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SURVIVAL, SITE FIDELITY, AND POPULATION TRENDS OF AMERICAN KESTRELS WINTERING IN SOUTHWESTERN FLORIDA

DANIEL M. HINNEBUSCH,[1,4] JEAN-FRANÇOIS THERRIEN,[1,2] MARC-ANDRÉ VALIQUETTE,[1,2] BOB ROBERTSON,[1,3] SUE ROBERTSON,[1] AND KEITH L. BILDSTEIN[1]

ABSTRACT.—The winter population ecology of American Kestrel (*Falco sparverius*), one of the most abundant and widely distributed raptors in North America, is poorly understood. We systematically searched a 225-km^2 area in Cape Coral, southwestern Florida, for American Kestrels during 14 winters (1 Dec–15 Mar, 1994–2008) to measure their annual apparent survival and to see if individuals returned to the same wintering area. We recaptured 101 of 2,958 banded kestrels during the study. We estimated annual apparent survival of 75% for males and 74% for females using a Cormack-Jolly-Seber model. These estimates are considerably higher than previous estimates for American Kestrels, but are similar to estimates reported for other species of *Falco*. Forty-six percent of the kestrels estimated to have survived were observed in the study area 1 year after recapture, based on year-specific color banding. All but six of 101 kestrels were recaptured within 1 km of where they were banded. Four of five kestrels banded as nestlings and subsequently recaptured in the study area were banded in southeastern Pennsylvania, suggesting migratory connectivity. Eighty percent of the kestrels trapped were females, but the proportion of females decreased annually (-3 ± 1% per year). Overall, the population decreased by an average of 7 ± 2% per year. Recent land-use change accompanied by increased human density and suburban expansion may be causing the observed trends. *Received 29 October 2009. Accepted 9 March 2010.*

American Kestrels (*Falco sparverius*) occur in open habitats throughout most of North and South America (Smallwood and Bird 2002). The American Kestrel, historically abundant throughout most of its range, has declined significantly since the 1970s (Sullivan and Wood 2005, Farmer et al. 2008). Potential causes for this decline include West Nile virus, organophosphate poisoning, increased predation by growing populations of Cooper's Hawks (*Accipiter cooperii*), population declines of Northern Flickers (*Colaptes auratus*), a primary cavity nester; and land-use changes (Sullivan and Wood 2005, Farmer et al. 2006, Medica et al. 2007, Farmer et al. 2008).

American Kestrels are partial migrants that undertake leapfrog migration (Roest 1957, Smallwood and Bird 2002). Individuals breeding at northern latitudes are more likely to migrate and move greater distances than individuals breeding farther south (Goodrich and Smith 2008). Banding returns indicate that most individuals that migrate to southwestern Florida breed in the northeastern United States or in southeastern Canada (Layne 1982). Individuals or, more rarely, pairs of kestrels maintain areas of exclusive use during winter (Cade 1955, Mills 1975). Males and females use different habitats in winter with males occupying areas with more woody vegetation (Smallwood and Bird 2002). This may be the result of later-migrating males selecting suboptimal habitat left vacant by females (Smallwood 1988), or because larger females dominate smaller males (Ardia and Bildstein 1997).

Site fidelity by migratory birds can be advantageous because individuals benefit from being familiar with a previously occupied territory (Spaans 1977, Nichols et al. 1983). Familiarity with a territory likely allows for more efficient foraging and predator avoidance (Hinde 1956, Clarke et al. 1993, Yoder et al. 2004). Evidence supporting winter site fidelity in American Kestrels is limited to studies of small numbers of band recoveries and observation of uniquely marked individuals. Return rates of 19% (four of 21 individuals) and 17% (eight of 47) were reported at wintering sites in central Ohio (Mills 1975) and southern Texas (Bolen and Derden 1980), respectively, for kestrels marked with patagial tags. Tabb (1977) reported a return rate of 2% (17 of 842) for kestrels banded at several sites in southern Florida, but that estimate is based entirely on recaptures because individuals could not be reliably identified without recapture. Several other species of raptors demonstrate winter site fidelity (Garrison and Bloom 1993, Harmata and Stahlecker 1993, Powers 1996).

[1] Hawk Mountain Sanctuary, Acopian Center for Conservation Learning, 410 Summer Valley Rd., Orwigsburg, PA 17961, USA.

[2] Université Laval, Département de biologie and Centre d'études nordiques, Québec, QC G1K 7P4, Canada.

[3] Deceased.

[4] Corresponding author; e-mail: hinnebusch@hawkmtn.org and osprey1984@yahoo.com

Moreover, satellite tracking has provided evidence for winter site fidelity by North American falcons, including Peregrine Falcon (*Falco peregrinus*) and Prairie Falcon (*F. mexicanus*), based on a small number of individuals (McGrady et al. 2002, Steenhof et al. 2005).

Survival estimates are essential for effective species' management and conservation (Crone 2001, Sandercock 2006). However, survival in the wild remains poorly known for the American Kestrel (Smallwood and Bird 2002). To date, two studies have estimated mortality rates using band recovery and territory occupancy (Roest 1957, Henny 1972), a technique that does not consider the probabilities of capture and detection biases and is further biased by territory vacancies that may not be the result of deaths of birds (Gould and Fuller 1995).

We report the results of a 14-year study of American Kestrels wintering in southwestern Florida. Specifically, we: (1) estimate annual apparent survival, (2) discuss a decrease in size of the observed population characterized by a decrease in number of females, (3) provide evidence for strong winter site fidelity, and (4) discuss evidence for migratory connectivity between winter territories in Florida and natal sites in the northeastern United States.

METHODS

Study Area.—We marked American Kestrels within ~275 km^2 containing 2,966 km of roads in the city of Cape Coral and adjacent Pine Island, west of Fort Myers, Lee County, Florida. The study site is on a peninsula along the Gulf of Mexico bordered to the east by the Caloosahatchee River and to the west by Matlacha Pass. Native cover includes slash pine (*Pinus elliottii*) woodlands and tidal marshes (Wesemann 1986, Millsap and Bear 2000). An extensive network of canals and roads was built in the area in the late 1950s (Bernard 1983, Zeiss 1983). The site now consists largely of single-family residences and unoccupied, but regularly mowed, lots (Millsap and Bear 2000). Parallel roads are ~100 m apart. The human population in 2000 was 102,286 (376.1/km^2). In 2006 it had grown 48% to 151,389 (556.7/km^2) (USCB 2009).

Data Collection.—BR and SR searched Cape Coral for American Kestrels each winter (1 Dec–15 Mar) for 14 years beginning in December 1994. Observers drove along each road in the study area at <25 km/hr while searching for kestrels, which often hunted from prominent perches and were easily observed (Bildstein and Collopy 1987). We surveyed each road once each winter and recorded male/female, location, and band color of all kestrels observed on our initial visit to each road.

We attempted to capture every kestrel observed by using a bal-chatri trap (25-cm-diameter, 7-cm-high) baited with two mice (*Mus musculus*) (Berger and Mueller 1959). Unless previously banded, captured kestrels were marked with a USGS aluminum band and a year-specific plastic, coil-style, color band (red, blue, white, yellow, black, or green), except for 1994–1995 and 1995–1996, when color bands were not used. Each color, except white, was used in 2 nonconsecutive years with bands being placed on different legs in different years. Wrap-around color bands were manufactured by Gey Band & Tag Company, Norristown, Pennsylvania, USA. A body-condition index was calculated for each captured bird by dividing the cube root of body mass by wing chord, which was used as a wing loading index for Merlins (*Falco columbarius*) by Temple (1972). If we were unable to capture a bird, we returned to the same site later in the season, usually in early March, and again attempted to trap it. However, observations of kestrels observed on a road after our initial survey of that road were not included in analyses. We indicated sites at which we banded or observed kestrels as the nearest intersection of roads. We obtained information on banding and recovery locations outside the Cape Coral study area from the Bird Banding Laboratory, USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA. We considered recovered banded kestrels to have been found during the breeding season if they were found between 1 April and 31 August (*sensu* Smallwood and Bird 2002).

Statistical Analyses.—We estimated annual apparent survival (Φ) and capture probability (p) using recapture data with a Cormack-Jolly-Seber (CJS) model of mark-recapture in MARK 5.1 software (White and Burnham 1999). The model was based on a single study site with 14 recapture occasions (1995–2008). We used a single biological state, treating the age of all individuals as after-hatch-year. Our global model allowed apparent survival and capture probability to vary with year and male/female, as well as an interaction between those covariates. We retained all models for which ΔAIC_c was <2 and used model averaging to estimate parameters.

The initial capture and recapture sites for each recaptured bird were identified using ArcGIS (ESRI 2009). We tested for a difference between males and females in inter-capture distance, the distance between the site of original capture and the recapture site, using the Mann-Whitney *U*-test. We used Spearman's rank correlation to test for a relationship between inter-capture distance and years between captures and body-condition index at time of initial capture. We compared average annual capture success rate for marked and unmarked kestrels using a paired *t*-test.

Observed population was estimated as the number of kestrels observed on the initial visit to all roads. Effort did not vary among years and we used observed population as an index of true population size to compare among years. We used the natural logarithms of the female proportion of the population and the number of kestrels observed each year to estimate the change in the female proportion of the population, and the annual percent change in the observed population, respectively, using simple linear regression. All statistical analyses used SAS 9.1 (SAS Institute Inc. 2003). Tests were considered significant if $P < 0.05$. All error terms, except as noted, represent one standard error.

RESULTS

We captured 2,958 American Kestrels (211 ± 27/year), including 2,365 females, 592 males, and one individual for which we did not record gender. We recaptured 101 kestrels (80 females and 21 males) at least 9 months after their initial capture (Table 1). The mean time between banding and recapture was 2.8 ± 0.2 years (range = 11 months to 9 years). No bird was recaptured more than once. Each year, an average of 192 ± 56 individuals marked in previous years with year-specific color bands were observed, but these birds were difficult to recapture. Overall annual capture rates of unbanded kestrels were much higher than recapture rates for banded birds (61 ± 2% vs. 4 ± 1%; $t = 29.5$, $P < 0.001$).

We retained three models for apparent survival and recapture probability with $\Delta AIC_c < 2$ (combined Akaike weight, $w_i = 0.86$; Table 2). We estimated male apparent survival at 75 ± 5% and female apparent survival at 74 ± 4% based on model averaging. Overall, the year effect was not retained as a covariate affecting apparent survival, suggesting constant adult apparent survival during the 14 years of study. Recapture probability, as estimated with the CJS model, was low during the study period. It was greatest in 1995–1996 (5% for males and 4% for females), but remained between 1 and 3% for both males and females in every subsequent year until 2007–2008, when no kestrels were recaptured.

The proportion of females in the observed population (banded and unbanded) decreased by 3 ± 1% annually ($R^2 = 0.79$, $F = 38.0$, $P < 0.001$). Females comprised 86% of the population in the first 3 years of study and 64% of the population in the last 3 years. The total number of kestrels observed in the study area decreased an average of 7 ± 2% per year ($R^2 = 0.54$, $F = 11.6$, $P = 0.007$). The number of females observed decreased an average of 10 ± 2% per year ($R^2 = 0.63$, $F = 17.3$, $P = 0.002$; Fig. 1) and the number of males increased by 4 ± 1% per year ($R^2 = 0.37$, $F = 5.9$, $P = 0.035$).

For kestrels color banded in year *n*, we observed an average of 34 ± 1% in year $n + 1$, 18 ± 1% in year $n + 2$, and 9 ± 1% in year $n + 3$ (Fig. 2). Considering our estimate of annual apparent survival with a CJS model, we observed, in year $n + 1$, 46% of the kestrels banded in year *n* that were still alive in year $n + 1$ (Fig. 2).

The longest inter-capture distance that could have occurred within our study area was 32 km. Mean distance between initial and second capture for recaptured kestrels was 488 ± 102 m (range = 0 to 7,887 m). All but six birds recaptured were caught <1 km from the initial capture site, and 75% were recaptured within 423 m (Fig. 3). There was no difference in inter-capture distance between males and females ($U = 1{,}208$, $P = 0.26$), and inter-capture distance was not correlated with years between captures ($r_s = 0.083$, $P = 0.41$). Inter-capture distance and body-condition index at time of initial capture exhibited a nearly significant, weak correlation ($r_s = 0.19$, $P = 0.061$).

Twenty-five banded kestrels were observed outside the study area (Fig. 4). We recaptured five females in Cape Coral that had been banded as nestlings, four of which had been banded in eastern Pennsylvania and one of which had been banded in central Nova Scotia. We also recaptured two females that had been banded as adults, one in April in Connecticut and one in September on the Delmarva Peninsula, Virginia. Eighteen (11 females and 7 males) kestrels banded in Cape Coral were found dead outside the study area, including 13 (7 females and 6 males) that were

TABLE 1. Percent of American Kestrel cohorts recaptured each year after banding in Cape Coral, southwestern Florida. ''*n*'' indicates the number of kestrels banded each year. Subsequent columns indicate the percent (above) and number (below) recaptured each year after banding.

		Year of Recapture												
Year	*n*	1995–1996	1996–1997	1997–1998	1998–1999	1999–2000	2000–2001	2001–2002	2002–2003	2003–2004	2004–2005	2005–2006	2006–2007	2007–2008
1994–1995	207	3	<1	<1	0	1	0	1	<1	<1	0	0	0	0
		7	1	1	0	2	0	2	1	1	0	0	0	0
1995–1996	431		1	<1	0	<1	0	<1	0	0	0	0	0	0
			5	2	0	1	0	2	0	0	0	0	0	0
1996–1997	161			2	0	1	1	0	1	0	0	0	0	0
				4	0	2	1	0	1	0	0	0	0	0
1997–1998	224				0	1	2	<1	1	<1	0	0	0	0
					0	3	5	1	2	1	0	0	0	0
1998–1999	190					2	1	0	1	1	1	1	0	0
						4	2	0	1	1	1	1	0	0
1999–2000	404						2	0	<1	<1	<1	<1	<1	0
							8	0	1	2	1	2	1	0
2000–2001	195							1	1	1	1	1	0	0
								2	1	2	1	1	0	0
2001–2002	218								1	2	<1	<1	0	0
									3	4	1	1	0	0
2002–2003	274									1	1	1	0	0
										4	2	2	0	0
2003–2004	175										2	1	1	0
											3	2	1	0
2004–2005	124											0	0	0
												0	0	0
2005–2006	114												1	0
													1	0
2006–2007	102													0
														0
2007–2008	139													

TABLE 2. Models of apparent survival (Φ) and recapture probability (p) for recaptured American Kestrels ($n = 101$) in southwestern Florida for which $w_i > 0.10$. Both apparent survival and recapture probability were allowed to vary with year and sex, as well as an interaction between year and sex, in the global model. We tested all possible models nested within the global model. The best model not included in model averaging [Φ(sex)/p(year + sex)] had $\Delta AIC_c = 2.25$ and $w_i = 0.13$.

Model	AIC_c	ΔAIC_c	w_i	Parameters	Variance
Φ(.)/p(year)	1209.07	0.00	0.39	14	119.36
Φ(.)/p(year + sex)	1209.64	0.57	0.30	15	117.92
Φ(sex)/p(year)	1210.72	1.65	0.17	15	118.99

recovered during the breeding season, although we were not able to ascertain if kestrels died in breeding areas or as migrants. Kestrels recovered during the breeding season included five in Quebec, one in New Brunswick, one in Maine, two in New York, two in Pennsylvania, one in Delaware, and one in South Carolina. Kestrels recovered during the non-breeding season included one each in New Brunswick, Ontario, New York, North Carolina, and South Carolina. No birds captured in Cape Coral were recaptured outside the study area and reported to the Bird Banding Laboratory.

DISCUSSION

The annual apparent survival estimates of 75% for males and 74% for females are considerably higher than those reported by Roest (1957) and Henny (1972) (43 and 55%, respectively). Both of these studies relied on band recoveries from dead birds or nest-site occupancy to evaluate annual mortality rates. Their estimates of annual apparent survival are based on a time when direct persecution by humans (Bildstein 2008) may have resulted in greater mortality. At least 24% of the recovered kestrel bands reported by Roest (1957) came from birds killed by people. Human-caused mortality in kestrels reported in Henny (1972) ranged from 16% for 1958–1965 to 48% for 1925–1945. Our estimates are similar to estimates reported for other species of *Falco* in North America, including 75–89% for Prairie Falcons (Enderson 1969, Steenhof et al. 2006), 62% for Merlins (Lieske et al. 2000), and 79–93% for

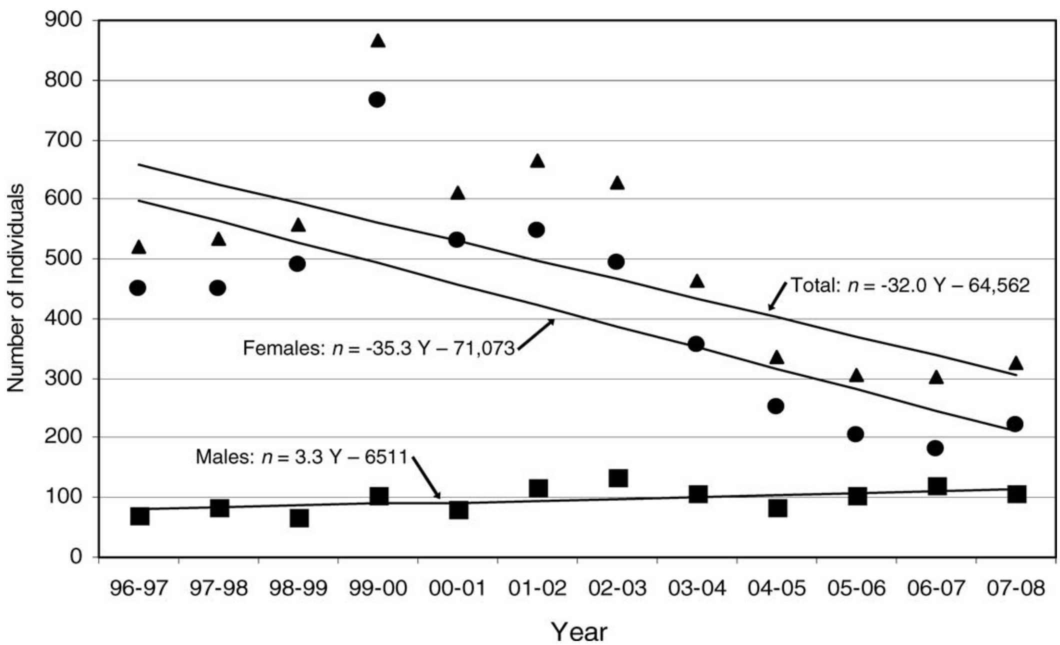

FIG. 1. Number of observations of female (circles), male (squares), and total (triangles) American Kestrels in Cape Coral, southwestern Florida, 1996–2008. ''n'' indicates number of kestrels and ''Y'' indicates the calendar year beginning in a winter season in the regression equations.

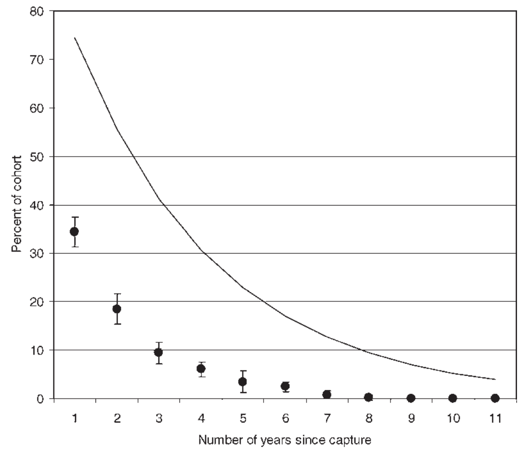

FIG. 2. Proportion of color-marked American Kestrel cohorts observed in Cape Coral, southwestern Florida and the estimated proportion surviving each year. Points indicate the average proportion of marked cohorts observed in the study area after each year. Vertical lines are 95% confidence intervals. The curve indicates the estimated surviving population based on annual adult apparent survival estimates from the CJS model in this study.

Peregrine Falcons (Court et al. 1989, Tordoff and Redig 1997). Survival estimates for Common Kestrels (*Falco tinnunculus*) in the United Kingdom were 80% for males and 66% for females (Dobson 1987). To our knowledge, this study reports the first estimates of annual apparent survival for American Kestrels using a CJS model.

We recognize use of year-specific color bands is not the most effective method to estimate annual apparent survival, recapture probability, and between-year inter-capture distances because it did not allow us to record individual encounter histories for kestrels that were not recaptured. Our estimate of apparent survival with the CJS model was based only on the 101 recaptured kestrels. We believe this estimate is reliable because it considers the low recapture probability.

The decline in the numbers of kestrels observed in the study area does not seem to be attributable to a decrease in adult survival over the study period as no year effect was retained in the models. However, the decrease in numbers of kestrels observed started in 2002, 3 years after discovery of West Nile virus in New York (Lanciotti et al. 1999). American Kestrels are susceptible to infection by West Nile virus (Komar et al. 2003) and exhibit symptoms that may decrease survival in wild birds (Nemeth et al. 2006). Ninety-five percent of tested American Kestrels breeding in Pennsylvania had antibodies indicating they had been exposed to the virus

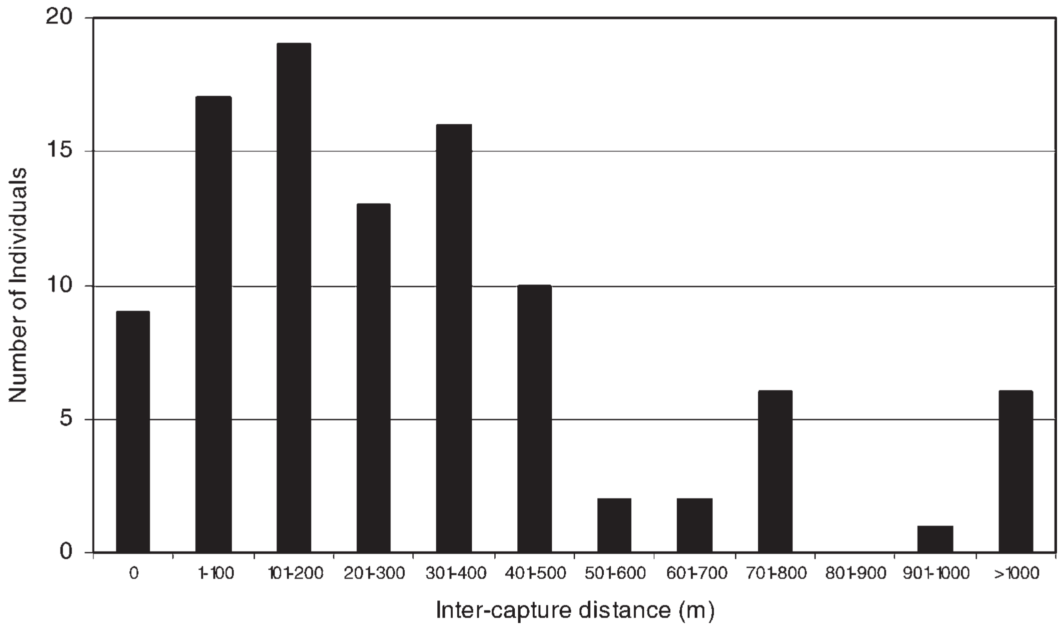

FIG. 3. Distances between capture and recapture sites between winter seasons for American Kestrels in Cape Coral, southwestern Florida. The greatest inter-capture distance was 7.9 km.

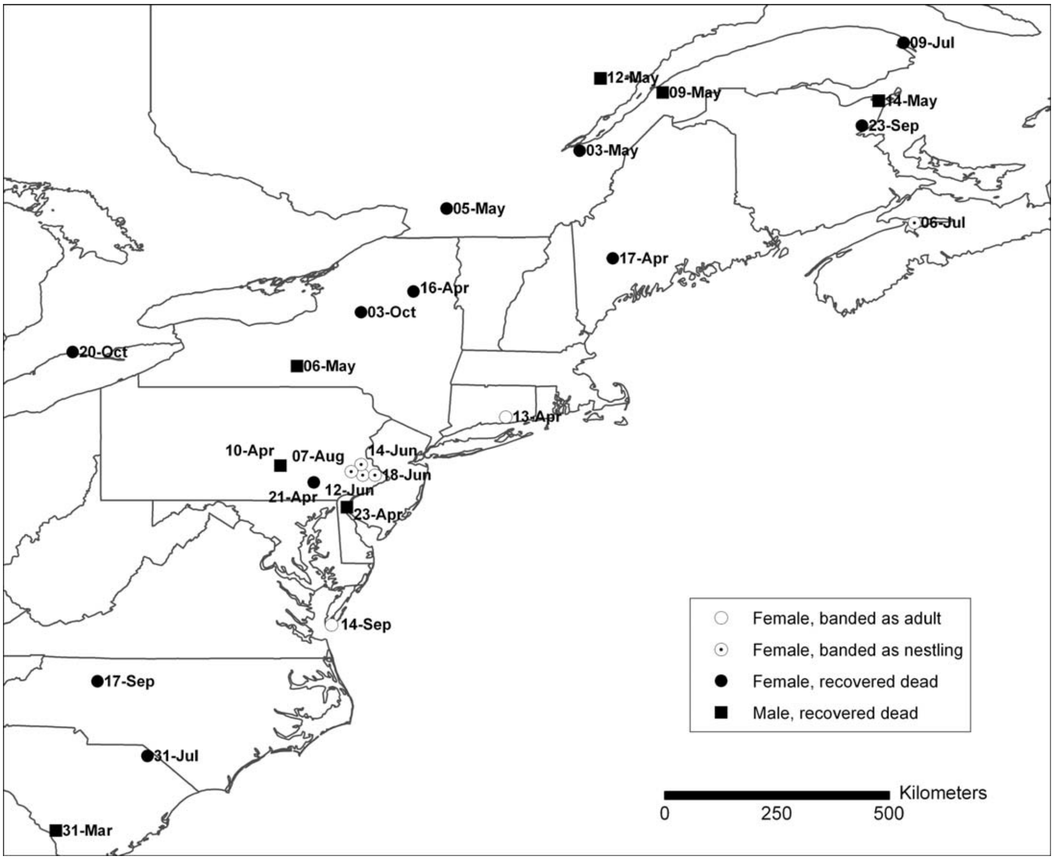

FIG. 4. Banding and band recovery sites for American Kestrels observed between 1 December and 15 March in Cape Coral, southwestern Florida. Males represented with squares and females with circles.

(Medica et al. 2007). The population decrease in our study area was characterized by a decrease in females. We believe this change in sex ratio could be due to land-use changes at the study site. Female kestrels occupy more open habitat in winter than males and, over the course of our study, land use in our study area shifted from open areas to more woody cover due to suburban development. The increase in number of males observed in the study area was relatively small compared to the decrease in the number of females observed. The observed increase in human population in the study area, combined with the suburban expansion of Cape Coral, has reduced the occurrence of good wintering habitat for kestrels. Those two factors seem to negatively affect the overall Cape Coral kestrel population as well as skew the sex ratio toward males.

American Kestrels wintering in Cape Coral, Florida exhibited strong winter site fidelity. Most kestrels that returned to the study area wintered a short distance (<1 km) from their previous wintering area, based on between-year inter-capture distances. The relatively large numbers of color-banded birds we saw, together with a small recapture rate, suggest the small number of recaptures was not due to emigration but rather to capture avoidance. Our observations of numerous color-banded kestrels in the area support strong winter site fidelity by American Kestrels. Our estimate of the proportion of birds observed in winters subsequent to capture is likely conservative due to loss of color bands (Nelson et al. 1980). Seven percent of the kestrels observed in the last year of our study (2007–2008) had an aluminum band and no color band. It is unlikely these kestrels had been banded in years when we did not use color bands (1994–1995 and 1995–1996) because we estimate that >96% of the kestrels banded in those years had already died by 2007–2008.

Four of five kestrels recaptured after being banded as nestlings outside the study area were banded within 42 km of each other in southeastern Pennsylvania, suggesting migratory connectivity in populations we studied. American Kestrels migrate singly or in small groups (Kerlinger et al. 1985), and juveniles migrate earlier than adults (Smallwood 1988, Mueller et al. 2000); thus, juveniles do not have the opportunity to follow adults on migration, as has been observed for some flocking migrants (Maransky and Bildstein 2001). Strong connectivity between natal and wintering areas has important conservation implications because a decrease in productivity in a local breeding population can drastically affect the population in wintering areas with which it is connected and vice versa. Recoveries of kestrels banded in the study area were distributed over a much wider range than were banding locations of nestlings recaptured in the study area, providing little evidence of connectivity between wintering and breeding areas for adults. We could not ascertain whether a recovered bird had died in its breeding areas or as a migrant in most cases. We cannot clearly state there is a lack of migratory connectivity in adult kestrels.

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