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Authors: Dykstra, Cheryl R., Hays, Jeffrey L., Simon, Melinda M., Wegman, Ann R., Williams, Kelly A., et al.

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DISPERSAL AND SURVIVAL OF RED-SHOULDERED HAWKS Banded IN SUBURBAN SOUTHERN OHIO, 1996–2018¹

CHERYL R. DYKSTRA²

Raptor Environmental, 7280 Susan Springs Drive, West Chester, OH 45069 USA

JEFFREY L. HAYS AND MELINDA M. SIMON

RAPTOR, Inc., 961 Barg Salt Run Road, Milford, OH 45150 USA

ANN R. WEGMAN

Cincinnati Museum Center, 1301 Western Avenue, Cincinnati, OH 45203 USA

KELLY A. WILLIAMS

Department of Biological Sciences, 430 Irvine Hall, Ohio University, Athens, OH 45701 USA

LAURA R. DYKSTRA

Calvin College, 3201 Burton Street SE, Grand Rapids, MI 49546 USA

ABSTRACT.—We used banding data to investigate dispersal and survival of Red-shouldered Hawks (*Buteo lineatus*) in two study areas in southern Ohio from 1996 to 2018. Of the 2448 nestlings we banded, 167 (6.8%) were encountered (dead or alive) some time after banding. Mean distance from the natal nest at the time of encounter was 31.6 ± 6.2 km (median = 10.0, range = 0.1–568.6 km, $n = 163$); natal dispersal distance averaged 16.0 ± 1.9 km (median = 9.0, range = 1.4–117.1 km, $n = 110$), and was significantly greater for females than for males. Most hawks dispersed <30 km, but 11 hawks (6.7%) dispersed >100 km from their natal nest. Of these long-distance dispersers, nine (82%) were <2 yr old, suggesting that some young birds wander widely prior to breeding. Dispersal distance differed by sex and age at encounter, with dispersal distance negatively correlated with age at encounter, and females dispersing farther (39.8 ± 12.3 km) than males (22.8 ± 9.86 km) and unknown-sex birds (33.9 ± 10.6 km; all $P < 0.05$; means estimated from the logistical regression model). Dispersal direction for all birds followed a uniform distribution ($P > 0.05$); however, dispersal direction of long-distance dispersers was not uniform ($P < 0.05$) but bimodal, with hawks encountered either to the south or to the northeast of the study area. Mean age at recovery was 2.6 ± 0.3 yr (median = 1.5 yr, range = 0.2–10.3 yr). As in other raptor species, apparent annual survival varied between age classes, with young birds (hatch-year and second-year) having lower apparent annual survival (0.49 ± 0.03) than adult birds (0.76 ± 0.03). Our study provides information on dispersal, survival, and causes of mortality of Red-shouldered Hawks, demographic data that are important for evaluating population trends and the sustainability of urban/suburban populations.

KEY WORDS: *Red-shouldered Hawk*; *Buteo lineatus*; circular statistics; dispersal; dispersal distance; mortality; RMark; suburban; survival; urban ecology.

DISPERSIÓN Y SUPERVIVENCIA DE INDIVIDUOS DE *BUTEO LINEATUS* ANILLADOS EN ÁREAS SUBURBANAS DEL SUR DE OHIO, 1996–2018

RESUMEN.—Usamos datos de anillado para investigar la dispersión y supervivencia de *Buteo lineatus* en dos áreas de estudio en el sur de Ohio, desde 1996 hasta 2018. De los 2448 polluelos que anillamos, 167 (6.8%) fueron encontrados (muertos o vivos) algún tiempo después de ser anillados. La distancia media desde el sitio de nacimiento al momento del encuentro fue de 31.6 ± 6.2 km (media = 10.0, rango = 0.1–568.6 km, $n = 163$). La distancia de dispersión desde el sitio de nacimiento promedió 16.0 ± 1.9 km (media = 9.0, rango

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² Email address: cheryldykstra@gmail.com

= 1.4–117.1 km, $n = 110$), y fue significativamente mayor para las hembras que para los machos. La mayoría de los individuos de *B. lineatus* se dispersaron <30 km, pero 11 individuos (6.7%) se dispersaron >100 km desde su lugar de nacimiento. De estos individuos dispersados a grandes distancias, nueve (82%) fueron menores de dos años, lo que sugiere que algunas aves jóvenes deambularon ampliamente antes de reproducirse. La distancia de dispersión varió entre sexos y edades al momento del encuentro, estando la distancia de dispersión negativamente correlacionada con la edad al momento del encuentro, dispersándose las hembras más lejos (39.8 ± 12.3 km) que los machos (22.8 ± 9.9 km) y que las aves de sexo desconocido (33.9 ± 10.6 km; $P < 0.05$ en todos los casos; medias estimadas a partir de un modelo logístico de regresión). La dirección de dispersión para todas las aves siguió una distribución uniforme ($P > 0.05$); sin embargo, la dirección de dispersión de los individuos dispersados a grandes distancias no fue uniforme ($P < 0.05$) sino bimodal, encontrándose individuos ya sea al sur o al noreste del área de estudio. La edad media al momento de la recuperación fue de 2.6 ± 0.3 años (media = 1.5 años, rango = 0.2–10.3 años). Como en otras especies de rapaces, la supervivencia anual aparente varió entre clases de edad, presentando las aves jóvenes (del año de eclosión y del segundo año) una supervivencia anual aparente menor (0.49 ± 0.03) que las aves adultas (0.76 ± 0.03). Nuestro estudio brinda información sobre dispersión, supervivencia y causas de mortalidad de *B. lineatus*, todos datos demográficos que son importantes para evaluar las tendencias poblacionales y la sustentabilidad de las poblaciones urbanas/suburbanas.

[Traducción del equipo editorial]

Natal dispersal, the movement of an animal from its birthplace to the location of its first breeding attempt (Greenwood and Harvey 1982), is an important characteristic of raptor life-history, with ramifications for gene flow and population genetics (Calabuig et al. 2008), demographics (Newton 1979, Katzner et al. 2012) and the selection of habitat for survival and reproduction (Newton and Marquiss 1983). Dispersal may be influenced by habitat fragmentation and urbanization, which can create patches of unsuitable areas interspersed with habitat (Martin et al. 2006) or may affect the type of habitat selected by the dispersing raptor (Katzner et al. 2012). Yet dispersal is poorly understood for many raptor species (Bildstein and Peterjohn 2012).

Many raptors exhibit sex-biased dispersal, in which females typically disperse farther than males (e.g., Peregrine Falcons [*Falco peregrinus*], Katzner et al. 2012, Faccio et al. 2013; Lesser Kestrels [*Falco naumanni*], Serrano et al. 2003; Cooper's Hawks [*Accipiter cooperii*], Mannan et al. 2004, 2007), the typical pattern for birds (Greenwood and Harvey 1982). It has been suggested that shorter dispersal distances are associated with the sex that invests the most in territory establishment and defense (Serrano et al. 2003, Solaro and Sarasola 2012). Kestrels dispersing longer distances have lower survival rates than short-distance dispersers, yet are more likely to colonize an empty territory (Serrano and Tella 2012), suggesting trade-offs in dispersal strategies.

Like dispersal, survival is a critical metric for understanding population dynamics and interpreting population trends in the face of changing environmental and climate conditions (Bildstein and Peterjohn 2012). Survival, not reproductive rate, is the most significant factor affecting lifetime reproductive success among long-lived birds such as raptors (Newton 1989). Survival varies by age class, with young raptors typically having lower annual survival rates than older ones (Lieske et al. 2000, Serrano and Tella 2012, Faccio et al. 2013, Horikoshi et al. 2018), and can also vary with dispersal distance (Bloom et al. 2011, Serrano and Tella 2012), and sex (Jonker et al. 2014, Colchero et al. 2017, Reynolds et al. 2017). Urbanization also might be expected to affect raptor survival due to numerous anthropogenic threats including collisions with vehicles and buildings, electrocution, and poisonings (Hager 2009, Dwyer et al. 2018). Yet in some species, survival in urban areas is high or is similar to that in nonurban areas (Cooper's Hawks, Mannan et al. 2008, Rosenfield et al. 2018; Mississippi Kites [*Ictinia mississippiensis*], Skipper 2013, 2018). Knowledge of a species' dispersal patterns and survival is important for understanding demography and conserving populations in novel environments such as urban landscapes.

The Red-shouldered Hawk (*Buteo lineatus*) is often described as a species that prefers remote regions of mature forest habitat characterized by bottomland riparian zones or other forested areas near water sources (Johnson 1989, Bosakowski et al. 1992, Bosakowski and Smith 1997). However, it has been

increasingly recognized as an adaptable member of many urban/suburban avian communities, particularly in California and the southeastern United States, where it nests in yards, parks, and remnant forests, and even occasionally on buildings (Dykstra et al. 2018).

Despite the species' apparent adaptability, Red-shouldered Hawk population trends appear equivocal in many areas. Breeding Bird Survey (BBS) results indicate stable or possibly slightly increasing trends in many regions between 2005 and 2015 (Sauer et al. 2017), but like many raptors, Red-shouldered Hawks are not well-surveyed by BBS methods (Dykstra et al. 2008). Meta-analysis of autumn migration counts revealed stable populations in eastern North America, but unknown trends in the west due to insufficient sample sizes (Bildstein et al. 2008). Recent assessments in southern California suggest a dramatic population decline among urban/suburban populations there, for unknown reasons (Dykstra et al. 2018).

Other than reproductive rate, demographic data for this relatively common species are sparse, and may be important for understanding how this species responds to urbanization and other changes in its environment. In the absence of modern telemetry data, banding data can provide valuable information on critical aspects of its life history including dispersal and survival.

The objectives of our banding study of urban/suburban Red-shouldered Hawks were to (1) investigate sex- and age-based differences in dispersal, (2) evaluate survival rates, and (3) document causes of mortality in an urban/suburban population.

METHODS

Study Areas. We banded nestling Red-shouldered Hawks in Hamilton, Clermont, Butler, and Warren Counties in suburban southwestern Ohio (SWOH hereafter), and in the Hocking Hills (HH hereafter) region of southeastern Ohio, in Hocking, Athens, Perry, and Vinton Counties. In SWOH, suburban development varied from densely populated (residential lots approximately 20 m × 35 m) to sparsely populated (>2.5-ha residential lots and undeveloped private land; Dykstra et al. 2000). Native forests in the SWOH study area are dominated by second-growth oak-hickory (*Quercus* spp. and *Carya* spp.) and beech-maple (*Fagus grandifolia* and *Acer saccharum*) associations, with lowland riparian forests characterized by sycamores (*Platanus occidentalis*)

and beech. We found nests on private land, in yards of residences or in nearby forested areas (Dykstra et al. 2003).

The HH study area, approximately 180 km east of the SWOH study area, is heavily forested with a sparse human population. We found nests in Wayne National Forest, Hocking State Forest, Zaleski State Forest, and associated private lands. The predominant forest type is oak-hickory, but plantations of white pine (*Pinus strobus*) and red pine (*P. resinosa*) are also common. Lowland forests are characterized by sycamores, silver maple (*Acer saccharinum*), beech, and river birch (*Betula nigra*). Proximity of nests to human activities varied widely, with some areas containing residential development, some recreational development such as hiking trails and picnic areas, and some fairly remote (Dykstra et al. 2000).

Banding. We used several techniques to locate Red-shouldered Hawk nests. We searched historical nesting territories known to us from previous work (Dykstra et al. 2000, 2003) and near sites where Red-shouldered Hawks responded to conspecific broadcasts. While traveling in the study area, we sighted some nests from roads, and other nests were reported to us by raptor rehabilitators, landowners, and birders.

We accessed nests using approved climbing techniques when the nestlings were approximately 2–5 wk old, between May and early July each year from 1996 to 2018. We banded the young with US Geological Survey (USGS) bands. We also banded most nestlings in SWOH with colored plastic bands (Haggie Engraving Company, MD, USA) inscribed with individual alphanumeric codes large enough to be read with binoculars or spotting scope.

Band Encounters. Following the USGS Bird Banding Lab (BBL) protocol, we defined a band recovery as a report of a hawk that had died, and a band encounter as any report of a banded hawk, dead or alive. Band encounter data were obtained in several ways, including the typical BBL "Report to the bander." We encountered banded hawks in the course of other fieldwork: we read some bands using a spotting scope or binoculars, and trapped some banded birds using a bal chati trap baited with a house mouse (*Mus musculus*) or European Starling (*Sturnus vulgaris*; Bloom et al. 2007). A local raptor rehabilitation organization, RAPTOR, Inc., reported any banded birds that were admitted injured to their facility. Increasingly in recent years, local photographers and birders reported banded birds through our study website (www.redshoulderedhawkstudy).

com) or shared photos of banded birds on Facebook pages devoted to local birding. We investigated most encounters by contacting the individual who had reported the band to obtain more detailed information, with the result that all encounters were described by a specific location (i.e., street address or intersection) rather than simply the 10-min block. We included encounter data from 1997–August 2018. Nestlings or fledglings encountered in the immediate vicinity of the nest were not included in our dataset.

We used a hand-held GPS unit or Google Earth maps to determine latitude and longitude of banding and encounter locations. We calculated dispersal distance in ArcGIS (NAD 1983, Ohio State Plane South coordinate system) as the distance between the banding and encounter locations. Following Dykstra et al. (2004) and Bloom et al. (2011), we classified hawks that moved >100 km between banding and encounter locations as long-distance dispersers. We also calculated the magnetic compass direction (angle between banding and encounter locations) for each encountered hawk (Veness 2015).

We determined cause of death for recovered birds from the BBL records or by carcass examination, and classified the circumstances of each encounter as (1) found dead with no other information, (2) found dead due to collision with vehicle, (3) found dead due to collision with an airplane, (4) found dead due to electrocution, (5) found dead due to predator, (6) found injured but subsequently died in captivity or was euthanized, (7) found injured and released after treatment, (8) trapped by us in the course of other research and released, (9) observed by us (i.e., color-band read), or (10) photographed by a birder or other member of the public.

We determined sex of some encountered birds by examination of the carcass, observation of behavior (i.e., copulation), presence/absence of a brood patch during breeding season, genetic determination, or by use of a sexing classification tree we developed for nestling Red-shouldered Hawks older than approximately 3 wk old (see Dykstra et al. 2012 for details of genetic determination and classification tree).

We estimated age of hawks at the time of encounter in days or years as appropriate for particular analyses of dispersal, assuming a hatch date of 23 April, the mean hatch date for SWOH 1997–1999 (Dykstra et al. 2004). To make data directly comparable to our earlier analysis of

dispersal (Dykstra et al. 2004), which was based on breeding phenology in our study area, we classified encounters into three categories based on the estimated age of the bird on the encounter date: <298 d, 298–663 d, and >663 d. Young birds <298 d were those encountered before 15 February of the year following the banding year, and thus were not breeding birds. Birds age 298–663 d were in immature plumage or in their first adult plumage prior to the breeding season and thus likely not breeding, although some immature-plumaged individuals do breed (Dykstra et al. 2008). Birds >663 d old were in adult plumage and presumably breeders. We choose 15 February as the cutoff date because most birds in our study area had begun breeding activities such as courtship and nest-building by that date (Dykstra et al. 2001a, 2004). In addition, to estimate survival using a Burnham model (below), we modeled age as time since marking (TSM). For this part of our analysis, we converted age (TSM) to a factor with three levels: juvenile (TSM = 0, encountered in same calendar year as banding, i.e., HY [hatch-year]); immature (TSM = 1, encountered in the calendar year after banding, i.e., SY [second-year]), and adult (TSM >2, i.e., ASY [after-second-year]).

Data Analysis. We present all results as mean $\pm$ 1 SE of mean, median, and range. Because of skewed distributions, we $\log_{10}$ -transformed distance from the natal nest and age at encounter data to meet assumptions of normality.

Dispersal distance and direction. Adult Red-shouldered Hawks in SWOH apparently are year-round residents (Dykstra et al. 2001b, 2004), with small year-round territories (165 ha; Dykstra et al. 2001b); thus we assumed that any encountered bird >663 d old was likely at or near its breeding location, regardless of the season. We further assumed that this location was the first breeding site for any individual >663 d old on the basis of high breeding-site fidelity (46 of 54 records, 85%) and very short breeding dispersal distances (mean = 1.7 km, $n = 8$; C. Dykstra and J. Hays unpubl. data). We used a general linear model to determine whether dispersal distance varied by sex, with age at encounter (in d) as a covariate. We used Rao's spacing test of uniformity in the package circular (Agostinelli and Lund 2017) to test for directionality in dispersal direction of all individuals and of long-distance dispersers separately. We used an analysis of variance for circular data with a likelihood ratio test to

Table 1. Dispersal distance of Red-shouldered Hawks banded as nestlings in southern Ohio and encountered after fledging ($n = 163$). For birds encountered more than one time, only the most recent encounter was included.

SEX	AGE AT ENCOUNTER	STATUS	n	DISTANCE FROM NATAL NEST (km)		
				MEAN $\pm$ SE	MEDIAN	RANGE
Female	<298 d	dead	4	204.2 $\pm$ 108.9	152.5	0.1–511.8
		alive	0			
	298–663 d	dead	6	65.8 $\pm$ 39.5	24.4	7.1–260.5
		alive	1	13.8	13.8	13.8
	>663 d	dead	11	23.8 $\pm$ 3.6	20.9	2.2–47.4
Male	<298 d	alive	25	15.3 $\pm$ 2.7	11.4	1.8–47.1
		dead	4	15.7 $\pm$ 4.9	19.1	1.5–23.2
	298–663 d	alive	3	2.3 $\pm$ 0.6	2.2	1.3–3.3
		dead	5	121.6 $\pm$ 111.7	9.3	7.2–568.6
	>663 d	dead	8	22.2 $\pm$ 12.4	10.7	1.5–107.7
Unknown sex	<298 d	alive	38	12.5 $\pm$ 3.8	4.6	1.4–117.1
		dead	14	69.5 $\pm$ 33.0	10.6	1.9–356.1
	298–663 d	alive	1	8.2	8.2	8.2
		dead	11	42.7 $\pm$ 33.2	5.1	0.6–373.3
	>663 d	alive	3	4.5 $\pm$ 1.8	4.5	1.3–7.6
		dead	16	18.8 $\pm$ 4.4	12.3	1.9–57.8
		alive	12	13.9 $\pm$ 4.1	7.8	1.8–44.2

determine if there were any differences in dispersal direction by sex, age, or survival in separate analyses.

Survival. We used a combined live-recapture dead-recovery model in RMark (Laake 2013) to analyze banding, recapture/resighting, and recovery data of Red-shouldered hawks banded as nestlings. We used a Burnham model to estimate survival (S , probability of surviving a time interval), the probability of being encountered alive (p , recapture probability conditioned on remaining in the sample region), the probability of being found dead and reported (r , recovery), and fidelity (F , fidelity rate: probability of remaining in the sampling region). Because all individuals were banded as nestlings, we did not use age at capture in models. Instead we modeled age as time since marking (TSM; see above). The Burnham model assumes that live encounters only occur in the sampling area while dead encounters occur outside of the sampling area. In our study, hawk bands were large enough for bands to be observed by the public; thus, live encounters could occur outside of the “sampling” area. Therefore, we could not estimate fidelity and so we fixed this parameter ($F = 1$). We first ran models with three age classes (HY, SY, ASY) to reflect TSM; however, due to the small number of encounters and recoveries of juvenile and immature birds (Table 1), not all parameters in the model were estimable (some parameters were singular). We

reran the models with the two younger age classes combined into one (HY/SY). Because we noticed an increasing number of encounters due to reports by photographers using digital cameras (Supplemental Materials, Fig. S1), we included two time periods (1996–2006 and 2007–2018) in models to determine if there were differences in apparent survival and the probability of being encountered alive between periods. We constructed a set of candidate models with an additive effect of time period and age class (TSM) on survival (S), live encounter (p), and dead recovery (r) with fidelity ($F = 1$) fixed. We removed models with non-estimable parameters then compared the remaining models using AIC_c (Burnham and Anderson 2002).

Encounter status. To investigate how dispersal distance and other factors influenced whether birds were found alive or dead, we used a logistic regression with binomial distribution to determine if the probability of being encountered alive (vs. dead) was related to sex, age at encounter, and dispersal distance. We used AIC_c for model selection (Burnham and Anderson 2002).

We determined if there were differences in age at encounter by sex with a general linear model with sex (male, female, and unknown). When differences were found, we used Tukey post hoc tests in package lsmeans (Lenth 2016) to determine which groups

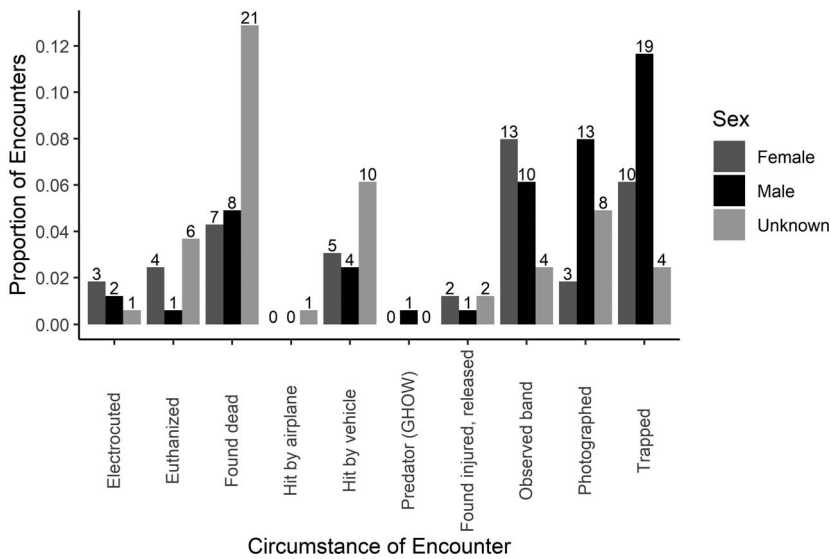


Figure 1. Red-shouldered Hawks banded as nestlings and encountered after banding, by circumstances of encounter and sex. Euthanized birds were found injured and presented to a rehabilitation organization but either died while under treatment or were euthanized due to severity of the injury. Values above bars indicate sample size. Predation event was by a Great Horned Owl (*Bubo virginianus*; GHOW).

differed. We then removed unknown-sex birds and used a logistic regression (binomial distribution) to determine if the probability of being detected alive differed between males and females and by age at encounter.

RESULTS

Between 1996 and 2018, we banded 2448 nestling Red-shouldered Hawks (1824 in the suburban SWOH study area and 624 in the rural HH study area). Of these, 163 (8.9%) from SWOH and 4 (0.64%) from HH were encountered some time after banding, for a total of 167 (6.8%). Encounter records of four SWOH birds lacked precise encounter location data and we removed these from the dataset, leaving a sample size of 163. Seventy-four hawks were either dead or died during rehabilitation and 89 were encountered alive, 21 of them on multiple occasions, most of which were re-observations of color-banded birds at the same breeding territory in a subsequent year. For all analyses other than survival using RMark (below), we included only the most recent encounter.

Most birds were trapped, photographed, observed, or simply found dead (Fig. 1). The cause of death was known for 38 birds, with half ($n = 19$) due to collision with a vehicle. Eleven birds (29%) were

found injured but then died or were euthanized while in rehabilitation, while six (16%) were electrocuted, one collided with an airplane (3%) and one was killed by a predator, a Great Horned Owl (*Bubo virginianus*).

Dispersal from the Natal Nest. For all hawks, regardless of age, the mean distance from the natal nest at the time of encounter was 31.6 ± 6.2 km (median = 10.0, range = 0.1–568.6, $n = 163$; Table 1). Most ($n = 138$; 85%) hawks dispersed <30 km, but 11 hawks (6.7%) dispersed >100 km from their natal nest (Fig. 2, 3). Of these long-distance dispersers, nine (82%) were ≤ 663 d old and thus were nonbreeders or likely nonbreeders. Four of the young long-distance dispersers were found north of our SWOH study area in summer (late June–August), four were south of SWOH in winter (November–February) and one was north of SWOH in winter (Appendix 1, Fig. 2).

Natal dispersal distance averaged 16.0 ± 1.9 km (median = 9.0, range = 1.4–117.1 km, $n = 110$). Natal dispersal was longer for females (17.9 ± 2.2 km, median = 18.8, range = 1.8–47.4, $n = 36$) than for males (14.2 ± 3.8 km, median = 5.5, range = 1.4–117.1, $n = 46$; t -test on log-transformed values, $t = 2.637$, $P = 0.010$; Table 1).

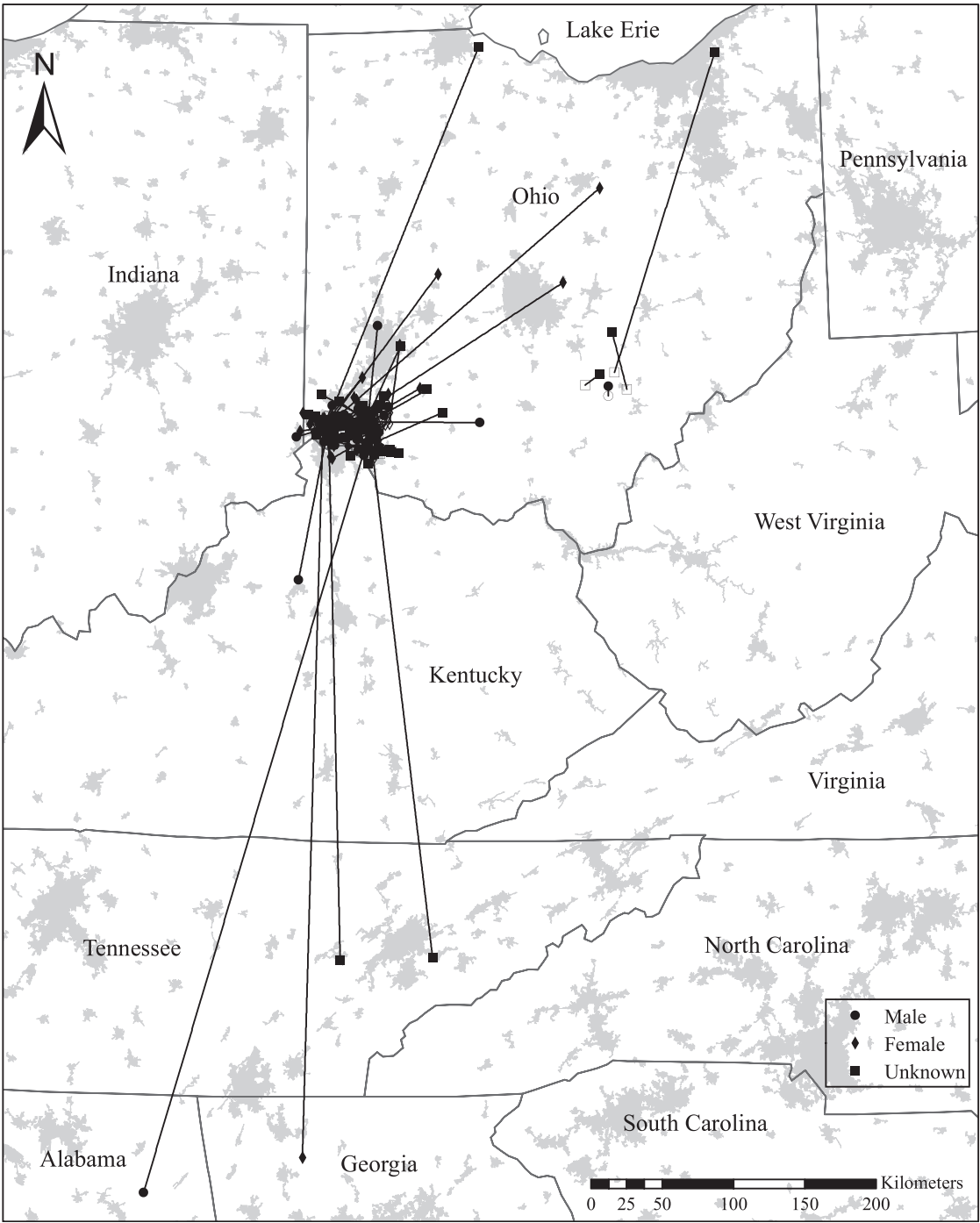


Figure 2. Dispersal of 163 Red-shouldered Hawks banded as nestlings in southern Ohio, USA, 1996–2018. Lines join natal sites and encounter locations. Banding sites are shown as open symbols; encounter sites as filled symbols. Gray shading indicates urban and suburban areas.

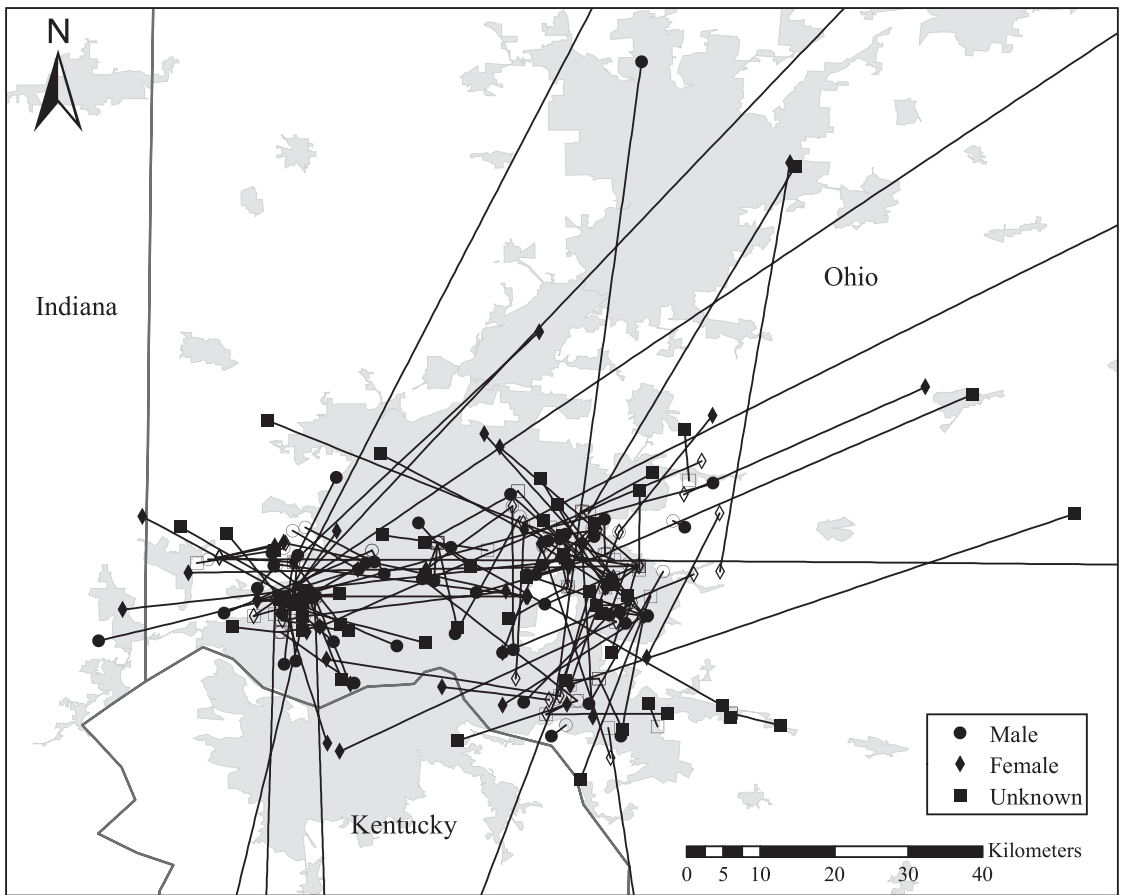


Figure 3. Dispersal of Red-shouldered Hawks banded as nestlings in southwestern Ohio, USA, 1996–2018 (detail of Fig. 2). Lines join natal sites and encounter locations. Banding sites are shown as open symbols; encounter sites as filled symbols. Gray shading indicates urban and suburban areas.

The best model indicated that dispersal distance differed by sex and age at encounter ($F_{3,159} = 5.5$, $P = 0.001$; $AIC_c = 286.0$, weight = 0.83). Dispersal distance was negatively correlated with age at encounter ($t = -2.91$, $P = 0.004$). Females dispersed farther (39.8 ± 12.3 km) than males (22.8 ± 9.9 km; $t = -2.99$, $P = 0.003$) and unknown-sex birds (33.9 ± 10.6 km, $t = -2.03$, $P = 0.04$; all means estimated from the model with sex and age at encounter).

Dispersal direction was uniform (Rao's spacing test of uniformity test statistic = 129.11, $P > 0.05$; Fig. 4a), and dispersal direction did not vary by sex ($\chi^2 = 1.02$, $P = 0.60$), age at encounter ($\chi^2 = 2.01$, $P = 0.37$), or survival ($\chi^2 = 0.0002$, $P = 0.99$). However, dispersal direction of long-distance dispersers did not follow a uniform distribution (Rao's spacing test of unifor-

mity test statistic = 200.31, $P < 0.05$) but instead appeared to be bimodal, with hawks encountered either to the south or to the northeast of the study area (Fig. 4b).

Survival. Mean age at recovery was 2.6 ± 0.3 yr (median = 1.5 yr, range = 0.2–10.3 yr, $n = 79$ birds, including the five found injured, then rehabilitated and released). For all further analysis involving hawk status (alive/dead) at encounter, we classified the birds found injured, rehabilitated, and then eventually released ($n = 5$) as dead rather than alive. These birds were injured severely enough that they could be captured by hand on the ground, and would likely have died had humans not intervened.

Apparent survival. The AIC_c -selected survival model included survival (S) as an effect of age category

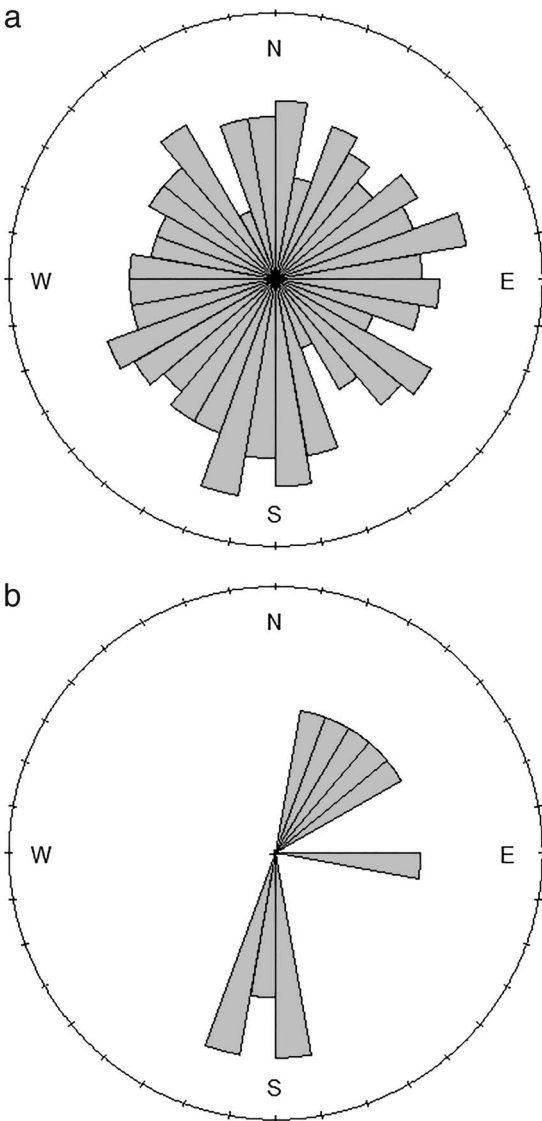


Figure 4. Dispersal direction for Red-shouldered Hawks banded as nestlings in southern Ohio: (a) all dispersing individuals ($n = 163$), (b) long-distance dispersers only ($n = 11$). Each bar in the circular histogram represents 10° and bar lengths are proportional to the number of observations (in each graph).

(TSM), encounter probability (p) as an additive effect of time period and age category (HY/SY vs. adult), recovery (r) as an effect of age category, and fidelity as a fixed effect ($AIC_c = 2397.25$, weight = 0.96, Appendix 2). Apparent annual survival varied between age categories, with the HY/SY birds having

lower annual survival (0.49 ± 0.03) than adult birds (0.76 ± 0.03).

Encounter probability was greater in the second half of our study (2007–2018) compared to the first (1996–2006) and greater in adults compared to HY/SY birds (Supplemental Materials, Fig. S2). Increased probability of being encountered alive was likely related to increased encounters due to photographers (Supplemental Materials, Fig. S1). Recovery probability also increased with age class (HY/SY: 0.02 ± 0.003 ; Adults: 0.12 ± 0.03).

Probability of being encountered alive. The best logistic regression model of the probability of being alive (vs. dead) at encounter included age (in yr) at encounter, sex (male, female, unknown) and dispersal distance (km) and explained 20.3% of the variability in the model. The probability of a hawk being encountered alive increased 21.7% per yr ($z = 2.82$, $P = 0.005$), and decreased 1.6% per km dispersed ($z = -1.92$, $P = 0.055$). Females and males did not differ in their probability of being encountered alive ($z = 1.44$, $P = 0.15$) but unknown-sex birds had a lower probability of being encountered alive ($z = -2.22$, $P = 0.03$) when dispersal distance and age were included in the models (Fig. 5).

DISCUSSION

Dispersal. Red-shouldered Hawks banded as nestlings in our study generally dispersed short distances, but a few birds, mostly young, were found much farther from their natal nests. The dispersal distance, with a mean of 31.6 km and median of 10.0 km, was similar to that we reported earlier from a smaller sample of this same population (mean of 38.5 km, median of 12.3 km, $n = 43$, Dykstra et al. 2004). Red-shouldered Hawks banded as nestlings in southern California, where the species is also resident, similarly dispersed only 55 km on average (median = 24 km, $n = 119$; Bloom et al. 2011). The California study differed slightly from ours in methodology: Bloom and colleagues included only birds that died (recoveries), whereas we included birds encountered alive or dead, which may have affected the means. Our data support this explanation, in that birds found dead were farther from their natal sites than were birds encountered alive (Table 1). Study-area bias resulting in underestimation of dispersal distance is not uncommon in dispersal studies because short-distance dispersers are more likely to be detected than long-distance dispersers (Koenig et al. 1996), and birds are more likely to be found and reported in areas of high human density than in

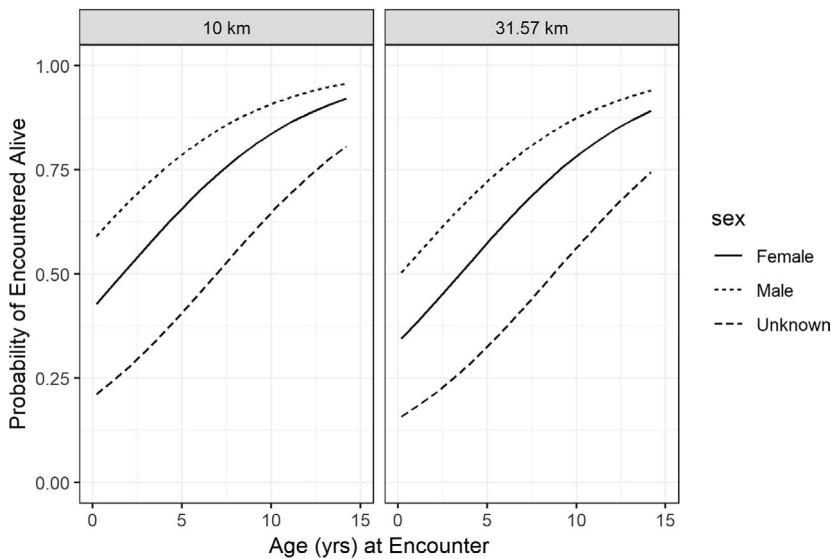


Figure 5. Probability of Red-shouldered Hawks banded as nestlings being encountered alive (vs. dead) by sex and age at encounter (yr), from the logistic regression model of encounter status (alive = 1, dead = 0), sex (female, male, unknown), and dispersal distance. Estimates shown at the median (10 km) and mean (31.57 km) dispersal distances.

rural areas (Bildstein and Peterjohn 2012). This was obvious from our very low encounter rate for the rural Hocking Hills region (0.6%) compared to the rate for suburban SWOH (8.9%), although some of this disparity may be attributed to the use of color bands in SWOH and not in HH. Nonetheless, we believe that our estimates of local dispersal were likely correct, as we found few birds that dispersed across the study area from the west side to the east side or vice versa, a distance of 30–50 km, despite similar research effort and human population density in both areas.

Natal dispersal distance in our study averaged 16 km (median = 9.0 km), similar to the 18 km we determined earlier from a much smaller sample size ($n = 20$ birds; Dykstra et al. 2004), and the 17 km reported by Jacobs and Jacobs (2002) for a sample of 11 birds in Wisconsin. In the current study, we were able to sex sufficient numbers of males and females for statistical comparison, in part due to a morphological method for sexing some nestlings (Dykstra et al. 2012). Female Red-shouldered Hawks dispersed farther than males, both in terms of natal dispersal and overall dispersal. Typically, female raptors disperse farther than males (Greenwood and Harvey 1982), a pattern documented for Peregrine Falcons (Katzner et al. 2012, Faccio et al. 2013), Lesser Kestrels (Serrano et al. 2003), Bald Eagles (*Haliaeetus*

leucocephalus; Millsap et al. 2014), Northern Goshawks (*Accipiter gentilis*; Byholm et al. 2003), Cooper's Hawks (Mannan et al. 2004, 2007), Eurasian Sparrowhawks (*Accipiter nisus*; Newton and Marquiss 1983), and White-tailed Eagles (*Haliaeetus albicilla*; Whitfield et al. 2009), among others. Species with greater degrees of size dimorphism may be more likely to show sex-biased dispersal distances, with females dispersing farther than males (Soutullo et al. 2006b). Researchers have proposed that shorter dispersal distances are associated with the sex that invests the most in territory occupancy and defense (Serrano et al. 2003, Solaro and Sarasola 2012). Males may also benefit more from philopatry, as familiarity with the local environment may improve hunting success and males do most of the breeding-season foraging in many raptor species, while females often primarily care for the young (Byholm et al. 2003, Dykstra et al. 2008). Our anecdotal observations may support these hypotheses for Red-shouldered Hawks. For example, in eight documented cases of breeding dispersal (defined as the movement from one breeding site to another), six dispersers were females and two were males (mean distance between breeding sites was 1.7 km; C. Dykstra and J. Hays unpubl. data), suggesting that females may be less attached to their territories. In contrast, during our call-playback surveys at occu-

pied territories, both male and female often responded together, suggesting similar levels of investment in nest defense (C. Dykstra unpubl. data). We note that the resident status of these birds may influence their territoriality, and that their sexual size dimorphism is only moderate, with mean masses averaging 768 g for females and 573 g for males (Dykstra et al. 2012). These caveats suggest that sex-biased difference in dispersal distance might be expected to be relatively small, as indeed it was (female natal dispersal distance averaged 26% longer than for males).

A small percentage of Red-shouldered Hawks dispersed >100 km from their natal area and most of these long-distance dispersers were young birds that had not reached typical breeding age. These young birds, representing 17% (9 of 53) of the birds ≤ 663 d old encountered in our study, were found primarily north of our study area in the summer, and south of our study area in winter, possibly suggesting some seasonality of their movements and indicating that some segments of this resident population may be more mobile than previously thought. Although southward movement in winter may describe a typical migration pattern, the northward movement seems to indicate that some young Red-shouldered Hawks may wander fairly widely prior to reaching breeding age, as do some other raptors (Soutullo et al. 2006a, 2006b, Mojica et al. 2008, Whitfield et al. 2009, Faccio et al. 2013, Morrison and Baird 2016, Watson et al. 2019). Three of the four young birds found well to the north in summer were recovered in August of their first year, just a few weeks after fledging. Similarly, radio-tagged young Red-shouldered Hawks in southern California remained in their natal areas for 4 wk after fledging, but then apparently dispersed rapidly, with only a few remaining in their natal region by 12 wk after fledging (Bloom et al. 2011). In southern California, long-distance dispersers found >100 km from their natal areas made up 8.4% of the recoveries and were also primarily young birds (9 of 10) that had not reached breeding age; some of these dispersed outside of the species' known breeding range and were thus considered vagrants (Bloom et al. 2011). Interestingly, most of the long-distance dispersers, including six of the eight individuals that were <1 yr old, moved northward from southern California (Bloom et al. 2011).

Post-fledging northward movement is also known from a few other species of raptors, including Bald Eagles (Broley 1947, Wood et al. 1998, Millsap et al.

2004, Linthicum et al. 2007, Mojica et al. 2008, Wood 2009, Hunt et al. 2009), Red-tailed Hawks (*Buteo jamaicensis*; Bloom et al. 2015), Ferruginous Hawks (*Buteo regalis*; Watson et al. 2019), and Lesser Kestrels (Olea 2001). Improved foraging prospects may have favored such northward movements (Wood et al. 1998, Linthicum et al. 2007, Olea 2001, Bloom et al. 2015).

Red-shouldered Hawks' ability to inhabit urban/suburban areas, in Ohio, California, and elsewhere throughout the species' range (Dykstra et al. 2018), combined with their capacity for long-distance dispersal, suggests that the species has the potential to colonize new areas (Bloom et al. 2011, Dykstra et al. 2018). This aptitude likely has survival value in the face of rapidly urbanizing landscapes throughout North America.

Survival. We used both recovery and recapture/resighting data to estimate an apparent annual survival rate of 0.49 for young birds (HY and SY together), and 0.76 for adult birds. The adult survival rate was within the typical range of adult survival rates of other raptor species, 0.61–0.84 (Cooper's Hawks, Rosenfield et al. 2018; Mississippi Kites, Skipper 2018; New Zealand Falcons [*Falco novaeseelandiae*], Horikoshi et al. 2018; Northern Goshawks, Reynolds et al. 2017; Common Buzzards [*Buteo buteo*], Jonker et al. 2014). Lower survival rates during the first year of life are typical for raptors (Newton 1979), including Red-shouldered Hawks. Henny (1972) used recovery data for Red-shouldered Hawks banded as nestlings from 1924–1945 to calculate a mortality rate of 0.58 during the first year, and 0.31 for all subsequent years, and similar rates during 1946–1965. In our earlier analysis, based on cumulative exponential distribution (CED) analysis of recovery data only, we estimated that 50% of SWOH Red-shouldered Hawks had died by age 1.2 yr, 75% by 2.4 yr, and 95% by 5.2 yr (Dykstra et al. 2004), which was similar to results for a small sample of birds banded in northern Ohio. Mean age at recovery in the current study was 2.6 yr (median = 1.5 yr), which was similar to the mean of 2.4 yr (median = 1.4 yr) reported earlier for Red-shouldered Hawks banded as nestlings and recovered (1945–2005, BBL unpubl. data, reported in Dykstra et al. 2008).

Raptors that disperse farther may have lower survival (Bloom et al. 2015) or lower reproductive success (Newton and Marquiss 1983, Forero et al. 2002) than those that disperse shorter distances. In our study, 9 of 11 long-distance dispersers were

young birds ≤ 663 d old, and all were found dead or had severe injuries that resulted in death (Appendix 1). Similarly, Red-shouldered Hawks that dispersed long distances from southern California were mostly young birds, and had lower survival than short-distance dispersers (Bloom et al. 2011). In our overall regression model, age, sex, and dispersal distance influenced the probability of being encountered alive (vs. dead), with dispersal distance negatively related to probability of being encountered alive. This result agrees with previous findings for other raptor species. Among Peregrine Falcons, first-year birds both dispersed the farthest and had the highest mortality rate, although a relationship was not detected statistically, as survival was significantly influenced only by age (Faccio et al. 2013). Long-distance dispersing likely incurs greater risk than shorter dispersals due to the hazards of travel, including unfamiliarity with the landscape or higher risk of predation (Newton and Marquiss 1983), and these risks may explain higher mortality.

Causes of Mortality. Causes of mortality documented in our study were typical for raptors in urban environments. Collisions are the most common cause of raptor mortality in urban landscapes, albeit with the caveat that birds injured or killed near roads and buildings may be more likely to be seen than those killed away from areas humans frequent (Hager 2009, Dwyer et al. 2018). Collisions with vehicles (50%) and planes (3%) were responsible for most mortality among Ohio Red-shouldered Hawks for whom cause of death was known. Electrocutions, the second-most important source of mortality for urban raptors (Dwyer et al. 2018), claimed another 16%. Collisions with buildings, vehicles, and utility lines were responsible for injuries to 81% of the Peregrine Falcons admitted for treatment (Sweeney et al. 1997) and most mortalities for which cause of death of urban peregrines was known (Katzner et al. 2012, Faccio et al. 2013), as well as 13% of mortalities of urban Lesser Kestrels in Spain (Tella et al. 1996). Electrocution caused most mortalities of urban Harris's Hawks (*Parabuteo unicinctus*; Dawson and Mannan 1995, Dwyer 2006, Dwyer and Mannan 2007, Boal and Dwyer 2018) and is a significant threat to population conservation (Boal and Dwyer 2018). Electrocution and collisions with vehicles caused most deaths among PTT-marked suburban Bald Eagles in Florida, resulting in first-year mortality of suburban birds that exceeded that of rural birds (Millsap et al. 2004).

Poisoning, particularly by anticoagulant rodenticides, is an important concern for urban raptors. We documented no poisonings during our study; however, we note that outdoor poison bait boxes are present in our study area (C. Dykstra unpubl. data) and that no hawk carcasses were submitted for chemical analysis. Anticoagulant exposure is common in some raptors, affecting 75–100% of individuals (Albert et al. 2010, Dwyer et al. 2018), and is likely most significant for Red-shouldered Hawks in urban/industrial situations, or at southern latitudes where rodent pests and rodenticide use are more prevalent. The number of occupied territories in southern California has declined dramatically over the last decade; although extended drought may have contributed, anecdotal evidence suggests that rodenticide poisoning or West Nile Virus may also have played a role (Dykstra et al. 2018).

The only clearly non-anthropogenic source of mortality of SWOH Red-shouldered Hawks was predation by Great Horned Owls, represented in this study by a carcass we found in an owl nest occupied by two owlets. Video-camera monitoring of nests in our study area revealed one Great Horned Owl predation of an incubating female and numerous predations of nestlings (Miller et al. 2015). Great Horned Owls are abundant in our SWOH study area (Holt 1996), and the fragmented landscape and abundant prey of suburban environments may promote increased populations of these generalist predators, relative to rural forested regions (Chace and Walsh 2006).

Conclusions. Our study provides baseline data on dispersal, survival, and causes of mortality of suburban Red-shouldered Hawks. The ability of this species to use urban/suburban landscapes and its potential for relatively long-distance dispersal in at least one component of the population suggest that it may fare well in the face of increasing urbanization. However, the wide range of urban/suburban environments, influenced variously by native habitat, prey base, pollution, and other factors, makes it likely that Red-shouldered Hawk populations in different locations will have different ecologies and population trends (Dykstra 2018). Future studies should focus on elucidating factors that affect demographic rates in this population and elsewhere, particularly in little-studied parts of the species' range.

SUPPLEMENTAL MATERIALS (available online). Figure S1: Encounter rate trends for Red-shouldered Hawks banded as nestlings in southern Ohio. Figure

S2: Probability of being encountered alive for Red-shouldered Hawks banded as nestlings by age category and time period.

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Appendix 1. Long-distance dispersal (>100 km) by Red-shouldered Hawks banded as nestlings in southern Ohio (SWOH = southwestern Ohio suburban study area; HH = Hocking Hills rural study area). All birds hit by vehicles were dead or were euthanized in captivity due to severity of the injury. In two cases where the month of encounter was known but exact date was not, we assumed an encounter date of the 15th of the month for analysis.

BAND NO.	STUDY AREA	SEX	CIRCUMSTANCES OF ENCOUNTER		BANDING DATE	ENCOUNTER DATE	ENCOUNTER LATITUDE (DEGREES)		ENCOUNTER LONGITUDE (DEGREES)	ENCOUNTER STATE	AGE AT ENCOUNTER (yr)	DISPERSAL DISTANCE (km)	DISPERSAL DIRECTION (DEGREES)
			ENCOUNTER										
2206-20464	SWOH	M	Hit by vehicle		23 May 2000	5 Nov 2002	38.25068°N		84.8524°W	KY	2.54	107.7	190.7
1156-11923	SWOH	M	Photographed		25 May 2012	8 Jan 2016	39.24457°N		83.3881°W	OH	3.71	117.1	90.1
2206-52993	SWOH	F	Found dead		10 May 2000	12 Jan 2001	40.18465°N		83.7194°W	OH	0.72	135.1	35.9
1156-14611	SWOH	F	Hit by vehicle		18 May 2014	18 Aug 2014	40.12287°N		82.6916°W	OH	0.32	169.9	56.8
1156-00242	HH	U	Found dead		25 May 2013	5 Aug 2013	41.55197°N		81.3875°W	OH	0.28	235.1	18.5
2206-43364	SWOH	F	Hit by vehicle		20 May 1997	27 Jun 1998	40.71417°N		82.3768°W	OH	1.18	260.5	48.5
2206-82872	SWOH	U	Found dead		27 May 2008	10 Aug 2008	41.61567°N		83.3683°W	OH	0.30	288.3	21.6
1156-04879	SWOH	U	Found dead		28 May 2011	Dec 2011	35.86352°N		83.7923°W	TN	0.65	356.1	173.2
816-04565	SWOH	U	Found dead		13 May 2003	15 Nov 2004	35.84977°N		84.5096°W	TN	1.57	373.3	178.5
2206-64532	SWOH	F	Hit by vehicle		24 May 2001	21 Dec 2001	34.60175°N		84.7937°W	GA	0.66	511.8	181.3
2206-82855	SWOH	M	Hit by vehicle		22 May 2008	Feb 2009	34.36832°N		86.0014°W	AL	0.82	568.6	196.5

Appendix 2. Models of apparent survival of Red-shouldered Hawks banded as nestlings. Burnham model of live encounters and dead recoveries was used to estimate survival (*S*), encounter probability (*p*), recovery probability (*r*) and fidelity (*F*) as a function of age category (HY/SY vs. adult) and time period (1996–2006, 2007–2018).

MODEL	PARAMETERS	AIC _c	ΔAIC	WEIGHT	DEVIANCE
S(~age.group)p(~time.bin + age.group)r(~age.group)F(~1)	7	2397.25	0	0.960	644.023
S(~age.group)p(~age.group)r(~age.group)F(~1)	6	2403.62	6.370	0.040	652.404
S(~age.group)p(~time.bin + age.group)r(~1)F(~1)	6	2419.15	21.900	0.000 ^a	667.934
S(~time.bin + age.group)p(~time.bin + age.group)r(~1)F(~1)	7	2420.31	23.062	0.000	667.085
S(~age.group)p(~time.bin)r(~age.group)F(~1)	6	2425.37	28.117	0.000	674.150
S(~age.group)p(~age.group)r(~1)F(~1)	5	2427.14	29.894	0.000	677.937
S(~age.group)p(~time.bin)r(~1)F(~1)	5	2433.58	36.332	0.000	684.375
S(~1)p(~time.bin)r(~1)F(~1)	4	2435.04	37.793	0.000	687.844
S(~time.bin)p(~time.bin)r(~1)F(~1)	5	2436.59	39.343	0.000	687.386
S(~1)p(~time.bin)r(~time.bin)F(~1)	5	2436.60	39.351	0.000	687.394
S(~time.bin)p(~time.bin)r(~time.bin)F(~1)	6	2438.34	41.087	0.000	687.121
S(~age.group)p(~1)r(~1)F(~1)	4	2444.30	47.053	0.000	697.104
S(~1)p(~1)r(~1)F(~1) ^b	4	2448.66	51.416	0.000	701.467

^a The weight of the third and following models was <0.0001; value shown is rounded.

^b Null model.