Nest Success of Southeastern American Kestrels Associated with Red-Cockaded Woodpeckers in Old-Growth Longleaf Pine Habitat in Northwest Florida

KATHLEEN E. GAULT[1,*], JEFFREY R. WALTERS[2], JOSEPH TOMCHO, JR.[1,3], LOUIS F. PHILLIPS, JR.[1,4], AND ANDREW BUTLER[1,5]

Abstract - The Southeastern American Kestrel (*Falco sparverius paulus*), a non-migratory subspecies of the widespread American Kestrel, has declined to the point that it is listed as threatened in Florida, the state in which it is most common. We studied the nesting biology of Southeastern American Kestrels in 1999 and 2000 at Eglin Air Force Base, FL, in old-growth longleaf pine savanna, a habitat type historically widely occupied by the kestrels. Most of the nest cavities we observed were in old-growth trees, both living and dead, and were originally excavated by Red-cockaded Woodpeckers (*Picoides borealis*) and then enlarged by other woodpecker species. Nesting success was 70% in 1999 and 56% in 2000. In 1999, 67% of eggs survived to become fledglings in successful nests, as did 58% in 2000. Nests in live pines and snags were equally successful, and nest success was positively related to cavity height in 1999. Reduced nesting success in 2000 may have been related to severe drought conditions. High nesting concentrations of up to 4 pairs per km^2 were observed. We suggest that stands of old-growth longleaf pine, with little or no hardwood midstory and a relatively high number of snags, inhabited by Red-cockaded Woodpeckers, may constitute high quality habitat for Southeastern American Kestrels. Therefore, loss of longleaf pine habitat, degradation of remaining longleaf habitat due to fire suppression and removal of old-growth and snags, and the decline of the Red-cockaded Woodpecker, a species on which kestrels may have depended as a source of nest cavities historically, may have contributed to the decline of the Southeastern American Kestrel.

Introduction

The American Kestrel (*Falco sparverius*) is the most widespread and abundant falcon in North America (Cade 1982, Johnsgard 1990). However, concerns exist about the status of the Southeastern American Kestrel, a non-migratory subspecies (*F. s. paulus* Howe and King 1902). In Florida, the state in which it is most common, the Southeastern American Kestrel is currently listed as threatened due to a substantial decrease in the population (Hoffman and Collopy 1988, McFarlane

[1]Virginia Tech RCW Research Team, PO Box 875, Niceville, FL 32588-0875. [2]Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061-0406. [3]Current address: 259N North Bear Creek Road, Asheville, NC 28806. [4]Current address: 726 North Eglin Parkway, Ft. Walton Beach, FL 32547. [5]Current address: 1209 Pinewood Lane, Crestview, FL 32539. [*]Corresponding author - rcwproj@earthlink.net.

1973). For example, the population in north-central Florida has declined an estimated 82% over 40+ years. There is little information on population status elsewhere in the subspecies' range, but its numbers are believed to be declining in Alabama and South Carolina as well (Smallwood 1990).

The preferred habitat of the Southeastern American Kestrel includes pasture-like areas, longleaf pine (*Pinus palustris*) sandhills, pine flatwoods, agricultural areas, parks, and golf courses (Bohall 1984, Bohall-Wood and Collopy 1986, Wiley 1978). The subspecies' decline is attributed to various human modifications of the landscape such as development, fire suppression, and removal of nest sites (snags) (Hoffman and Collopy 1988). In particular, open longleaf pine savannas, the former distribution of which closely matches the range of the Southeastern American Kestrel (Smallwood 1990), have declined by over 95% (Frost 1993). Most longleaf habitat was lost to clearing for agriculture and development, and conversion to larger, faster growing species such as slash (*P. elliottii*) and loblolly pine (*P. taeda*). What remained was degraded by fire suppression and loss of old growth. Fire suppression allows the development of a hardwood midstory, eliminating the open stand structure kestrels require (Hoffman and Collopy 1987). In Florida, habitat is being managed for several endangered and threatened species, including the Red-cockaded Woodpecker (*Picoides borealis*), eastern indigo snake (*Drymarchon corais couperi*) and gopher tortoise (*Gopherus polyphemus*), which are closely linked to the loss of longleaf pine-turkey oak sandhills, and the circumstantial evidence suggests a similar link with the decline of the Southeastern American Kestrel (Smallwood and Bird 2002).

American Kestrels are secondary cavity nesters, relying on cavities constructed by several species of woodpecker (Raphael 1985) such as Northern Flicker (*Colaptes auratus*), Red-headed Woodpecker (*Melanerpes erythrocephalus*) and Pileated Woodpecker (*Dryocopus pileatus*) (Stys 1993). Southeastern American Kestrels also nest in snags of various tree species including longleaf pine, turkey oak (*Quercus laevis*) and live oak (*Quercus virginiana*) (Hoffman and Collopy 1987). Use of cavities in live trees by kestrels is thought to be unusual (Hoffman 1983) because most primary cavity nesters excavate cavities in snags. The Red-cockaded Woodpecker is one of few species to excavate cavities in live pine trees, and it is associated with the Southeastern American Kestrel by virtue of extensive range overlap and a similar requirement for open pine stands (Smallwood and Bird 2002, USFWS 2003). These woodpeckers live in territorial family groups, and each territory contains a cluster of several cavity trees (Walters 1990). Only old pines (i.e., > 100 years old) contain sufficient heartwood in which to excavate a cavity (Conner et al. 1994). The entrance diameter of Red-cockaded Woodpecker cavities typically is only five cm (Jackson 1978), and therefore unaltered cavities are not large enough to accommodate kestrels. However, other larger woodpecker species often enlarge Red-cockaded Woodpecker cavities and thus enable larger secondary cavity users such as Wood Ducks (*Aix sponsa*), Eastern Screech-Owls (*Megascops asio*) and fox squirrels (*Sciurus niger*) to occupy them. The size of many of these enlarged cavities is appropriate for Southeastern American Kestrels. Thus in open pine savannas, where Red-cockaded Woodpeckers are present, Southeastern American Kestrels have access to nest sites not available in other habitats. Since populations of secondary cavity nesters, including American Kestrels, often are limited by nest site availability (Newton 1998, Smallwood and Bird 2002), this may explain the correlation between the distribution and abundance of these three species: longleaf pine, Red-cockaded Woodpecker, and Southeastern American Kestrel.

Eglin Air Force Base in northwest Florida is one of the few locations where this relationship may be examined. Eglin supports significant populations of both Red-cockaded Woodpeckers and Southeastern American Kestrels, and is one of the only areas in which substantial amounts of old-growth longleaf pine remain. While there has been some degradation of longleaf habitat by past periods of fire suppression and encroachment by sand pine (*P. clausa*), currently much of the old-growth pine is in good condition. On Eglin, unlike virtually anywhere else, both Red-cockaded Woodpecker cavities and old-growth (as opposed to second-growth) snags are available to Southeastern American Kestrels in large numbers, as they likely were historically. In this paper we present two years of data on reproductive success of Southeastern American Kestrels nesting in both live pines and snags in Red-cockaded Woodpecker cavity tree clusters on Eglin. Our objectives were to assess the value of cavities in live pines and old-growth snags as nest sites, and to evaluate productivity in an area similar to historic habitat.

Field-Site Description

Eglin Air Force Base is located in Santa Rosa, Okaloosa, and Walton counties in the western panhandle of Florida and encompasses approximately 188,000 ha. Although 10% of the area consists of cleared test ranges, the majority of the base is forested. Six major ecological associations occur on Eglin (Kindell et al. 1997); we restricted our study to two types of longleaf communities, the Sandhills Ecological Association and the Flatwoods Ecological Association. The sandhills community type, characterized by rolling sandhill ridges dissected by streams, occupies the majority (78%) of the base land area. Vegetation includes an overstory of longleaf pine, a midstory of oaks (predominantly turkey oak) and ground cover consisting of various forbs and grasses including gopher apple (*Licania michauxii*), bluestem (*Andropogon* spp.), and bracken fern (*Pteridium aquilinum*). The flatwoods community is characterized by an open canopy of longleaf and/or slash pine with little or no midstory and dense ground cover consisting of wiregrass (*Aristida stricta*), saw palmetto (*Serenoa repens*), and gallberry (*Ilex glabra*).

The amount of old-growth longleaf pine on Eglin is unusual compared to other landscapes in the southeast. Hardesty et al. (1997) reported that about 25% of the pines within the home ranges of 25 groups of Red-cockaded Woodpeckers on Eglin were > 100 years of age, and about 10% were > 150 years old. At other locations, for example Camp Lejeune Marine Base in North Carolina, trees > 100 years of age typically comprise < 1% of the pine timber (Zwicker and Walters 1999). Currently, all longleaf pine (both live and dead) is protected on Eglin. Forestry operations consist of removing off-site slash pine and sand pine and replanting longleaf in order to return the habitat to historic conditions. Prescribed fire, particularly growing season fire, is an integral part of this restoration process. Unlike in many state and national forests, dead trees are not salvaged and therefore numerous snags exist on the landscape. Snags are particularly numerous on Eglin because of tree mortality due to frequent lightning strikes, prescribed fires, and wildfires. Eglin has a large population of Red-cockaded Woodpeckers; in 2000 there were 301 active Red-cockaded Woodpecker cavity tree clusters and over 6000 Red-cockaded Woodpecker cavity trees (unpubl. data, K. E. Gault). Compared to other longleaf areas, on Eglin there appears to be greater availability of cavities for Southeastern American Kestrels and other secondary cavity nesters.

Methods

Searches for American Kestrel nests were largely coincident with monitoring activities at Red-cockaded Woodpecker clusters in 1999 and 2000. We monitored Red-cockaded Woodpecker breeding activity in 130 active clusters. Beginning the first week of April, each cluster was visited weekly to check for eggs and nestlings. Prior to this, we scouted for likely kestrel nest sites in the vicinity of each woodpecker cluster by looking for suitable sized cavities and kestrels in the area. During weekly visits to each cluster we continued to search for kestrel nests by observing behavior of kestrels and checking cavities using a Treetop Peeper (™ Sandpiper Technologies). In 2000, we also visited all known nest sites from the previous year. We did not search for kestrel nests outside of woodpecker clusters. Our goal was to locate ten nests in each tree type (live or dead) each year, and we looked for additional nests only when time permitted.

Once kestrel nests were found, we checked them every two weeks using the Treetop Peeper to record numbers of eggs and nestlings. We assumed, based on findings of Heintzelman and Nagy (1968), that one egg was laid every other day, and counted back from hatching in order to determine nest initiation dates. In order to avoid inducing young to fledge early, we last visited nests one week prior to the projected fledging date. If there were young still present at this last visit, we counted the nest as successful. After the nestlings had fledged we returned to the nest site to search for fledglings and in many cases we observed them, but we did not search beyond the vicinity of the nest site.

Nest success was calculated both as a proportion of the nests that successfully fledged young and also using the Mayfield method (Mayfield 1960, 1961, 1975). In calculating the daily and period survival rates using the Mayfield method, we broke the nesting cycle into two periods (Hensler 1985); the incubation period and the nestling period. We used 30 days as the complete length of each period (Wiley 1978). If a nest was found during the nestling cycle, it was not included in the calculations for the incubation cycle. If a nest failed between visits, we counted half the number of days between visits as the number of exposure days. In making the calculations we used only the days between actual visits. Days preceding the initial detection of the nest were not counted and neither were days after the last visit to the nest.

If a nest failed, we monitored the site for several weeks afterwards to detect renesting attempts, and we visited successful nest sites for several weeks post-fledging to detect double brooding attempts.

At each visit, we attempted to sex any adults that were present and record which sex was incubating, brooding or delivering food. We also collected the following data at each of the kestrel nest sites: date found, tree height, cavity height, cavity orientation, tree type (live tree or snag), and cavity type (old Red-cockaded Woodpecker cavity or not). We tested for differences in nest success based on these variables using a Mann-Whitney U test, and used logistic regression to simultaneously test relationships of all these variables to nest success. We did not use any statistical tests to compare data between years because in 2000 we searched for, and found, nests in the same cavities as in 1999. The 2000 data therefore are not random and not independent from the 1999 data.

Results

In 1999, we found 31 Southeastern American Kestrel nests in 29 different Red-cockaded Woodpecker clusters, 15 in live pine trees and 16 in snags. In 2000, we located 37 nests in 32 different clusters, 17 in live trees and 20 in snags. All of the nests in both years were in longleaf pine trees. Of the 30 cavities used as kestrel nest sites in 1999 (one cavity was used twice), 52% were reused in 2000. Forty-seven percent of cavities in snags and 94% of those in live pines were originally created by Red-cockaded Woodpeckers. The two cavities in live trees that were not created by Red-cockaded Woodpeckers appeared to be limb scars that were enlarged by another species of woodpecker.

Nest initiation dates ranged from 3 April to 23 June in 1999 and from 22 March to 20 June in 2000. The first three nests located in 2000 were in the same cavities as the first three found in 1999. In both years, last nests were renesting attempts. We did not observe any attempts at double brooding in either year.

The majority of nests contained five eggs, but few nests hatched all five eggs and fewer still fledged five young (Fig. 1). Mean clutch size

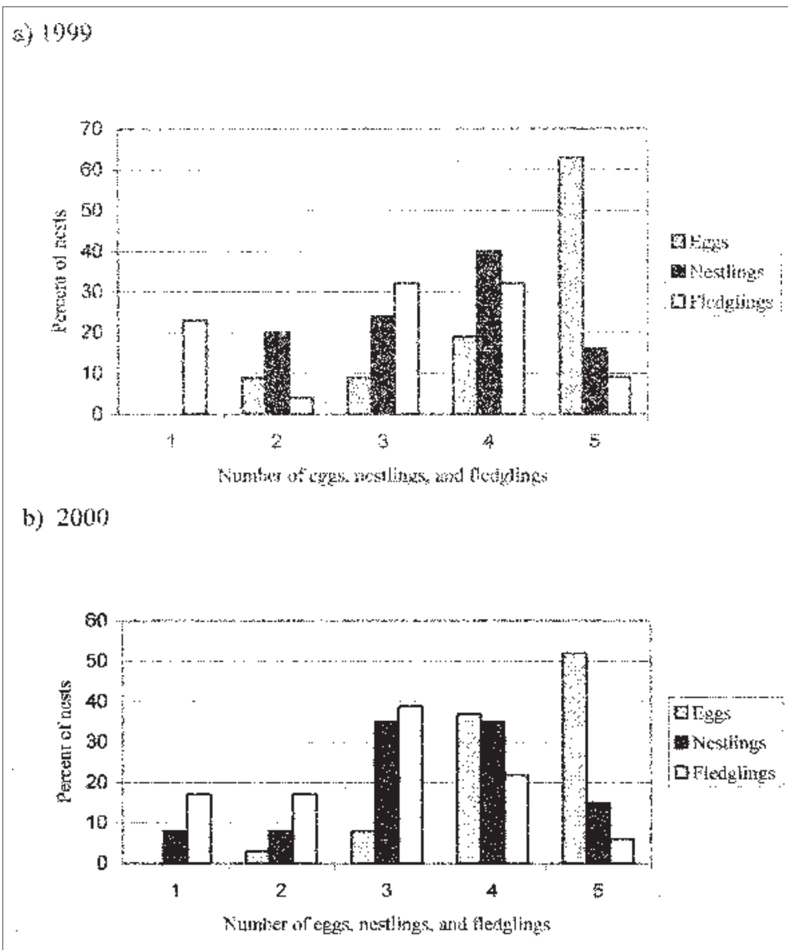

Figure 1. Frequency distributions of clutch sizes, nestlings per nest, and fledglings per nest for Southeastern American Kestrels on Eglin Air Force Base, Florida in (a) 1999 (N = 31) and (b) 2000 (N = 37).

(± SD) was similar in the two years (4.4 ± 0.9 in 1999 and 4.3 ± 1.0 in 2000) with a range of two to five eggs per clutch. Of 66 observations of incubating adults, the female was sitting on the eggs in 92% of them. Mean number of nestlings for all nests that hatched (3.5 ± 1.0 in 1999 and 3.4 ± 1.0 in 2000) and for successful nests (3.6 ± 1.0 in 1999 and 3.6 ± 1.1 in 2000) were nearly identical between years. Mean number of fledglings per successful nest was slightly lower in 2000 (2.7 ±1.2) than in 1999 (3.1 ± 1.3). Partial brood loss from successful nests occurred in both years. In 1999, 81% of eggs hatched and 84% of nestlings fledged so that 67% of eggs survived to become fledglings. In 2000, 83% of eggs hatched but only 60% of nestlings fledged and thus only 58% of eggs survived to become fledglings.

Nest success differed between the two years. In 1999, 70% of kestrel nests fledged young, whereas only 56% of nests fledged young in 2000. Using the Mayfield method of estimating nest success (rate ± SD), we calculated a 75% ± 10% overall success rate for nests in 1999 and a 58% ± 9% overall success rate in 2000. In both years the majority of nests that failed did so at the egg stage (75% in 1999 and 79% in 2000). Using the Mayfield method (rate ± SD), we calculated that in 1999 the probability of survival for the egg stage was 89% ± 7% while the probability of survival for the nestling stage was 84% ± 8%. In 2000, the probability of survival for the egg stage was only 69% ± 8% while the survival rate for the nestling stage was 83% ± 9%.

We observed only a single renesting attempt in 1999, hence only 11% of nest failures were followed by renesting. We observed five renesting attempts in 2000 (one successful), thus 33% of nest failures were followed by renesting. Two of the nests that we considered renesting attempts were not located in the same cavity as the original nest even though the first nest cavity was still available and appeared to be in good condition. Although the adults were not marked, we assumed that these were renesting attempts based on proximity to the original nest cavity and timing of nest initiation relative to the original nest failure.

We calculated means of several nest site variables for both successful and unsuccessful nests (Table 1). Cavity height was significantly higher for successful nests than unsuccessful nests (Mann-Whitney U = 90, *P* =

Table 1. Mean (± SD) of nest site variables for successful and unsuccessful Southeastern American Kestrel nests on Eglin Air Force Base, Florida, in 1999 and 2000 (first nesting attempts only).

	1999		2000	
Variable	Successful	Unsuccessful	Successful	Unsuccessful
Sample Size	21	9	19	14
Cavity Height	9.3 ± 2.7 m*	7.5 ± 2.8 m*	8.4 ± 2.9 m	8.7 ± 1.8 m
Tree Height	19.8 ± 3.4 m	18.4 ± 4.0 m	17.6 ± 4.2 m	19.0 ± 3.7 m
Cavity Orientation	187 ± 101°	190 ± 91°	221 ± 80°	200 ± 118°

* Within-year values are significantly different, see text for details.

0.045) in 1999. However, cavity height was not related to nest success in 2000 (Mann-Whitney U = 285, P = 0.451). None of the other nest site variables were significantly different between successful and unsuccessful nests in either year. In particular, nests in live trees and those in snags were equally successful (Table 2). We were unable to use all the variables in a logistic regression model of nest success because tree height and cavity height were highly correlated with one another, as were tree type and cavity type. Therefore we dropped two variables, tree height and cavity type, from the analysis. With three variables included in the analysis (tree type, cavity height, cavity orientation), the model was not a significant predictor of nest success ($\chi^2 = 3.46$, N = 70, df = 3, $P = 0.46$).

The causes of the majority of nest failures (96%) were undetermined. There was circumstantial evidence that three nest failures were due to predation, however. In one case, we found a Corn Snake (*Elaphe guttata guttata*) in a kestrel nest cavity with one remaining egg. This cavity was located 7.3 m above ground in a snag. In the second case, we observed a snake (Corn Snake or Gray Rat Snake, *Elaphe obsoleta spiloides*) in a nest cavity in a snag at a height of 12.7 m. This nest should have contained nestlings at the time of the discovery of the snake, but we were unable to confirm whether or not the eggs ever hatched. In the last case we observed eggshell fragments at the bottom of a kestrel nest tree approximately two weeks after incubation had begun indicating a possible incidence of predation. The following week a Red-bellied Woodpecker nest was observed in the nest cavity, suggesting that the Red-bellied Woodpecker may have removed the contents of the kestrel nest. In 2000, one nest failed when the cavity tree was burned during a prescribed fire.

Although we did not attempt to estimate densities of kestrels, we observed some nests in sufficiently close proximity to be noteworthy. In 1999, two clusters contained two kestrel nests (185 m apart and 200 m apart, respectively) and three of the four nests fledged young. In 2000, we observed two kestrel nests in each of three different woodpecker clusters and three kestrel nests in a single woodpecker cluster. In the cluster with three kestrel nests, two of the nests were approximately 30 m apart, and the third nest was approximately 200 m from the first two. In the three clusters

Table 2. Proportion of Southeastern American Kestrel nests in live trees and snags on Eglin Air Force Base, Florida, that were successful, in 1999 and 2000 (first nesting attempts only). Actual proportions of nests successfully producing young (% success) and Mayfield estimates of success (± SD) are presented.

Category	N	% success	Mayfield success %
1999 Live trees	15	80	82 (± 11)
1999 Snags	15	60	71 (± 13)
2000 Live trees	16	56	51 (± 13)
2000 Snags	16	56	63 (± 12)

that each had two kestrel nests, the distances between nests were 125 m, 165 m, and 167 m. We documented another square-kilometer area, encompassing three active Red-cockaded Woodpecker clusters, with a very high density of three kestrel nests in 1999 and four kestrel nests in 2000.

Discussion

In general, reproductive parameters for Southeastern American Kestrels nesting in Red-cockaded Woodpecker clusters on Eglin are similar to those reported from other areas. Clutch sizes were similar to the range of three to five described by Wiley (1978) and hatching rates were on the upper end of the ranges (64–89%) reported for American Kestrels by Balgooyen (1976), Heintzelman and Nagy (1968), Smith et al. (1972), and Stys (1993). Of the previous studies, all recorded data from natural nest sites except for Heintzelman and Nagy (1968), who studied reproduction in kestrels using nest boxes. Also, similar to Wiley (1978) and Johnsgard (1990), we observed females incubating the majority of the time, in fact a greater percentage of the time than reported by Balgooyen (1976) who observed females incubating 80–85% of the time. The proportion of nestlings fledged from successful nests in 1999, 84%, was intermediate to rates reported by Balygooyen (1976) (98%) and Smith et al. (1972) (76%). However, the fledging rate in 2000 (60%) was considerably lower than previously reported rates. We realize that we may have overestimated the number of fledglings per successful nest because our last visit to the nest was one week prior to fledging, but the error involved likely is small. The similarity of our two estimates of nest success suggest we estimated this parameter accurately.

The lower fledging rate and poor reproductive success in 2000 may have been related to drought conditions that existed across north Florida. Rainfall was 25–50 cm below normal in 2000, and this followed two previous years of lower than normal rainfall (pers. comm., Florida Climate Center, Tallahassee, FL). For Red-cockaded Woodpeckers on Eglin, 2000 was the poorest year reproductively since monitoring began in 1992 (Walters et al. 2002). The coincidental declines in productivity of the two species suggest that an environmental factor such as drought was the cause.

An average nest cavity height of 8.6 m was slightly higher than that reported by Hoffman (1983) (7.25 m), and cavity height was related to nesting success in one year (1999). Higher nest cavities might provide greater protection from climbing nest predators such as snakes. However, one snake successfully preyed upon a nest that was 12.7 m high, indicating that a high nest does not guarantee immunity against predation by snakes. Nest height is probably not a factor in predation by other bird species or nest loss due to environmental factors, which may explain the lack of effect of nest height in 2000.

While some aspects of the kestrel's breeding biology were similar to other studies, we observed some differences. Our findings agree with those of Hoffman (1983) and Hoffman and Collopy (1987) in that the majority of nest cavities were in longleaf pine. However, unlike in north-central Florida where almost all of the nest cavities were located in snags (Hoffman 1983), we observed kestrels nesting in live pine trees frequently. Hoffman (1983) conducted his study in an area in which there were no Red-cockaded Woodpeckers and therefore few or no cavities in live pine trees. The majority (70%) of kestrel nest cavities we observed at Eglin were originally excavated by Red-cockaded Woodpeckers and then enlarged by other woodpecker species. The more than 6000 documented Red-cockaded Woodpecker cavity trees on Eglin (unpubl. data, K.E. Gault) thus provide a large number of current and future nest sites for kestrels and other cavity nesting species.

Southeastern American Kestrels exhibit a high degree of territory fidelity, often using the same territory during successive years (Bohall-Wood and Collopy 1986). Over half of the nest cavities we monitored during 1999 were reused in 2000. The use of nest cavities in live pines supports territory fidelity as live trees are likely to persist from one year to the next, whereas snags deteriorate quickly. Although all of the 1999 nest cavities in live trees were still available as nest sites in 2000, several of the snags had fallen over or were broken at the cavity, making them unusable as nest sites in 2000. Since we detected no difference in nest success rate between live trees and snags, there should be no disadvantage to using live trees as nest sites, and kestrels using live trees would have the advantage of increased nest site longevity.

We observed exceptionally high local nesting densities of kestrels in several instances. We recognize that we did not conduct a complete population survey and that on average breeding densities at Eglin are probably lower than the extremes that we observed. However, our observations indicate that when suitable nest sites are readily available, as they are in Red-cockaded Woodpecker clusters in old-growth longleaf habitat, high breeding densities are possible. In one area we observed a nesting density of at least 4 pairs per km^2, and in several others we observed densities of at least 2 pairs per km^2. These densities are considerably higher than the 0.41 pairs per km^2 reported by Hoffman and Collopy (1987) and the 0.67 pairs per km^2 reported by Bohall (1984) in longleaf pine-turkey oak habitat elsewhere in Florida that lacked Red-cockaded Woodpeckers. That population densities of kestrel can be increased by providing nest boxes (Hamerstrom et al. 1973, Smallwood and Collopy 1993, Toland and Elder 1987) supports the notion that cavities excavated by Red-cockaded Woodpeckers might effect kestrel numbers.

We concur with Hoffman and Collopy (1988) that loss of longleaf pine habitat and degradation of remaining longleaf due to fire suppression are major factors in the decline in numbers of Southeastern American Kestrels. To these factors we would add habitat degradation due to loss of old-growth longleaf and the decline of the Red-cockaded Woodpecker. The 82% decline in the Southeastern American Kestrel population in Florida between the early 1940's and 1983 reported by Hoffman and Collopy (1988) is similar to the decline in longleaf during the same period. At present, approximately 3% of the original longleaf pine forests remain, and most of what remains is degraded (Frost 1993, Ware et al. 1993).

We propose that loss of longleaf forest generally, and of old growth stands and Red-cockaded Woodpeckers within remaining longleaf forests, results in loss of good quality kestrel nest sites. Old-growth snags, which are unavailable in most areas, may make particularly good nest sites, although this possibility has yet to be investigated. More importantly, Red-cockaded Woodpeckers require old-growth for cavity excavation (Conner et al. 1994). We have shown that these woodpeckers provide nest sites for the Southeastern American Kestrel, both in live trees and, when their cavity trees die, snags. As for habitat degradation due to fire suppression, the kestrel prefers open habitat with scattered pines (Bohall-Wood and Collopy 1986, Wiley 1978). Midstory encroachment resulting from lack of fire closes the canopy and makes habitat unusable by kestrels. Midstory encroachment also makes the habitat unsuitable for Red-cockaded Woodpeckers (Jackson 1994, Walters 1991).

The potential impact of Red-cockaded Woodpeckers on the population dynamics of Southeastern American Kestrels due to their effect on nest site limitation has not been sufficiently appreciated. Increases in nesting densities of kestrels in response to nest boxes (Hamerstrom et al. 1973, Smallwood and Collopy 1993, Toland and Elder 1987) suggest that kestrel populations may often be limited by availability of nest sites (see also Newton 1998), and our study indicates that kestrels will readily use cavities that have originally been created by Red-cockaded Woodpeckers as nest sites. The decline of the Red-cockaded Woodpecker, as a result of habitat loss and degradation and the resulting loss of potential nest sites, may have as much to do with the decline of the Southeastern American Kestrel as habitat loss itself.

Acknowledgments

We thank the Department of Defense, Eglin Air Force Base, for funding our work with Red-cockaded Woodpeckers and other cavity-nesting species on Eglin. Carl Petrick and Bruce Hagedorn from Eglin's Natural Resources Branch provided ideas, information, and assistance in many forms. We also appreciate the contributions of Richard McWhite, Dennis Teague, and others in Eglin's Natural Resources Branch, and the support of the Military Command and Range Control. This work was conducted under Research Work Order 41, through the

Virginia Cooperative Fish and Wildlife Research Unit in the Department of Fisheries and Wildlife Science at Virginia Tech. We appreciate the assistance of Unit biologists Michael Vaughan and Richard Neves, and others associated with the USGS-BRD Research Work Order System, particularly Shannon Fennell. Jim Kowalsky assisted with data collection.

Literature Cited

Balgooyen, R.G. 1976. Behavior and ecology of the American Kestrel (*Falco sparverius*) in the Sierra Nevada of California. University of California Publication in Zoology 103:1–87.

Bohall, P.G. 1984. Habitat selection, seasonal abundance, and foraging ecology of American Kestrel subspecies in north Florida. M.S. Thesis, University of Florida, Gainesville, FL. 97 pp.

Bohall-Wood, P.G., and M.W. Collopy. 1986. Abundance and habitat selection of two American Kestrel subspecies in north-central Florida. Auk 103:557–563.

Cade, T.J. 1982. The Falcons of the World. Comstock-Cornell University Press, Ithaca, NY. 188 pp.

Conner, R.N., D.C. Rudolph, D. Saenz, and R.R. Schaefer. 1994. Heartwood, sapwood, and fungal decay associated with Red-cockaded Woodpecker cavity trees. Journal of Wildlife Management 58:728–734.

Frost, C.C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Pp. 17–44, *In* S.M. Hermann (Ed.), The Longleaf Pine Ecosystem: Ecology, Restoration, and Management. Tall Timbers Fire Ecology Conference Proceedings, No. 18. Tall Timbers Research Station, Tallahassee, FL. 418 pp.

Hamerstrom, F., F.N. Hamerstrom, and J. Hart. 1973. Nest boxes: An effective management tool for kestrels. Journal of Wildlife Management 37:400–403.

Hardesty, J.L, K.E. Gault, and H.F. Percival. 1997. Ecological correlates of Red-cockaded Woodpecker (*Picoides borealis*) foraging preference, habitat use and home range size in northwest Florida (Eglin Air Force Base). Final Report, Research Work Order 99, Florida Cooperative Fish and Wildlife Unit, University of Florida, Gainesville, FL. 82 pp.

Heintzelman, D.S., and A.C. Nagy. 1968. Clutch sizes, hatchability rates, and sex ratios of sparrow hawks in eastern Pennsylvania. Wilson Bulletin 80:306–311.

Hensler, G.L. 1985. Estimation and comparison of functions of daily nest survival probabilities using the Mayfield method. Pp. 289–301, *In* B.J.T. Morgan and P.M. North (Eds.), Statistics in Ornithology. Springer-Verlag, New York, NY. 418 pp.

Hoffman, M.L. 1983. Historical status and nest-site selection of the American Kestrel (*Falco sparverius paulus*) in Florida. M.S. Thesis, University of Florida, Gainesville, FL. 100 pp.

Hoffman, M.L., and M.W. Collopy. 1987. Distribution and nesting ecology of the American Kestrel (*Falco sparverius paulus*) near Archer, Florida. Pp. 47–57, *In* D.M. Bird and R. Bowmen (Eds.), The Ancestral Kestrel. Raptor Research Report 6, Raptor Research Foundation, Vermillion, SD. 178 pp.

Hoffman, M.L., and M.W. Collopy. 1988. Historical status of the American Kestrel (*Falco sparverius paulus*) in Florida. Wilson Bulletin 100:91–107.

Jackson, J.A. 1978. Pine bark redness as an indicator of Red-cockaded Woodpecker activity. Wildlife Society Bulletin 6:171–172.

Jackson, J.A. 1994. Red-cockaded Woodpecker (*Picoides borealis*). Pp. 1–20. *In* A. Poole and F. Gill (Eds.). Birds of North America, No. 85. The Birds of North America, Inc., Philadelphia, PA.

Johnsgard, P.A. 1990. Hawks, Eagles, and Falcons of North America. Smithsonian Institution Press, Washington, DC. 397 pp.

Kindell, C.E., B.J. Herring, C. Nordman, J. Jensen, and L.G. Chafin. 1997. Natural community survey of Eglin Air Force Base. 1993–1996: Final report. Florida Natural Areas Inventory, Tallahassee, FL. 124 pp.

McFarlane, R.W. 1973. Florida's sparrow hawk. Florida Naturalist 46:20–22.

Mayfield, H. 1960. The Kirtland's Warbler. Cranbrook Institute of Science, Bloomfield Hills, MI.

Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

Newton, I. 1998. Population Limitation in Birds. Academic Press, San Diego, CA.

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

Smallwood, J.A. 1990. American Kestrel and Merlin. Pp. 29–37, *In* B.G. Pendleton, M.N. LeFranc, Jr., and B.A. Milsap (Eds.), Proceedings of the Southeast Raptor Management Symposium and Workshop. National Wildlife Federation, Washington, DC. 245 pp.

Smallwood, J.A., and D.M. Bird. 2002. American Kestrel (*Falco sparverius*). Pp. 1–32. *In* A. Poole and F. Gill (Eds.), Birds of North America, No. 602. The Birds of North America, Inc., Philadelphia, PA.

Smallwood, J.A., and M.W. Collopy. 1993. Management of the threatened Southeastern american Kestrel in Florida: Population responses to a regional nest box program (abstract). Journal of Raptor Research 27:81.

Smith, D.G., C.R. Wilson, and H.W. Frost. 1972. The biology of the American Kestrel in central Utah. Southwestern Naturalist 17:73–83.

Stys, B. 1993. Ecology and habitat protection needs of the Southeastern American Kestrel (*Falco sparverius paulus*) on large-scale development sites in Florida. Florida Game and Fresh Water Fish Comm., Nongame Wildlife Program Tech. Report No. 13, Tallahassee, FL . 35 pp.

Toland, B.R., and W.H. Elder. 1987. Influence of nest-box placement and density on abundance and productivity of American Kestrels in central Missouri. Wilson Bulletin 99:712–717.

U.S. Fish and Wildlife Service. 2003. Recovery plan for the Red-cockaded Woodpecker (*Picoides borealis*): Second revision. U.S. Fish and Wildlife Service, Atlanta, GA. 296 pp.

Walters, J.R. 1990. The Red-cockaded Woodpecker: A "primitive" cooperative breeder. Pp. 69–101, *In* P.B. Stacey and W.D. Koenig (Eds.), Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior. Cambridge University Press, Cambridge, UK. 615 pp.

Walters, J.R. 1991. Application of ecological principles to the management of endangered species: The case of the Red-cockaded Woodpecker. Annual Review of Ecological Systems 22:505–523.

Walters, J.R., C.A. Haas, and K.E. Gault. 2002. Adaptive management of Red-cockaded Woodpeckers on Eglin Air Force Base, Florida: Experimental study. Unpublished report.

Ware, S., C.C. Frost, and P.D. Doerr. 1993. Southern mixed hardwood forest: The former longleaf pine forest. Pp. 447–493, *In* W.H. Martin, S.G. Boyce and A.C. Echternacht (Eds.), Biodiversity of the Southeastern United States: Lowland Terrestrial Communities. John Wiley and Sons, Inc., New York, NY. 502 pp.

Wiley, J.W. 1978. Southeastern American Kestrel. Pp. 32–34, *In* H.W. Kale, III (Ed.), Rare and endangered Biota of Florida. Volume II, Birds. University of Florida Press, Gainesville, FL.

Zwicker, S.M., and J.R. Walters. 1999. Selection of pines for foraging by Red-cockaded Woodpeckers. Journal of Wildlife Management 63:843–852.