

# NORTH AMERICAN FAUNA



United States Department of the Interior  
Fish And Wildlife Service



**Frontispiece.** Adult female Cooper's hawk *Accipiter cooperii* equipped with a backpack-mounted radio-transmitter.

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# Ecology of the Cooper's Hawk in North Florida

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## Abstract

We studied adult Cooper's hawks *Accipiter cooperii* on two study areas in north Florida from 1995 to 2001, an area dominated by large plantations managed for northern bobwhite *Colinus virginianus* and an area of mixed farmland and woods with no direct bobwhite management. We monitored 76 Cooper's hawk nesting attempts at 31 discrete nest areas, and radio-tagged 19 breeding males and 30 breeding females that we radio-tracked for up to 5 y. Nesting density (565 to 1,494 ha per occupied nest area) was comparable but productivity (1.8 and 2.8 young fledged per occupied and successful nest area, respectively) was lower than for the species elsewhere. Prey may have been more limiting than in other areas studied because chipmunks *Tamias striatus*, an important prey elsewhere, were absent. Annual Cooper's hawk survival averaged 84% for males and 81% for females, except in 1998 when survival was substantially lower. Average annual home-range size for male Cooper's hawks was 15.3 km<sup>2</sup> inclusive of one nesting area. Female annual ranges averaged 30.3 km<sup>2</sup>, and included from three to nine nesting areas. Daily space use was similar between the sexes, but females had separate breeding and nonbreeding ranges whereas males were sedentary. Females used the same nonbreeding areas among years, but switched nesting areas 68% of the time compared with only 17% for males. Birds comprised 88% of the breeding and 98% of the nonbreeding season diet of Cooper's hawks by frequency. Important prey species all year were mourning doves *Zenaida macroura*, blue jays *Cyanocitta cristata*, and northern bobwhite; during summer, cattle egrets *Bubulcus ibis*, northern mockingbirds *Mimus polyglottos* and northern cardinals *Cardinalis cardinalis* were also important; and during autumn and winter, killdeer *Charadrius vociferus*, yellow-billed cuckoos *Coccyzus americanus*, and chickens were important. Female Cooper's hawks took larger prey than males; females were responsible for most cattle egret and chicken kills; whereas, males took most blue jays, killdeer, northern mockingbirds, and northern cardinals. Of avian prey brought to nests, 64% were nestling birds. Most adult male Cooper's hawks were adept at raiding bird nest boxes. Male Cooper's hawks captured 85% of the prey fed to nestlings. Female Cooper's hawks relied on males for food from early March until young were  $\geq 12$  d old, and 6 of 10 breeding females monitored intensively were never observed foraging for their broods. Most prey brought to nestling Cooper's hawks was captured within 2 km of nests, and foraging effort was consistent throughout the day. During the nonbreeding season, most prey captures occurred before 0900 hours or at dusk. Northern bobwhite made up 2% of male and 6% of female Cooper's hawk prey annually by frequency; this extrapolated to 18 bobwhite/year/adult Cooper's hawk on both study areas, 59% of which were captured between November and February. Outside the breeding season, male Cooper's hawks foraged evenly over their home range whereas females tended to focus on prey concentrations. Because female Cooper's hawks were so adept at finding and exploiting prey hotspots, perhaps the best strategy for reducing predation on bobwhite is habitat management that produces an even distribution of bobwhite across the landscape.

Keywords: *Accipiter*; Cooper's hawk; diet; Florida; foraging; home range; predation

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## Introduction

The Cooper's hawk *Accipiter cooperii* has a broad distribution across temperate North America, ranging from both coasts north into southern Canada and southward into Florida and northern Mexico (Rosenfield and Bielefeldt 1993; American Ornithologists' Union 2008). The biology of the Cooper's hawk, particularly the bird's breeding ecology, has been well-studied in northern and western parts of the species' range (Henny and Wight 1972; Reynolds and Wight 1978; Millsap 1982; Rosenfield and Bielefeldt 1993; Rosenfield et al. 1995; Boal and Mannan 1999; Nenneman et al. 2002; Rosenfield et al. 2007; Stout et al. 2007). However, in the southeastern United States near the southern limits of the Cooper's hawk's range, little work has been done with this species and most aspects of population biology are poorly documented (Layne 1986; Toland and Millsap 1996). This is surprising given the widespread and increasing interest in the Cooper's hawk in the Southeast as a significant predator of the declining northern bobwhite (hereafter, bobwhite; *Colinus virginianus* [Stoddard 1978; Rollins and Carrol 2001; Link et al. 2008]). Little information is available on ranging behavior and home range characteristics for the Cooper's hawk anywhere. Murphy et al. (1988) reported the breeding home range of a single male Cooper's hawk in Wisconsin; Boal and Mannan (2000) studied the breeding-season home ranges of urban Cooper's hawks in Tucson, Arizona; and Roth et al. (2005) reported on winter home ranges of Cooper's hawks in Indiana. No study has looked at year-round home ranges, annual variation in seasonal ranges, or compared home range characteristics of males and females.

We initiated a study of aspects of population biology and foraging ecology of the Cooper's hawk in northern Florida and south-central Georgia in 1992 to help answer questions about the role of this predator in affecting bobwhite populations, and to collect basic information on breeding biology, survival, ranging behavior, diet, and foraging behavior in this poorly studied part of the species' range. From 1995 to 2001, we used conventional raptor population monitoring techniques and radio-telemetry to intensively study Cooper's hawks on two study areas in north Florida and adjacent southern Georgia. One of our study areas, Tall Timbers, was situated in an area dominated by large, privately owned hunting plantations heavily managed for bobwhite. The second area, Dowling Park, consisted of farmland and mixed-oak woodlands with little or no bobwhite management.

Previous studies have shown that both drought (Snyder and Wiley 1976) and excessive precipitation in the prelaying period (Newton and Marquiss 1984) can negatively affect reproductive success in *Accipiter* hawks, and there is ample evidence that reproductive

potential can vary spatially under differing ecological conditions (Snyder and Wiley 1976; Boal and Mannan 1999; Rosenfield et al. 2000). We hypothesized that these factors would affect measures of reproductive success in our study populations, and that poor reproductive conditions would be associated with larger home-range sizes because of the need for foraging adults to cover more area to find sufficient food, and lower annual survival of breeding adults because of negative effects on body condition from increased foraging (see Rosenfield and Bielefeldt 1999). We also hypothesized that observed variation in reproduction and ranging behavior would be reflected by differences in diet and foraging behavior. Finally, we hypothesized that predation rates would be proportional with relative abundance among important prey species on both study areas, including predation on northern bobwhite.

Herein we summarize our findings, which we believe advance understanding of Cooper's hawk ecology in three important ways. First, as already suggested, this is the first comprehensive study of the breeding biology and foraging ecology of the species in southeastern part of its range. We believe findings from our study areas should be broadly applicable to breeding Cooper's hawks across much of the Atlantic coastal plain of the Southeast, from North Carolina south and westward into eastern Texas. Second, our work provides some of the first contemporary estimates of annual survival, seasonal and annual home-range size, and breeding and nonbreeding season diet for the species, as well as the first quantitative estimates of the annual predation rate of adult Cooper's hawks on northern bobwhite. Finally, as we discuss later, we believe our study population was more food-stressed than many of the other Cooper's hawk populations studied to date; thus, our work offers unique insights into the ecology of this species under a different set of environmental conditions than most prior work.

## Study Sites

### Tall Timbers

The 14.7-km<sup>2</sup> Tall Timbers study area, where we conducted initial surveys in 1994, was centered on the Tall Timbers Research Station in northern Leon County, Florida and adjacent Grady County, Georgia within the Red Hills physiographic region. We selected the Tall Timbers study area because of its long history with bobwhite research (Masters 2011) and its proximity to bobwhite hunting plantations. The Tall Timbers study area consisted largely of private lands, so we were dependent on permission from many different landowners to enter property to study hawks. Access to private lands was seasonally intermittent (access was not allowed while hunting was occurring) or denied on many of the private plantations near or adjacent to the Tall Timbers Research Station, which hampered our ability to collect information there.



The Tall Timbers study area consisted of plantations actively managed for hunting of bobwhite. Much of this area was longleaf pine *Pinus palustris* turkey oak *Quercus laevis* high pine upland forest (Myers and Ewel 1990) prior to settlement, but during our study uplands were dominated by large loblolly pines *Pinus taeda* with scattered laurel *Quercus laurifolia* and live *Quercus virginiana* oaks and a heavy shrub and herbaceous understory. Bottomland forests along drainages consisted of laurel oaks, live oaks, sycamore *Platanus occidentalis*, short-leaf pine *Pinus echinata*, and hickory *Carya* spp. Active land management consisted mainly of application of frequent prescribed fire during winter and summer, as well as hardwood thinning via mechanical and herbicide treatments.

Climate in north Florida was temperate to subtropical, with a bimodal precipitation pattern associated with summer thunderstorms and midwinter cyclonic systems. Tallahassee, the closest National Oceanic and Atmospheric Administration weather-monitoring site to the Tall Timbers Study Area, receives an average of 158.8 cm of precipitation annually, with a monthly peak of 21.6 cm in July. Highs average 17.7°C in January and 32.9°C in July, with minimum average daily lows of 4.3°C in January (all climate information from Southeast Regional Climate Center (2007) for the period 1947–2000 unless otherwise noted). There was a strong El Niño event during the winter of 1997–1998. Such events typically produce wetter than normal conditions in Florida (NOAA 2007), and February rainfall in 1998 was substantially above normal (Southeast Regional Climate Center 2007).

### Dowling Park

The Dowling Park study area, where we conducted initial Cooper's hawk surveys starting in 1992, was 202 km<sup>2</sup> in size, and was located in Suwannee County, Florida between the towns of Live Oak and Dowling Park in the Northern Highlands physiographic region (Figure 1). We selected the Dowling Park area because of its relative proximity to Tall Timbers, but absence of bobwhite management. Thus, the two areas provided a geographically proximate comparison of Cooper's hawk biology on landscapes with and without an emphasis on bobwhite management. As with Tall Timbers, most of the Dowling Park study area was privately owned, but we were granted access essentially to the entire study area.

The Dowling Park study area consisted of large expanses of cultivated and fallow farmland interspersed with oak woodlots of varying size. Prior to settlement, the area was largely high pine upland forest, and some tracts of this community type were extant during our study. However, for the most part, upland forests during our study were dominated by laurel and live oak, often with a few remnant overstory longleaf pines and interspersed with blocks of planted loblolly pine.

The only lowlands on the study area were along the western border, and consisted of bottomland hardwood forest dominated by live oak, sweet gum *Liquidambar styraciflua*, and tulip tree *Liriodendron tulipifera* along the floodplain of the Suwannee River. Cultivated farmland on the study area produced corn, tobacco, and watermelon. Cattle grazing and red junglefowl (chicken) farms were common.

Live Oak, the closest National Oceanic and Atmospheric Administration weather-monitoring site to the Dowling Park Study Area, receives an average of 135.6 cm of precipitation annually, with peak monthly precipitation averaging 17.9 cm in July. High temperatures average 19.3°C in January and 33.6°C in July, with minimum average daily lows of 5.3°C in January. The Dowling Park study area was also affected by the El Niño event of 1998, and experienced the highest February precipitation amount for the 53-y period of record for Live Oak in that year (37.8 cm).

## Methods

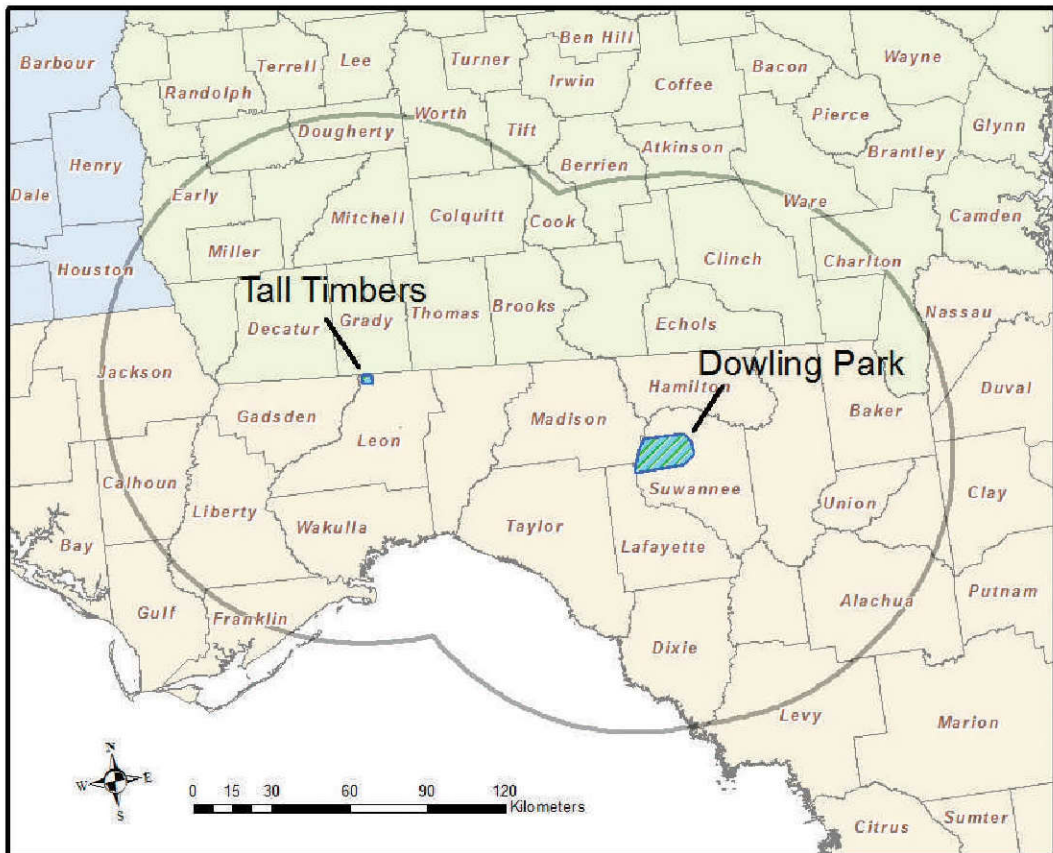
### Study period

We initiated field work searching for Cooper's hawk nest areas in 1992 on Dowling Park and 1994 on Tall Timbers, and we continued to collect information on reproductive activity through the breeding season of 2000. We restricted our analyses of reproductive data to the period 1995–2000, years in which we had relatively complete sampling of all nest areas on each study area. In 1995, we initiated radio-tracking of breeding adult Cooper's hawks on both study areas, and radio-tracking continued through the start of the breeding season in 2001. Prey data were collected from individual radio-tagged Cooper's hawks and prey remains were collected at nests from 1995 to 2001.

### Definitions

We defined the "breeding season" as 1 March to 15 August, and the "nonbreeding season" as 16 August to 28 (or 29) February. For some analyses we split the nonbreeding season into a "postbreeding season" (16 August–31 October) and a "winter season" (1 November–28 [29] February). Cooper's hawks in, or mostly in, definitive plumage were considered to be  $\geq 2$  y old, or "after second year (ASY)." Cooper's hawks in juvenal plumage (or just beginning a molt into definitive plumage) in January through July were considered "second year (SY)."

We defined a "nest area" (synonymous with nest territory) as the area within 1.0 km (one-half the mean internest distance on the Dowling Park study area) of a nest structure used by Cooper's hawks for nesting during  $\geq 1$  y. We selected this distance for delineating discrete nest areas based on the maximum distance between successive nests of nondispersing, radio-tagged, adult male Cooper's hawks



**Figure 1.** Map showing locations of the Dowling Park and Tall Timbers intensive Cooper's hawk study areas (blue hatched areas) in north Florida and south Georgia. Circles buffering the study areas depict the 100-km-radius area we searched by aircraft for dispersing Cooper's hawks. Cooper's hawks that we relocated within the aerial search area were monitored and were included in the study.

between years. A nest area was considered an "occupied nest area" in a given year if a pair of Cooper's hawks attended a nest in which eggs were likely laid (i.e., eggs or an incubating female were seen, or down was visible on the nest structure and Cooper's hawks were seen in association with the nest). A "nest" was a structure used for nesting (e.g., where eggs were laid) by Cooper's hawks within a nest area. We defined Cooper's hawk "nest density" as the number of Cooper's hawk nest areas over the duration of the study in each study area divided by the number of ha in each study area. We calculated the "density of occupied nesting areas" as the number of occupied nest areas divided by the number of ha in each study area.

"Start date" for a nest was the date on which incubation was estimated to have begun based on direct observation or backdating based on the age of young when handled for banding (usually between 14 and 20 d of age). An occupied nest area in which  $\geq 1$  young was raised to 24 d of age was considered a "successful nest area," and "nest success" was the proportion of occupied nest areas that were successful.

"Brood size" was the number of young in an occupied nest that survived to  $\sim 24$  d of age, and "brood size at successful nests" was the number of young raised to  $\sim 24$  d considering only successful nests. We made brood counts of young at this age from video cameras mounted on nests, from observations from blinds at nests of young responding to prey deliveries, and by using a mirror pole to view nest contents. The earliest that video-monitored Cooper's hawks left the immediate area of the nest structure (i.e., fledged) on our study areas was 29 d; thus, 24 d represented 83% of fledging age. Rosenfield et al. (2007) recommend using 70% of fledging age as the cutoff for Cooper's hawk productivity counts based on the increased likelihood of missing individuals that have left the nest as nestling age increases. Given that we observed no individual leaving the nest before 29 d, we felt that 24 d of age was a safe age to use for this cutoff, and we found it preferable to 18 d because it was closer to the actual age at which the young fledged. From a practical perspective, this choice probably mattered little because we observed no brood mortality in our study between 18 d and 24 d.



“Home range” describes the area included within the 95% fixed-kernel contour of a set of location data. We use the term “core area” to describe the area included within the 50% fixed-kernel contour of a set of location data. We selected these isopleths to describe utilization distributions of Cooper's hawks because they are commonly used for other taxa (e.g., Babcock 1995; Plowman et al. 2006). The daily range (DR) and daily core area (DCA) are the home range and core area estimates calculated from a single-day's locations for an individual Cooper's hawk. The seasonal range (SR) and seasonal core area (SCA) are the home range and core area estimates calculated from locations accumulated over a season for an individual Cooper's hawk; seasons analyzed were the breeding and nonbreeding seasons. The annual range (AR) and annual core area (ACA) are the home range and core area estimates calculated from locations accumulated during 1 y for an individual Cooper's hawk.

We considered an individual Cooper's hawk to have moved when it changed its ranging pattern such that it was using an area that did not overlap with any previously used area, and when that change persisted for more than 28 d. We used 28 d for this cutoff because radio-tagged hawks were monitored at least once each 14 d; therefore, 28 d typically included at least two tracking intervals. Female Cooper's hawks that permanently left their nest areas and ceased caring for young before the young were 29 d of age (fledging age) were considered to have deserted their broods and mate (following Fujioka 1989, and Kelly and Kennedy 1993). Female Cooper's hawks were considered to have dispersed from the study areas if they undertook a postbreeding movement of >100 km; some dispersing females returned to the study area in subsequent seasons or years.

In our analyses of foraging behavior, we defined a foraging bout as the interval between when a radio-tagged hawk initiated a hunting foray (usually when it left the immediate nest area after delivering a prey item) until the next prey item was captured.

Variables are defined and assigned an acronym at the time of first mention in the text. All variables are also listed and defined in Appendix A.

## Locating nest areas

Cooper's hawk nest areas were located through systematic searches of potential nesting habitat on both study areas starting in mid-March and continuing through late April, when females at occupied nest areas initiated incubation behavior. Thus, these searches were timed to correspond with the month prior to Cooper's hawk egg-laying on our study areas. Based on our experience with the range of habitat conditions used by Cooper's hawks for breeding in north Florida, we considered potential nesting habitat as any wooded area >0.5 ha in size with trees >5 m tall. We identified potential suitable nesting areas from aerial photography and Landsat

satellite imagery, and confirmed them on the ground. By 1995, all potential nesting habitat on both study areas had been searched on foot during at least one breeding season. Areas within 1 km of previously documented Cooper's hawk nesting areas, areas of seemingly suitable nesting habitat that were  $\geq 1$  km from other known occupied nest areas, and locations where radio-tagged female Cooper's hawks concentrated activity during early mornings in March and April were resurveyed each subsequent year. Our search protocol included thorough foot searches of possible nest stands by knowledgeable observers, where we looked for urates, prey remains, molted Cooper's hawk feathers, and visible stick nests. We also visited many prospective nest areas within 30 min of sunrise, listening for Cooper's hawk vocalizations (Stewart et al. 1996) or playing broadcast Cooper's hawk calls (Rosenfield et al. 1988). Previously occupied nest areas and potential nesting habitat where evidence of Cooper's hawk activity was found during the initial search were resurveyed again in late April and May to confirm occupancy status. Collectively, we believe our search protocol resulted in the detection of all Cooper's hawk nesting attempts where pairs reached the stage of egg-laying on both study areas each year.

We did not take quantitative measures of habitat at nest areas, but did subjectively record notes on habitat at each nest. Trees supporting nests were identified to species following Kurz and Godfrey (1962), and nest tree heights were determined using a range pole or by direct measurement.

## Capture and radio-tagging

We attempted to capture all breeding Cooper's hawks at nest areas where eggs hatched. We captured Cooper's hawks in mist nets surrounding a rehabilitated but nonreleasable great horned owl *Bubo virginianus*, as described by Bloom et al. (2007). Initially we waited until Cooper's hawk young were  $\geq 10$  d old before attempting to capture adults, but after determining with radio-telemetry that captured males immediately reinitiated hunting and that captured females immediately returned to nests, we began trapping as soon as we judged that hatching was completed. Because we targeted breeding adult Cooper's hawks that hatched eggs, our initial sample did not include adults that failed to breed or whose nests failed early in the nesting cycle. However, some of the adults we followed for multiple years did fail to successfully nest in subsequent years. Nevertheless, our sample of captured and radio-tagged Cooper's hawks was biased toward successful breeders, as is the case with most studies that have relied on a marked sample of Cooper's hawks. It should be kept in mind that our findings, as well as those of many previous studies, may not be representative of the breeding population as a whole.

We weighed captured hawks to the nearest g with a triple-beam balance, and then measured unflattened





**Figure 2.** After second year male (right) and female (left) Cooper's hawk, showing 11-g very high frequency transmitters.

wing cord, tail length, hind-claw length, tarsus length, tarsus width, bill depth, and culmen. Wing cord and tail were measured to the nearest mm using a meter stick, and other measurements were taken to the nearest 0.1 mm using dial calipers. Wing, tail, and hind claw measurements followed Baldwin et al. (1931). Tarsus width was the lateral width of the tarsus at the narrowest point. Tarsus length was the length of the tarsometatarsus from the point of articulation with the metatarsals to the point of articulation with the tibia and fibula. One of us (B.A.M.) assigned an iris-color score to each captured Cooper's hawk by comparing the iris (or a photograph of the iris) with the color chart from Palmer (1962). We initially scored iris color with seven levels: 1) yellow, 2) yellow-orange, 3) orange-yellow, 4) orange, 5) orange-scarlet, 6) scarlet-orange, and 7) scarlet. However, we found it difficult to replicate some scoring, so we converted scores to one of five levels following Rosenfield et al. (1992): 1) yellow, 2) light orange (combining yellow-orange and orange-yellow), 3) orange, 4) dark orange (combining orange-scarlet and scarlet-orange), and 5) red. In calculating mean eye-color scores for each study area, we treated each recapture of the same individual in a different year as an independent sample.

We banded all captured hawks with U.S. Geological Survey bands, and equipped them with

a very high frequency radio-transmitter package with tip-switch mortality sensors (American Wildlife Enterprises, Monticello, Florida). Transmitters were attached to Cooper's hawks using the Y-backpack harness design described by Buehler et al. (1995), except that we used 6.35-mm-wide Teflon ribbon (Bali Ribbon, Bali, Pennsylvania) and we padded the suture points with neoprene. Initially, both males and females were equipped with 24-mo, 11-g very high frequency transmitter packages (Figure 2). Beginning in 1998, we switched to 12-mo, 7.5-g very high frequency transmitter packages on males. Seven female and 11 male Cooper's hawks were monitored for >1 y, up to a maximum of 5 y for one female.

Radio-tagged Cooper's hawks were located from the ground at least once every 14 d. If a signal could not be detected from the ground, we thoroughly searched a 100-km-radius area around each study area from a fixed-wing aircraft. If we relocated a hawk during the aerial flights, we resumed regular ground checks at the new location. Cooper's hawks with transmitters not approaching their expected maximum battery life that could not be relocated were assumed to have emigrated >100 km from the study area. We continued to search for these hawks on both study areas during the course of scheduled tracking, as well as on all subsequent flights to find other missing hawks. We could not distinguish between hawks that had dispersed and hawks whose radio-transmitters had failed, and some transmitters may have failed in association with catastrophic mortalities (e.g., vehicle collisions). However, based on the high reliability we experienced with our radio-transmitters, we suspect most missing hawks actually dispersed. We had only one known partial transmitter failure, and we were able to recapture and replace the transmitter on that individual. For the purposes of survival rate estimation, individuals were censored from the analysis for intervals over which their status was unknown.

## Productivity

Nest structures in nest areas were checked with a mirror mounted on a 20-m range-pole (Figure 3) when they were discovered each year, and nest stage (preincubation, incubation, or nestling) was recorded. We revisited nests at least once every 14 d to determine whether or not the nesting effort was still ongoing and to estimate the age of nestlings. We estimated the laying date from our direct observations, but we refined that estimate based on the age of nestlings during subsequent visits, giving particular weight to age estimates during visits when young were handled for banding. We estimated the age of nestlings by comparing the plumage stage with photographs of nestlings of known age from north Florida nests, and from photographs of birds that had been hand-raised by falconers. We were unable to accurately estimate start dates at most unsuccessful nests, so these nest areas are excluded





**Figure 3.** Checking the contents of a Cooper's hawk nest using a 20-m range-pole with mirror attachment.

from start date estimates. Consequently, our start-date estimates are for successful nests only, and do not represent an unbiased sample of all nesting attempts. We restricted our analyses to the period 1995–2000, years when we had a relatively complete understanding of the nesting population on both study areas and when all nest areas were monitored for occupancy well before egg-laying commenced.

We were interested in possible differences in ranging behavior between good and poor reproductive years, and between nest areas with consistently high reproduction and poor reproduction. For these analyses, we ranked nest sites (SITERANK) and years (YEARRANK) from best to worse according to cumulative performance across three variables: 1) nest area occupancy, 2) relative start date, and 3) brood size. Ranks were mean standardized scores (average of standardized  $z$ -scores) for brood size (best = largest brood size), proportion of years occupied (best = highest percent of years occupied), and relative start date (best = earliest start date). The predicted direction of trends was based on observations for the closely related Eurasian sparrowhawk *Accipiter nisus* (Newton and Marquiss 1984; Newton 1985; Kostrzewa 1996; Sergio and Newton 2003).

### Survival

We immediately recovered carcasses of any hawks with transmitters emitting mortality signals. The

likely proximate cause of death was obvious for most Cooper's hawk mortalities even though it was often several days to 2 wk after death before we recovered carcasses. In questionable cases, we submitted carcasses to the Laboratory of Wildlife Disease Research, Pathobiology Department, College of Veterinary Medicine at the University of Florida for necropsy. In cases of predation, carcasses that had been plucked were classified as killed by an avian predator, most likely either a great horned owl or red-tailed hawk *Buteo jamaicensis* (or in some cases, another Cooper's hawk). In cases where the Cooper's hawk carcass was under a known great horned owl roost or under a Cooper's hawk prey-handling perch, we assigned the mortality to that species. Although we believe it unlikely, it is possible that in some cases the predator identified was a secondary scavenger and not the mortality agent.

### Ranging behavior

We were interested in how individual Cooper's hawks used the landscape at three temporal (daily, seasonal, and annual) and two spatial (home range and core area) scales. From the breeding season in 1996 through June 1997, we explored radio-tracking methods for accomplishing these objectives. We intensively radio-tracked three adult male and three adult female Cooper's hawks during this period. Not all radio-tagged hawks survived or remained available to us for the full period, but we obtained at least four usable DR and DCA estimates from all individuals during the nonbreeding season and from three males and two females for the breeding season (overall, we obtained 112 DR and DCA estimates). Tracking sessions consisted of following individual radio-tagged hawks for  $\geq 8$  h continuously, obtaining triangulated (or visual) location estimates as close to every 15 min as possible. We tracked hawks in rotating order.

We accepted two types of locations for these and subsequent range analyses. First, we included visual location estimates—those that were visually confirmed or where the observer was considered to be within 50 m of the transmitter as evidenced by signal strength. Second, we included triangulated estimates where the  $\geq 2$  triangulation stations were within 1 km of the estimated transmitter position, and where the angle formed by the intersection of the azimuths was between  $45^\circ$  and  $125^\circ$ . Triangulated transmitter locations were estimated from the intersections of their azimuths using Program LOCATE II (Nams 2001). We estimated error in triangulated locations by deploying 10 test transmitters in areas frequented by radio-tagged Cooper's hawks, and then comparing the actual locations to triangulated location estimates for each person who assisted with the radio-tracking component of the study. Participants in trials were blind to the actual locations of test transmitters.



Based on the recommendations of Swihart and Slade (1985), we considered sets of locations yielding a Schoener index value  $\geq 1.96$  to satisfy assumptions of statistical independence. We generated area observation curves (Odum and Kuenzler 1955) for the 95% isopleths of home range estimates for the six Cooper's hawks tracked during the exploratory phase of our study to determine the number of locations necessary to achieve asymptotes of the home-range size estimates for the period of interest. We used these results to establish minimum sample-size requirements for range estimates throughout the study.

Although locations were obtained every 15 min throughout the day for DR and DCA estimates, it was not practical to maintain this sampling intensity for tracking more than six individuals for long periods of time. Moreover, for estimates of SR and AR, locations collected at this frequency did not meet assumptions of independence. Accordingly, we sought a less intensive, more statistically robust sampling approach to estimate seasonal and annual ranges. We evaluated three possible sampling frames for calculating SR and AR estimates: 1) locations obtained every 15 min for 4-h time blocks; 2) locations obtained once every 4 h over 12-h time blocks; and 3) a single location each day.

We used the Animal Movement extension version 2.0 (Hooge and Eichenlaub 2000) in ArcView 3.2 to calculate range estimates. We calculated fixed-kernel, harmonic mean, and minimum convex polygon estimates of DR, DCA, SR, SCA, AR, and ACA for the six radio-tagged Cooper's hawks tracked during the exploratory phase for each day that met our sample size criteria. We used the least-squares cross-validation procedure to determine the appropriate smoothing factor for fixed-kernel ranges. We compared estimates from all three analysis approaches to determine which best met our objectives. We used range estimates from the preferred analysis approach in all subsequent analyses. For AR calculations for individual Cooper's hawks that moved within a year, we calculated utilization-area estimates for each use area separately and then added them together. For male and female Cooper's hawks simultaneously occupying adjacent nest areas, we calculated the extent of spatial overlap between breeding and nonbreeding SR and SCA in ArcView 3.2.

## Movements and dispersal

We measured the distance between the most recently used nest area for a given individual Cooper's hawk and the geographic centroid of the subsequent winter home range (nest-to-wintering-area distance); the distance between successive nest areas (breeding dispersal distance, *sensu* Greenwood and Harvey 1982); and the distance between the

geographic centroids of successive wintering ranges (interyear wintering-area distance). In cases where hawks moved between two or more discrete winter home ranges, we used the most distant one from the prior nest area to calculate nest-to-wintering-area distance. Some Cooper's hawks that were not found during search flights subsequently reappeared on a study area. In such cases, we assumed the hawks moved  $>100$  km from their prior nest area for the period during which they could not be found. We used a default value of 100 km as the movement distance for these individuals, even though the real distance was likely greater. Accordingly, many of our dispersal distance estimates underestimate actual movement distances.

## Diet

We collected information on Cooper's hawk diet three ways: 1) collection of prey remains near nests in nest areas during the breeding seasons from 1992 to 2000 (prey remains data set); 2) blind and video-camera observations at nests from 1998 to 2000 (direct observation data set); and 3) collection of prey remains from prey captures by radio-tagged Cooper's hawks during radio-tracking sessions from 1995 to 2001 (radio-tracking data set). These data sets had different advantages and biases; but in general, data sets based on prey remains are considered inherently biased because prey types that leave little in the way of remains (e.g., nestling birds, reptiles, small mammals) are underrepresented (Bielefeldt et al. 1992; Lewis et al. 2006).

During each nest visit, we collected and removed all prey remains (feathers, fur, skeletal parts) found under the nest tree or nearby food-handling perches. Remains were packaged separately with data on the time and nest area. Each package was sent to the U.S. National Museum, Smithsonian Institution, for identification of parts to the lowest taxonomic level possible through comparison with museum material by taxa experts.

From 1996 through 1998, we observed Cooper's hawk nests from ground blinds in an effort to obtain information on feeding rates and nestling diets. We had difficulty identifying prey from ground blinds, so in 1998 we placed video home system (VHS) cameras at all nests in Dowling Park at which both breeding adults were radio-tagged and at which young were raised to  $>7$  d of age. We simultaneously videotaped, conducted ground-based blind observations, and radio-tracked both adult Cooper's hawks at sample nests for 12-h shifts starting at dawn. We did not employ video cameras on the Tall Timbers study area because we were unable to follow radio-tagged adults when they traveled off Tall Timbers on to neighboring private property. In 1999 and 2000, we continued to videotape at all Dowling Park nests with young where both adults



were radio-tagged, but we switched to digital video cameras (Sandpiper Technologies, Inc., <http://www.sandpipertech.com/info.html> [last visited 27 September 2012]) to improve the quality of the imagery. In 1999 we also ceased simultaneous ground-blind observations, and we altered our sampling period to run from noon to dark on the first day, and dawn to noon on the next day.

All videotaped prey deliveries were reviewed by at least two observers with experience identifying raptor prey (Video S1). To aid in identification, we prepared a catalog of photographs of museum specimens of likely prey species that emphasized features such as feet and bills, which we found particularly useful for identification. We compared prey brought to nests with the photographs in the catalog to aid in identification. Whenever possible, prey items were identified to Class, Order, Family, Genus, Species, sex, and age. Collectively, this approach provided us with data from 1998 through 2000 on the temporal and spatial history of foraging bouts conducted by both parent Cooper's hawks, as well as on the age of prey items captured.

During radio-tracking sessions, we watched for any signs that Cooper's hawks had made a prey capture (e.g., cessation of hunting or flight to a known prey-handling area). When we suspected a kill had been made, we triangulated on the hawk's position from a distance that would not cause disturbance, and then we waited for the hawk to leave. Once the hawk left the area, we conducted a thorough search of the area for prey remains. As with remains from nest sites, all remains located during tracking sessions were collected, bagged with proper identification, and sent to the U.S. National Museum, Smithsonian Institution, for identification of parts to the lowest taxonomic level possible. During the breeding season, prey remains from radio-tagged hawks provided information to supplement information gleaned from video at nests. Prey remains data from radio-tagged hawks was the primary source of diet information for Cooper's hawks from the nonbreeding season.

We followed the approach of Bielefeldt et al. (1992) in estimating mass of prey. For avian species with adult mass <27 g, we assumed they fledged at >90% of adult mass, so all birds in this category were recorded as the adult mass regardless of age. Nestlings of birds with adult mass between 28 and 59 g were assigned 70% of adult mass as nestlings, 90% of adult mass as fledglings, and 95% of adult mass as juveniles or age unknown; birds in the 60–91-g range were recorded as 65%, 85%, and 90% of adult mass for the same age categories, respectively; and birds >92 g were recorded as 55%, 80%, and 85% of adult mass, respectively. Woodpeckers and cavity-nesting passerines that fledged at near adult size were assigned 95% of the mass of adults. Avian

prey mass was as reported by Dunning (1992), except that for bobwhite we used seasonal average mass by sex, as determined from samples of trapped birds at Tall Timbers (Tall Timbers Research Station, Leon County, Florida; V. Carter, personal communication), and for American kestrels we estimated average mass from individuals trapped and banded by T.F.B. near the Dowling Park study area. We estimated a minimum and maximum likely mass for mammals based on information by Whittaker (1995); we assigned the smaller mass for juveniles and the larger for adults. In cases where age was not certain, we used 75% of the larger mass. For reptiles, we used mass from specimens collected in northern Florida (Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida; K. Enge, personal communication).

### Avian prey availability

We conducted avian point counts in July 1998 and February, May, and July 1999 and 2000 on Tall Timbers ( $n = 38$  points) and Dowling Park ( $n = 50$  points). Point counts were conducted following the U.S. Geological Survey Breeding Bird Survey protocol (<https://www.pwrc.usgs.gov/bbs/index.cfm?CFID=10606059&CFTOKEN=11573326> [last visited 11 November 2012]) using the same observer throughout. One departure from Breeding Bird Survey protocol was that juvenile and fledgling birds, when heard or seen, were counted and recorded separately from adults. Fledglings and juveniles (grouped as one category) were counted when begging noises were heard, if adults were heard or seen feeding young, or when fledglings were actually seen. In the latter cases, we were generally able to identify the fledglings to species.

We recognize and acknowledge that avian point counts, unadjusted for detectability differences among species, probably provide a biased representation of availability of some avian prey species to Cooper's hawks. For comparisons of diet between study areas or seasons, where such biases would be consistent across comparisons, the effects of detectability biases on results are probably minor. However, in comparisons of use versus availability, this bias could have a more pronounced effect and should be considered as a possible explanation for observed differences.

### Statistical analyses

We employed traditional forms of hypothesis testing in some cases, but in many others we used information-theoretic methods in exploratory analyses to assess the relative weight of evidence for a series of alternative a priori models, hierarchical subsets of a global model, in explaining variation in a particular response variable (Burnham and Anderson 1998). Akaike's Information Criterion (AIC)

values corrected for small sample size ( $AIC_c$ ) provided the relative strength of evidence for each model. In cases where the variance-inflation factor ( $\hat{c}$ ) for the global model  $>2.0$ , we used quasi- $AIC_c$  ( $QAIC_c$ ) values in model selection. We used the “AICcmodavg” package (Mazerolle 2010) in R (R Development Core Team 2010) for model selection in most cases, except we used Program MARK (Burnham and Anderson 1998; Cooch and White 2005) for analysis of survival and nest survival models. The model statistics (e.g., parameter counts, AIC values) we report are those provided by the respective software program. We used the “modavg” function in R to generate parameter estimates and unconditional standard errors (SE) for multi-model inference. We used the “modavgpred” function in R to generate model-averaged predictions and unconditional SEs based on the suite of plausible models when such predictions were desired. Fits were obtained using either generalized linear models for binomial data with a logit-link function (nest site occupancy, nest success, survival, bobwhite capture probability); Poisson regression in generalized linear models with a log-link function (brood size at successful nests); or linear models with an identity-link function; nest chronology, home range comparisons).

AIC weights ( $w$ ) were calculated from  $QAIC_c$  values to aid in model selection following Burnham and Anderson (1998). We considered models within 2.0  $QAIC_c$  units to be competitive; we only include competitive and global models in tables reporting model selection results. Variables included in competitive models were further evaluated using the “modavg” function to determine whether the 90% model or model-averaged coefficient confidence intervals overlapped 0. Variable values and SEs were predicted according to the suite of best models (taking into account the likely contribution of each variable) using the “modavgpred” function in R.

We reviewed the literature and identified a list of variables a priori that we postulated might function as covariates and affect Cooper's hawk reproductive metrics, ranging behavior, survival, or bobwhite capture probability, either singly or in combination. As our study progressed, we also identified additional factors that we speculated might be responsible for observed variation in one or more life-history traits. We incorporated these variables into the global models that we evaluated using information-theoretic methods, and assessed the weight of evidence for their effect on Cooper's hawk ecology on our study areas using model ranking as described above. The variables and rationale for including them in models are described below (phrases in parenthesis are model terms used for the effects in the tables, and unless otherwise noted, hypotheses were developed a priori):

1. Study Area (AREA). We expected that, because of the marked differences in landscape features between the two study areas and possible associated differences in prey availability, that nest site occupancy; nest chronology; nest success; brood size; brood size at successful nests; annual survival; daily, seasonal, and annual home-range and core area sizes; home range overlap; probability of female dispersal; and daily probability of bobwhite capture would differ for Cooper's hawks between study areas. We had no a priori basis for predicting the direction of differences in study area effects for the various response variables, except that we expected daily probability of bobwhite capture to be higher on Tall Timbers given the management emphasis on that species there. AREA was treated as a factor in models, with two levels: 1) Dowling Park and 2) Tall Timbers.
2. Female Age (AGE). Based on findings with *Accipiter* hawks in some other studies (Snyder and Wiley 1976; Millsap 1982; Newton and Marquiss 1984; Boal 2001a), we expected that nesting attempts involving SY females would start later; be less successful; result in smaller broods; and have smaller brood sizes at successful nest sites compared with nesting attempts involving ASY females. AGE was treated as a factor in models, with two levels: 1) SY and 2) ASY.
3. Eye Color (EYE). We predicted that eye color score would be negatively associated with the probability of dispersal by females because those females with eyes approaching red were likely older. We hypothesized that older females likely dominated younger individuals, and were less prone to have to travel as far to find suitable nesting areas. In this case we used eye color as a coarse surrogate for age, because there is a general but nonspecific progression from yellow to red irises with age in some female Cooper's hawk populations (Rosenfield et al. 2003). All SY females, and only SY females, had yellow or yellow-orange irises, and thus SY females fell into two distinct groups for this analysis. We treated EYE score as an integer in models, and recognize that this treatment implies that distances between adjacent scores are equal (Powers and Xie 2008).
4. Fixed year effects (TIME). We recognized that there might be a temporal trend in Cooper's hawk nest-area occupancy, nest survival, brood size, and brood size at successful nests over the duration of the study because several sources (Layne 1986; Sauer et al. 2011) suggest the summer Cooper's hawk population in the



southeastern Atlantic coastal plain was increasing prior to and during our study. Our rationale for these predictions was that if Cooper's hawk populations were changing in size and growing toward saturation, nest area occupancy and productivity might vary with time, either increasing or decreasing, depending on how close the breeding population was to saturation. We treated years as integers for TIME in models.

5. Nonfixed year effects (YEAR). We postulated that reproductive measures, ranging behavior, and bobwhite predation rate might vary nondirectionally among years based on annual variation in weather and other abiotic factors. YEAR, where included in a model, was a factor with six levels: 1) 1995, 2) 1996, 3) 1997, 4) 1998, 5) 1999, and 6) 2000. We also evaluated subsets of YEAR as fixed effects in some models, as described below:
  - a. Late Winter–Early Spring Precipitation (PRECIP). Based on work with the Eurasian sparrowhawk and northern goshawk *Accipiter gentilis* (Newton 1978; Newton and Marquiss 1984; Newton 1986; Kenward 2006), we expected atypically wet late winter early springs to be associated with lower nest-area occupancy and delayed nest chronology; and with poorer nest success, lower brood sizes, lower brood sizes at successful nests, and higher rates of female dispersal. PRECIP was included in models as a factor with three levels: 1) years with average January through April precipitation (within 1 SD of the long-term average, based on Southeast Regional Climate Center [2007]; 1995, 1996, and 2000); 2) years with lower than average January through April precipitation ( $>1$  SD lower than average; 1999); and 3) years with higher than average January through April precipitation ( $>1$  SD above average; 1997 and 1998).
  - b. Year 1998 (YR1998). The year 1998 was unique in two respects. First, as noted previously, it was an El Niño year and had record late winter early spring precipitation. In that respect, the premise that 1998 might differ from other years was a subset of the PRECIP hypothesis. However, 1998 was also the year where we switched to lighter transmitters on male Cooper's hawks. Given these two possible effects, we speculated a posteriori that nest site occupancy and nest chronology might be delayed, and if so, that nest success, brood size, and brood size at successful nests would be lower than average in 1998 due to climatic factors. We expected these effects to be the result of lowered foraging success, so we also expected daily, seasonal, and annual home-range sizes; home range overlap between adjacent males; annual survival; and probability of female dispersal to be larger in 1998 than in other years. We did not expect heavy transmitters to have an effect on reproductive or ranging variables, but we did expect male survival to increase with the change in transmitter weight in 1998. YR1998 was included in models as a factor with two levels: 1) YEAR = 1998 and 2) YEAR  $<>$ 1998.
  - c. Before and after 1998 (YRGROUP). As an extension of covariate 5b, we hypothesized that the 1998 effects on nest-area occupancy, chronology, brood size, brood size at successful nests, annual survival, probability of female dispersal, and increased male survival might carry over into subsequent years, or that they might differ between the years prior to and after year 1998. YRGROUP was included in models as a factor with two levels: 1) YEAR  $<$  1998 and 2) YEAR  $\geq$  1998.
  - d. Before, during, and after 1998 (YR-STRATA). As another extension of 5b, we postulated that the combination of effects associated with the year 1998 might result in differences in nest-area occupancy; chronology; brood size; brood size at successful nests; annual survival; and probability of female dispersal before, after, and during the year 1998. We did not expect a YRSTRATA effect on male survival. YRSTRATA was included in models as a factor with three levels: 1) YEAR  $<$  1998, 2) YEAR = 1998, and 3) YEAR  $>$  1998.
6. Interaction between temporal effects and AREA (AREA\*YEAR, AREA\*TIME). As an extension of 1, 4, and 5, we predicted there might be a difference in the fixed and nonfixed effects of year between study areas with respect to nest site occupancy, chronology, brood size, brood size at successful nests, survival, and female dispersal because the El Niño precipitation was considerably greater on Dowling Park than Tall Timbers. Therefore, we included the interaction term and logical subsets (e.g., AREA\*YR1998) in models evaluating these relationships.

7. Sex (SEX). We predicted that annual survival, daily range, seasonal range, and annual range values might differ between male and female Cooper's hawks, based on findings for other species of *Accipiter* hawks (Newton 1986; Kenward 2006). Based on findings with other species, we suspected that female ranges would be smaller than male ranges during the breeding season and larger at other times of the year, and that male ranges would be largest during the breeding season and smaller at other times of the year. We had no a priori belief about the direction of differences in survival rate. SEX was treated as a factor in models, with two levels: 1) female, and 2) male.
8. Season (SEASON). Consistent with findings in other *Accipiter* hawks (Newton 1986; Kenward 2006), we postulated that Cooper's hawk daily and seasonal range size and predation rates on bobwhite would differ between the breeding and nonbreeding seasons. SEASON was treated as a factor in models, with two levels: 1) breeding season, and 2) nonbreeding season. However, for the purposes of bobwhite predation-rate analyses, we identified an additional level. Several authors have speculated that Cooper's hawk predation on bobwhite is greatest during winter and early spring, related to the decreased availability of escape cover at this time of the year (Stoddard 1978; Mueller and Atkinson 1985; Mueller 1989; Guthery 2000; Carter et al. 2002; Cox et al. 2004). Given this information, we suspected that Cooper's hawk predation on bobwhite might be greater after the first hard winter frost and before spring regrowth began. On our study area, this was the period between early November and the end of February. For bobwhite predation models, SEASON was treated as a factor with three levels: 1) winter, where month = November, December, January, or February; 2) breeding, where month = March, April, May, June, or July; or 3) postbreeding, where month = August, September, and October.
9. Interaction between sex and season (SEX\*SEASON). As noted above, we expected the seasonal differences in daily and seasonal ranges to follow different patterns for males and females because of the different roles played by the sexes during the breeding season. As such, this interaction covariate is an extension of covariates 7 and 8.
10. Interaction between sex and study area (SEX\*AREA). Because of slight differences in the proportion of SY breeding females between study areas (see Results), we included an a posteriori covariate that allowed the effect of study area on survival to vary between sexes. High proportions of relatively young breeding females are indicative of high female mortality or rapidly increasing populations in raptors (Newton 1979).
11. Three-way interaction between sex, season, and study area (SEX\*SEASON\*AREA). We included this three-way interaction in models for daily and seasonal range size to allow for possible complex differences in the effect of these variables on range size between sexes, study areas, and seasons.
12. YEARRANK (YEARRANK). We expected daily, seasonal, and annual ranges; home range overlap; and probability of female dispersal to be larger in lower ranked (poorer) years. If prey availability was the primary factor driving year ranks, we postulated that Cooper's hawks would have to forage more widely to find sufficient food in poor years, and that females would be more likely to disperse. We also expected prey delivery rates to be greater in better years. YEARRANK was treated as a factor in models, with three levels: 1) high-ranked years (lower one-third of ranks, where one was the best ranked year), 2) moderate-ranked years (middle one-third of ranks), and 3) low-ranked years (lower one-third of ranks).
13. SITERANK (SITERANK). Similar to 12, we expected daily, seasonal, and annual ranges; home range overlap; and probability of female dispersal to be larger on or from lower ranked (poorer) sites, assuming that prey availability was the primary factor driving site ranks. We expected that Cooper's hawks would have to forage more widely to find sufficient food on, and that females would be more likely to disperse from, poor-quality nest areas. Accordingly, we also expected prey delivery rates at nests on lower ranked sites to be lower than on higher ranked sites. SITERANK was treated as a factor in models, with three levels: 1) high-ranked sites (lower one-third of ranks, where one was the best ranked nesting area), 2) moderate-ranked sites (middle one-third of ranks), and 3) low-ranked sites (lower one-third of ranks).
14. Number of young (YOUNG). We postulated that the breeding season range of adult male and female Cooper's hawks would increase proportionally with brood size because of the greater resource requirements of larger broods. We treated brood size as an integer in models.

We used Program MARK (Cooch and White 2005) to evaluate models involving nest success and survival. The nest survival module in Program MARK was used to evaluate nest success models; we used a nesting period of 54 d (30 d incubation



[Rosenfield and Bielefeldt 1993] and 24-d nestling period) in nest survival models. We used known-fate models in MARK to evaluate survival. We used all Cooper's hawks that were radio-tagged from 1995 to 2000 that survived >10 d after radio-tagging in survival models. The six individuals that died within 10 d of radio-tagging were excluded because we suspected these mortalities might have been associated with capture and handling effects. Individual hawks were retained in the survival data set until their transmitter battery failed, they emigrated from the study area, or they died. All Cooper's hawks of unknown status over a survival interval were censored from the analysis for that interval. We recaptured and replaced expiring transmitters on four individuals.

For hypotheses regarding rates of predation on bobwhite, we used the radio-tracking prey data set to estimate the probability of capture of a bobwhite on a given day. Although this data set probably underrepresented actual prey-capture rates because many smaller prey were likely overlooked, we believe it accurately reflected capture rates for larger prey such as bobwhite because they required considerable handling time (in our experience, usually >2 h). Because of the long handling time, we were able to detect when Cooper's hawks captured larger prey. To minimize the potential of including days when bobwhite were captured but missed, we only included the following tracking sessions in these analyses: 1) during the nonbreeding season, only tracking sessions during which a given hawk was radio-tracked for  $\geq 4$  h and at least one prey capture was confirmed or on which tracking occurred for  $\geq 8$  h, and 2) during the breeding season, only tracking sessions lasting  $\geq 8$  h or paired 4-h tracking sessions on sequential days. We assumed that on days tracking occurred for  $\geq 8$  h and no prey captures were detected, either no prey were captured, or one or more small prey were captured but the captures went undetected. We estimated the proportion of days when bobwhites were captured according to variables included in the best-fitting models, and then expanded that value to estimate the number (and SE) of northern bobwhite captured by sampled Cooper's hawks over a year.

In addition to information-theoretic methods, we used standard parametric and nonparametric approaches and graphical techniques to address a number of other questions. In cases where we employed standard hypothesis testing, we gave preference to parametric tests when assumptions of the tests could be met either with the raw data or through transformation of the raw data. Unless otherwise noted, the arcsine transformation was applied to all proportions before parametric analyses; daily, seasonal, and annual home-ranges sizes were square-root transformed; and counts were log

(ln)-transformed. Throughout, we use  $\alpha \leq 0.10$  as our threshold for statistical significance to lessen chances of Type II error. We use  $n$  to designate sample size for tests, SE for standard error, and  $df$  for degrees of freedom.

We used linear models and 2-way analysis of variance (ANOVA) to evaluate the effects of nest start date and prior adult experience at a particular nest area on brood size at successful nests. Based on general trends in raptors, we expected to find higher brood sizes at successful nests where the start date was early, and we expected to find higher measures of reproductive success at nests where adults had been in residence for  $\geq 1$  y (Newton 1979). We distinguished between Cooper's hawks with and without prior-years' experience at a nest area based on banding and radio-tagging records. We compared brood size at successful nests attended by radio-tagged and non radio-tagged adult males and females with 2-way ANOVA with interaction to determine whether radio transmitters had an effect on nest success and productivity. We did not evaluate brood size at all nests (i.e., successful and unsuccessful) because only adult Cooper's hawks with young were captured and radio-tagged; thus, radio-tagged hawks were more likely to be successful because their nests had already survived at least to hatching.

We supplemented daily range-size model analyses with graphical evaluation of annual trends in daily range size for Cooper's hawks of both sexes. Because DR varied by sex and among individuals, we created a standardized measure of DR size for these analyses by dividing DR estimates for each radio-tagged Cooper's hawk each day by the AR for that hawk. The resulting metric was the proportion of the AR used on a daily basis at the 95% contour-level (PAHR). We fitted a smoothed line and confidence bands to the PAHR distribution using locally weighted scatterplot smoothing (LOESS) regression in the R package GGPlot2 (R Development Core Team 2010).

For diet analyses, we considered prey species that made up  $\geq 4\%$  of any data set by frequency to be important prey. We used frequency rather than biomass because biomass was strongly affected by one capture of a very heavy prey species. We chose  $\geq 4\%$  as our break point for distinguishing important prey because there was a gap in the frequency distribution for several of the data sets at this level. We used chi-square contingency tables, with the null hypothesis that frequencies of important prey species were equal, to look for differences in diet between Cooper's hawk sexes, between study areas, and between seasons. If we rejected the null hypothesis, we excluded species in order of decreasing contribution to the original chi-square until differences among cells became nonsignificant (Zar 1984). We

**Table 1.** Sample sizes and measurements of breeding adult male and female Cooper's hawks on two north Florida study areas, 1995–2000. All males were >2 y old, whereas five females were in their second year (SY). Tail length differed between female age classes (mean SY = 212 [SE = 2] mm, ASY = 205 [SE = 2] mm), but all other measurements were similar between female age classes and for both sexes between study areas and are pooled below (see text).

Sex	n	Mean (SE)							
		Wing cord (mm)	Tail (mm)	Hind claw (mm)	Tarsus width (mm)	Tarsus length (mm)	Culmen (mm)	Bill depth (mm)	Mass (g)
Female	30	262 (2)	206 (2)	23.9 (0.2)	6.5 (0.4)	77.0 (0.7)	19.7 (0.2)	14.2 (0.2)	523 (22)
Male	19	233 (1)	180 (2)	20.3 (0.1)	6.3 (0.9)	68.8 (1.0)	16.4 (0.1)	12.8 (0.3)	288 (19)

compared mean weight of prey between Cooper's hawk sexes, and against the mean weight of available prey, using 1-way ANOVA, and visually using box plots. We transformed prey weights to the log-scale for these analyses.

We looked for daily and seasonal temporal patterns in prey capture rates for radio-tagged Cooper's hawks by calculating the number of prey captures made per hour of radio-tracking during the breeding season and nonbreeding season. We included in this analysis all days on which focal hawks were tracked for  $\geq 4$  h. Data were pooled across sexes because we had insufficient data on prey capture rates for females during the breeding season for meaningful comparison. We used linear regression to determine the degree to which SITERANK and YEARRANK explained variation in breeding-season prey-capture rates. We only collected data for these analyses on Dowling Park due to access restrictions around Tall Timbers.

We transformed raw-count totals for each avian species that comprised  $\geq 4\%$  of avian detections at point counts on each study area to observed abundance ranks. Similarly, we rank-transformed prey-capture frequencies for each important avian prey species from the full prey-capture data set by study area and season. We plotted the abundance rank against the capture rank following the approach by Kenward (2006). Prey species plotted above a diagonal line through the origin were represented more in the prey capture data set than expected based on abundance rank, while those below the line were represented less often than expected. We recognize that this is a crude measure of prey selection, given unaccounted-for differences in detectability among avian species on point counts and biases in the full prey-frequency data set. Nevertheless, we believe the results provide coarse insight into prey preferences by Cooper's hawks on our study areas.

Our data sets included many cases where the same individual Cooper's hawks and Cooper's hawk nest areas were sampled in successive years. In these cases we treat the years, individuals, and nest areas as statistically independent replicates unless otherwise

noted. We believe this was tenable because the individual Cooper's hawks aged a year between samples, and could have been (and in many cases were) replaced by new recruits between years. As such, each year's breeding population consisted of a new assortment of individuals under a different set of environment conditions.

## Results

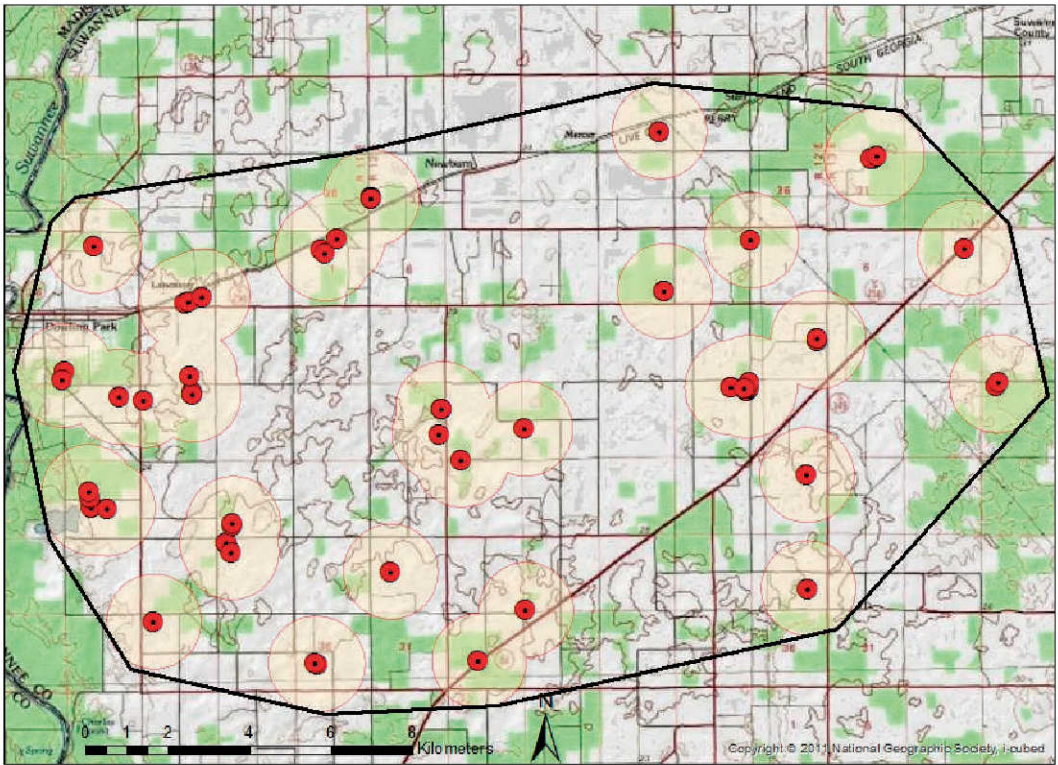
### Breeding biology and survival

*Characteristics of breeding adult Cooper's hawks.* We captured 30 different breeding female and 19 breeding male Cooper's hawks (Table 1; Table S1). We found no differences in measurements or mass of breeding Cooper's hawks of either sex between Tall Timbers and Dowling Park (independent-sample *t*-tests,  $P > 0.10$  for all). After second year females and SY females differed in tail length (independent-sample *t*-test,  $t = 3.12$ ,  $df = 19.59$ ,  $P < 0.001$ ) but all other measurements were similar between age classes. Overall, female Cooper's hawks averaged 1.8 times larger than males in mass, and 1.1 times larger in wing cord.

All breeding male Cooper's hawks and 70 of 76 (92%) breeding females were classified as ASY. Second year females were present at 3 of 18 (17%) occupied nest areas on Tall Timbers and 3 of 58 (5%) occupied nest areas on Dowling Park; the difference was not significant (2-sample test for equality of proportions with continuity correction,  $\chi^2 = 1.2$ ,  $df = 1$ ,  $P = 0.28$ ). Mean eye-color score of breeding females did not differ between study areas (Dowling Park = 3.1, SE = 0.3, sample size [ $n$ ] = 30; Tall Timbers = 2.5, SE = 0.3,  $n = 11$ ; independent-sample *t*-test,  $t = 1.5$ ,  $df = 21.7$ ,  $P = 0.13$ ).

*Nest area density, location, and reuse.* We identified 26 nest areas on the Dowling Park study area, and 5 on Tall Timbers, yielding densities of 776 ha and 294 ha per nest area, respectively (see below for densities of occupied nest areas). Additional nest areas outside the original study-area boundaries were located based on movements of radio-tagged Cooper's hawks, but these are not included in density





**Figure 4.** Map of Cooper's hawk nest areas on the Dowling Park study area, Suwannee County, Florida, 1995–2000, showing the regular spacing of nest sites in suitable habitat. Circles denote locations of occupied nests in one or more years, and nests are buffered with a 1-km-radius circle (one-half the mean internest area distance).

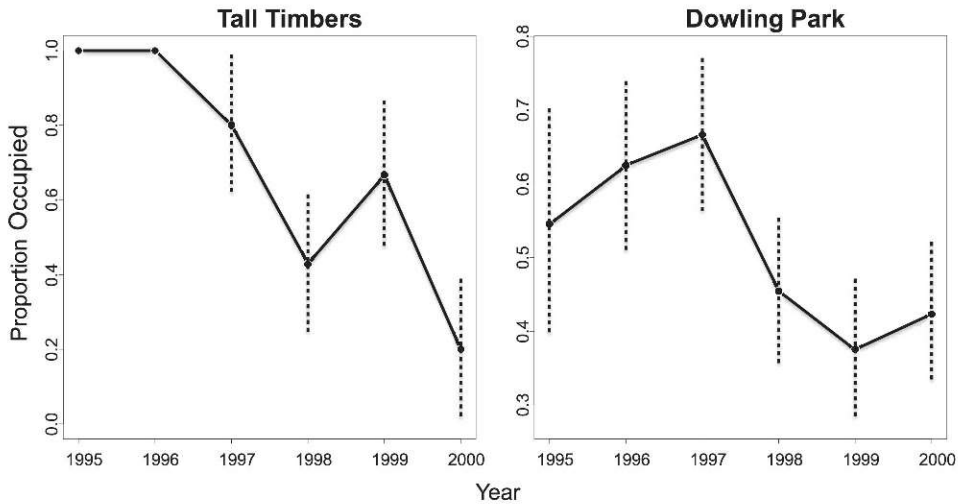
estimates. Cooper's hawk nests averaged 2.0 (SE = 0.1,  $n = 26$ ) km apart on Dowling Park and 1.7 (SE = 0.17,  $n = 5$ ) km apart on Tall Timbers, a nonsignificant difference (1-way ANOVA:  $F = 0.09$ ,  $df = 1,29$ ,  $P = 0.34$ ). The closest simultaneously occupied nests were 1.1 km apart on Dowling Park and 1.3 km apart on Tall Timbers. On Dowling Park, where our study area was large enough to develop a comprehensive sense of nest spacing, nest areas were relatively evenly spaced across the landscape where there was suitable nesting habitat (Figure 4).

All five nest areas on Tall Timbers were in bottomland forests along ephemeral drainages or small streams, areas that were seasonally flooded (mainly during summer) and as a result had very little understory vegetation. All 26 nest areas on Dowling Park were in uplands that were historically longleaf pine-dominated sandhills. Exclusion of fire had allowed laurel oaks and other hardwoods to encroach under the pines. Canopy closure was high in nest stands on Dowling Park, and as a result understory vegetation was sparse. Although most nests at Dowling Park were in fairly large woodlots ( $\geq 10$  ha), three were in small linear stands of oak trees along old fencerows embedded in large blocks

of planted loblolly pine, and one was in a tree-lined fencerow bordered by a field.

On both study areas, nests were usually within 100 m of a substantial habitat edge, most often the border of the nest woodlot and an open field. Most nests also adjoined a small forest opening, such as a glade, trail, or unimproved road. Of the 77 nest structures located, 62 (81%) were in laurel oaks, 8 (10%) were in live oaks, 2 (3%) were in American beech *Fagus grandifolia*, and one (1%) each were in spruce pine *Pinus glabra*, sweet gum, cherry *Prunus* spp., water oak *Quercus nigra*, and red oak *Quercus rubra*. Laurel oak was the most frequent nest tree species on both study areas. Nest heights were not measured at every nest area, but two nests that represented the extremes were 5.5 m and 24.8 m above ground. Most nests were between 11 and 18 m above ground.

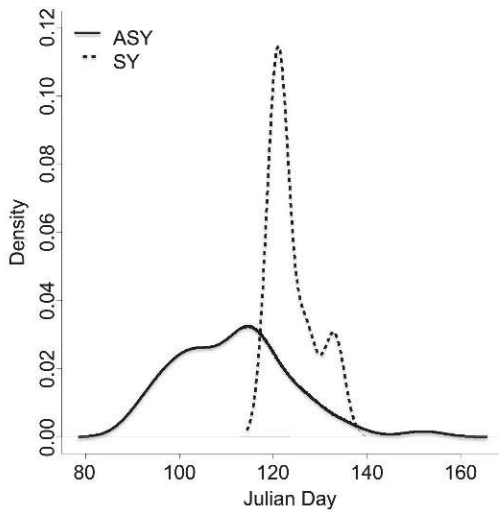
In 38 (79%) of 48 instances where Cooper's hawks occupied a nest area in  $\geq 2$  consecutive years, they built a new nest; 10 times (21%) they reused the previous year's nest. At one nest area that was occupied each year of our study, Cooper's hawks reused the same nest 3 y in succession. At another area where both the adult male and female from the preceding year had been replaced by new birds, the



**Figure 5.** Proportion of Cooper's hawk nest areas occupied annually on two north-Florida study areas, 1995–2000. Error bars are the SE.

same nest was reused. At a third area, Cooper's hawks and red-shouldered hawks *Buteo lineatus* alternated in the use of a nest structure over 4 y. In cases where Cooper's hawks constructed a new nest, the new nest averaged 159 m ( $n = 38$ ,  $SE = 35$ , range = 15–1,000 m) from the prior-year's nest; the extreme case involved a male and female Cooper's hawks radio-tagged the previous year.

*Nest area occupancy.* We detected radio-tagged female Cooper's hawks for at least a few days at most nest areas early in the breeding season each year, but breeding activity did not proceed to the point where a nest area was classified as occupied in all cases. Overall, we classified 76 nest areas (out of 146 possible nest area  $\times$  year combinations) as occupied: 58 on Dowling Park and 18 on Tall Timbers (Table S2). Competitive nest-area occupancy models all included temporal effects, and several included a study area effect (Table 2), but only the model-averaged coefficient for YRGROUP, TIME, and TIME\*AREA did not include 0. Model-based estimates of nest-area occupancy were 68% ( $SE = 6\%$ ) for 1995 through 1997, and 42% ( $SE = 5\%$ ) for 1998 through 2000. The decreasing trend was apparent on both study areas, but appeared more directly related to the year 1998 on Dowling Park (Figure 5). Over all years, the average occupied nest density was 565 ha and 1,494 ha per occupied nest area on Tall Timbers and Dowling Park, respectively.



**Figure 6.** LOESS-smoothed frequency distribution of Cooper's hawk nest start date by age of female (SY = second year, ASY = after second year) from two north Florida study areas, 1995–2000. The mean start day for ASY females was 21 April, and for SY females it was 3 May. Smoothing was done in R using the scatter-plot smoothing package (R Development Core Team 2010) default criteria.

*Nesting chronology.* The mean start date for successful nests was 22 April ( $SE = 1.6$  d,  $n = 59$ ; range = 31 March–30 May, the latter being a re-nesting effort). Competitive models included female-age and several temporal effects (Table 2), but only the female-age effect had a model-averaged coefficient that did not include 0. The model-based estimated start date for successful nests with ASY females was 21 April ( $SE = 1.5$  d), compared with 3 May ( $SE = 4.8$  d) for nests with SY females (Figure 6).

*Nest success.* Competitive nest-success models included female-age and temporal effects, but the highest-ranked model was the constant (intercept



**Table 2.** Competitive and global models examined to explain variation in Cooper's hawk nest chronology, nest area occupancy, nest survival, brood size, and brood size at successful nests on two north-Florida study areas, 1995–2000. Sample size was 76 occupied nests at 31 nest areas. Model ranking was based on Akaike's Information Criterion (AIC) corrected for small sample size (AIC<sub>c</sub>). All competitive models (within 2 AIC units of the top model) and the global model are shown. Chronology was evaluated with linear models using an identity-link function; occupancy and nest survival were evaluated with binomial generalized linear models using a logit-link function; and brood size and brood size at successful nests were evaluated with Poisson generalized linear model using a log-link function.

Variable	Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub>	ΔAIC <sub>c</sub> <sup>c</sup>	ω <sup>d</sup>	∑ω <sup>e</sup>
Chronology	YR1998 + AGE	5	463.37	0	0.23	0.23
	AGE	3	463.42	0.06	0.22	0.45
	YRSTRATA + AGE	6	463.78	0.42	0.18	0.63
	YEAR + AGE + AREA + TIME + YRSTRATA + PRECIP + YR1998 + YRGROUP + AREA*TIME	14	470.79	7.42	0.01	0.99
Occupancy	YRGROUP	2	196.99	0	0.22	0.22
	YRGROUP*AREA	4	197.19	0.19	0.20	0.43
	YRGROUP + AREA	3	197.48	0.49	0.18	0.6
	TIME	2	198.78	1.79	0.09	0.69
	YRSTRATA	3	198.96	1.97	0.08	0.78
	YEAR + AREA + TIME + PRECIP + YRGROUP + YRSTRATA + YR1998 + AREA*YEAR + AREA*TIME	12	210.29	13.3	0	1.00
Nest survival	CONSTANT	1	130.69	0	0.36	0.036
	AGE	2	131.27	0.58	0.27	0.55
	AREA	2	132.41	1.71	0.13	0.69
	YR1998	2	132.5781	1.8849	0.12	0.81
	AGE + AREA + YEAR	17	151.82	21.13	<0.01	1.00
Brood size	CONSTANT	1	277.79	0	0.21	0.21
	AREA	2	279.15	1.37	0.11	0.32
	YRGROUP	2	279.16	1.37	0.11	0.43
	YR1998	2	279.63	1.84	0.08	0.52
	AGE	2	279.74	1.95	0.08	0.60
	YEAR + AREA + TIME + AREA*YEAR + AGE + AREA*TIME	13	297.62	19.83	0	1.00
Brood size at successful nests	CONSTANT	1	158.44	0	0.23	0.23
	AREA	2	159.45	1.01	0.14	0.36
	TIME	2	160.17	1.73	0.09	0.46
	AGE	2	160.32	1.88	0.09	0.55
	YEAR + AREA + TIME + AREA*YEAR + AGE + AREA*TIME	13	189.63	31.20	0	1.00

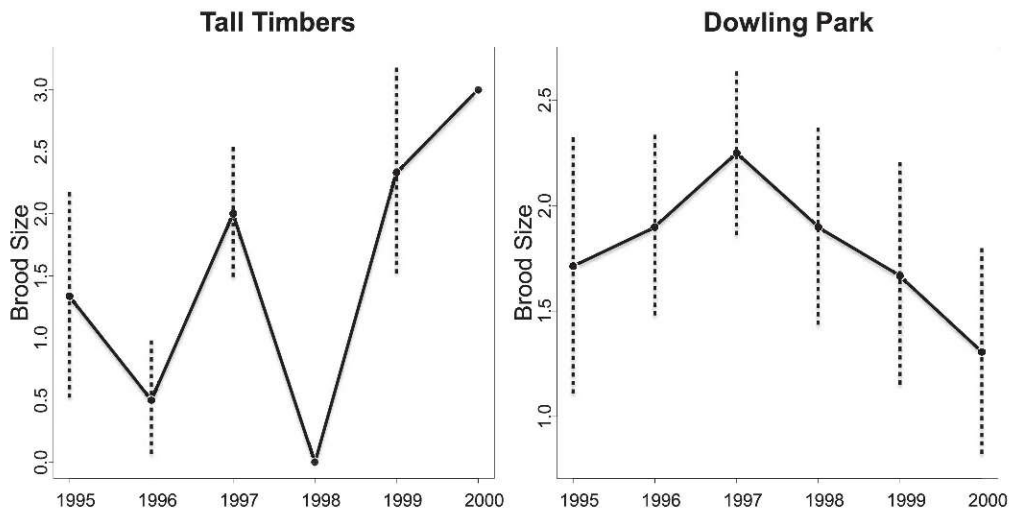
<sup>a</sup> AGE = a factor in models, with two levels: 1) SY and 2) ASY. YEAR = a factor with six levels: 1) 1995, 2) 1996, 3) 1997, 4) 1998, 5) 1999, and 6) 2000. AREA = a factor with two levels: 1) Dowling Park and 2) Tall Timbers. TIME = an integer, with years as values. YRGROUP = a factor with two levels: 1) YEAR <1998 and 2) YEAR ≥1998. YRSTRATA = a factor with three levels: 1) 1995–1997; 2) 1998; 3) 1999–2000. PRECIP = a factor in models with three levels: 1) years with annual precipitation within 1 SD of the average; 2) years with annual precipitation > 1 SD above the average; and 3) years with annual precipitation < 1 SD below the average. YR1998 = a factor with two levels: 1) 1998, 2) <>1998. CONSTANT = constant intercept (only) model. A \* denotes inclusion of an interaction term between the effects.

<sup>b</sup> Number of model parameters.

<sup>c</sup> Change in AIC<sub>c</sub> from the top-ranked model.

<sup>d</sup> Model weight.

<sup>e</sup> Cumulative model weight.



**Figure 7.** Brood size of Cooper's hawks on two north Florida study areas, 1995–2000. Points are annual means and dotted lines denote the SE.

only) model (Table 2). Female age and year effects had model-averaged coefficients with confidence intervals that included 0, so the weight of evidence was for the constant-only model. Daily nest survival as derived from this model averaged 0.991 (SE = 0.002), or 62% over the 54-d nesting period.

We determined the stage of nest failure at all 28 nests that were unsuccessful: 1) 7 failed either before or shortly after eggs were laid, 2) 11 failed during incubation, and 3) 10 failed with young. We could determine the cause of failures at 11 nest areas: 1) weather accounted for 3 failures (2 in a single tornado in 1997 and 1 in a hurricane in 1995); 2) 3 nests were depredated (1 clutch by gray squirrels *Sciurus carolinensis*), 1 by an unidentified mammal, and 1 by a great horned owl); 3) 2 nests were abandoned after timber cutting or road construction started within 100 m of the nests; 4) 2 nests were abandoned after adult males died (in both cases males were radio-tagged); and 5) fire ants *Solenopsis wagneri* caused the death of 1 brood when they prematurely jumped from the nest (Video S2).

**Productivity.** Overall, Cooper's hawk brood size averaged 1.79 (SE = 0.18,  $n = 76$ , range = 0–5; Figure 7) and brood size at successful nests averaged 2.78 (SE = 0.24,  $n = 49$ , range = 1–5). Brood size at successful nests did not differ between nest areas with and without radio-tagged adult males (1-way ANOVA,  $F = 0.30$ ,  $df = 1,46$ ,  $P = 0.59$ ) or females (1-way ANOVA,  $F = 1.54$ ,  $df = 1,46$ ,  $P = 0.31$ ). The highest-weighted brood-size model and brood-size at successful nest model was the constant intercept-only model, but other competitive models suggested temporal and study area effects (Table 2). However, coefficient confidence intervals for all effects for both response variables included 0, so we

accepted the intercept-only model as the model with the strongest evidence in both cases.

There was a weak decrease in brood size at occupied nests with increasing start date (adjusted  $R^2 = 0.06$ ,  $F = 5.0$ ,  $df = 1,57$ ,  $P = 0.03$ ); the relationship held when nest areas with SY females were removed from the analysis (adjusted  $R^2 = 0.07$ ,  $F = 4.7$ ,  $df = 1,51$ ,  $P = 0.03$ ). There was no difference in brood size among nest areas where the male, the female, or both adults were known to have been resident at the nest area during the preceding year (1-way ANOVA; experience-effect  $F = 0.357$ ,  $P = 0.70$ ). However, brood size at nests where at least one adult was known to be new to the nest area (1.7 [SE = 0.18,  $n = 70$ ]) was lower than at nests where at least one adult had been resident on the nest area previously and the other member of the pair was not known to be new (2.8 [SE = 0.61,  $n = 6$ ]; 1-way ANOVA; experience-effect  $F = 3.20$ ,  $df = 1,74$ ,  $P = 0.08$ ). Based on nest area occupancy, nest start, and productivity information provided above, we computed SITERANK and YEAR-RANK scores (Tables 3 and 4).

**Survival rates.** We used data from 16 male and 26 female radio-tagged Cooper's hawks to estimate annual survival rates (Table S1). The highest-weighted models (Table 5) suggested a year 1998 and a year 1998\*sex interaction effect on survival rates. The model-averaged estimates of survival in years other than 1998 was 84% (SE = 4) for males and 81% (SE = 6) for females. Annual survival in 1998 was 57% (SE = 9) for males and 36% (SE = 11) for females.

**Seasonal pattern and causes of mortality.** Overall, the number of mortalities of radio-tagged Cooper's hawk by month did not differ from a uniform distribution ( $\chi^2_2 = 1.73$ ,  $P = 0.42$ ; Figure 8).



**Table 3.** Cooper's hawk nest areas ranked by reproductive output on two north Florida study areas. Only nest areas that were occupied >1 y between 1995 and 2000 were evaluated. Ranks were assigned according to mean standardized scores for average annual brood size, proportion of years occupied, and average relative nest start date.

Nest area	Brood size	Occupancy	Relative start date <sup>a</sup>	Mean sample standard score <sup>b</sup>	Rank
SUWA017028	4.00	1.00	37	2.00	1
SUWA017001	3.60	1.00	28	1.57	2
SUWA017015	3.40	1.00	29	1.54	3
SUWA017027	2.00	1.00	25	0.98	4
SUWA017019	2.00	1.00	16	0.67	5
SUWA017010	1.83	0.50	29	0.57	6
LEON017001	1.80	0.83	19	0.54	7
SUWA017022	1.25	0.75	26	0.54	7
SUWA017005	1.33	0.67	21	0.32	8
SUWA017016	1.20	1.00	12	0.31	9
SUWA017029	0.00	1.00	—	0.30	10
SUWA017020	1.00	0.50	27	0.24	11
LEON017004	1.25	0.50	24	0.20	12
LEON017003	0.67	0.50	27	0.14	13
SUWA017009	0.80	0.33	29	0.06	14
SUWA017017	1.00	0.60	17	0.01	15
SUWA017023	1.00	0.33	20	-0.20	16
SUWA017003	0.60	0.20	22	-0.38	17
SUWA017006	0.33	0.50	12	-0.48	18
SUWA017021	0.00	0.50	—	-0.49	19
SUWA017026	0.00	0.50	—	-0.49	19
LEON017002	0.33	0.50	7	-0.67	20
LEON017005	0.00	0.33	—	-0.76	21
SUWA017025	0.00	0.33	—	-0.76	21
SUWA017007	0.00	0.17	11	-0.98	22
SUWA017008	0.00	0.33	6	-0.99	23
SUWA017013	0.00	0.17	—	-1.01	24
SUWA017011	0.50	0.33	0	-1.04	25
SUWA017012	0.33	0.17	5	-1.09	26
SUWA017004	0.00	0.00	—	-1.28	27
SUWA017024	0.00	0.00	—	-1.28	27

<sup>a</sup> Expressed as days before the latest nest start date over all nest areas.

<sup>b</sup> Average of sample standard scores (z-scores) for occupancy, brood size, and start date.

However, for males equipped with heavy (11-g) transmitters, mortality was not evenly distributed ( $\chi^2 = 6$ ,  $df = 2$ ,  $P = 0.05$ ), with most deaths occurring in the prebreeding period of late January through March. After 1998, when males were equipped with 6-g transmitters, there was no seasonal bias in mortality ( $\chi^2 = 2$ ,  $df = 2$ ,  $P = 0.37$ ). We recaptured three male and six female Cooper's hawks after they had worn their transmitters for  $\geq 1$  y, and observed no evidence of abrasion or feather damage related to the transmitter or backpack.

Avian predation was the most frequent cause of mortality among male Cooper's hawks for which a cause of death could be determined (7 of 13 cases). In four cases, all involving males equipped with heavy transmitters that were killed between mid-January and mid-March, mortalities occurred in close proximity to the nest sites on the nest areas where the males were resident. Two of these carcasses were recovered under known Cooper's hawk prey-handling perches and two were on the ground under brush or on logs. Based on the

**Table 4.** Study years ranked according to mean standardized scores for mean brood size, proportion of nest sites occupied, and mean nest start date of Cooper's hawks on two study areas in north Florida, 1995–2000.

Year	Occupancy	Brood size	Relative start date <sup>a</sup>	Mean sample standard score <sup>b</sup>	Rank
1997	0.58	1.5	9	1.16	1
1995	0.50	1.14	7	0.37	2
1996	0.57	1.05	0	-0.17	3
1999	0.37	0.759	8	-0.31	4
2000	0.34	0.645	10	-0.33	5
1998	0.33	0.74	5	-0.72	6

<sup>a</sup> Expressed as days before the latest average annual nest start-date over all nest areas.

<sup>b</sup> Average of sample standard scores (z-scores) for occupancy, brood size, and start date.

condition of the carcasses and their location, we believe all four of these males were killed by Cooper's hawks. Of remaining depredated male Cooper's hawks, a red-tailed hawk was responsible in one case, a great horned owl in another, and in two cases we suspected red-tailed hawks or great horned owls but could not be certain. The cause of death for three males that died in 1998 could not be determined, but two were extremely emaciated.

Avian predation accounted for three of eight female Cooper's hawk mortalities, one likely from a great horned owl and the other two either by a great horned owl or a red-tailed hawk. Two other female Cooper's hawks died after they appeared to have been trapped, one in a funnel-trap used to capture bobwhite and another in a leg-hold trap at a bobwhite breeding facility. A third female was also captured in a bobwhite trap on a hunting plantation but was released alive. One female Cooper's hawk was found dead on a road, likely hit by a vehicle.

The cause of death for one female could not be determined.

In both cases where adult males died while young were in the nest, females abandoned the young within 24 h and all nestlings died. The oldest young in these cases were 7 and 11 d old, respectively. In all three cases where adult female Cooper's hawks died while young were in the nest, the male continued to bring food to the nest and all young survived to ≥24 d of age.

**Ranging behavior**

*Radio-tracking data quality and protocols.* During the 12-mo exploratory radio-tracking period, we obtained 2,229 acceptable locations from the six radio-tagged Cooper's hawks, representing 112 complete tracking days. Area-observation curves indicated that 20 locations were adequate to describe the DR and DCA, but that 50 were necessary for SR, SCA, AR, and ACA estimates. We

**Table 5.** Competitive and global models examined to explain variation in Cooper's hawk annual survival on two north-Florida study areas, 1995–2001. Sample size was 16 male and 26 female Cooper's hawks trapped at nest areas and fitted with backpack-mounted radio-transmitters; many individuals were monitored for >1 y, up to a maximum of 5 y. Model ranking was based on Akaike's Information Criterion (AIC) corrected for small sample size (AIC<sub>c</sub>). All competitive models (within 2 AIC units of the top model) and the global model are shown. Survival was estimated in Program MARK using a sin-link function.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub>	ΔAIC <sub>c</sub> <sup>c</sup>	ω <sup>d</sup>	∑ω <sup>e</sup>
SEX*YR1998	4	140.92	0	0.54	0.54
YR1998	2	141.36	0.44	0.43	0.97
SEX + YEAR + AREA	22	164.02	23.11	<0.001	1

<sup>a</sup> YEAR = a factor in models, with six levels: 1) 1995, 2) 1996, 3) 1997, 4) 1998, 5) 1999, and 6) 2000. AREA = a factor with two levels: 1) Dowling Park and 2) Tall Timbers. YR1998 = a factor with two levels: 1) 1998, and 2) <>1998. SEX = a factor with two levels: 1) female, and 2) male. A \* denotes inclusion of an interaction term between the effects.

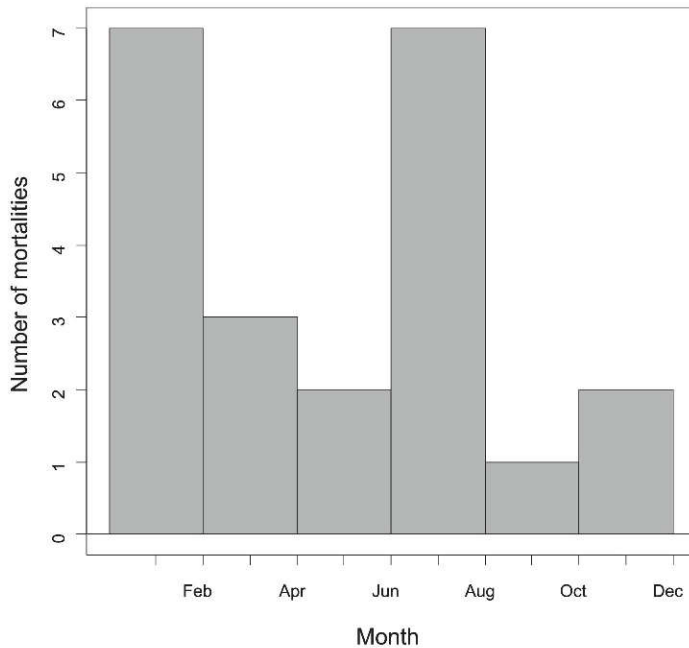
<sup>b</sup> Number of parameters estimated in the model.

<sup>c</sup> Change in AIC<sub>c</sub> from highest-ranked model.

<sup>d</sup> Model weight.

<sup>e</sup> Cumulative model weight.





**Figure 8.** Number of deaths recorded by month for radio-tagged Cooper's hawks on two north Florida study areas, 1995–2000.

established these as minimum sample sizes for estimating home ranges at each spatial scale.

Cooper's hawk home ranges calculated using the fixed-kernel, harmonic mean, and minimum convex polygon methods were not different in size (1-way ANOVAs on square-root-transformed area estimates,  $P > 0.10$  in all cases). However, the fixed-kernel method yielded home ranges that consistently appeared more sensitive to actual utilization of the landscape. In addition, when subsamples of the data were subjected to fixed-kernel analysis, home range estimates closely approximated those calculated from the full data set. For these reasons, we chose to use the fixed-kernel method in subsequent analyses. Of the sampling frames tested, sets of locations collected  $>4$  h apart during 12-h sampling periods and sets consisting of one location per individual per day produced Schoener index values  $>1.96$ , indicating suitable levels of statistical independence among locations. Because of the larger sample size relative to effort involved, we settled on the former sampling frame for collection of data sets to calculate SR, SCA, AR, and ACA estimates. We estimate our average distance error for triangulated positions was 68 m (SE = 6.1,  $n = 60$ ).

**Daily range size.** We had sufficient data to calculate estimates of 112 Cooper's hawk DR and DCA (Table S3). Over the entire year, male DR averaged 291.5 (SE = 37.2) ha, and female DR averaged 196.0 (SE = 34.5) ha. Model analysis suggested DR and DCA varied seasonally, between sexes, between

study areas, and that there were interaction effects between area and season, area and sex, and sex and season (Table 6). However, the only variables with coefficient confidence intervals that did not include 0 for both DR and DCA were sex, season, and the interaction between sex and season. Box plots of DR and DCA showed a general pattern of relatively large male and small female DR and DCA during the breeding season and relatively similar daily ranges between sexes during the nonbreeding season (Figure 9). The daily range of male Cooper's hawks in the first half of the breeding season greatly exceed that of females, averaging about 40% of the AR (Figure 10). By about 125 d after egg-laying, and for the remainder of the year, daily ranges of males and females were similar in size.

**Seasonal range size.** We obtained sufficient radio-tracking locations to estimate 20 breeding and 16 nonbreeding SR for male, and 20 breeding and 13 nonbreeding SR for female Cooper's hawks (Table S4). Seasonal ranges were obtained from 16 different male and 12 different female Cooper's hawks; 8 females and 5 males were tracked over  $>1$  y, though not all provided enough data for multiple seasonal-range estimates. Model analysis suggested that SR and SCA varied between study areas, and that there was an interaction effect between sex and season (Table 7). Both study area and the sex\*season interaction had coefficient confidence intervals that did not include 0. In general, SR and SCA were similar between sexes during the breeding season,

**Table 6.** Competitive and global linear models examined to explain variation in size of 112 square-root-transformed daily ranges (95% fixed-kernel home-range contour, DR) and square-root-transformed daily core areas (50% fixed-kernel home-range contour, DCA) for three adult male and three adult female Cooper's hawk on two north Florida study areas, 1996–1997. Estimates are based on 2,229 acceptable locations (see text) collected during 112, 8-h tracking days over 12 mo. Model ranking was based on Akaike's Information Criterion (AIC) corrected for small sample size (AIC<sub>c</sub>). All competitive models (within 2 AIC units) of the top model and the global model are shown. Models were fit with an identity-link function.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub>	ΔAIC <sub>c</sub> <sup>c</sup>	ω <sup>d</sup>	∑ω <sup>e</sup>
<b>DR</b>					
AREA + SEASON + SEX + AREA*SEASON + AREA*SEX + SEASON*SEX	8	455.35	0	0.57	0.57
AREA + SEASON + SEX + AREA*SEASON + AREA*SEX + SEX*SEASON + AREA*SEASON*SEX	9	456.84	1.50	0.27	0.85
<b>DCA</b>					
AREA + SEX*SEASON	6	352.05	0	0.69	0.69
AREA + SEASON + SEX + AREA*SEASON + AREA*SEX + SEX*SEASON + AREA*SEASON*SEX	9	355.31	3.26	0.13	1.00

<sup>a</sup> AREA = a factor in models, with two levels: 1) Tall Timbers, and 2) Dowling Park. SEASON = a factor with two levels: 1) breeding, and 2) nonbreeding. SEX = a factor with two levels: 1) female, and 2) male. A \* denotes inclusion of an interaction term between the effects.

<sup>b</sup> Number of model parameters.

<sup>c</sup> Change in AIC<sub>c</sub> from the top-ranked model.

<sup>d</sup> Model weight.

<sup>e</sup> Cumulative model weight.

but larger for females during the nonbreeding season (Figure 11). Male SR averaged 14.6 (SE = 1.9) km<sup>2</sup> during the breeding season and 13.4 (SE = 4.0) km<sup>2</sup> during the nonbreeding season; whereas, female SR averaged 16.5 (SE = 4.2) km<sup>2</sup> during the breeding season and 32.4 (SE = 6.9) km<sup>2</sup> during the nonbreeding season.

*Annual home ranges.* We obtained sufficient radio-tracking data to estimate 18 male and 11 female Cooper's hawk ARs and ACAs (Table S4). This represented data from 12 males and 6 females (4 males and 3 females were tracked for >1 y and provided sufficient data to calculate >1 AR and ACA estimate each). Model analysis suggested AR and ACA differed between sexes and study areas; coefficient confidence intervals for both variables did not include 0 (Table 8). Annual range and ACA of both sexes were larger on Dowling Park than on Tall Timbers; and AR, but not ACA, was larger for females than males (Figure 12). Over all years, male AR averaged 15.3 km<sup>2</sup> (SE = 2.7) and female AR averaged 30.3 km<sup>2</sup> (SE = 5.8).

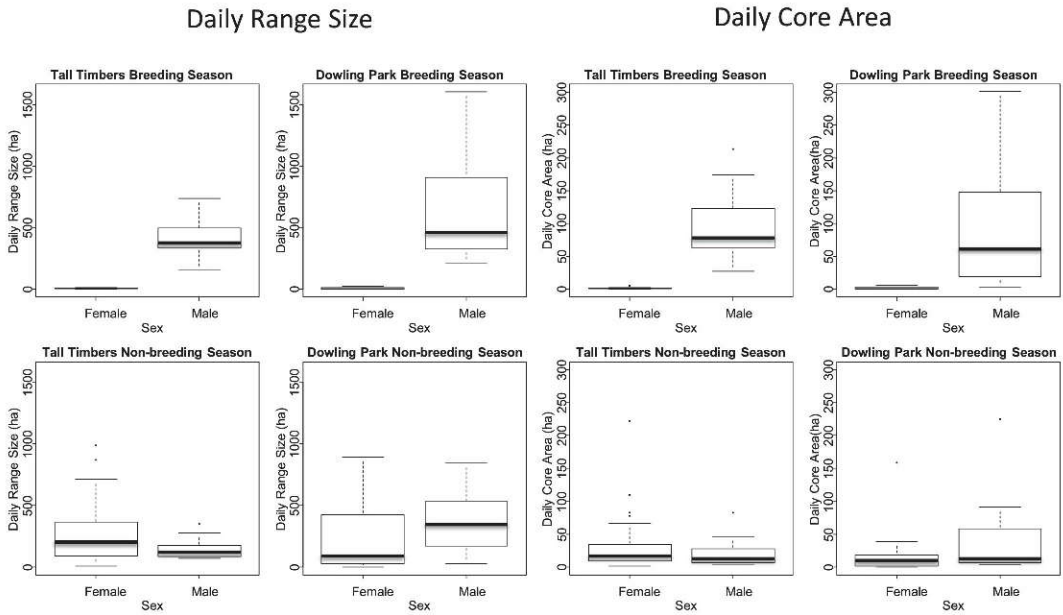
*Seasonal and annual range overlap.* We had sufficient data to calculate reciprocal overlap in SR of 10 neighboring adult male Cooper's hawks (Table S5). Seasonal range overlap ranged from 0% to 65%, and averaged 13% (SE = 3). Seasonal core areas were overlapped by SR of neighboring males in 21% of the cases. Most male AR and SR included only a single nest area (Figure 13). Model selection

suggested overlap was influenced by YEARRANK, SITERANK, and AREA (Table 9), and coefficient confidence intervals for all variables did not include 0. Overlap of adjacent adult male Cooper's hawk SR averaged 11% (SE = 3) on Dowling Park and 17% (SE = 3) on Tall Timbers. Seasonal range overlap was substantially lower for males occupying high-ranked nest areas compared with those of average or low rank, and overlap was greater in high-ranked years compared with average or low-ranked years (Figure 14). We had sufficient data to calculate overlap between AR over successive years for five male Cooper's hawks. Overlap of male successive-year AR averaged 64% (SE = 7), and for successive ACA, overlap averaged 85% (SE = 8).

Seasonal range of eight neighboring resident female Cooper's hawks ranged from 9% to 81%, and averaged 32% (SE = 8). These female SR overlapped known AR of three to seven adult male Cooper's hawks, and included from five to nine known Cooper's hawk nest areas. We had sufficient data to calculate overlap between AR over successive years for four female Cooper's hawks. Overlap of female successive-year AR averaged 15% (SE = 1), and for successive ACA, overlap averaged 21% (SE = 2); the overlap between years was primarily on the nonbreeding range.

*Dispersal and movement.* We measured breeding dispersal for 12 males and 25 females, nest-to-winter distance for 16 males and 28 females, and interyear wintering-area distance for 5 males and 5





**Figure 9.** Box plots for daily range size (95% fixed-kernel contour) and daily core-area size (50% fixed-kernel contour) for three adult male and three adult female Cooper's hawks on two north Florida study areas, April 1996 through June 1997. The horizontal heavy line in boxes is the median, boxes cover the median 50% of values (interquartile range), the whiskers extend outward from box hinges 1.5 times the interquartile range, and points beyond whiskers are outside values.

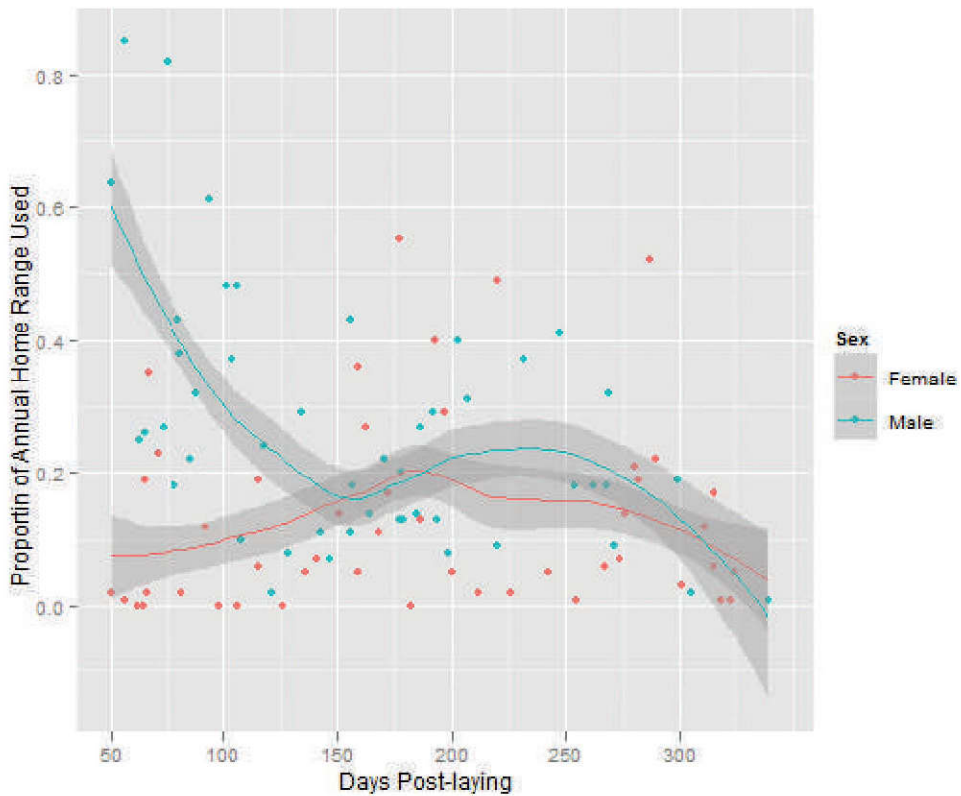
females (Table S6). Only 2 males (17%) changed nest areas between years compared with 17 females (68%), a significant difference (*t*-test for proportions,  $t = 3.75$ ,  $df = 21$ ,  $P = 0.001$ ). Of 10 instances where both members of a pair were known to be alive between years, the pair remained together in only 1 case (10%). The mean breeding dispersal distance was 0.6 (SE = 0.6) km for males and  $\geq 42.5$  (SE = 12.8) km for females (Figure 15). However, 10 (36%) females had nest-to-wintering area or breeding dispersal distances >100 km (e.g., outside our search area), so the mean underestimated true breeding dispersal for females. We know that two of these females had nest-to-wintering area distances of about 140 km because they dispersed from the Dowling Park study area and were detected on search flights around Tall Timbers. Considering only females that had known breeding dispersal distances, the mean dispersal distance was 4.2 km (SE = 1.6,  $n = 15$ ). Using only these known female breeding-dispersal distances, the difference between sexes in breeding dispersal was significant (1-way ANOVA,  $F = 3.23$ ,  $df = 1,24$ ,  $P = 0.09$ ). Nest-to-wintering area distance was greater for females than males (1-way ANOVA, nest-to-wintering area effect  $F = 28.60$ ,  $df = 1,42$ ,  $P < 0.001$ ), but interyear wintering area distance was similar between the sexes (interyear wintering-area distance effect  $F = 0.99$ ,  $df = 1,9$ ,  $P = 0.35$ ; Figure 15).

The highest-weighted model for predicting female long-distance (>100 km) postbreeding dispersal included only eye color, but the constant-only model was also competitive (Table 10).

The 90% confidence interval for the coefficient for eye color did not include 0. Eye color scores for dispersing females averaged 3.1 (SE = 0.5), compared with 4.7 (SE = 0.6) for females that did not disperse. Annual breeding-dispersal distance and the average distance between breeding and nonbreeding areas decreased with the progression from a yellow to red iris (Figure 16). Movements by females were most frequent in March and April and again in October and November (Figure 17). In the two cases where males changed nest areas between years, both moved to adjacent nest areas with equal or higher SITERANK scores after the death of the resident male on the adjacent nesting area. In one case, the previous nest area remained vacant; but in another, the vacated nest area was reoccupied by a new pair of Cooper's hawks.

**Diet**

*Sample sizes, data quality, and biases.* The direct-observation data set consisted of 729 h of simultaneous videotape and radio-tracking data involving 8 different male and 9 different female Cooper's hawks at 10 nest attempts at 8 different



**Figure 10.** Annual variation in daily range size (95% fixed-kernel contour) relative to the annual home-range size for three adult male and three adult female Cooper's hawks on two north Florida study areas, June 1996 through April 1997. Time on the X-axis is measured in days post-egg-laying, based on the nest start date in 1996 for each individual. The Y-axis is the proportion of each individual's annual home range (95% fixed-kernel contour) used per day. Lines are the LOESS-smoothed lines fit to the daily values in R (R Development Core Team 2010) using default criteria. The gray-shaded area bounding each line is the 90% confidence band.

nest areas on the Dowling Park study area in 1998, 1999, and 2000 (Table S7).

The prey-remains data set consisted of samples collected from 1992 (though mostly after 1995) to 2000 in association with 16 nest attempts at 5 nest areas on the Tall Timbers study area, and 69 nest attempts at 26 nest areas on the Dowling Park study area (Table S8). In contrast to the videotape data set, prey remains were identified with complete accuracy thorough visual comparison with museum collections.

The radio-tracking data set consisted of 3,176 h of radio-tracking of 12 male and 8 female Cooper's hawks at Dowling Park and Tall Timbers, from 1995 to 2000 (Table S9). This data set provided all of the data on diet during the nonbreeding period. The main problem with this data set was a bias in favor of larger prey (prey >100g) because large prey took longer to consume. The longer a Cooper's hawk fed on a kill, the greater the chance we would detect the capture and that we would be able to triangulate successfully on the feeding location. We suspect that we frequently failed to notice when very small and some moderate-sized prey were captured

because the meal was consumed before we could detect that a prey capture had occurred or establish an accurate feeding location.

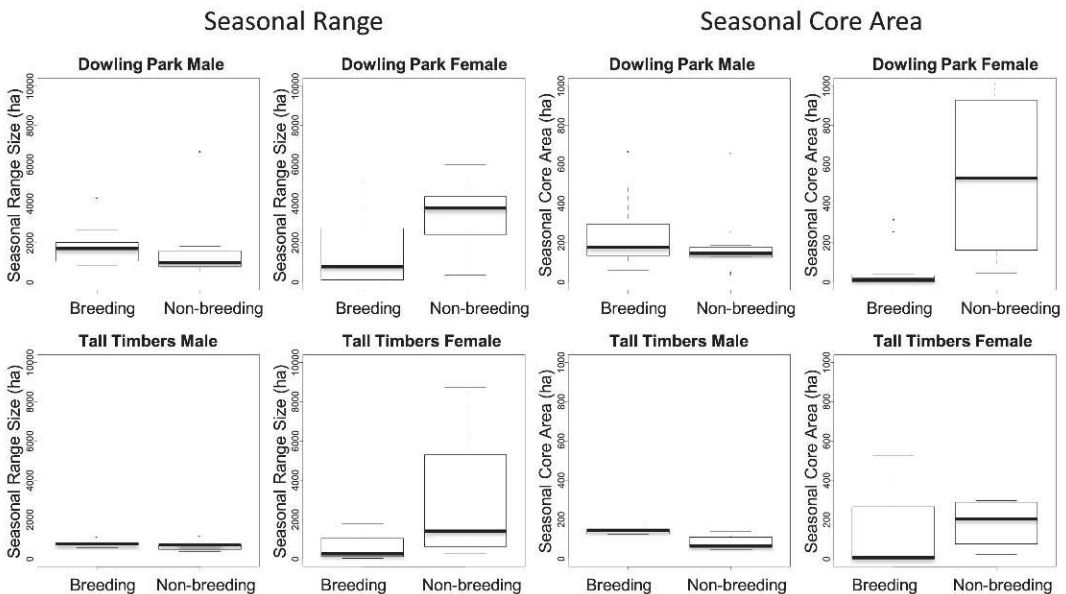
*Breeding season diet.* Breeding-season prey items collected over all data sets represented 1,100 individuals from 3 Classes,  $\geq 15$  Orders, and  $\geq 69$  species (Table 11). Birds comprised 87.5% of prey items by frequency and 74.6% of the biomass delivered to nestlings. The following species were determined to be important prey: mourning doves (scientific names of prey are given in Appendix B; 14.5%), blue jays (13.5%), cattle egrets (4.9%), northern mockingbirds (4.5%), northern bobwhites (4.5%), and northern cardinals (4.3%). The data set that included only direct prey observations provided similar results except that birds comprised a slightly smaller percentage by frequency and a greater percentage by biomass (84.6% and 85.2%, respectively). The proportional representation of important prey species in the pooled data set differed between study areas ( $\chi^2 = 54.5$ ,  $df = 5$ ,  $P < 0.001$ ; Figure 18), but when we dropped bobwhites and northern cardinals (the two species



**Table 7.** Competitive and global linear models examined to explain variation in size of 69 square-root-transformed seasonal ranges (95% fixed-kernel home-range contour, SR) and square-root-transformed daily core areas (50% fixed-kernel home-range contour, SCA) for 16 adult male and 12 adult female Cooper's hawk on two north Florida study areas, 1996–2000. Model ranking was based on Akaike's Information Criterion (AIC) corrected for small sample size (AIC<sub>c</sub>). All competitive models (within 2 AIC units of the top model) and the global model are shown. Models were fit with an identity link function.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub>	ΔAIC <sub>c</sub> <sup>c</sup>	ω <sup>d</sup>	∑ω <sup>e</sup>
<b>SR</b>					
AREA + SEX*SEASON	6	386.44	0	0.65	0.65
YR1998 + YRSTRATA + YRGROUP + YOUNG + SITERANK + YEARRANK + PRECIP + AREA*SEX*SEASON	16	398.64	12.20	0	1.00
<b>SCA</b>					
AREA + SEX*SEASON	6	278.93	0	0.62	0.62
SEX*SEASON	6	280.58	1.64	0.27	0.89
YR1998 + YRSTRATA + YRGROUP + YOUNG + SITERANK + YEARRANK + PRECIP + AREA*SEX*SEASON	16	295.68	16.75	0	1.00

<sup>a</sup> AREA = a factor in models, with two levels: 1) Tall Timbers, and 2) Dowling Park. SEASON = a factor with two levels: 1) breeding, and 2) nonbreeding. SEX = a factor with two levels: 1) female, and 2) male. YOUNG = an integer, the number of young raised to 24 d of age. SITERANK = a factor with three levels: 1) above average, 2) average, 3) below average. YEARRANK = a factor with three levels: 1) above average, 2) average, 3) below average. PRECIP = a factor in models with three levels: 1) years with annual precipitation within 1 SD of the average; 2) years with annual precipitation > 1 SD above the average; and 3) years with annual precipitation < 1 SD below the average. YRGROUP = a factor with two levels: 1) YEAR < 1998 and 2) YEAR ≥ 1998. YRSTRATA = a factor with three levels: 1) 1995–1997, 2) 1998, 3) 1999–2000. YR1998 = a factor with two levels: 1) 1998, 2) <>1998. A \* denotes inclusion of an interaction term between the effects.  
<sup>b</sup> Number of model parameters.  
<sup>c</sup> Change in AIC<sub>c</sub> from the top-ranked model.  
<sup>d</sup> Model weight.  
<sup>e</sup> Cumulative model weight.



**Figure 11.** Box plots for seasonal range (95% fixed-kernel contour) and seasonal core area (50% fixed-kernel contour) size for 16 adult male and 12 adult female Cooper's hawks on two north Florida study areas, 1996 through 2000. The horizontal heavy line in boxes is the median, boxes cover the median 50% of values (interquartile range), the whiskers extend outward from box hinges 1.5 times the interquartile range, and points beyond whiskers are outside values.

**Table 8.** Competitive and global linear models examined to explain variation in size of 27 square-root-transformed annual ranges (95% fixed-kernel home-range contour, AR) and square-root-transformed annual core areas (50% fixed-kernel home-range contour, ACA) from 16 adult male and 11 adult female Cooper's hawk on two north Florida study areas, 1996–2000. Model ranking was based on Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ). All competitive models (within 2  $AIC_c$  units of the top model) and the global model are shown. Models were fit with an identity link function.

Model <sup>a</sup>	$K^b$	$AIC_c$	$\Delta AIC_c^c$	$\omega^d$	$\sum \omega^e$
<b>AR</b>					
AREA + SEX	4	130.24	0	0.67	0.67
YEAR + TIME + YOUNG + SITERANK + YEARRANK + PRECIP + SEX + AREA	10	148.34	18.10	0	1.00
<b>ACA</b>					
AREA + SEX	4	108.84	0	0.27	0.27
AREA	3	109.43	0.59	0.20	0.47
SEX	3	110.28	1.44	0.13	0.60
YEAR + TIME + YOUNG + SITERANK + YEARRANK + PRECIP + SEX + AREA	10	126.92	18.08	0	1.00

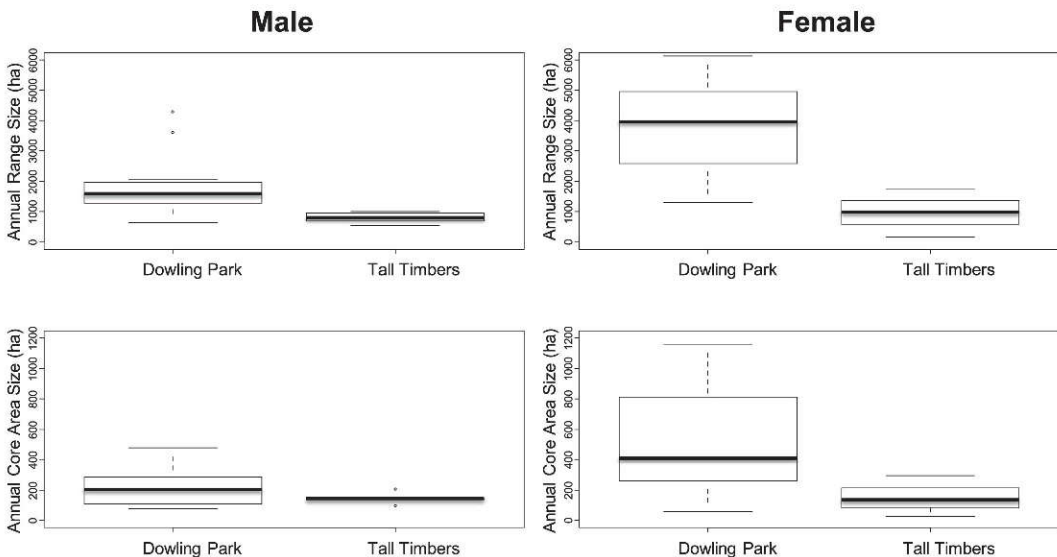
<sup>a</sup> AREA = a factor in models, with two levels: 1) Tall Timbers, and 2) Dowling Park. SEX = a factor with two levels: 1) female, and 2) male. TIME = an integer with years as values. YOUNG = an integer, the number of young raised to 24 d of age. SITERANK = a factor with three levels: 1) above average, 2) average, 3) below average. YEARRANK = a factor with three levels: 1) above average, 2) average, 3) below average. YEAR = a factor with six levels: 1) 1995, 2) 1996, 3) 1997, 4) 1998, 5) 1999, and 6) 2000. PRECIP = a factor in models with three levels: 1) years with annual precipitation within 1 SD of the average; 2) years with annual precipitation > 1 SD above the average; and 3) years with annual precipitation < 1 SD below the average. A \* denotes inclusion of an interaction term between the effects.

<sup>b</sup> Number of model parameters.

<sup>c</sup> Change in  $AIC_c$  from the top-ranked model.

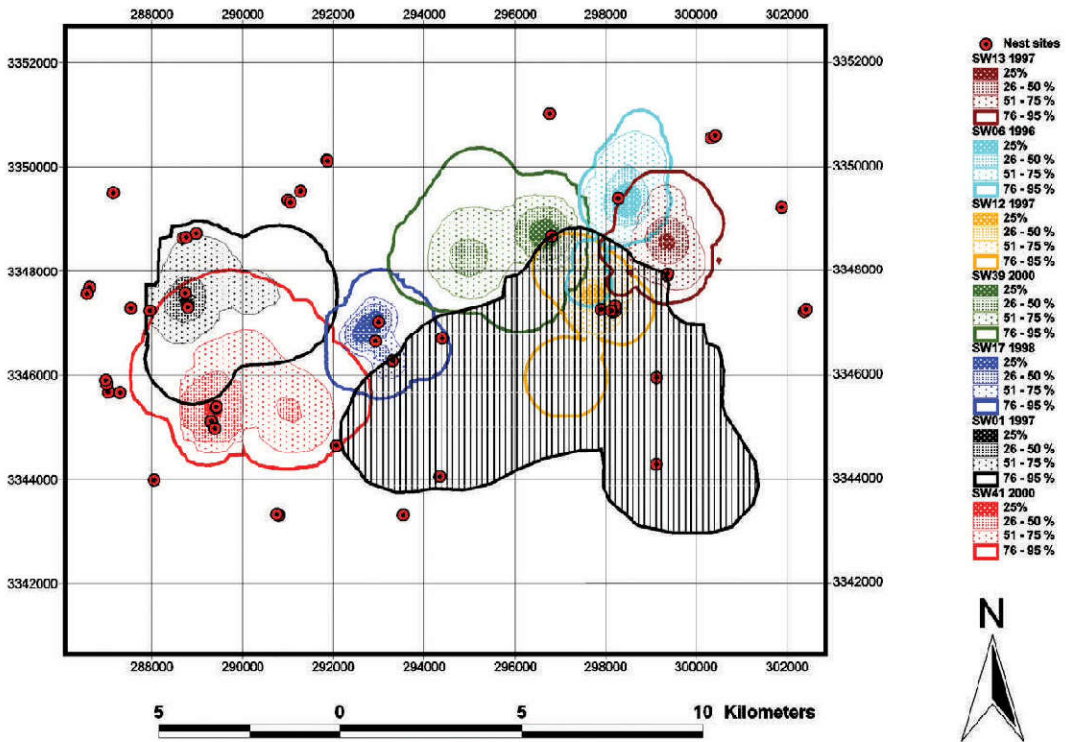
<sup>d</sup> Model weight.

<sup>e</sup> Cumulative model weight.



**Figure 12.** Box plots for annual range size (95% fixed-kernel contour) and annual core-area (50% fixed-kernel contour) size for 16 adult male and 11 adult female Cooper's hawks on two north Florida study areas, 1996 through 1999. The horizontal heavy line in boxes is the median, boxes cover the median 50% of values (interquartile range), and the whiskers extend outward from box hinges 1.5 times the interquartile range.





**Figure 13.** Map of annual ranges of seven adult male Cooper's hawks occupying contiguous nesting areas on the Dowling Park study area, north Florida, 1997-2000. The bold perimeter of the annual range of each male is the 95% fixed-kernel contour; 75%, 50% and 25% contours are also shown. The black cross-hatched area in the southeastern quarter of the study area is the 95% fixed-kernel annual range of female Cooper's hawk SW08, the mate of male SW12 (orange annual range) in 1997 when these two annual ranges were measured. The grid units are Universal Transverse Mercator coordinates in meters.

that contributed most to the chi-square value in descending order) the difference became nonsignificant ( $\chi^2 = 1.6$ ,  $df = 3$ ,  $P = 0.67$ ).

Nestling and fledgling birds comprised 64% of 60 prey items of known age brought to nests in the direct-observation data set. The percentage of nestling and fledgling birds brought to nests was 69.2% in 1998, 35.0% in 1999, and 84.6% in 2000; these percentages differed among years ( $\chi^2 = 7.47$ ,  $df = 2$ ,  $P = 0.02$ ), but the difference became nonsignificant when the year 1999 was dropped from the analysis ( $\chi^2 = 0.49$ ,  $df = 1$ ,  $P = 0.48$ ).

*Nonbreeding season diet.* We collected 197 prey items during the nonbreeding period, representing 2 Classes,  $\geq 12$  Orders, and  $\geq 42$  species (Table 11). Birds comprised 97.5% of these records by frequency and 85.6% by biomass. Mourning dove (27.9%), bobwhite (12.2%), blue jay (8.6%), killdeer (5.1%), yellow-billed cuckoo (5.1%), and domestic chicken (4.6%) were important prey in this data set.

We collected 151 prey items on the Dowling Park study area and 46 on Tall Timbers that were identifiable to species. The frequency of important prey species in the nonbreeding data set differed between study areas ( $\chi^2 = 22.92$ ,  $df = 6$ ,  $P < 0.001$ ;

Figure 19), but not when bobwhites were dropped from the analysis ( $\chi^2 = 2.29$ ,  $df = 5$ ,  $P = 0.81$ ).

*Comparison of male and female prey.* We were certain of the sex of the hawk that captured 392 of the breeding season and 116 of the nonbreeding season prey items in the direct-observation and radio-tracking data sets: 290 of these prey items were identified to species. Important prey species in this data set were cattle egrets, bobwhite, blue jays, chickens, northern mockingbirds, mourning doves, northern cardinals, and killdeer. The proportional representation of important prey species in this data set differed between sexes ( $\chi^2 = 45.07$ ,  $df = 8$ ,  $P < 0.001$ ; Figure 20), but not when cattle egrets, blue jays, and chickens (species contributing most to the chi-square value in descending order) were sequentially dropped from the analysis ( $\chi^2 = 6.02$ ,  $df = 5$ ,  $P = 0.30$ ). Because a large number of prey were not identified to species, and fewer large than small prey were unidentified, we suspect our sample probably underrepresented male Cooper's hawk prey compared with female prey.

We were able to estimate the weights of 421 of the 508 prey items captured by Cooper's hawks of known sex (we were able to estimate weights but

**Table 9.** Competitive and global linear models examined to explain variation in arcsine-transformed proportion of annual ranges (95% fixed-kernel contour) that overlapped between 10 pairs of male Cooper's hawks simultaneously occupying adjacent nest sites on two north Florida study areas, 1996–2000. Model ranking was based on Akaike's Information Criterion (AIC) corrected for small sample size (AIC<sub>c</sub>). All competitive models (within 2 AIC units of the top model) and the global model are shown. Models were fit with an identity link function.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub>	ΔAIC <sub>c</sub> <sup>c</sup>	w <sup>d</sup>	∑w <sup>e</sup>
SITERANK	4	2.98	0	0.32	0.32
YEARRANK	4	3.25	0.27	0.28	0.59
AREA	3	4.58	1.61	0.14	0.73
SEASON + YEAR + SITERANK + YEARRANK + AREA + SITERANK*YEARRANK	10	16.77	13.80	0	1.00

<sup>a</sup> AREA = a factor in models, with two levels: 1) Dowling Park, and 2) Tall Timbers. SEASON = a factor with two levels: 1) breeding, and 2) nonbreeding. SITERANK = a factor with three levels: 1) above average, 2) average, 3) below average. YEAR = a factor with six levels: 1) 1995, 2) 1996, 3) 1997, 4) 1998, 5) 1999, and 6) 2000. YEARRANK = a factor with three levels: 1) above average, 2) average, 3) below average. A \* denotes inclusion of an interaction term between the effects.

<sup>b</sup> Number of model parameters.

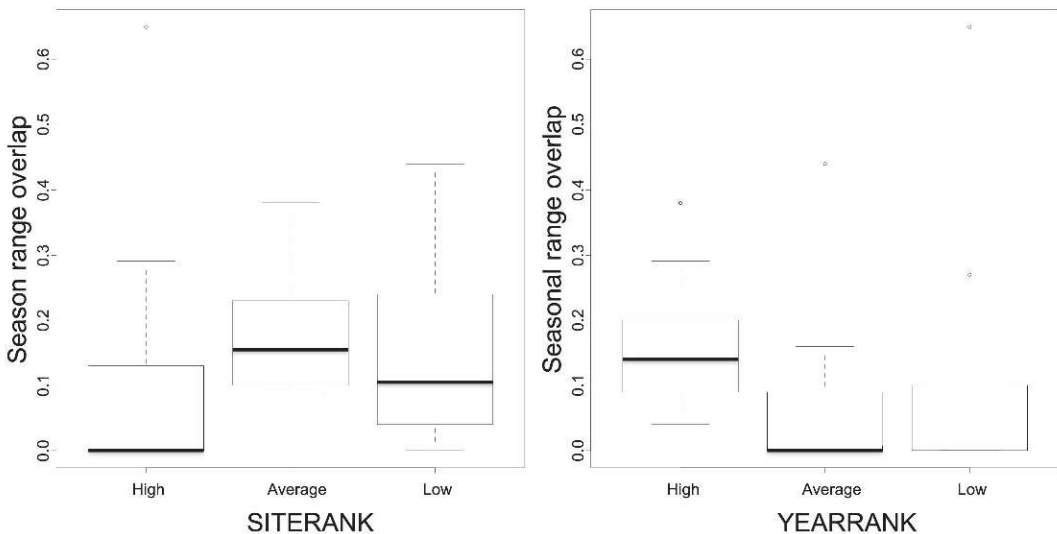
<sup>c</sup> Change in AIC<sub>c</sub> from the top-ranked model.

<sup>d</sup> Model weight.

<sup>e</sup> Cumulative model weight.

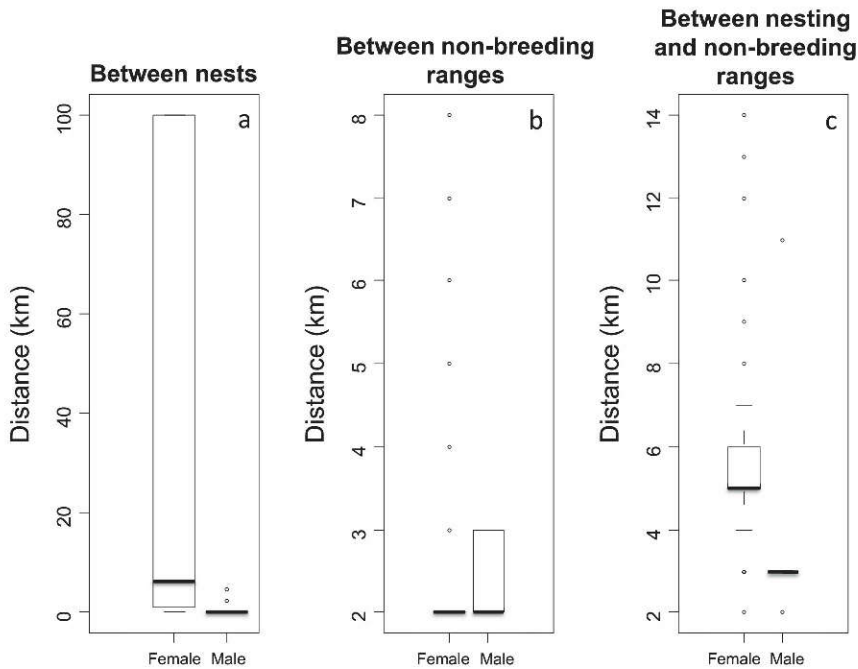
could not determine the species for many nestling birds brought to nests). Considering all prey-weight data, female Cooper's hawks captured larger prey on average than did males (mean = 109.9 g [SE = 1.2, n = 55] for females compared with 71.5 g [SE = 1.1, n = 235] for males; independent-sample *t*-test on log-transformed values, *t* = 2.6, *df* = 62.9, *P* = 0.01; Figure 21). However, there was no difference in mean prey weight of male and female Cooper's hawks during the breeding season in the direct-observation

data set (female mean = 90.7 g [SE = 1.5, n = 17], male mean = 63.4 g [SE = 1.1, n = 69]; independent-sample *t*-test on log-transformed values, *t* = 0.93, *df* = 17.4, *P* = 0.37) or in the radio-tracking data set from the breeding season (female mean = 83.1 g [SE = 1.8, n = 4] vs. male mean of 79.0 g [SE = 1.1, n = 33]; independent-sample *t*-test on log-transformed values, *t* = 0.1, *df* = 3.1, *P* = 0.94). Mean prey weights from the nonbreeding season radio-tracking data set were different between



**Figure 14.** Proportional overlap of adult male Cooper's hawk seasonal ranges (95% adaptive kernel contour) on two north Florida study areas, 1996–2000. Data are from 10 pairs of male Cooper's hawks simultaneously occupying adjacent nest sites. The horizontal heavy line in boxes is the median, boxes cover the median 50% of values (interquartile range), and the whiskers extend outward from box hinges 1.5 times the interquartile range. There was no difference in overlap of seasonal ranges between the breeding and nonbreeding season, so seasons were pooled for the box plots.





**Figure 15.** Box plots of distance between **(a)** successive years' nest sites (breeding dispersal distance in text), **(b)** successive years' nonbreeding season use areas (interyear wintering area distance in text), and **(c)** nonbreeding and breeding season ranges (nest-to-wintering area distance in text) for adult male and female Cooper's hawks on two north Florida study areas, 1995–2000. Samples sizes were as follows: **(a)** 12 males and 25 females; **(b)** 5 males and 5 females; and **(c)** 16 males and 28 females. The horizontal heavy line in boxes is the median, boxes cover the median 50% of values (interquartile range), and the whiskers extend outward from box hinges 1.5 times the interquartile range.

sexes (female mean = 146.5 g [SE = 1.2,  $n = 29$ ] vs. male mean of 81.5 g [SE = 1.1,  $n = 81$ ]; independent-sample  $t$ -test of log-transformed values,  $t = 3.0$ ,  $df = 47.8$ ,  $P = 0.004$ ).

*Use versus availability of avian prey.* We detected 17,964 birds on 1,140 point counts from July 1998 through July 2000 (Table S10). We detected more birds per count on average at Tall Timbers than at

**Table 10.** Competitive and global generalized linear models examined to explain variation in the proportion of adult female Cooper's hawks that undertook long-distance (>100 km) postbreeding dispersal, based on data from 28 radio-tagged adult female Cooper's hawks on two north Florida study areas, 1996–2000. Model ranking was based on Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ). All competitive models (within 2  $AIC_c$  units of the top model) and the global model are shown. Models were fit with a logit-link function.

Model <sup>a</sup>	$K^b$	$AIC_c$	$\Delta AIC_c^c$	$\omega^d$	$\sum \omega^e$
EYE	2	38.74	0	0.64	0.64
CONSTANT	1	40.64	1.91	0.25	0.89
YEAR + SITERANK + YEARRANK + EYE + AREA + WING	12	68.81	30.07	0	1.00

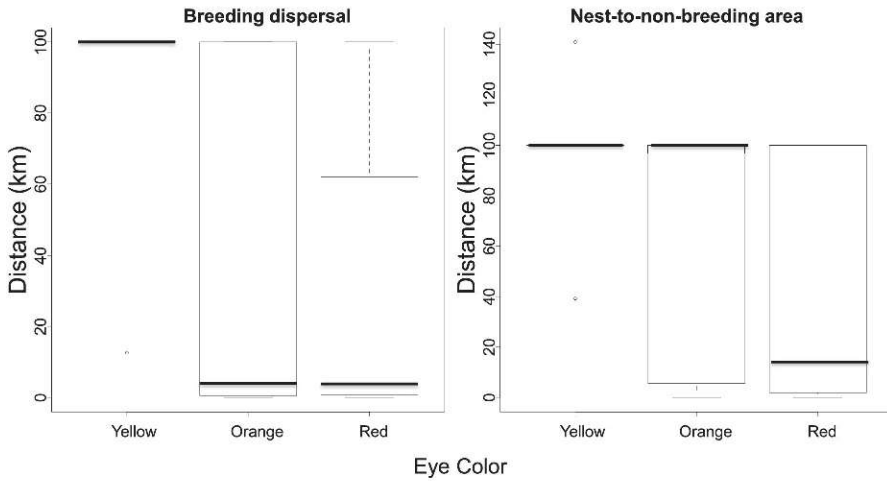
<sup>a</sup> CONSTANT = constant (intercept-only) model. SITERANK = a factor with three levels: 1) above average, 2) average, 3) below average. YEARRANK = a factor with three levels: 1) below average, 2) average, and 3) above average. EYE = an integer containing the eye color score, 1–6 (see text). YEAR = a factor with six levels: 1) 1995, 2) 1996, 3) 1997, 4) 1998, 5) 1999, and 6) 2000. AREA = a factor with two levels: 1) Dowling Park, 2) Tall Timbers. WING = an integer with the unflattened wing cord.

<sup>b</sup> Number of model parameters.

<sup>c</sup> Change in  $AIC_c$  from the top-ranked model.

<sup>d</sup> Model weight.

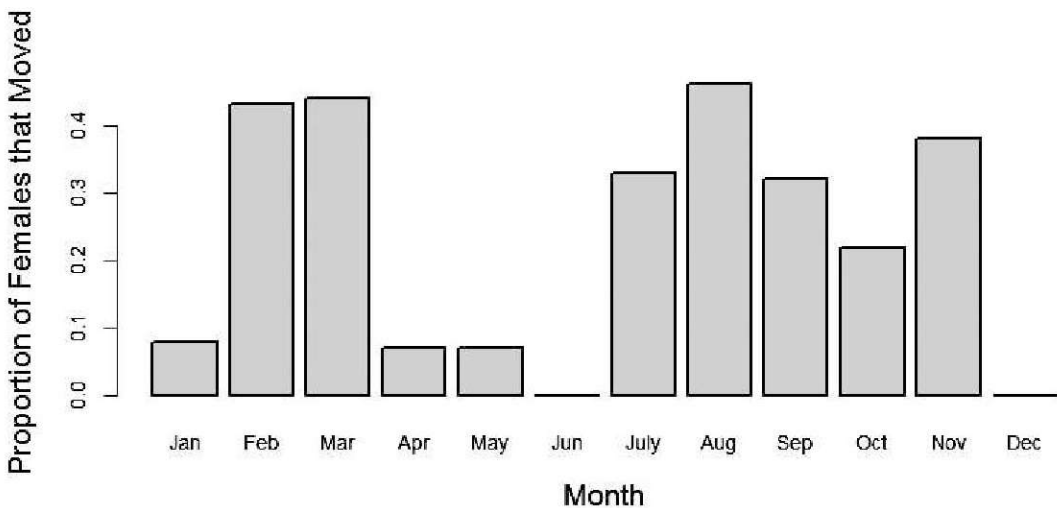
<sup>e</sup> Cumulative model weight.



**Figure 16.** Box plot showing distance between sequential years' nesting areas (breeding dispersal in text) and nest-to-nonbreeding area (nest-to-wintering distance in text) as a function of eye color for 25 and 28 adult female Cooper's hawks, respectively, on two north Florida study area, 1996–2000. The horizontal heavy line in boxes is the median, boxes cover the median 50% of values (interquartile range), and the whiskers extend outward from box hinges 1.5 times the interquartile range. The category "yellow" includes eye color scores 1 and 2; the category "orange" includes eye color scores 3 and 4; and the category "red" includes eye color scores 5 and 6.

Dowling Park (mean = 14.0, SE = 0.02 for Tall Timbers compared with mean = 12.6, SE = 0.02 for Dowling Park; 1-way ANOVA,  $F = 10.9$ ,  $df = 1,1139$ ,  $P < 0.001$ ), and there was no difference in the average number of birds detected per point across years (1-way ANOVA,  $F = 1.47$ ,  $df = 1,1138$ ,  $P = 0.23$ ). Among important prey species, we detected blue jays, mourning doves, and northern mockingbirds more frequently on Dowling Park, and we detected northern cardinals more frequently on Tall Timbers (Figure 22).

Plots of ranked abundance based on observations on point counts versus rank frequency in Cooper's hawk prey captures by study area and season showed that blue jays, northern bobwhite, and mourning doves were captured more frequently than expected in more than one season on both study areas (Figure 23). Selection toward other important prey species (cattle egrets, yellow-billed cuckoos, northern cardinals, northern mockingbirds, and killdeer) was also evident in at least one season on one study area.



**Figure 17.** The proportion of radio-tagged female Cooper's hawks that moved (see text for definition) by month on two north Florida study areas, 1996–2000.



**Table 11.** Prey of Cooper's hawks on two north Florida study areas, 1992–2001. Scientific names and sources of body mass measurements are given in Appendix A.

Class	Order	Species	Frequency by season		Mean mass	Total mass	% Freq.	% Weight
			Breeding	Non-breeding				
<b>Aves</b>			962	192	112.4	129,709.6	88.97	75.78
	<b>Caprimulgiformes</b>		2		108.0	216.0	0.15	0.13
		Chuck-will's-widow	2		108.0	216.0	0.15	0.13
	<b>Charadriiformes</b>		9	10	92.3	1,753.7	1.46	1.02
		Killdeer	9	10	92.3	1,753.7	1.46	1.02
	<b>Ciconiiformes</b>		61	3	308.9	19,769.6	4.93	11.55
		Cattle egret	54	3	312.7	17,821.1	4.39	10.41
		Green heron	2		180.2	360.4	0.15	0.21
		Little blue heron	1		305.6	305.6	0.08	0.18
		Snowy egret	2		333.9	667.8	0.15	0.39
		Unknown	2					
	<b>Columbiformes</b>		174	61	105.5	24,792.5	18.12	14.48
		Common ground-dove	6	2	28.8	230.4	0.62	0.13
		Eurasian collared-dove	4	3	133.0	931.0	0.54	0.54
		Mourning dove	159	55	106.9	22,876.6	16.50	13.37
		Rock pigeon	1		311.0	311.0	0.08	0.18
		Unknown	4	1				
	<b>Cuculiformes</b>		12	10	61.1	1,344.2	1.70	0.79
		Yellow-billed cuckoo	12	10	61.1	1,344.2	1.70	0.79
	<b>Falconiformes</b>		5	2	103.1	721.7	0.54	0.42
		American kestrel	5	2	103.1	721.7	0.54	0.42
	<b>Galliformes</b>		63	34	332.5	32,252.5	7.48	18.84
		Northern bobwhite	50	24	143.2	10,596.8	5.71	6.19
		Chicken	11	9	532.7	10,654.0	1.54	6.22
		Unknown	1					
		Wild turkey	1	1	5,336.0	10,672.0	0.15	6.23
	<b>Gruiformes</b>		1	1	491.0	982.0	0.15	0.57
		American coot		1	642.0	642.0	0.08	0.38
		Common moorhen	1		340.0	340.0	0.08	0.20
	<b>Passeriformes</b>		514	63	56.4	32,542.8	44.49	19.01
		American crow	1		403.0	403.0	0.08	0.24
		Bachman's sparrow	1		20.2	20.2	0.08	0.01
		Baltimore oriole		1	33.8	33.8	0.08	0.02
		Blue grosbeak	3		26.5	79.5	0.23	0.05
		Blue jay	148	17	79.7	13,150.5	12.72	7.68
		Blue-gray gnatcatcher	2		6.0	12.0	0.15	0.01
		Brown thrasher	15	2	54.4	924.8	1.31	0.54
		Brown-headed cowbird	7		42.0	294.0	0.54	0.17
		Carolina chickadee	1		10.2	10.2	0.08	0.01
		Carolina wren	14	1	20.5	307.5	1.16	0.18
		Cedar waxwing	1		31.8	31.8	0.08	0.02
		Chipping sparrow		3	12.3	36.9	0.23	0.02

**Table 11.** Continued.

Class	Order	Species	Frequency by season		Mean mass	Total mass	% Freq.	% Weight
			Breeding	Non-breeding				
		Common grackle	33	1	100.9	3,430.6	2.62	2.00
		Common yellowthroat		2	10.1	20.2	0.15	0.01
		Dark-eyed junco	1		19.6	19.6	0.08	0.01
		Eastern bluebird	8	2	29.4	294.0	0.77	0.17
		Eastern kingbird	2		41.4	82.8	0.15	0.05
		Eastern meadowlark	7	3	83.2	832.0	0.77	0.49
		Eastern towhee	6		38.2	229.2	0.46	0.13
		European starling	11		73.9	812.9	0.85	0.47
		Field sparrow	1	2	12.5	37.5	0.23	0.02
		Gray catbird	1		31.4	31.4	0.08	0.02
		Great crested flycatcher	5		32.2	161.0	0.39	0.09
		Hermit thrush	1		29.5	29.5	0.08	0.02
		House sparrow	2	1	26.2	78.6	0.23	0.05
		Loggerhead shrike	8	0	45.3	362.4	0.62	0.21
		Northern cardinal	47	4	42.6	2,171.7	3.93	1.27
		Northern mockingbird	50	2	45.8	2,381.2	4.01	1.39
		Northern parula	1		8.6	8.6	0.08	0.01
		Ovenbird		1	19.4	19.4	0.08	0.01
		Purple martin	1		19.4	19.4	0.08	0.01
		Pine warbler	2	4	11.9	71.4	0.46	0.04
		Red-winged blackbird	4	3	51.2	358.7	0.54	0.21
		American robin	7	3	73.6	735.6	0.77	0.43
		Rose-breasted grosbeak	1		73.6	73.6	0.08	0.04
		Savannah sparrow		1	16.9	16.9	0.08	0.01
		Song sparrow		1	20.8	20.8	0.08	0.01
		Swamp sparrow		1	17.0	17.0	0.08	0.01
		Tufted titmouse	6		21.6	129.6	0.46	0.08
		Unknown	109	2				
		White-crowned sparrow		1	27.7	27.7	0.08	0.02
		White-throated sparrow		2	25.9	51.8	0.15	0.03
		Wood thrush	5		43.7	218.4	0.39	0.13
		Yellow-rumped warbler	1	3	12.5	50.0	0.31	0.03
		Yellow-throated warbler	1		9.4	9.4	0.08	0.01
	<b>Piciformes</b>		43	3	90.7	4,172.2	3.55	2.44
		Downy woodpecker	4		26.8	107.4	0.31	0.06
		Northern flicker	4		130.4	521.4	0.31	0.30
		Pileated woodpecker	4	1	285.6	1,427.9	0.39	0.83
		Red-bellied woodpecker	21	1	60.7	1,335.7	1.70	0.78
		Red-cockaded woodpecker	1		42.4	42.4	0.08	0.02
		Red-headed woodpecker	4		71.2	284.6	0.31	0.17
		Unknown	5					
		yellow-bellied sapsucker		1	50.3	50.3	0.08	0.03



**Table 11.** Continued.

Class	Order	Species	Frequency by season		Mean mass	Total mass	% Freq.	% Weight
			Breeding	Non-breeding				
	<b>Strigiformes</b>		9	2	160.0	1,760.0	0.85	1.03
		Eastern screech-owl	9	2	160.0	1,760.0	0.85	1.03
	<b>Unknown</b>		69	3				
		Unknown	69	3				
<b>Mammalia</b>			39	5	939.8	41,351.2	3.39	24.16
	<b>Carnivora</b>		1		661.0	661.0	0.08	0.39
		Striped skunk	1		661.0	661.0	0.08	0.39
	<b>Lagomorpha</b>		14	3	1,294.1	21,999.7	1.31	12.85
		Eastern cottontail	14	3	1,294.0	21,998.0	1.31	12.85
	<b>Rodentia</b>		14	1	221.6	3,324.0	1.16	1.94
		Gray squirrel	1	1	555.0	1,110.0	0.15	0.65
		Southern flying squirrel	5		72.5	362.5	0.39	0.21
		Unknown small rodent	8					
	<b>Unknown</b>		10	1				
		Unknown	10	1				
<b>Reptilia</b>			9		11.5	103.5	0.69	0.06
	<b>Squamata</b>		9		12.1	108.9	0.69	0.06
		Broad-headed skink	1		31.0	31.0	0.08	0.02
		Green anole	2		5.0	10.0	0.15	0.01
		Six-lined racerunner	1		9.0	9.0	0.08	0.01
		Unknown	5					
<b>Unknown<sup>a</sup></b>			90					
	<b>Unknown</b>		90					
		Unknown	90					
<b>Total</b>			1,100	197	131.8	171,164.3	100	100

<sup>a</sup> Unknown prey at the Class- and Order-level are mostly items brought to nests that could not be identified at any level.

The majority of avian biomass on both study areas consisted of species weighing between 30 g and 145 g, although cattle egrets were comparatively abundant and caused a bimodal distribution in avian prey weights, with the second peak at 370 g. Considering all prey over both seasons, the mean weight of female prey was not different from the mean weight of available prey (mean = 109.9, SE = 1.2 g), whereas the mean weight of male prey was less than the mean weight of available prey (mean = 71.5, SE = 1.05; 1-way ANOVA,  $F = 11.0$ ,  $df = 2,8442$ ,  $P < 0.001$ ; Tukey Honestly Significant Difference test for 1) mean females vs. mean of available prey  $P = 0.70$ , and 2) males vs. available  $P < 0.001$ ; Figure 24). However, if cattle egrets are excluded from the available prey distribution and diet, the mean weight of male prey did not differ from the mean weight of remaining available avian prey; whereas, females captured heavier prey on average (1-way ANOVA,  $F = 11.2$ ,  $df = 2,6588$ ,  $P < 0.001$ ; Tukey Honestly

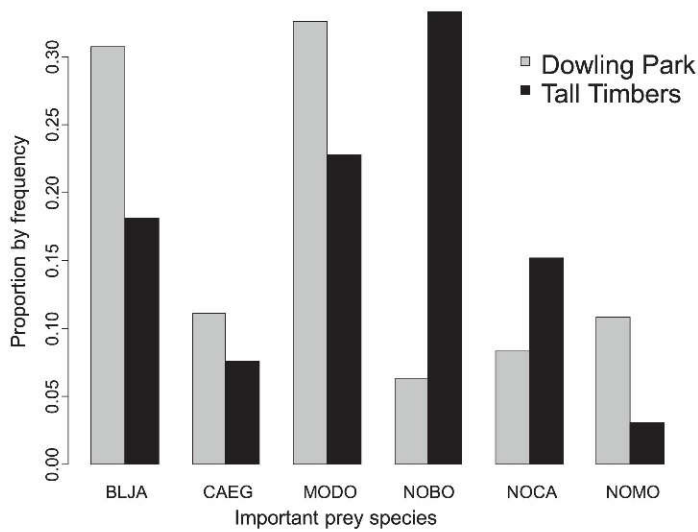
Significant Difference test for 1) mean females vs. mean of available prey  $P < 0.001$ , and 2) males vs. available  $P = 0.25$ ).

The average number of fledgling birds detected per point on July bird counts was 0.03 (SE = 0.01) in 1998, 0.11 (SE = 0.01) in 1999, and 0.06 (SE = 0.01) in 2000; these means were not different (1-way ANOVA,  $F = 0.19$ ,  $df = 1, 788$ ,  $P = 0.66$ ).

**Foraging behavior**

Results in this section are based on 243 prey captures by 27 radio-tagged Cooper's hawks (12 females and 15 males) during 1,170 h of systematic radio-tracking, primarily during 1998-2000.

*Factors affecting prey-capture rates.* Prey capture rates during the breeding season (including the prelaying and incubation period) averaged 0.28 per h (SE = 0.14,  $n = 853$  h), compared with 0.14 per h (SE = 0.01,  $n = 317$  h) during the nonbreeding season (independent-sample  $t$ -test,  $t = 8.06$ ,  $df = 142.2$ ,  $P < 0.001$ ; Table S11).

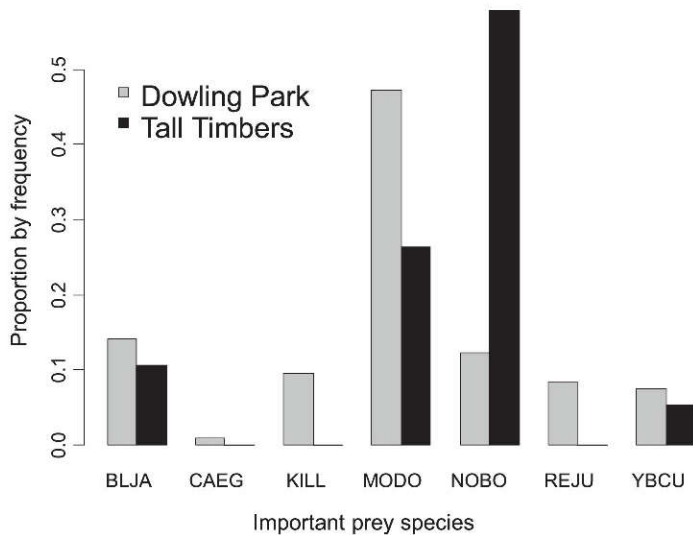


**Figure 18.** Proportion by frequency in pooled prey data set of important prey species in the breeding season diet of Cooper's hawks on two north Florida study areas, 1995–2001. Prey data are a combination of prey remains, direct observation, and radio-tracking data sets (see text for description). Important prey consist of prey species that individually made up >4% of the pooled data set by frequency. Alpha codes are defined in Appendix B.

Adult female Cooper's hawks did no detectible foraging during periods they were being monitored from March through May, during which time they presumably relied on their mates for food. After May, only 4 of 10 intensively monitored female Cooper's hawks were observed to reinitiate foraging activity; the remaining 6 did no detectible foraging during the entire breeding season while they were being monitored. Overall during the breeding

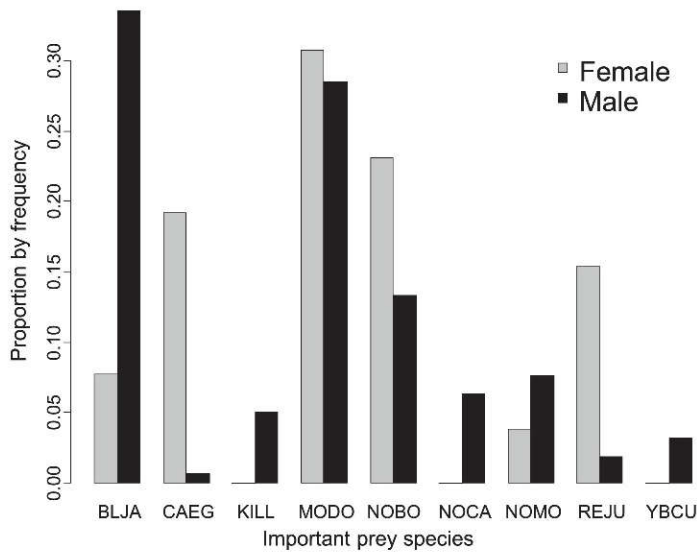
season, males were responsible for 84.7% of all prey captures observed, including all prey captured before young were 12 d of age (Figure 25).

During the breeding season, hourly prey-capture rates remained relatively stable from 0700 hours until dusk (Figure 26). During the nonbreeding season, prey captures peaked between 0900 hours and 1000 hours, with another abbreviated peak in the evening. There was no evidence of an increase in



**Figure 19.** Proportion by frequency of important prey species in the nonbreeding season diet of Cooper's hawks on two north Florida study areas, 1995–2001, from the radio-tracking data set (see text). Important prey consists of prey species that individually made up >4% of the data set by frequency. Alpha codes are defined in Appendix B.

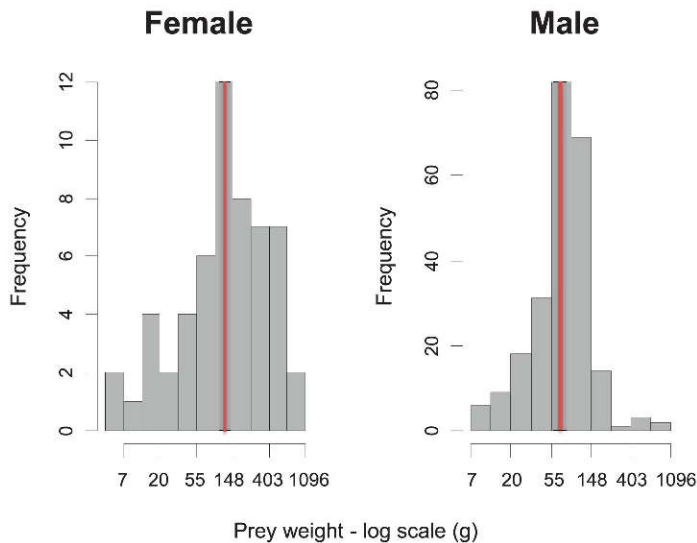




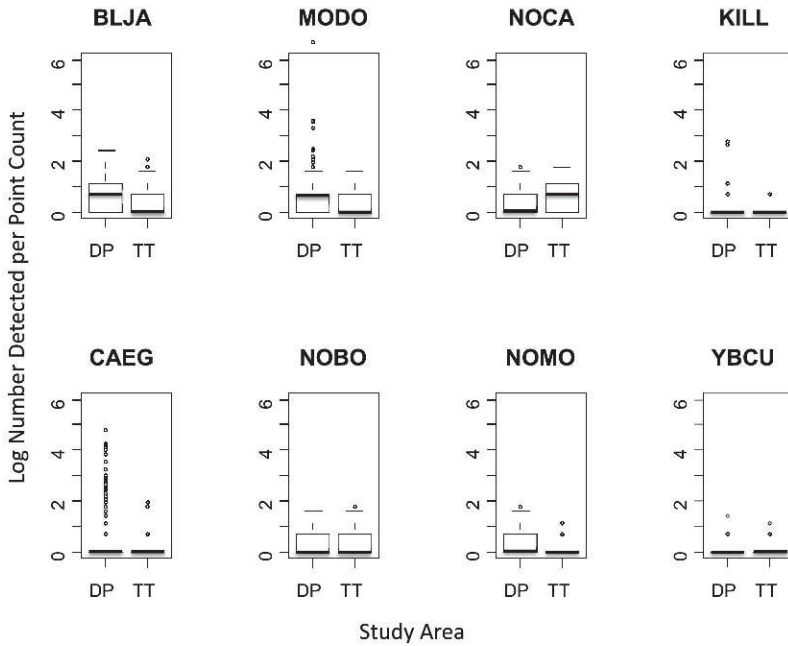
**Figure 20.** Proportion by frequency of important prey species in the diet of male and female Cooper's hawks on two north Florida study areas, 1995–2001. Prey data are from a combination of the direct observation and radio-tracking data sets (see text for description). Important prey consists of prey species that individually made up >4% of the pooled data set by frequency. Alpha codes are defined in Appendix B.

breeding-season prey-delivery rate with nestling age, even when the effects of brood size, the rank of the nest area, and year rank were accounted for as covariates (Analysis of Covariance, effect of nestling age  $F = 0.825$ ,  $df = 2,98$ ,  $P = 0.441$ ). There was also no evidence of a trend toward increasing biomass of prey deliveries as nestlings grew ( $R^2 = 0.008$ ,  $F = 1.41$ ,  $df = 1,184$ ,  $P = 0.236$ ).

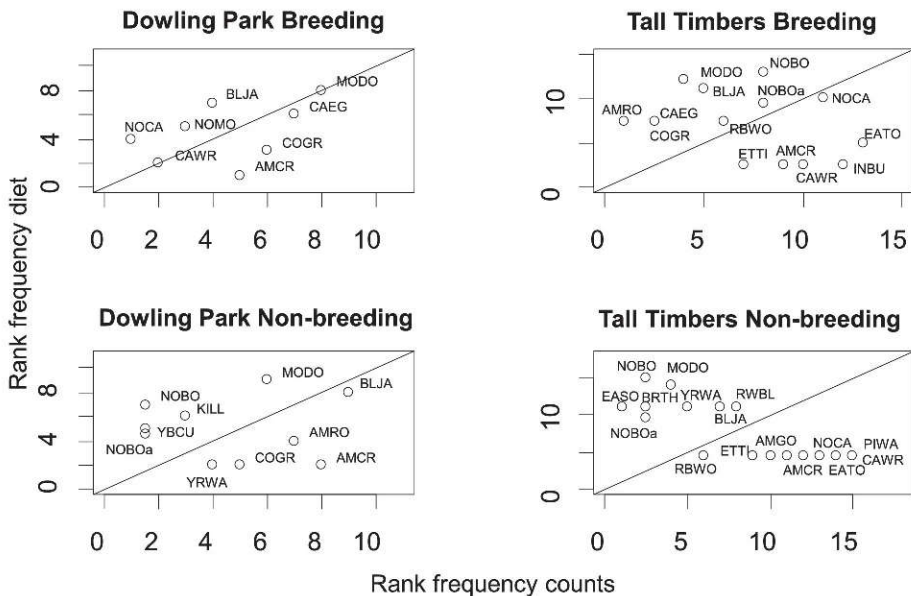
YEARRANK and SITERANK explained a high proportion of the variation in breeding-season prey-capture rates (multiple-regression  $R^2 = 90.6$ ,  $F = 33.9$ ,  $df = 2,7$ ,  $P < 0.001$ ; Figure 27). Average hourly prey-delivery rates per day at nests where female Cooper's hawks remained in attendance throughout the breeding season was 0.39 (SE = 0.03,  $n = 62$  h), compared with 0.31 (SE = 0.03,  $n$



**Figure 21.** Histogram of weights of prey captured by adult male and adult female Cooper's hawks on two north Florida study areas, 1995–2001. Data are from the direct observation and radio-tracking data sets, where sex of the captor was known. Dark-orange vertical lines denote the mean prey weight for each sex.

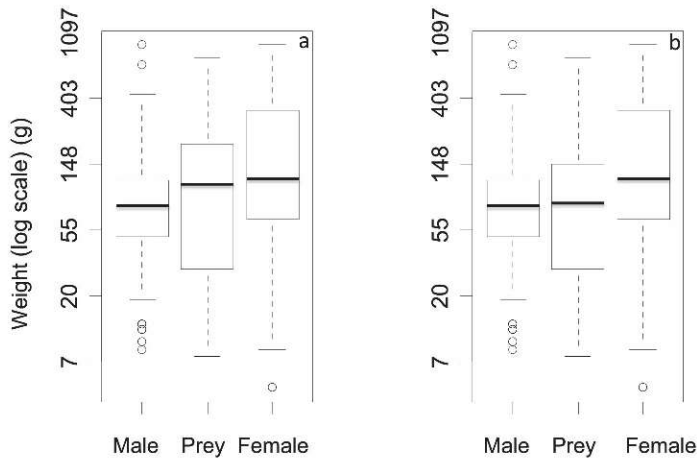


**Figure 22.** Box plots of the log-transformed number of detections of important Cooper's hawk prey species at 1,140 point-count stations on two north Florida study areas, 1998 through 2000. The horizontal heavy line in boxes is the median, boxes cover the median 50% of values (interquartile range), and the whiskers extend outward from box hinges 1.5 times the interquartile range. Alpha codes are defined in Appendix B.



**Figure 23.** Plots of relative ranks of avian species that comprised >4% of detections in seasonal point counts against rank frequencies of avian species that comprised >4% of seasonal Cooper's hawk prey on two north Florida study areas. Prey data are from the period 1995–2001, whereas point counts were conducted each year from 1998 to 2000. High ranks represent avian species detected most frequently in the diet or on bird counts. Alpha codes are described in Appendix B. The code NOBOa is an adjusted rate of predation for northern bobwhite, based on a detailed analysis of the radio-tracking prey data set (see text).





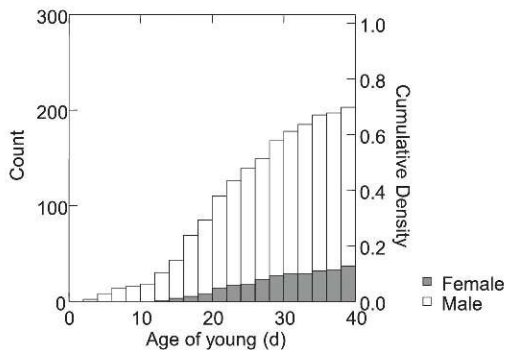
**Figure 24.** Box plots of male and female Cooper's hawk prey weights compared with weights of available avian prey (Prey) on two north Florida study areas, 1998–2000. Figure (a) includes all available prey encountered on point counts. Figure (b) excludes cattle egrets. The horizontal heavy line in boxes is the median, boxes cover the median 50% of values (interquartile range), and the whiskers extend outward from box hinges 1.5 times the interquartile range.

= 45 h) at areas where females deserted (independent-sample *t*-test,  $t = 2.16$ ,  $df = 102.6$ ,  $P = 0.03$ ). At nest areas where females deserted, prey delivery rates up to 3 d prior to desertion averaged 0.34 per h (SE = 0.027,  $n = 38$ ); whereas, 3 d prior to and after desertion, delivery rates averaged 0.13 per h (SE = 0.05,  $n = 7$ ; independent-sample *t*-test,  $t = 3.77$ ,  $df = 9.6$ ,  $P = 0.004$ ). Because females contributed so little to prey biomass brought to nests, it is unlikely that the drop in prey delivery rates immediately prior to and after females deserted was due to their decreased contribution. Rather, declines in prey delivery rates appeared to precede female nest abandonment. Males continued to

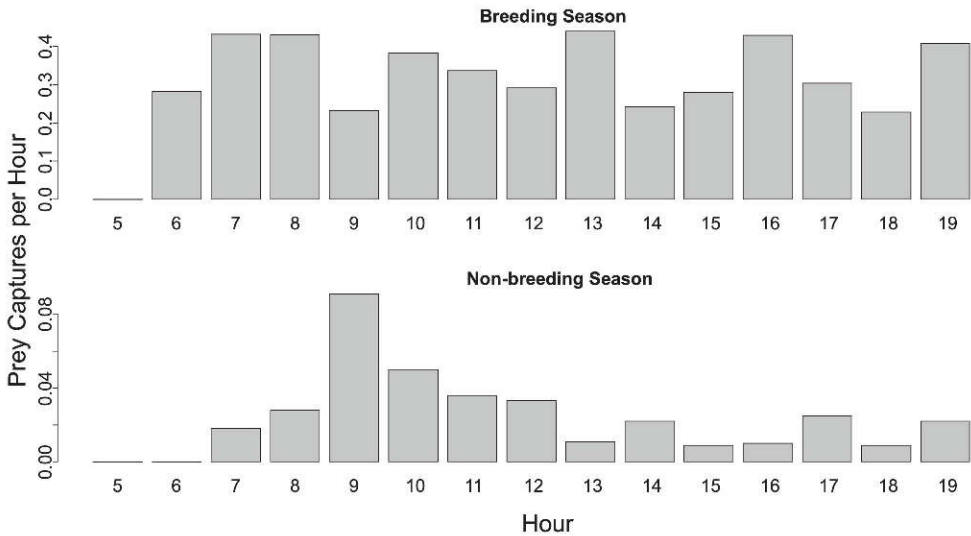
provision young at nest areas where females deserted, and we observed no nestling mortality after females departed.

*Foraging distance and time.* Radio-tagged Cooper's hawks attending young on the Dowling Park study area captured prey between 150 m and 4.8 km from nests (Figure 28; Table S11). The mean distance from the nest to prey capture sites did not differ between males and females (mean distance for males = 1.9 km [SE = 0.1,  $n = 109$ ], and 2.3 km [SE = 0.3,  $n = 19$ ] for females; 1-away ANOVA,  $F = 2.1$ ,  $df = 1,122$ ,  $P = 0.15$ ). Prey capture distance tended to increase over the course of the day ( $R^2 = 0.09$ ,  $F = 12.30$ ,  $df = 1,122$ ,  $P = 0.001$ ) and with nestling age ( $R^2 = 0.03$ ,  $F = 3.60$ ,  $df = 1,126$ ,  $P = 0.006$ ; Figure 29). The length of individual foraging bouts tended to increase over the day ( $R^2 = 0.06$ ,  $F = 5.79$ ,  $df = 1,91$ ,  $P = 0.02$ ), but not with chick age ( $R^2 = 0.01$ ,  $F = 0.08$ ,  $df = 1,122$ ,  $P = 0.373$ ; Figure 30).

*Diet and foraging specialization by individuals.* We observed several instances of individual diet and foraging-style specializations among radio-tagged Cooper's hawks. After the breeding season most females moved to, and subsequently revisited, sites with obvious concentrations of prey. These included night roosts of cattle egrets ( $n = 1$ ), bird feeders at homes ( $n = 1$ ), wildlife feeding stations on plantations ( $n = 2$ ), dove-hunting fields ( $n = 2$ ), release stations for pen-reared bobwhite ( $n = 2$ ), poultry farms ( $n = 2$ ), and night roosts of rock pigeons ( $n = 1$ ). One female followed from 1997 to 2001 spent each nonbreeding season near a single poultry farm, where she captured young chickens through a small hole in a corner of a brooder barn. Another female consistently hunted near a farmhouse that had many



**Figure 25.** Cumulative prey deliveries to nests by male and female breeding adult Cooper's hawks. Captures and prey deliveries were determined from simultaneous radio-tracking of adult Cooper's hawks and videotaping at nests over 720 h. Data are from 8 different male and 9 different female Cooper's hawks at 10 nest attempts at 5 different nest sites on the Dowling Park study area, north Florida, 1998–2000.



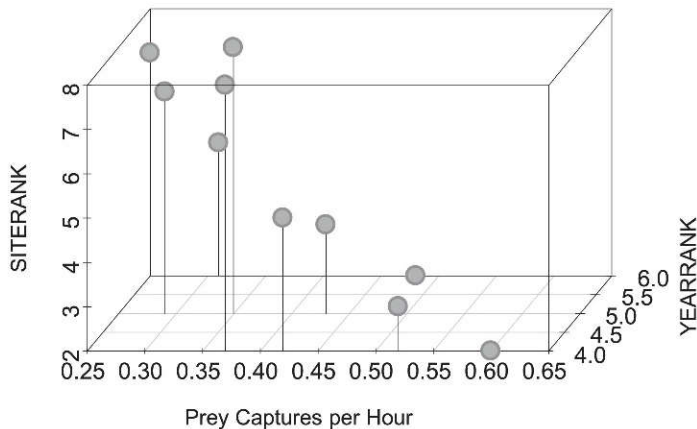
**Figure 26.** Hourly prey-capture rates (number prey captures per h of radio-tracking) during the breeding and nonbreeding seasons by radio-tagged adult Cooper's hawks of both sexes on two north Florida study areas, 1995–2001.

free-ranging chickens; we observed her capturing them on four occasions.

For the 10 pairs at nests where we video-recorded prey deliveries, foraging effort was skewed toward nestling and fledgling birds (64% of known-aged prey; 2-sample test for equality of proportions of adult vs. young birds in prey captures with continuity correction,  $\chi^2 = 35.8$ ,  $df = 1$ ,  $P < 0.001$ ). All of the intensively tracked males on the Dowling Park study area and one Tall Timbers male regularly checked bird nest boxes for prey. Three male Cooper's hawks made regular forays to one or more purple martin houses within their home ranges

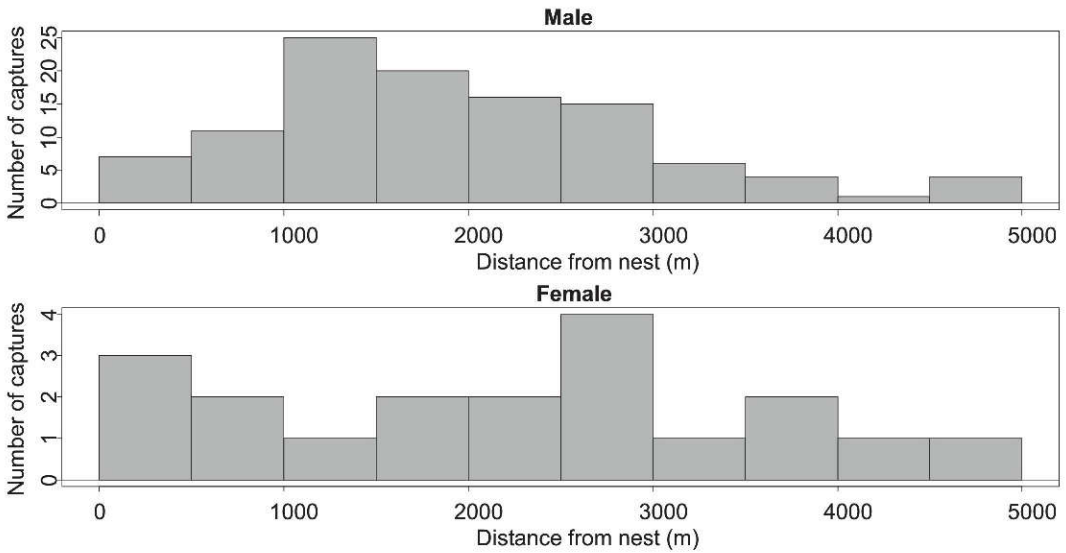
where they primarily captured European starlings. We observed male Cooper's hawks capture prey at purple martin, eastern bluebird, and American kestrel nest boxes. Whether at nest boxes or other nest sites, once male Cooper's hawks located the nest, they would make repeated visits until, presumably, all available nestlings had been captured.

*Predation on northern bobwhite.* A total of 416 did not meet our criteria for inclusion in analyses of bobwhite capture rates (Table S12). Model analyses suggested that bobwhite capture rates were affected by season and the interaction between sex and season (Table 12); only season had a coefficient



**Figure 27.** Relationship between SITERANK, YEARRANK, and mean prey-delivery rates at Cooper's hawk nest sites on two north Florida study areas, 1998–2000. Low ranks represent nest areas and years when indicators of reproductive success were greatest (see text). Prey delivery rates are from 10 nest areas where both adults were radio-tagged and where prey deliveries were videotaped concurrently with radio-tracking of both adults.





**Figure 28.** Distance from nest to locations of prey captures by radio-tagged breeding adult Cooper's hawks on the Dowling Park study area, north Florida, 1998–2000. Data are from 8 different male and 9 different female radio-tagged Cooper's hawks at 10 nest attempts on 8 different nest areas.

confidence interval that did not include 0. Model predictions were a capture rate (number of bobwhite captures per Cooper's hawk per day) of 0.09 (SE = 0.03) during winter, 0.01 (SE = 0.01) during the nonbreeding season, and 0.04 (SE = 0.01) during the breeding season. Expanded based on the number of days in each season, the predicted number of bobwhite captured per adult Cooper's hawk per season was: winter = 10.7 (SE = 1.2); postbreeding = 0.76 (SE = 0.76); and breeding = 6.7 (SE = 1.7). Annually, we estimate each adult Cooper's hawk captured 18.2 (SE = 3.6) bobwhite.

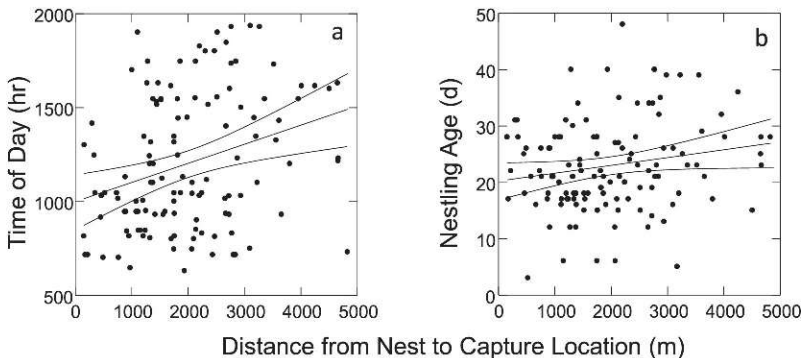
Assuming 1) a 14-h foraging day during the breeding season, 2) a 12-h foraging day at other times of the year (based on radio-tracking activity estimates), 3) an average of four prey captures per day during the breeding season (0.28 per h, with 85% by

males) and 4) one prey capture per day at other times of the year for both sexes, we estimated that male Cooper's hawks captured about 850 prey items per y, and females about 290 prey items per y. Based on the above calculations, we estimate that bobwhite comprised about 2% of adult male and 6% of adult female Cooper's hawk prey over the course of a year on both study areas. We provide adjusted estimates of the frequency of bobwhite in the Cooper's hawk diet in Figure 23 (NOBOa) based on this analysis.

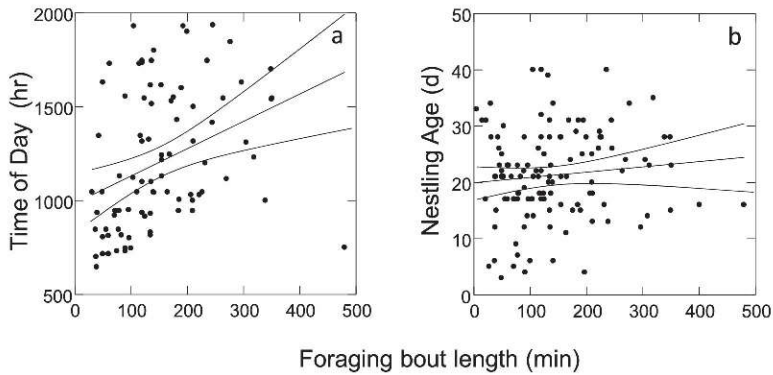
**Discussion**

**Nesting density and reproduction**

Cooper's hawk nest-area density was 2.6 times greater on Tall Timbers than on Dowling Park. Nesting habitat did not appear limiting on either



**Figure 29.** Relationship between distance from the nest to prey capture sites with (a) time of day, and (b) age of nestlings, for radio-tagged adult Cooper's hawks on the Dowling Park study area, north Florida, 1998–2000. Regression lines are bounded by 90% confidence intervals. Data are from 8 different male and 9 different female radio-tagged Cooper's hawks at 10 nest attempts on 8 different nest areas.



**Figure 30.** Relationship between foraging bout length with (a) time of day, and (b) age of nestlings, for radio-tagged adult Cooper's hawks on the Dowling Park study area, north Florida, 1998–2000. Regression lines are bounded by 90% confidence intervals. Data are from 8 different male and 9 different female radio-tagged Cooper's hawks at 10 nest attempts on 8 different nest areas.

study area, so we suspect nesting density was influenced by other factors. Territoriality and prey availability were the most likely limiting factors, based on limiting factors for *Accipiter* hawks elsewhere (Newton 1979, 1986; Kenward 2006). Density of occupied nests of Cooper's hawk elsewhere ranged from 272 to 2,321 ha per nest across a range of habitats and locales throughout the species' range (Reynolds and Wight 1978; Millsap 1982; Reynolds 1989; Rosenfield et al. 1991, 1995; Boal and Mannan 1999; Nenneman et al. 2002; Stout and Rosenfield 2010), so our observations are within the reported range. Nest area occupancy, and thus the density of occupied nest areas, varied temporally on our study areas and decreased during and after the El Niño year of 1998. We discuss nest area occupancy further below.

Studies across a wide range of latitudes and environmental conditions indicate that Cooper's hawks lay eggs from mid-April to late-May, with laying occurring in most locales from late April to early May (see summaries by Rosenfield and Bielefeldt 1993; Boal and Mannan 1999; Nenneman et al. 2002). Our results conform to this general pattern. Snyder and Wiley (1976) found that egg-laying by Cooper's hawks in Arizona was triggered by the arrival in mass of small migrant songbirds. That was unlikely the trigger in our study areas because most avian prey were resident species; however, seasonal shifts in the distribution and availability of resident prey might have been important in triggering nesting by the Cooper's hawks we studied.

Reports of Cooper's hawk nest success range from 47 to 91%, with most around 70% (as summarized in Rosenfield and Bielefeldt 1993; also Rosenfield et al. 1995; Boal and Mannan 1999; Nenneman et al. 2002; Rosenfield et al. 2007; Stout et al. 2007); estimates of brood size at occupied nests range from 1.6 to 2.8, and brood size at successful nests range

from 2.7 to 4.0 (as summarized in Rosenfield and Bielefeldt 1993; also Rosenfield et al. 1995; Boal and Mannan 1999; Nenneman et al. 2002; Rosenfield et al. 2007; Stout et al. 2007). Estimates of nest success and brood size at occupied nests can be biased high if early nest failures are not taken into account (Steenhof and Newton 2007) as we have done, and results of some of these earlier studies may not be comparable to our findings. Brood size at successful nests is likely more comparable among studies, though some researchers (e.g., Rosenfield et al. 1995) considered nests successful that survived shorter periods of time than the 24 d we used here. Despite these differences, we believe it is reasonable to conclude that measures of nesting success and productivity for Cooper's hawks in our study are at the lower end of values found in most previous studies for this species; this perhaps is not surprising given the southeastern Atlantic coastal plain was near the southern periphery of the Cooper's hawk's range during our study. Interestingly, the study area with the most similar reproductive measures to north Florida was in North Dakota at the northern periphery of the species' range (Rosenfield et al. 2007).

We found no support for any hypothesized effects on nest success, but we did find support for a temporal and study area effect on brood size. These findings are consistent with the possibility that the El Niño event in 1998 contributed to the overall low fecundity we observed. However, productivity metrics both before and after 1998 were low compared with other studies, so it is unlikely weather alone was responsible. Some factors affecting nest success and brood survival were unique to our study areas (e.g., fire ants), but neither these, nor other predators or mortality agents in common with other studies, appeared to cause atypical levels of nest failure or brood loss on our study areas. We considered five other potentially interrelated explanations for low fecundity in our study population:



**Table 12.** Competitive and global generalized linear models examined to explain variation in the proportion of days that radio-tagged adult Cooper's hawks captured northern bobwhite on two north Florida study areas, 1996–2000, based on data from 12 female and 15 male Cooper's hawks tracked from 1 to 5 y. Model ranking was based on Akaike's Information Criterion (AIC) corrected for small sample size (AIC<sub>c</sub>). All competitive models (within 2 AIC units of the top model) and the global model are shown. Models were fit with a logit-link function.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub>	ΔAIC <sub>c</sub> <sup>c</sup>	ω <sup>d</sup>	∑ω <sup>e</sup>
SEX*SEASON	6	143.60	0	0.50	0.50
SEASON	3	144.43	0.84	0.33	0.83
AREA + YEAR + SEX + SEASON + SEX*SEASON	11	150.11	8.22	0.02	0.95

<sup>a</sup> SEX = a model factor, with two levels: 1) female, and 2) male. SEASON = a factor with three levels: 1) nonbreeding (16 August through 31 October); 2) winter (1 November through 28 February), and 3) breeding (1 March through 15 August). AREA = a factor with two levels: 1) Dowling Park, and 2) Tall Timbers. YEAR = a factor with six levels: 1) 1995, 2) 1996, 3) 1997, 4) 1998, 5) 1999, and 6) 2000. A \* denotes inclusion of an interaction term between the effects.

<sup>b</sup> Number of model parameters.

<sup>c</sup> Change in AIC<sub>c</sub> from the top-ranked model.

<sup>d</sup> Model weight.

<sup>e</sup> Cumulative model weight.

1. There is a general tendency in many raptor species for clutch size, and thus reproductive potential, to decline with decreasing latitude (Newton 1979). Rosenfield and Bielefeldt (1993) reviewed available information and observed no such effect for Cooper's hawks, and the larger brood sizes observed in Arizona (Millsap 1982; Boal and Mannan 1999) were at latitudes only slightly greater than our study areas in Florida (32° vs. 30°N latitude).
2. Our study area is near the southern edge of the Cooper's hawk's breeding range (Foland and Millsap 1996); thus, environmental conditions for reproduction may be marginal relative to other locales studied. Several of the studies reporting much higher fecundity than Florida are at or near the northern periphery of the species' range, but so was the study with the most similar results to ours, in North Dakota (Rosenfield et al. 2007). A potentially important factor at the southern edge of the Cooper's hawk's breeding range in eastern North America is the absence of Eastern chipmunks *Tamias striatus* and other small ground squirrels, important components of the diet in many other areas (Bielefeldt et al. 1992). This is an important component of the food limitation hypothesis (number 5) below.
3. Many of the comparable Cooper's hawk studies occurred during a period of post-DDT population growth and recovery (Henny and Wight 1972; Bednarz et al. 1990; Rosenfield and Bielefeldt 1993), and our results might simply reflect natural reproductive values in a stable, saturated population. The fact that brood size at successful nests was inversely related to nest density on our two study areas provides some support for this hypothesis, but the relationship is confounded by the slightly greater proportion of less productive SY female breeders on the more densely populated Tall Timbers area. We also note that other contemporary studies of apparently fully recovered Cooper's hawk populations (e.g., Boal and Mannan 1999; Boal 2001a; Rosenfield et al. 2007) found higher brood sizes and successful brood sizes than we did, and in one 21-y study in Wisconsin, there was a positive correlation between annual productivity and occupied nest-area density (Stout et al. 2010).
4. Comparatively high turnover rates for female Cooper's hawks at nest areas may have had a negative effect on productivity. We observed higher brood sizes at nests with experienced adults; thus, the comparatively high and apparently natural rates of female breeding dispersal may have contributed to low overall productivity.
5. Prey resources may have been unusually limiting on our study areas compared with other locations where Cooper's hawk breeding biology has been studied. There are no comparable measures of prey availability among studies, so this hypothesis cannot be assessed directly. However, there are several lines of evidence to support this concept, which are discussed under "Diet and foraging habits" below. We suspect this is the most likely ultimate factor contributing to low productivity in our Cooper's hawk study population, and may have set the stage for other proximate contributing factors (such as high female turnover in number 4 above).

## Survival and causes of mortality

Most estimates of survival rates of Cooper's hawks are from samples of breeding adults. Henny and Wight (1972) estimated annual survival rates of adult Cooper's hawks of between 63% and 79% based on banding data across the species' range. Annual survival of adult male Cooper's hawks in Wisconsin was estimated at 81% over a 26-y period, based on mark recapture methods (Rosenfield et al. 2009). In Arizona, Mannan et al. (2008) estimated 64% annual first-year survival of radio-tagged Cooper's hawks, and 66% and 81% annual survival of second-year and older adults, respectively, based on mark recapture models. Roth et al. (2005) observed 75% survival of radio-tagged adult Cooper's hawks over a 110-d interval during winter in Indiana in one of the only studies that has targeted Cooper's hawks not captured at nests. Annual adult survival-rate estimates for close congeners have ranged from 81% for the goshawk in North America (Squires and Reynolds 1997), 80% (Kenward et al. 1999) to 84% (Tomberg and Colpaert 2001) for goshawks in Europe, and around 70% for the Eurasian sparrowhawk (Newton 1975; Newton et al. 1983, 1997). Adult Cooper's hawk survival rates we observed were similar to those estimated elsewhere, with the exception of the low survival rate observed in 1998. The proportion of SY female breeders is potentially an indirect indicator of survival for that sex (Newton 1979), and our observations of 5–12% SY female breeders falls within the range observed elsewhere for Cooper's hawks (6–26%; Reynolds and Wight 1978; Millsap 1982; Boal 2001a; Rosenfield et al. 2007; Stout et al. 2007).

Despite the small sample size, our analyses suggested survival rates of both sexes of Cooper's hawks in north Florida were unusually low in 1998. At least three of the males that died in 1998 were in poor general body condition, something we did not see in any other year in our study. In addition to low survival, Cooper's hawks exhibited comparatively low nest-area occupancy in 1998. Meteorologically, the strong El Niño event during the winter of 1997–1998 was associated with the wettest late winter and early spring on record in north Florida. Newton (1978) and Newton and Marquiss (1984) found that Eurasian sparrowhawks had difficulty obtaining sufficient food for breeding during cold wet springs, and atypical weather related to El Niño events have produced broad-scale changes in the winter distribution of some species of raptors in North America (Kim et al. 2008). Our point-count samples showed that the number of fledgling birds was lowest in 1998, and this may have contributed to the poor conditions in that year. However, there was also a strong inverse relationship between prey-capture rates and YEARRANK, which suggests that reduced foraging success in 1998 may have also been a contributing factor.

Difficult forging conditions may also have contributed to the high Cooper's hawk mortality rates in 1998, but other factors were also likely involved. Rosenfield and Bielefeldt (1999) noted that breeding male Cooper's hawks in Wisconsin declined in mass over the course of the breeding season. Although Rosenfield and Bielefeldt (1999) observed no inter-year variation in male body mass in their study, it seems logical that declines in mass might be greatest in years when foraging is particularly difficult. We hypothesize that this may have occurred in our study in 1998, and that low prey resources that year may have required those male Cooper's hawks that did breed that year to exert more effort in foraging than usual, which in turn resulted in more males being in low condition and vulnerable to disease and other mortality factors after the breeding season. Female Cooper's hawks contributed only about 15% of prey brought to nestlings and did not increase foraging effort to compensate for reduced provisioning by males; hence, it is unlikely that they suffered poorer body condition as a result of increased foraging demands. Rather, that females were also affected is evidence disease may have played a part in the high mortality that year. Although West Nile virus did not reach Florida until 2001 (Blackmore et al. 2003), many other mosquito-borne aviviruses were present in Florida during 1998 (Thomas et al. 2003). Rainfall rates, mosquito abundance, and prevalence of encephalitic virus activity are correlated in Florida (Day and Alan 1989); thus, it is possible that high rainfall during 1998 and attendant increases in mosquito abundance could have increased exposure of Cooper's hawks to one or more of these aviviruses that year.

The temporal pattern of mortality in male Cooper's hawks was substantially different for individuals with 10-g compared with 6.5-g transmitters. Most mortality of males with 10-g transmitters occurred immediately prior to breeding, after they had worn the transmitters for nearly a year with no negative effects on productivity. Most of these males were killed near prospective nest areas, and we believe most were killed by Cooper's hawks. No males wearing 6.5-g transmitters died under similar circumstances, leading us to conclude that the 3.5 g of additional weight with the heavy transmitters was critical. We suspect males wearing 10-g transmitters were at a disadvantage in early courtship encounters with their much larger prospective mates, or in territorial disputes with other males. The 10-g transmitters were 3.4% of mean male Cooper's hawk body weight, compared with 2.3% for the 6.5-g transmitters. Because we lacked a control sample of marked hawks without transmitters, we have no means to assess whether the 6.5-g transmitters on males or the 10-g transmitter on females also affected survival. However, it is noteworthy that



our estimate of annual survival for both sexes in years other than 1998 was comparable to annual survival estimates of color-banded female Cooper's hawks in Arizona (81%; Mannan et al. 2008).

Other studies have reported negative effects of transmitters on raptors. Reynolds et al. (2004) found markedly lower apparent survival of breeding male goshawks wearing tail-mount transmitters but no effect on survival from backpack-mounted transmitters, even though backpacks weighed more (3.4% of mean body weight compared with 1.5% for tail-mounts). Steenhof et al. (2006) found that prairie falcons *Falco mexicanus* that shed transmitters had higher annual apparent survival than falcons that did not. Several studies have reported lower survival, lower productivity, or behavioral changes for radio-tagged spotted owls *Strix occidentalis*, tawny owls *Strix aluco*, and burrowing owls *Athene cunicularia* (Paton et al. 1991; Foster et al. 1992; Petty et al. 2004; Gervais et al. 2006; Chipman et al. 2007), though Sunde (2006) found no effect of transmitters on tawny owl survival in another study. Our results provide further evidence that encumbering raptors with transmitters can affect survival, though in our case the effect was not apparent until nearly 9 mo after initial transmitter deployment and appeared to be related to transmitter weight.

### Ranging behavior and dispersal

Previous studies of ranging behavior of radio-tagged Cooper's hawks have been limited to the breeding or winter season, with breeding season information exclusively for males. Breeding-season home-range size of radio-tagged adult male Cooper's hawks was 0.66 km<sup>2</sup> in urban areas of Tucson, Arizona (Mannan and Boal 2000); 0.78 km<sup>2</sup> for a single male in a suburban area in Wisconsin (Murphy et al. 1988); and 1.2 km<sup>2</sup> in a rural area of northern New Mexico (Kennedy 1989). Roth et al. (2008) radio-tagged six urban and eight rural wintering Cooper's hawks in Indiana, and found average winter home ranges of 3.9–14.9 km<sup>2</sup>. Roth et al.'s sample included a mixture of male, female, adult, and immature Cooper's hawks; they found no evidence of a difference in winter seasonal home-range size between sexes, but there was evidence of a difference with age (adults used smaller home ranges), and ranges of Cooper's hawks in urban landscapes were smaller than in rural areas. Mannan et al. (2004) found that seasonal home-range sizes of nine juvenile Cooper's hawks in Arizona averaged 7.71 km<sup>2</sup> during winter, with no difference between sexes.

Male Cooper's hawks in our study had much larger breeding season ranges (14.6 km<sup>2</sup>) than in these prior studies, and nonbreeding season ranges of both sexes (13.4–32.4 km<sup>2</sup>) in north Florida were much larger than those observed in most other

studies. One possible explanation for this is that differences in data collection and analysis approaches render the results incomparable. However, we found no difference in daily range size of north Florida Cooper's hawks calculated using different estimation procedures, and we suspect this finding extends across studies. We did find support for the hypothesis that daily and seasonal ranges of Cooper's hawk differed over the year, and the patterns of seasonal shifts differed between males and females. Thus, estimates of range size in our study were very sensitive to the time of year in which observations were collected. To be valid, our findings suggest that comparisons of seasonal range size between study areas or populations would need to be carefully coordinated so that samples were phenologically identical. We suspect that this probably accounts for some of the differences observed between ours and other studies, but the magnitude of differences are so great we believe spatial use by Cooper's hawks on our study areas exceeded that of most other populations of this species studied so far. Our results, combined with those of prior studies, suggest that seasonal and annual range sizes of Cooper's hawks are highly variable across different landscapes. The large home ranges for the rural Cooper's hawks in our study also contributes to a growing body of evidence indicating that ranges of individual Cooper's hawks are smaller in urban settings (Mannan and Boal 2000; Roth et al. 2008), suggesting higher relative availability of prey there.

Unlike Mannan et al. (2004) and Roth et al. (2008), we found support for the hypothesis that nonbreeding-season range size of Cooper's hawks differed between the sexes. Annual home ranges of female Cooper's hawks were larger because, unlike males, most females in our study maintained separate breeding and nonbreeding ranges, and as a result their cumulative space use was much larger than for males over the course of a year. The moves by females between seasonal ranges typically occurred immediately before and after the breeding season, and were therefore captured in nonbreeding-season range-size estimates. When measured on a daily basis, space use by males and females was similar during the nonbreeding season. During the breeding season, the pattern was reversed: daily range size did differ between Cooper's hawk sexes, but the overall breeding-season range size did not. We attribute breeding season differences to the dissimilar roles of the sexes at this time of year. Female Cooper's hawks have a primary role in caring for young (Meng 1951; Snyder and Wiley 1976; Rosenfield and Bielefeldt 1993), and this is consistent with our finding that they stayed within 100 m of their nests for several weeks prior to and during incubation and until the young were about



12 d old. Conversely, males have a primary role in foraging throughout the breeding season (Meng 1951; Snyder and Wiley 1976; Rosenfield and Bielefeldt 1993), and our findings show they traversed 20–80% of their entire annual range each day while feeding young. The only exception was early in the breeding season prior to egg-laying, when males also stayed fairly close to the nest. As the breeding season progressed, females traveled more widely. Although daily range size remained small, space use by female Cooper's hawks over the entire breeding season was similar to that by males. This same general pattern of annual space use by the sexes has been observed in the Eurasian sparrowhawk, except that female sparrowhawk ranges are larger than male ranges during every season (Newton 1986).

We also found support for the hypothesis that seasonal and annual range sizes of Cooper's hawks differed between study areas, with the smallest seasonal and annual ranges consistently occurring on Tall Timbers where Cooper's hawk nest density was also greatest. Kenward (1982) and Newton (1986) found that home ranges in their studies of the goshawk and Eurasian sparrowhawk, respectively, were smallest where prey abundance and amount of preferred foraging habitat was greatest, and this was generally true in Roth et al.'s (2008) study of wintering Cooper's hawks in Indiana. We found higher avian prey abundance in our study on Tall Timbers, which is consistent with the smaller Cooper's hawk home ranges there. We believe the more contiguous natural landscapes, application of bobwhite management practices, and absence of large blocks of agricultural land on Tall Timbers provided a greater density of favorable foraging habitat than was available on Dowling Park. As such, Cooper's hawks probably required less space to meet their seasonal foraging requirements on Tall Timbers, and responded numerically by increasing density.

In the only other study of home range overlap for Cooper's hawks, Mannan and Boal (2000) found breeding season ranges of males in Tucson, Arizona, to be generally exclusive. The general pattern we observed for adult male Cooper's hawks was one of partitioning the landscape into regularly spaced home ranges with exclusive nesting areas and, as distance from the nests increased, increasingly shared foraging areas. As was observed for Cooper's hawks in Tucson (Boal 2001b) and for sparrowhawks (Newton 1986), we suspect male Cooper's hawks in north Florida defend their home ranges from other males, with a priority on excluding same-sex trespassers from nesting areas. Female annual ranges in our study overlapped extensively, and ranges of individual females overlapped annual ranges of many males and included up to nine nest areas.

This pattern resembles what Mannan (2010) observed for juvenile Cooper's hawks in Tucson, Arizona; he speculated that by overlapping several nest areas, juveniles were able to repeatedly assess whether vacancies, and thus breeding opportunities, existed in their home ranges. We suspect this was also the case among adult female Cooper's hawks on our study area, in that by overlapping many nesting areas they were able to obtain constant feedback on the status of prospective future nesting areas.

During February and early March, radio-tagged female Cooper's hawks, and to a lesser extent radio-tagged males, began focusing their activity around nest areas within their home range. Most female Cooper's hawks moved among several different nest areas during this period. Early in the nesting season female occupancy of nest areas was not exclusive; on one occasion in late February, we observed two radio-tagged females at the same nest area over the course of several days. By the second week in March and through April, as the start of incubation approached, females tended to settle in on a single nesting area. We suspect that females moved among nests in February and March to evaluate nesting areas and their respective resident males. At this time, females probably were competing among themselves to settle on the optimum nesting area, as has been observed for Eurasian sparrowhawks (Newton 1986) and goshawks (Kenward 2006), and is suggested for Cooper's hawks by evidence of age-related mate selection (Boal 2001a) and by female-on-female aggression around nests (Boal 2001b). For male Cooper's hawks, this was a time when daily ranges were smallest, and those on the most productive home ranges or with the most experience probably were able to focus more of their time provisioning visiting females. This was also apparently a risky time for male Cooper's hawks, because this is when several radio-tagged males were killed (often, we suspect, by other Cooper's hawks). We do not know the sex of individual Cooper's hawks responsible for these deaths, but C. Boal (2001b and personal communication, Lubbock, Texas) observed instances of intense fighting by male Cooper's hawks early in the breeding season around nests in Tucson, and we observed females chasing resident males on a few occasions in our study. As we noted previously, male mortality early in the breeding season in north Florida was solely of individuals wearing heavy transmitters; thus, it is possible the added weight compromised these males in aggressive interactions with either prospective mates or other males attempting to acquire the nest area.

Breeding dispersal in north Florida Cooper's hawks was female-biased (*sensu* Greenwood and Harvey 1982). Male Cooper's hawks in our study almost always occupied the same home range between years, except in two cases where males



moved to an adjacent nesting area of equal or higher quality. Rosenfield et al. (1996) observed a similar pattern for male Cooper's hawks in Wisconsin (1996); although, in that longer term study, male nest-area fidelity was complete. Conversely, female Cooper's hawks in north Florida changed nesting areas between years nearly 70% of the time, and in general showed a higher degree of fidelity to the nonbreeding than the breeding season range. We found support for hypotheses that female Cooper's hawk breeding dispersal was greatest among what were likely younger individuals. Our finding of high site fidelity by male Cooper's hawks is consistent with what has been observed in other studies, but the high rate of breeding dispersal by female Cooper's hawks in our study contradicts findings from other areas; Rosenfield and Bielefeldt (1996) reported 15% breeding dispersal among female Cooper's hawks in a long-term study in Wisconsin, and Mannan et al. (2007) found <10% breeding dispersal in either sex in Tucson, Arizona. Natal dispersal in Cooper's hawks also appears to be female-biased (Rosenfield and Bielefeldt 1992; Rosenfield et al. 1996; Mannan et al. 2004, 2007). This same pattern has been observed for the goshawk (Kenward 2006) and Eurasian sparrowhawk (Newton 1986).

Our findings that distance between breeding and nonbreeding ranges of female Cooper's hawks decreased as eye color darkened suggests that female Cooper's hawks on our study areas become more sedentary with age. As we stated earlier, we suspect this is because older females outcompeted younger females for high-ranking nest areas in close proximity to their nonbreeding ranges. This implies a fitness advantage of breeding dispersal from nest areas (if they are distant from the nonbreeding range) to nest areas closer to the nonbreeding range. Such an advantage might accrue if the nesting areas open to young females are generally of lower quality (and thus passed over by older females), and if by breeding on or near their nonbreeding range, females would have greater familiarity with prey resources and be better able to supplement the male's foraging efforts for the brood. The late start date of nests with SY females provides some support for first part of this hypothesis, because it suggests that younger females probably had to search extensively to find territory-holding males not already paired with preferred ASY females (Boal 2001a).

The process of nest area selection and pair formation by Cooper's hawks may have been more involved on our study areas than at other locations with lower rates of female breeding dispersal and more persistent pair bonds. In north Florida, adult females essentially redistributed themselves among nest areas annually, so female versus female competition for nest sites and "testing" of resident males was likely widespread each year. The large

breeding dispersal distances of female Cooper's hawks, high female turnover rates, large female annual ranges, and the comparatively low measures of reproductive success were all possible consequences of this breeding system.

### Diet and foraging habits

Food availability can be the primary factor regulating populations of *Accipiter* hawks (Newton 1986; Kenward 2006). Our results suggest this was the case for Cooper's hawks nesting in north Florida. Cooper's hawk productivity in our study was directly related to prey delivery rates by males, both among nest sites and across years. The ability of a male Cooper's hawk to attract and retain a female at a nest site appeared to be strongly tied to his provisioning rate. Female Cooper's hawks quickly deserted nest sites where males were not providing sufficient food and returned to their own nonbreeding-season home ranges.

At least two lines of evidence suggest prey may have been generally limiting for the Cooper's hawk populations we studied relative to others. The strongest evidence of this is that prey delivery rates to nests in our study averaged fewer than 0.3 per h, compared with 0.34–0.9 prey deliveries per h in other studies (Fitch et al. 1946; Snyder and Wiley 1976; Kennedy and Johnson 1986; Murphy et al. 1988; Estes and Mannan 2003). Although comparatively low prey-delivery rates might be offset if biomass of the prey captured was relatively large, that was not the case in our study because the most common prey species were the same or similar to prey in most other studies (see below). Secondary evidence that prey may have been unusually limiting was the comparatively poor reproductive performance of Cooper's hawks in our study, as discussed previously. Although we noted several factors that might have contributed to poor reproductive success, the low rate of prey delivery was likely the most important among these.

Cooper's hawks on our study areas appeared to feed primarily on birds (89% of the diet by frequency and 76% by biomass). Birds are prominent in most other studies of Cooper's hawk diet during the breeding season studies, ranging from 26% to 90% of observed prey (Errington 1932; Fitch et al. 1946; Hammerstrom and Hammerstrom 1951; Meng 1951; Craighead and Craighead 1956; Snyder and Wiley 1976; Kennedy 1980; Janik and Mosher 1982; Millsap 1982; Bielefeldt et al. 1992; Bosakowski et al. 1992; Peterson and Murphy 1992; Estes and Mannan 2003; Cava et al. 2012). We are aware of only one other nonbreeding diet study for the Cooper's hawk that used methods similar to ours (Roth and Lima 2006), and that study found that birds comprised >90% of observed prey.

Bielefeldt et al. (1992) contended that studies of Cooper's hawk diet based on prey remains overes-



timated the proportion of birds in the diet because bird parts are more persistent and noticeable around nests than are remains of other Orders of prey. They assert that birds likely comprised <50% of the Cooper's hawk's diet by frequency in many of the populations studied, with small mammals, particularly chipmunks, making up most of the remainder of the diet. Our findings support the contention that prey remains provide a biased representation of the importance of various taxa in the diet. However, in our case prey remains underrepresented the importance of birds in the diet based on biomass, likely because nestling birds were not accounted for in prey remains samples. Though biases described by Bielefeldt et al. (1992) certainly applied to aspects of our findings, and we identified and reported additional kinds of biases as well, we feel confident that birds comprised >75% of the Cooper's hawk diet in north Florida by biomass and frequency throughout the year. Surprisingly, reptiles, an important component of the Cooper's hawk diet in a few other studies (Fitch et al. 1946; Estes and Mannan 2003), were not captured frequently by either sex of Cooper's hawk in our study despite their relatively high abundance (Enge 1997). Given that reptiles were not taken often as prey, the reliance on avian prey in north Florida was a necessity because ground-dwelling squirrel and chipmunk species commonly captured in other Cooper's hawk diet studies (Bielefeldt et al. 1992) are absent from our study areas. Some urban Cooper's hawk populations maintain high productivity without using mammalian prey (Boal and Mannan 1999; Rosenfield et al. 2010), but this is likely possible because of the greater abundance of suitable avian prey species in urban environments (Estes and Mannan 2003; Roth et al. 2008). In rural north Florida, we suspect the lack of a small ground squirrel component in the prey community was a key factor limiting the reproductive potential of Cooper's hawks breeding there.

Although Cooper's hawks preyed upon 76 species in our study, a few avian species made up the majority of the diet. Dominance of a few prey species has been observed in most other Cooper's hawk diet studies (Meng 1951; Snyder and Wiley 1976; Kennedy 1980; Janik and Mosher 1982; Millsap 1982; Bielefeldt et al. 1992; Bosakowski et al. 1992; Peterson and Murphy 1992; Estes and Mannan 2003; Cava et al. 2012). In our study, the list of important prey species by frequency varied between study areas, seasons, and sexes. Mourning doves, blue jays, and northern bobwhite were important prey in all seasons on both study areas. Most of these species, or close relatives, have been reported as common prey of Cooper's hawks in other studies (Meng 1951; Snyder and Wiley 1976; Kennedy 1980; Janik and Mosher 1982; Millsap

1982; Bielefeldt et al. 1992; Bosakowski et al. 1992; Peterson and Murphy 1992; Estes and Mannan 2003; Roth and Lima 2003), except that Roth and Lima (2003) reported a lack of predation on blue jays in their study of wintering Cooper's hawks in Indiana.

Several authors noted that Cooper's hawks focus on ground- and shrub-oriented prey (Reynolds and Meslow 1984; Bielefeldt et al. 1992; Bosakowski et al. 1992; Cava et al. 2012). This was true in our study, because most of the avian taxa preferentially selected by Cooper's hawks primarily occur in these vegetation strata (Dickson and Noble 1978; Reynolds and Meslow 1984; Bielefeldt et al. 1992; Bosakowski et al. 1992). A notable exception, however, was the heavy reliance on nestling birds by male Cooper's hawks during the breeding season as observed in this study, by Bielefeldt et al. (1992), and at least during the latter stages of the nesting cycle by Cava et al. (2012). We frequently observed male Cooper's hawks searching the tree canopy for nests, as well as removing nestling birds from nest boxes. These behaviors accounted for 64% of the prey male Cooper's hawks brought to their nests in our study. Cooper's hawk predation has been identified as a possible factor in the decline of American kestrels in North America (Farmer et al. 2006). Although Smallwood et al. (2009) found no direct statistical relationship between negative population trends in American kestrels and population increases in Cooper's hawks in Breeding Bird Survey data, our findings provide empirical evidence that in at least some settings, Cooper's hawks can and do target kestrel nest boxes as sources of prey. Given this, nest box programs may increase the vulnerability of American kestrels to predation by Cooper's hawks.

With the exception of mourning doves and northern bobwhite that were taken regularly by both male and female Cooper's hawks in our study, the sexes focused on different species of prey. Blue jays (and other medium and small passerine birds) were primarily taken by male Cooper's hawks, and chickens and cattle egrets were taken exclusively by females. The choice of different prey resulted in the disparity we observed in mean prey size between Cooper's hawk sexes over the year. Prey size partitioning by male and female Cooper's hawks has been observed or postulated in other studies (Selander 1966; Storer 1966; Reynolds 1972; Snyder and Wiley 1976). These authors hypothesized that extreme sexual size dimorphism has been selected for in this raptor because it allows partitioning of food resources between the sexes and increases the cumulative foraging niche, which is advantageous during the breeding season. However, many Cooper's hawk populations studied during the breeding season have not shown sexual food partitioning



(Snyder and Wiley 1976; Kennedy 1980; Kennedy and Johnson 1986). Our results provide additional evidence against the breeding season niche-expansion hypothesis because the diet differences we observed between sexes were only evident at other times of the year.

The potential advantage of sexual prey-size partitioning by Cooper's hawks during the breeding-season was further offset by the inconsistent effort exerted by females toward hunting in our study. Female Cooper's hawks accounted for only 15% of prey deliveries at nests overall, and females at over half the nest sites we monitored intensively were not observed foraging at all. Significantly, the response by female Cooper's hawks to declining prey delivery rates by males was to desert the nest area and brood, not to increase foraging efforts to augment prey deliveries to young. Kelly and Kennedy (1993) investigated theoretical factors associated with female brood desertion in Cooper's hawks and concluded desertion was an effective strategy that balanced probabilities for current brood survival with survival and future reproductive potential of the female. Our findings support this hypothesis, because at all nest sites where breeding female Cooper's hawks deserted but breeding males remained alive, all young fledged successfully. Most of these females were not observed foraging or providing food to the broods; hence, they were consuming resources brought by the male that otherwise would have gone to the nestlings. The nest desertion strategy was not effective in maximizing production when the male Cooper's hawk died, because in all these cases the females promptly deserted their nests and all abandoned nestlings died.

At the 4 of 10 intensively studied nests where female Cooper's hawks did regularly capture prey for their broods, female foraging efforts appeared opportunistic. In these cases, hunting female Cooper's hawks primarily ambushed birds in fields bordering the nest woodlot or captured small prey close to the nest. Two of these female Cooper's hawks nested in relatively close proximity to their nonbreeding ranges, and these females occasionally returned to the nonbreeding areas and brought prey back to their nests. This not only explains the seemingly contradictory long-distance foraging forays by females in Figure 28, but it also suggests the possibility that one reason females contributed so little prey was that they were not familiar with foraging opportunities around their nests. In all but 1 of 10 cases in the direct observation data set, the female had no prior experience (to our knowledge) hunting in the vicinity of her nest. Opportunism was also an element of female Cooper's hawk foraging behavior during the nonbreeding season. Although male Cooper's hawks were restricted year-round to a

home range centered on their nest area, females moved over much larger areas almost nomadically, and exploited concentrations of prey at places such as chicken farms, home bird and bobwhite feeders, cattle egret night roosts, and cattle feedlots. Once such a site was located, the female Cooper's hawks stayed and exploited it until, presumably, it became unprofitable.

We believe any selective advantages conferred by prey size partitioning on our study areas most likely accrued outside the breeding season. Boal and Mannan (1996) suggested this might be the case for goshawks in Arizona, after having failed to find evidence of prey size partitioning for that species during the breeding season. In our case, we suspect that the broader foraging niche of female Cooper's hawks facilitated their opportunistic, wide-ranging foraging behavior during the nonbreeding season by allowing them to take advantage of a wider range of situations where prey were concentrated. The wide-ranging behavior, coupled with a focus on larger sized prey, may also serve to lessen competition for prey resources between male and female Cooper's hawks with overlapping nonbreeding ranges.

Storer (1966), Reynolds (1972), and to a lesser degree Schoener (1969), hypothesized that the smaller size of male *Accipiter* hawks was advantageous because the greatest biomass of prospective avian prey are in smaller size classes, and a smaller male more closely matches the size distribution of potential prey. Our findings initially contradicted this hypothesis, because we found that the average size of female Cooper's hawk prey closely matched the average size of available avian prey, while males focused on smaller sized birds. However, this relationship was heavily driven by one prey species, the cattle egret. When cattle egrets were dropped from the diet and bird-count data sets, the average size of remaining male avian prey did closely match the average size of what was available and avian prey of females tended to be heavier than average. Cattle egrets exhibited a heavily clumped distribution on our study areas owing to their flocking behavior and tendency to use large, communal night roosts. As such, both by virtue of their size and distribution, they were favored female Cooper's hawk prey and essentially unavailable to males. Thus, exclusive of the anomaly associated with this one avian species, our findings generally support the idea that male Cooper's hawks were focusing foraging effort on the most abundant weight-classes of available avian prey.

A component of this theory as advanced by Reynolds (1972) was that a closer match in size between male Cooper's hawks and smaller avian prey was advantageous because of the great agility of small birds; hawks closer in size were likely more of a match in terms of quickness and maneuverability.



Sonsthagen et al. (2012) provide indirect support for this hypothesis by showing that genetic and morphological differentiation in breeding Cooper's hawks across the northern part of the species' range suggests that overall body size may be tracking prey size. Although such a relationship may be true overall, as noted by Bielefeldt et al. (1992) and observed in our study, breeding male Cooper's hawks forage mainly on fledgling and nestling birds, prey for which agility may not always be necessary. This casts doubt on the premise that advantages of increased agility in male Cooper's hawks are associated with foraging efficiency during the breeding season, but leaves open the possibility that benefits accrue at other times of the year. In this context, our findings lend support to the modified "agile male" hypothesis advanced by Bielefeldt et al. (1992) and Boal and Mannan (1996) that smaller male size might be advantageous outside the breeding season, but with one further amendment: this advantage is heightened by virtue of male Cooper's hawk's residency on a comparatively small home range of fixed size. Because of this, male Cooper's hawks in our study had less freedom to search out and exploit prey concentrations. Consequently, they were more dependent than females on continuously distributed prey species. Male Cooper's hawks may benefit by being more closely matched in size with the majority of prospective prey during late summer, autumn, and winter for two reasons. First, to the extent that smaller predator size facilitates capture of smaller prey, smaller size for male Cooper's hawks would increase foraging efficiency because most encounters would be with smaller sized prey. Second, capturing fully grown birds is presumably harder than capturing nestlings and fledglings; thus, increased agility by male Cooper's hawks might increase foraging effectiveness at these times of the year.

Temporal and spatial dynamics of foraging behavior of Cooper's hawks has not been widely studied. Murphy et al. (1988) studied the foraging behavior of a single breeding male Cooper's hawk in Wisconsin whose seasonal home range was 784 ha; this individual spent the majority of his time within 0.5 km of the nest, and 99% of all foraging was within 2 km of the nest. Breeding male Cooper's hawks in our study also captured most prey within 2 km of the nest, but nearly 35% was captured >2 km away, and <10% of prey were captured within 0.5 km of the nest. This is consistent with the finding that breeding-season home ranges of male Cooper's hawks in Florida were larger than in other locations studied. However, because nest spacing in our study was similar to that in Wisconsin (Murphy et al. 1988) and elsewhere, the more wide-ranging foraging by male Cooper's hawks in our study probably resulted in more overlap between adjacent males in their use of peripheral hunting areas.

Because male foraging distance increased over the breeding season, overlap in foraging by males on abutting territories probably also increased as young developed. As we noted earlier, measured breeding-season home-range overlap for male Cooper's hawks in our study was considerably greater than in the only other study that looked at this (Mannan and Boal 2000). The little foraging that breeding female Cooper's hawks did in our study was fairly evenly distributed within 5 km of the nest.

Murphy et al. (1988) noted that the single breeding male Cooper's hawk in their Wisconsin study hunted at about the same rate throughout the day, a pattern similar to what we observed. This contrasts with findings of Fitch et al. (1946) and Fischer (1986) in the western United States, who found daily lulls in foraging activity of breeding Cooper's hawks, perhaps associated with inactive periods for prey. Outside the breeding season, Cooper's hawks in our study concentrated their foraging activity in the morning before 1000 hours and in the evening at dusk. This matches closely the pattern observed by Roth and Lima (2007) in a study of wintering Cooper's hawks in Indiana. In our study, nonbreeding Cooper's hawks rarely made more than one prey capture per day, and on most days those kills happened in the early morning.

Cooper's hawks in our study did not increase their prey delivery rate or the biomass of prey brought to nests as young grew. This is consistent with findings in other studies (Snyder and Snyder 1973; Estes and Mannan 2003). Snyder and Snyder (1973) suggested that male Cooper's hawks hunt at their maximum capacity during the brood stage, and prey availability determines prey capture rates. Our results support this hypothesis.

### Predation on northern bobwhite

One of our major objectives in this study was to evaluate predation by Cooper's hawks on bobwhite. Much of the information discussed previously applies generally to bobwhite as an important prey species of Cooper's hawks in our study. In this section, we focus the discussion more on the specific attributes of Cooper's hawk utilization of bobwhite as prey in an effort to hone in on the factors that influenced that use.

Our radio-tracking data set suggested bobwhite captures by Cooper's hawks occurred on about 5% of days over the course of the year. These estimates call into question the findings from our prey remains data set that bobwhite comprised 34% of breeding and 57% of winter Cooper's hawk prey at Tall Timbers by frequency. As noted previously, prey remains data are biased in favor of prey remains that have high persistence, and bobwhite remains (as well as those from other moderate to large birds) are persistent. However, because we were unable to



follow radio-tagged Cooper's hawks onto private lands around Tall Timbers to determine prey captures there, it is possible that bobwhite predation rates by Cooper's hawks off Tall Timbers were higher, and that the actual difference between the two estimates is less. In spite of this possibility, we believe the radio-tracking data set provided a more reliable estimate of Cooper's hawk bobwhite capture frequency. Our initial estimates of rank-abundance of bobwhite in the diet in Figure 23 are therefore likely inflated, and we believe the adjusted estimates are more credible (and we note that estimates of the frequency of other moderate to large birds in the diet inferred from the prey remains data set alone might be similarly biased). Even the adjusted estimates suggest bobwhite were preferred prey, which is not surprising considering the bobwhite is a ground-dwelling bird within the size range captured by both male and female Cooper's hawks.

We found that resident Cooper's hawk predation on bobwhite in north Florida was relatively modest and occurred mostly during winter. Previous studies on bobwhite in the same part of Florida and elsewhere have shown that  $\geq 60\%$  of annual bobwhite mortality is from raptors, mainly Cooper's hawks and northern harriers *Circus cyaneus*, and that raptor mortality occurs mostly during late winter and spring (Stoddard 1978; Mueller 1989; Carter et al. 2002; Cox et al. 2004). Thus, the predation rate of adult Cooper's hawks on bobwhite that we observed was considerably lower than what prior studies of bobwhite have suggested, but our observations on temporal pattern of that predation are consistent with findings in those other studies. Stoddard (1978) and Mueller (1989) contend that much of the late winter and spring bobwhite predation in north Florida and south Georgia is from Cooper's hawks on northbound migration. Because we did not study that component of the Cooper's hawk population, our study sheds no light on this aspect of Cooper's hawk predation. However, we suggest that another possibility may account for the disparity: the above-cited radio-telemetry based estimates of bobwhite mortality may overestimate natural rates of raptor predation because radio-tagged quail are especially susceptible to hawk predation, as suggested by Guthery and Lusk (2004). We have no direct evidence on this point, but it is notable that Mueller (1989) reported recovering the remains of >27 bobwhite from one Cooper's hawk nest on Tall Timbers during his intensive bobwhite radio-telemetry study there, while we only observed a total of 50 bobwhite over 6 y at 76 intensively monitored occupied Cooper's hawk nest areas on both our study areas.

Sandercock et al. (2008) found that winter survival of adult bobwhite had the greatest effect of any demographic variable on variance in population

growth rate. Thus, despite relatively modest rates of Cooper's hawk predation, the effect of that mortality on bobwhite populations might not be inconsequential. For that reason, management efforts to reduce predation on bobwhite by Cooper's hawks deserve consideration. Our results suggest a number of factors that might influence Cooper's hawk predation rates on bobwhite, and as we noted earlier, we believe these findings should have broad application across the Atlantic coastal plain of the southeastern United States. First, the prevalence of predation on bobwhite by Cooper's hawks during winter suggests a possible relationship between predation rates on quail and availability of escape cover. By the early part of the winter season, overnight frosts were common in all years of our study and herbaceous and shrub escape cover was reduced substantially from that available in other seasons. We suspect Cooper's hawks were more successful finding and capturing bobwhite under these conditions. Several authors have noted the importance of escape cover in predator avoidance for bobwhite (Stoddard 1978; Mueller and Atkinson 1985; Guthery 2000). Mueller et al. (1989) speculated that bobwhite were highly susceptible to Cooper's hawk predation after prescribed burning at Tall Timbers for similar reasons. Although a subsequent study by Carter et al. (2002) failed to find an increase in raptor predation on bobwhite after fire in Texas, based on our observations we agree with Mueller et al. that winter fires probably make bobwhite more susceptible to Cooper's hawk predation, at least in north Florida.

A second factor that might influence bobwhite predation by Cooper's hawks is the prevalence of factors that result in quail being concentrated in distribution rather than dispersed over the landscape, as was observed by Kenward (1999) for goshawks and ring-necked pheasants *Phasianus colchicus*. Female Cooper's hawks in particular were attuned to finding and exploiting situations where prey was concentrated. Gamebird feeders and food plots were visited by radio-tagged Cooper's hawks regularly; and when and where these features concentrated bobwhite, Cooper's hawk predation likely increased.

A third factor that could affect bobwhite predation is the release of pen-reared quail. Some radio-tagged female Cooper's hawks traveled long distances and temporarily settled in areas where bobwhite had been stocked, and although we were unable to monitor the diets of these individuals because of access restrictions, we suspect they were feeding on released quail. Naive pen-reared bobwhite are probably easy targets for Cooper's hawks by themselves, but they may have an indirect impact on native bobwhite populations by attracting unnaturally high densities of Cooper's hawks to local areas during the nonbreeding season, and by

focusing the attention of those foraging hawks on bobwhite. A further consideration is that if releases of pen-reared quail are accompanied by a reduction in habitat management efforts, populations of other Cooper's hawk prey species that benefit from such management (Ford et al. 2002) might decline, leaving bobwhite to absorb the full effect of the functional response by hawks.

A final factor that must affect bobwhite predation rates by Cooper's hawks is bobwhite abundance. Bobwhite populations temporally and spatially fluctuate with environmental and other factors (Guthery 1997, 2000), and the opportunistic nature of foraging by female Cooper's hawks suggests they should respond functionally with higher predation rates and numerically by concentrating in higher densities in years and locations when quail populations are high. Thus, managers should reasonably expect a functional and numerical response of hawks to changes in bobwhite abundance. Such a temporal difference in abundance might explain some of the disparity between our observed Cooper's hawk predation rates on bobwhite at Tall Timbers and rates inferred by Mueller (1989).

Our findings suggest several management actions that could be taken to reduce the vulnerability of bobwhite to Cooper's hawk predation on our study areas and perhaps elsewhere in the southeastern United States. First, the overall philosophy of habitat management to allow unconstrained use of space through time by bobwhite (Guthery 1997) seems particularly suited to minimizing Cooper's hawk predation by favoring a dispersed rather than clumped or concentrated distribution of quail across the landscape. Second, delaying prescribed burning in north Florida until after early March, when resident female Cooper's hawks are no longer hunting and are being fed by males, would likely lessen predation, as was suggested by Mueller et al. (1989). Such a burning regime more closely approximates the natural fire regime in north Florida, and has many other ecosystem benefits (Myers and Ewel 1990). Finally, the possible role of released pen-reared bobwhite in attracting and focusing Cooper's hawk predation on quail should be considered by land managers before undertaking such releases. In general, land management aimed at maintaining a natural, diverse, and dispersed mix of cover and food should afford the greatest benefits to bobwhite in reducing their vulnerability to Cooper's hawk predation.

### Supplemental Material

Please note: *North American Fauna* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

**Video S1.** Example of the digital video recordings of prey deliveries to Cooper's hawk nests obtained during this study. The first clip shows adult male Cooper's hawk SW37 delivering an adult northern mockingbird to his brood at nest area SUWA017022 on 24 May 2000. The second clip shows adult female Cooper's hawk SW18 delivering a broad-headed skink to her brood at nest SUWA017015 on 19 June 1999; the nest contains the carcass of an adult mourning dove delivered by the adult male a few minutes earlier. The third clip shows adult female Cooper's hawk SW33 delivering to the nest a cattle egret that she captured the previous day; this video was taped at nest area SUWA017005 on 29 May 1999. The final clip shows the same nest 1 h later, with the female delivering a fledgling blue jay captured by the adult male. All adult Cooper's hawks in these video clips are wearing radio-transmitters.

Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S1> (212739 KB AVI).

**Video S2.** Video recorded at nest area SUWA017022 on 25 May 2000, 1514–1528 hours. Fire ants were first seen in this nest on 24 May 2000, when they swarmed a northern mockingbird carcass delivered to the nestlings by the adult male Cooper's hawk. By 25 May 2000, the fire ants were causing visible agitation in the nestlings, resulting in this chick jumping to its death. On 31 May 2000 the nest failed and all remaining young disappeared.

Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S2> (356456 KB AVI).

Field descriptions for supplemental data sets. Metadata file for supplemental Tables S1–S12.

Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S3> (39 KB PDF).

**Table S1.** Supplemental information on Cooper's hawks captured and radio-tagged on two north Florida study areas, 1995–2000.

Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S4> (43 KB XLS).

**Table S2.** Supplemental information on Cooper's hawk nest areas monitored on two north Florida study areas, 1995–2000.

Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S5> (73 KB XLS).

**Table S3.** Supplemental information on daily ranges of Cooper's hawks monitored on two north Florida study areas, 1996–1997.

Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S6> (43 KB XLS).

**Table S4.** Supplemental information on seasonal and annual ranges of Cooper's hawks monitored on two north Florida study areas, 1995–2000.

Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S7> (46 KB XLS).



**Table S5.** Supplemental information on seasonal range overlap for Cooper's hawks on two north Florida study areas, 1995–2000.  
Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S8> (27 KB XLS).

**Table S6.** Supplemental information on dispersal for Cooper's hawks on two north Florida study areas, 1995–2000.  
Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S9> (27 KB XLS).

**Table S7.** Supplemental information on breeding season videotaping and radio-tracking intervals by hour for Cooper's hawks on two north Florida study areas, 1998–2000.  
Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S10> (44 KB XLS).

**Table S8.** Supplemental information on prey of Cooper's hawks on two north Florida study areas, 1995–2000.  
Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S11> (498 KB XLS).

**Table S9.** Supplemental information on non-breeding radio-tracking intervals by hour for Cooper's hawks on two north Florida study areas, 1995–2000.  
Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S12> (24 KB XLS).

**Table S10.** Supplemental information on results of point counts of birds on two north Florida Cooper's hawk study areas, 1998–2000.  
Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S13> (829 KB XLS).

**Table S11.** Supplemental breeding-season foraging information for radio-tagged Cooper's hawks on the Dowling Park study area, north Florida, 1998–2000.  
Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S14> (58 KB XLS).

**Table S12.** Supplemental information on northern bobwhite capture rates for Cooper's hawks on two north Florida study areas, 1995–2000.  
Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S15> (148 KB XLS).

**Reference S1.** Millsap BA. 1982. Distributional status of Falconiformes in westcentral Arizona - with notes on ecology, reproductive success and management. U.S. Department of the Interior, Bureau of Land Management, Technical Note 355.  
Found at DOI: <http://dx.doi.org/10.3996/nafa.78.0001.S16> (4.4 MB PDF).

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**Appendix A.** A list of variable acronyms used in the text and tables, and short definitions.

Variable	Name	Description
ACA	Annual core area	50% fixed-kernel contour of a single year's location data (e.g., breeding, nonbreeding)
AGE	Age	Cooper's hawk age
AR	Annual range	95% fixed-kernel contour of a single year's location data (e.g., breeding, nonbreeding)
AREA	Study area	Dowling Park or Tall Timbers
ASY	After-second-year	A Cooper's hawk in its third or later year of life
DCA	Daily core area	50% fixed-kernel contour of a single day's location data
DR	Daily range	95% fixed-kernel contour of a single day's location data
EYE	Eye color	Cooper's hawk eye color
PRECIP	Late winter and early spring precipitation	Late winter and early spring precipitation in relation to average
PAHR	Proportion annual home range used on a daily basis	The proportion of the annual home range of an individual covered by that individual on a given sampled day
SCA	Seasonal core area	50% fixed-kernel contour of a single season's location data (e.g., breeding, nonbreeding)
SEASON	Season	SEASON was treated as a two-factor variable in most models, with the levels: 1) breeding season, and 2) nonbreeding season. For bobwhite predation models, SEASON was treated as a factor with three levels: 1) winter, where month = November, December, January, or February; 2) breeding, where month = March, April, May, June, or July; and 3) postbreeding, where month = August, September, and October.
SEX	Sex	A factor in models, with two levels: 1) female, and 2) male
SITERANK	Nest area rank	Rank of Cooper's hawk nest areas based on several productivity metrics
SR	Seasonal range	95% fixed-kernel contour of a single season's location data (e.g., breeding, nonbreeding)
SY	Second-year	A Cooper's hawk in its second year of life
TIME	Time	An integer time series over years of the study
YEAR	Year	A factor with six levels: 1) 1995, 2) 1996, 3) 1997, 4) 1998, 5) 1999, and 6) 2000
YEARRANK	Year rank	Rank of years based on several Cooper's hawk productivity metrics
YOUNG	Number of young	Brood size at 24 d of age
YR1998	Year 1998	A factor with two levels: 1) YEAR = 1998 and 2) YEAR <>1998
YRGROUP	Year group	A factor with two levels: 1) YEAR <1998 and 2) YEAR >1998
YRSTRATA	Year strata	A factor with three levels: 1) YEAR <1998, 2) YEAR = 1998, and 3) YEAR >1998

**Appendix B.** Scientific names and weights of Cooper's hawk prey. Scientific names of birds follow American Ornithologists' Union (2008), names of mammals follow Baker et al. (2003), and names of reptiles follow Carothers (2008).

<b>Order</b>					
<b>Common name</b>	<i>Genus</i>	<i>Species</i>	<b>Alpha code</b>	<b>Adult weight (g)</b>	<b>Source</b>
AVES					
Caprimulgiformes					
Chuck-will's-widow	<i>Caprimulgus</i>	<i>carolinensis</i>	CWWI	120.0	Dunning 1992
Charadriiformes					
Killdeer	<i>Charadrius</i>	<i>vociferus</i>	KILL	97	Dunning 1992
Ciconiiformes					
Cattle egret	<i>Bubulcus</i>	<i>ibis</i>	CAEG	338	Dunning 1992
Green heron	<i>Butorides</i>	<i>virescens</i>	GRHE	212	Dunning 1992
Little blue heron	<i>Egretta</i>	<i>caerulea</i>	LBHE	340	Dunning 1992
Snowy egret	<i>Egretta</i>	<i>thula</i>	SNEG	370	Dunning 1992
Columbiformes					
Common ground-dove	<i>Columbina</i>	<i>passerina</i>	COGD	30	Dunning 1992
Eurasian collared-dove	<i>Streptopelia</i>	<i>decaocto</i>	ECDO	149	Dunning 1992
Mourning dove	<i>Zenaida</i>	<i>macroura</i>	MODO	119	Dunning 1992
Rock pigeon	<i>Columba</i>	<i>livia</i>	ROPI	345	Dunning 1992
Cuculiformes					
Yellow-billed cuckoo	<i>Coccyzus</i>	<i>americanus</i>	YBCU	64	Dunning 1992
Falconiformes					
American kestrel	<i>Falco</i>	<i>sparverius</i>	AMKE	111	Florida Fish and Wildlife Conservation Commission files
Galliformes					
Northern bobwhite	<i>Colinus</i>	<i>virginianus</i>	NOBO	154	Tall Timbers Research Station
Red junglefowl (Chicken)	<i>Gallus</i>	<i>gallus</i>	REJU	500	Dunning 1992
Wild turkey	<i>Meleagris</i>	<i>gallopavo</i>	WITU	7,400	Dunning 1992
Gruiformes					
American coot	<i>Fulica</i>	<i>americana</i>	AMCO	720	Dunning 1992
Common moorehen	<i>Gallinula</i>	<i>chloropus</i>	COMO	302	Dunning 1992
Passeriformes					
American crow	<i>Corvus</i>	<i>brachyrhynchos</i>	AMCR	448	Dunning 1992
Bachman's sparrow	<i>Aimophila</i>	<i>aestivalis</i>	BASP	20	Dunning 1992
Baltimore oriole	<i>Icterus</i>	<i>galbula</i>	BAOR	34	Dunning 1992
Blue grosbeak	<i>Passerina</i>	<i>caerulea</i>	BLGR	28	Dunning 1992
Blue jay	<i>Cyanocitta</i>	<i>cristata</i>	BLJA	87	Dunning 1992
Blue-gray gnatcatcher	<i>Poliptila</i>	<i>caerulea</i>	BGGN	6	Dunning 1992
Brown thrasher	<i>Toxostoma</i>	<i>rufum</i>	BRTH	69	Dunning 1992
Brown-headed cowbird	<i>Molothrus</i>	<i>ater</i>	BHCO	49	Dunning 1992
Carolina chickadee	<i>Poecile</i>	<i>carolinensis</i>	CACH	10	Dunning 1992
Carolina wren	<i>Thryothorus</i>	<i>ludovicianus</i>	CAWR	19	Dunning 1992
Cedar waxwing	<i>Bombycilla</i>	<i>cedrorum</i>	CEWA	32	Dunning 1992
Chipping sparrow	<i>Spizella</i>	<i>passerina</i>	CHSP	12	Dunning 1992



## Appendix B. Continued.

Order					
Common name	Genus	Species	Alpha code	Adult weight (g)	Source
Common grackle	<i>Quiscalus</i>	<i>quiscula</i>	COGR	114	Dunning 1992
Common yellowthroat	<i>Geothlypis</i>	<i>trichas</i>	COYE	10	Dunning 1992
Dark-eyed junco	<i>Junco</i>	<i>hyemalis</i>	DEJU	19	Dunning 1992
Eastern bluebird	<i>Sialia</i>	<i>sialis</i>	EABL	32	Dunning 1992
Eastern kingbird	<i>Tyrannus</i>	<i>tyrannus</i>	EAKI	44	Dunning 1992
Eastern meadowlark	<i>Sturnella</i>	<i>magna</i>	EAME	89	Dunning 1992
Eastern towhee	<i>Pipilo</i>	<i>erythrophthalmus</i>	EATO	41	Dunning 1992
European starling	<i>Sturnus</i>	<i>vulgaris</i>	EUST	82	Dunning 1992
Field sparrow	<i>Spizella</i>	<i>pusilla</i>	FISP	13	Dunning 1992
Gray catbird	<i>Dumetella</i>	<i>carolinensis</i>	GRCA	37	Dunning 1992
Great crested flycatcher	<i>Myiarchus</i>	<i>crinitus</i>	GCFC	34	Dunning 1992
Hermit thrush	<i>Catharus</i>	<i>guttatus</i>	HETH	31	Dunning 1992
House sparrow	<i>Passer</i>	<i>domesticus</i>	HOSP	28	Dunning 1992
Loggerhead shrike	<i>Lanius</i>	<i>ludovicianus</i>	LOSH	47	Dunning 1992
Northern cardinal	<i>Cardinalis</i>	<i>cardinalis</i>	NOCA	45	Dunning 1992
Northern mockingbird	<i>Mimus</i>	<i>polyglottos</i>	NOMO	49	Dunning 1992
Northern parula	<i>Parula</i>	<i>americana</i>	NOPA	9	Dunning 1992
Ovenbird	<i>Seiurus</i>	<i>aurocapilla</i>	OVEN	19	Dunning 1992
Purple martin	<i>Progne</i>	<i>subis</i>	PUMA	49	Dunning 1992
Pine warbler	<i>Dendroica</i>	<i>pinus</i>	PIWA	12	Dunning 1992
Red-winged blackbird	<i>Agelaius</i>	<i>phoeniceus</i>	RWBL	64	Dunning 1992
American robin	<i>Turdus</i>	<i>migratorius</i>	AMRO	77	Dunning 1992
Rose-breasted grosbeak	<i>Pheucticus</i>	<i>ludovicianus</i>	RBGR	46	Dunning 1992
Savannah sparrow	<i>Passerculus</i>	<i>sandwichensis</i>	SASP	20	Dunning 1992
Song sparrow	<i>Melospiza</i>	<i>melodia</i>	SOSP	25	Dunning 1992
Swamp sparrow	<i>Melospiza</i>	<i>georgiana</i>	SWSP	17	Dunning 1992
Tufted titmouse	<i>Baeolophus</i>	<i>bicolor</i>	TUTI	22	Dunning 1992
White-crowned sparrow	<i>Zonotrichia</i>	<i>leucophrys</i>	WCSP	28	Dunning 1992
White-throated sparrow	<i>Zonotrichia</i>	<i>albicollis</i>	WTSP	26	Dunning 1992
Wood thrush	<i>Hylocichla</i>	<i>mustelina</i>	WOTH	48	Dunning 1992
Yellow-rumped warbler	<i>Dendroica</i>	<i>coronata</i>	YRWA	13	Dunning 1992
Yellow-throated warbler	<i>Dendroica</i>	<i>dominica</i>	YTWA	9	Dunning 1992
Piciformes					
Downy woodpecker	<i>Picoides</i>	<i>pubescens</i>	DOWO	27	Dunning 1992
Northern flicker	<i>Colaptes</i>	<i>auratus</i>	NOFL	132	Dunning 1992
Pileated woodpecker	<i>Dryocopus</i>	<i>pileatus</i>	PIWO	287	Dunning 1992
Red-bellied woodpecker	<i>Melanerpes</i>	<i>carolinus</i>	RBWO	62	Dunning 1992
Red-cockaded woodpecker	<i>Picoides</i>	<i>borealis</i>	RCWO	44	Dunning 1992
Red-headed woodpecker	<i>Melanerpes</i>	<i>erythrocephalus</i>	RHWO	72	Dunning 1992
Yellow-bellied sapsucker	<i>Sphyrapicus</i>	<i>varius</i>	YBSA	51	Dunning 1992
Strigiformes					
Eastern screech-owl	<i>Megascops</i>	<i>asio</i>	EASO	200	Dunning 1992

**Appendix B.** Continued.

<b>Order</b>					
<b>Common name</b>	<i>Genus</i>	<i>Species</i>	<b>Alpha code</b>	<b>Adult weight (g)</b>	<b>Source</b>
MAMMALIA					
Carnivora					
Striped skunk	<i>Mephitis</i>	<i>mephitis</i>	STSK	522	Whitaker 1995
Lagomorpha					
Eastern cottontail	<i>Sylvilagus</i>	<i>floridanus</i>	EACO	900	Whitaker 1995
Rodentia					
Gray squirrel	<i>Sciurus</i>	<i>carolinensis</i>	GRSQ	400	Whitaker 1995
Southern flying squirrel	<i>Glaucomys</i>	<i>volans</i>	SRFS	45	Whitaker 1995
REPTILIA					
Squamata					
Broad-headed skink	<i>Plestiodon</i>	<i>laticeps</i>	BHSK	31	Florida Fish and Wildlife Conservation Commission files
Green anole	<i>Anolis</i>	<i>carolinensis</i>	GRAN	5	Florida Fish and Wildlife Conservation Commission files
Six-lined racerunner	<i>Aspidoscelis</i>	<i>sexlineata</i>	SLRR	9	Florida Fish and Wildlife Conservation Commission files