nest box after removing the wood shavings, or by placing these materials on top of the wood shavings. Nesting substrate for kestrels was wood shavings, grass (nests built by starlings), or bare wood (nests in which >50% of the floor of the nest box lacked nesting material).

In 1990 we experimentally adjusted the size of kestrel broods to two siblings in 15 nests and five siblings in nine nests to study the influence of brood size on foraging efficiency (Varland and Loughin 1992). Because these adjustments were made when young were ready to fledge, data on reproductive success (e.g., brood size, fledging success) were recorded according to the status of these nests before the manipulations occurred.

Statistical analyses.—We used the traditional apparent success method (nests fledging at least one young) and the Mayfield method (Mayfield 1961, 1975) to estimate nesting success. The Mayfield method avoids overestimates of nesting success that result when some nesting failures, especially those early in the nesting cycle, are undetected. Because intervals between our nest visits were not constant, we used the maximum likelihood estimator (MLE) of the survival rate as described by Bart and Robson (1982). For these computations, we used a PC SAS version of "Program MAYFIELD" (Krebs 1989:609–611). We calculated the probability of nest survival by Mayfield analysis for the incubation and brood-rearing periods, which are both 29 days (Bird and Palmer 1988). We used a normal statistic on transformed daily survival rates, as suggested by Bart and Robson (1982), to test for differences in the probability of survival between the two periods for each year, and we used one-way ANOVA to test for differences across all years. Kestrels entering the brood-rearing period must have first survived the incubation period. Thus, tests for differences in survival between periods were made on data sets that were not independent of one another, because they contained some of the same birds. Caution should be used in interpreting results of the tests.

The observational unit (N) was the nest. For each nest, we determined clutch size, hatching success (% of eggs laid that hatched), brood size (number of birds in a brood where at least one egg was laid), fledging success (% of young hatched that fledged), and number of birds in a brood to fledge. Only kestrels $\geq$22 days old on the last nest visit were classified as having fledged (Steenhof 1987). We computed the yearly means for clutch size, hatching success, brood size, fledging success, and number of birds in a brood to fledge by averaging across nests. We used the Kruskal-Wallis test (Randles and Wolfe 1979) to test for differences among years for each of the parameters of nesting success.

We tested for associations of nest box occupancy and nesting success with nest box orientation (north vs south). For these analyses, we used the Chi-square test for contingency tables to test for differences in each of the five years of the study. We used the Cochran-Mantel-Haenszel (CMH) test (Agresti 1990:230) to evaluate differences across years.

RESULTS AND DISCUSSION

Nest box occupancy.—Nest box occupancy by kestrels averaged 45.1% for the five years of the study, 1988–1992 (Table 1). This occupancy rate is within the range of rates reported for kestrels occupying nest boxes in other areas of North America (average = 41.8; Table 2).

We detected no significant association between nest box occupancy and box orientation (north vs south) for each year of the study (Chi-square test: 1988, $P = 0.18$; 1989, $P = 0.05$; 1990, $P = 0.86$; 1991, $P = 0.37$; 1992, $P = 0.98$) or for the years combined (CMH test, $P = 0.92$). Other studies have reported that kestrels prefer to use nest boxes facing east or south (Balgooyen 1976, Raphael 1985, Toland and Elder 1987). In California, kestrels occupied cavity nests in trees facing east significantly more often than expected (Balgooyen 1976), an observation corroborated in additional work by Raphael (1985). Toland and Elder (1987) found that 68% of kestrel nests in natural cavities and 67% of the nests in nest boxes faced east or south, but they did not evaluate these occupancy rates in the context of cavity availability.

TABLE 1

REPRODUCTIVE SUCCESS OF AMERICAN KESTRELS ALONG INTERSTATE HIGHWAY 35 IN CENTRAL IOWA, 1988–1992

Variable	1988 (N) Mean ± SE	1989[a] (N) Mean ± SE	1990[b] (N) Mean ± SE	1991 (N) Mean ± SE	1992 (N) Mean ± SE	All Years (N) Mean ± SE	*P*-values[c]
Occupancy (%)[d]	(50) 36.0	(66) 37.9	(90) 57.8	(50) 46.0	(50) 48.0	(5) 45.1 ± 3.9	—
Apparent success (%)[e]	(18) 77.8 ± 0.1	(25) 72.0 ± 0.1	(52) 51.9 ± 0.1	(23) 82.6 ± 0.1	(24) 60.0 ± 0.1	(5) 68.9 ± 5.7	—
Clutch size	(11) 4.8 ± 0.2	(20) 5.0 ± 0.1	(15) 4.8 ± 0.1	(18) 4.8 ± 0.1	(16) 4.8 ± 0.1	(5) 4.8 ± 0.1	0.28
Hatching success (%)	(11) 67.3 ± 13.6	(20) 63.2 ± 8.6	(15) 44.0 ± 10.7	(18) 75.6 ± 8.6	(16) 62.5 ± 10.8	(5) 62.5 ± 5.2	0.23
Brood size	(18) 3.7 ± 0.4	(26) 2.6 ± 0.4	(47) 2.2 ± 0.3	(22) 3.8 ± 0.4	(21) 3.2 ± 0.4	(5) 3.1 ± 0.3	0.01
Fledging success (%)	(15) 93.3 ± 6.7	(15) 91.7 ± 6.8	(28) 85.7 ± 6.7	(18) 98.9 ± 1.1	(16) 85.0 ± 8.7	(5) 90.9 ± 2.6	0.72
Fledglings per brood	(18) 3.6 ± 0.5	(24) 2.3 ± 0.4	(47) 1.9 ± 0.3	(21) 3.8 ± 0.4	(20) 2.8 ± 0.5	(5) 2.9 ± 0.4	0.01

[a] One nest box occupied twice: first nest was successful, and outcome of the second was unknown.
[b] One nest box occupied twice: first nest was unsuccessful, and second was successful.
[c] Kruskal-Wallis test.
[d] Except for four nest boxes in 1989 and one in 1990, European Starlings initiated nesting in every nest box not occupied by kestrels.
[e] % of nests that fledged at least one young.

TABLE 2

REPRODUCTIVE SUCCESS (MEAN) OF AMERICAN KESTRELS USING NEST BOXES IN NORTH AMERICA

Location (reference)	No. of nest boxes available	Occupancy (%)	Apparent success (%)[a]	Clutch size	Hatching success (%)	Fledging success (%)	Brood size	Fledglings per brood
Iowa								
This study	50–90	45	69	4.8	62	91	3.1	2.9
Wisconsin								
(Hamerstrom et al. 1973)	50	25	20	—	—	—	—	—
Utah								
(Stahlecker 1979)	25	73	—	—	—	—	—	3.1
West Virginia								
(Wilmers 1982)	60–91	27	73	4.6	67	95	—	—
California								
(Bloom and Hawks 1983)	40–65	31	83	4.3	79	90	4.0	3.1
Missouri								
(Toland and Elder 1987)	22–61	53	73	5.0	71	98	—	4.5
Wyoming								
(Wheeler 1992)	35–42	—	—	4.7	81	90	3.7	—

[a] % of nests that fledged at least one bird.

Mean nest box occupancy by starlings between 1988 and 1992 was 52.2%. Except for five nest boxes not used by any avian species, starlings initiated nesting in every nest box not occupied by kestrels. Not all these nests, however, contained eggs or young. We removed starling nests from nest boxes when they were found, often before eggs were laid.

We have indirect evidence that kestrels evicted starlings from nest boxes. For those kestrel nests in which the nesting substrate was recorded (N = 115), 53% consisted of wood chips, 37% of grass, and 10% of bare wood. The nests with grass substrate were built by starlings and abandoned, at least in some cases, because they were taken over by kestrels.

We never observed kestrels remove starling eggs from a nest box, but on several occasions we found starling eggs or egg fragments beneath nest boxes in which kestrels were nesting. At one site, a male kestrel flew from a nest box as we approached. We found the female sitting on top of nine starling eggs. We banded her and returned to the nest six days later to find that the kestrel pair and starling eggs were gone. The female was observed incubating five kestrel eggs 11 days later in a box about 1.6 km from her first nest. The nest box in which this female was first seen was reoccupied by starlings.

Although our observations provide evidence that kestrels evicted starlings from nest boxes, starlings probably caused kestrels to abandon their nests as well (cf Wilmers 1987, Weitzel 1988). We checked 33 kestrel nests after nest failure and found that in 14 of these nests starlings had subsequently initiated nesting. We found kestrel eggs or egg fragments beneath three of these nest boxes. We do not know what caused any of these 33 nest failures, but harassment by starlings may have been responsible for some of the losses.

Nesting success.—Apparent nesting success averaged 68.9% between 1988 and 1992 (Table 1). We found no significant association between apparent nesting success and nest box orientation for each year of the study (Chi-square test: 1988, $P = 0.42$; 1989, $P = 0.78$; 1990, $P = 0.46$; 1991, $P = 0.85$; 1992, $P = 0.88$) or for the years combined (CMH test, $P = 0.55$). Apparent nesting success for kestrels using nest boxes elsewhere in North America ranged between 20 and 83% (average = 62.2%; Table 2). In Missouri, nesting success for American Kestrels was 78% for boxes on utility poles, 64% for boxes on buildings and silos, and 7% in natural cavities in trees (Toland and Elder 1987).

Using the Mayfield method, we detected a significantly lower probability of survival during the incubation stage than in the brood rearing stage for 1989 and 1990 (Z test; Table 3) and for the years combined (ANOVA, $F_{1,4} = 10.7$, $P = 0.03$). During the five years of the study, 49 of 142 kestrel nests failed; 40 of the failures occurred during the incubation stage and nine during the brood rearing stage.

TABLE 3
SURVIVAL RATES OF AMERICAN KESTREL NESTS ALONG INTERSTATE HIGHWAY 35 IN CENTRAL IOWA, 1988–1992[a]

	Incubation period	Brood rearing	*P*-values[b]
1988			
Survival rate	76%	93%	0.24
95% CI[c]	56–100%	81–100%	
(N)	(18)	(15)	
1989			
Survival rate	64%	94%	0.02
95% CI	47–86%	83–100%	
(N)	(25)	(16)	
1990			
Survival rate	39%	84%	<0.01
95% CI	25–61%	71–100%	
(N)	(52)	(33)	
1991			
Survival rate	86%	100%	N.S.[d]
95% CI	73–100%	—[e]	
(N)	(23)	(20)	
1992			
Survival rate	75%	81%	0.66
95% CI	59–95%	63–100%	
(N)	(24)	(18)	

[a] Survival rates were determined by the Mayfield method (Mayfield 1961, Mayfield 1975).
[b] *Z*-test based on daily survival rates.
[c] CI = confidence interval.
[d] Determination of nonsignificance based on confidence interval for incubation period.
[e] Confidence interval test cannot be calculated because all nests monitored were successful.

Incubation stage.—The median date of the start of incubation in 1988–1992 was 24 April. The earliest date of incubation initiation for these five years was 1 April, while the latest date was 23 June. American Kestrel clutch size averaged 4.8 over the five years of the study, with no significant difference among years (Kruskal-Wallis test; Table 1). Clutch sizes for kestrels using nest boxes elsewhere in North America were similar to those in our study (Table 2). The median hatching date for 1988–1992 was 23 May. The earliest date of hatching was 30 April and the latest 22 July.

Mean hatching success for 1988–1992 was 62.5%, and we detected no significant difference among years (Kruskal-Wallis test; Table 1). Hatching success in our study was lower than the rates reported for kestrels elsewhere (Table 2), but these differences may be attributable mainly to an extremely low hatching success rate in 1990. Values for the other years were comparable to those from other studies.

In our study, all 12 clutches on a substrate of bare wood failed during the incubation stage. Egg chilling due to insufficient substrate for insulation probably was the primary reason for egg failure on bare wood. Starlings, however, may have been indirectly responsible for these nest failures, as they generally removed wood chips from nest boxes while building their nests.

We accidentally broke one egg in each of four clutches of five eggs while handling the adult kestrels in these nest boxes. We do not know what caused the other mortalities during the egg stage; factors such as egg infertility, addling, removal by starlings, nest abandonment, and predation probably were responsible. Predation was probably not a major factor contributing to nest failure, as the nest boxes were attached to steel I-beams. On one occasion, however, we found raccoon (*Procyon lotor*) scat on the lid of a nest box about 20 m above the ground, so mammalian predation may have occurred in a few cases.

Brood rearing stage.—The average brood size for 1988–1992 was 3.1, and the average number of young in a brood to fledge was 2.9 (Table 1). We detected a significant difference among years for each of these two measures of reproductive success (Kruskal-Wallis test; Table 1). Mean brood size and number of birds to fledge were lower in our study than in others, but the differences may not be significant (Table 2).

In our study, 12 nests exhibited some brood loss. All brood members died in nine nests, and partial brood losses occurred in the other three. In seven of the 12 nests, including the three with partial brood losses, the young disappeared. Young from these nests may have been cannibalized by their parents and/or siblings (Bortolotti et al. 1991). We found no evidence (e.g., partially eaten young), however, to support this.

We determined that starvation was the cause of death for one brood of two, but we do not know how the other birds died. The low rate of nest failure during brood rearing and, in particular, the low rate of starvation among nestlings indicate that parents were able to provision their young.

A lack of prey, however, may have contributed to nest failure during the incubation stage. Nest desertion because of limited prey was the most important cause of nest failure during incubation for the Eurasian Kestrel (*Falco tinnunculus*) in Holland (Cave 1968).

Fledging success averaged 90.9% over the five years of the study and there was no significant difference among years (Kruskal-Wallis test; Table 1). The fledging success in our study was similar to the rates for kestrels using nest boxes in other areas (average = 93.3%; Table 2).

The median fledging date for the five years of the study was 20 June. The earliest date of fledging was 25 May, and the latest was 20 August. Only two of 16 mortalities among the 61 radio-marked fledglings died because of collisions with vehicles along the interstate (Varland et al. 1993). This suggests that traffic along the interstate was not a major source of mortality for fledglings.

Reproductive success of kestrels nesting in nest boxes along I-35 was similar to that of kestrels using nest boxes in other settings across North America. The I-beams to which the boxes were attached provided a strong support and a high perch so that nests were not easily accessed by predators. Nest boxes on interstate signs have given kestrels nesting opportunities that would not exist otherwise across much of Iowa's agricultural landscape.

ACKNOWLEDGMENTS

This paper is a contribution of the Iowa Cooperative Fish and Wildlife Research Unit, U.S. Fish and Wildlife Service; Iowa State Univ. (ISU); Iowa Dept. of Natural Resources (IDNR); and the Wildlife Management Institute. It is Journal Paper No. J-15121 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, Project No. 2845. Support was received from the Iowa Dept. of Transportation, IDNR Nongame Program, Iowa Ornithologists' Union, North American Bluebird Society, Iowa Science Foundation, Big Bluestem Audubon Society of Ames, Iowa, Max McGraw Wildlife Foundation, Iowa Agriculture and Home Economics Experiment Station, and the ISU Dept. of Animal Ecology. We are grateful to Mike Meetz, IDNR Nongame Technicians Bruce Ehresman and Pat Schlarbaum, and ISU students Tami Holmes, Kathy Andersen, Kandi Moeller, Patrick Emge, Vern Windsor, Brian Warson, and Jason Humble for assistance in the field. We thank Carroll Rudy for the drawing and Ding-Hwa Lei for writing the PC SAS computer program for Program MAYFIELD. We also thank Erv Klaas, who provided advice, and Tom Carpenter, Jim Dinsmore, Larry Igl, John Smallwood, and an anonymous reviewer who read drafts of the paper and provided helpful comments.

LITERATURE CITED

AGRESTI, A. 1990. Categorical data analysis. John Wiley and Sons, New York, New York.

BALGOOYEN, R. G. 1976. Behavior and ecology of the American Kestrel (*Falco sparverius*) in the Sierra Nevada of California. Univ. Calif. Publ. Zool. 103:212–224.

BART, J. AND D. S. ROBSON. 1982. Estimating survivorship when the subjects are visited periodically. Ecology 63:1078–1090.

BENT, A. C. 1938. Life histories of North American birds of prey. U.S. Natl. Mus. Bull. 170.

BIRD, D. M. AND R. S. PALMER. 1988. American Kestrel. Pp. 253–290 *in* Handbook of North American birds, vol. 5 (R. S. Palmer, ed.). Yale Univ. Press, New Haven, Connecticut.

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., K. L. WIEBE, AND W. M. IKO. 1991. Cannibalism of nestling American kestrels by their parents and siblings. Can. J. Zool. 69:1447–1453.

CAVE, A. J. 1968. The breeding of the kestrel, *Falco tinnunculus* L., in the reclaimed area Oostelijk Flevoland. Netherl. J. Zool. 3:313–407.

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

KALMBACH, E. R. AND W. L. MCATEE. 1930. Homes for birds. U.S.D.A. Bull. No. 1456.

KREBS, C. J. 1989. Ecological methodology. Harper and Row, New York, New York.

MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255–261.

———. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456–466.

RANDLES, R. H. AND D. A. WOLFE. 1979. Introduction to the theory of nonparametric statistics. John Wiley and Sons, New York, New York.

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

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

STEENHOF, K. 1987. Assessing raptor reproductive success and productivity. Pp. 157–170 *in* Raptor management and techniques manual (B. A. Giron Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird, eds.). National Wildlife Federation, Washington, D.C.

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

VARLAND, D. E. AND T. M. LOUGHIN. 1992. Social hunting in broods of two and five American Kestrels after fledging. J. Raptor Res. 26:74–80.

———, E. E. KLAAS, AND T. M. LOUGHIN. 1993. Use of habitat and perches, causes of mortality and time until dispersal in post-fledging American Kestrels. J. Field Ornithol. 64:169–178.

WEITZEL, N. 1988. Nest-site competition between the European Starling and native breeding birds in northwestern Nevada. Condor 90:515–517.

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. 1982. Kestrel use of nest boxes on reclaimed surface mines in West Virginia and Pennsylvania. M.Sc. thesis, West Virginia Univ., Morgantown, West Virginia.

———. 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. Found., Inc. and Macdonald Raptor Res. Centre of McGill Univ., Ste. Anne de Bellevue, Quebec.