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RESEARCH ARTICLE

Demography and metapopulation dynamics of an urban Cooper's Hawk subpopulation

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ABSTRACT

Cooper's Hawks (*Accipiter cooperii*) have been extending their breeding range into urban areas, prompting questions about the relative importance of cities to the demography and conservation of these raptors. A key unanswered question is how urban subpopulations interact with their precedent exurban subpopulations. Two general models have been proposed to describe relationships among subpopulations in a metapopulation: (1) source–sink, where immigrants from sources sustain sinks; and (2) balanced dispersal, where dispersal is proportionally equal among subpopulations. I evaluated whether either of these models predict metapopulation dynamics of urban and exurban Cooper's Hawks in central New Mexico using demographic data in a Bayesian integrated population model. All urban female Cooper's Hawks began breeding in their first year; 69% settled at nests in the urban subpopulation and 31% emigrated and settled in an exurban subpopulation. The high rate of female emigration was likely because of a shortage of breeding urban males, caused by a 1 yr delay in male age-at-first-breeding. Emigration exceeded immigration by nearly 30%, making a balanced-dispersal model implausible. Although the urban subpopulation was a source, the primary recipient subpopulation was not a sink; urban emigrants appeared to have a competitive advantage obtaining exurban nest sites. High urban winter prey abundance supported year-long residency among urban female Cooper's Hawks, whereas nearly all exurban females migrated. Resident urban females that emigrated settled on exurban nesting territories before migrants returned, and thus without direct competition from them. Previous metapopulation models do not incorporate the concept that differences in dispersal behavior between subpopulations can drive dispersal dynamics in a metapopulation. These findings provide further evidence that patch dynamics in a metapopulation can be complex, and may be governed by factors other than just demographic rates and connectivity.

Keywords: Accipiter cooperii, balanced dispersal model, Bayesian integrated population model, Cooper's Hawk, metapopulation dynamics, source–sink model, urban wildlife

Demografía y dinámica metapoblacional de una subpoblación urbana de *Accipiter cooperii*

RESUMEN

La especie *Accipiter cooperii* ha estado extendiendo su rango reproductivo a áreas urbanas, generando preguntas sobre la importancia relativa de las ciudades para la demografía y la conservación de esta rapaz. Una pregunta clave sin respuesta es cómo las subpoblaciones urbanas interactúan con sus subpoblaciones precedentes suburbanas. Dos modelos generales han sido propuestos para describir las relaciones entre las subpoblaciones en una metapoblación: (1) fuente-sumidero, donde los inmigrantes desde las fuentes mantienen los sumideros; y (2) dispersión balanceada, donde la dispersión es proporcionalmente igual entre las subpoblaciones. Evalué si alguno de estos modelos predice la dinámica metapoblacional urbana y suburbana de *A. cooperii* en el centro de Nuevo México usando datos demográficos en un modelo poblacional integrado bayesiano. Todas las hembras urbanas de *A. cooperii* comenzaron criando en su primer año; 69% se establecieron en nidos en la subpoblación urbana y 31% emigraron y se establecieron en una subpoblación suburbana. La alta tasa de emigración de hembras se debió probablemente a una escasez de machos reproductivos urbanos, causada por un desfasaje de un año en la edad de los machos del primer año reproductivo. La emigración excedió la inmigración por aproximadamente 30%, haciendo que el modelo de dispersión balanceada sea inviable. Aunque la subpoblación urbana fue una fuente, la principal subpoblación receptora no fue un sumidero; los emigrantes urbanos parecieron tener una ventaja competitiva para obtener los sitios de anidación suburbanos. La alta abundancia urbana de presas en invierno sostuvo el comportamiento de residencia de las hembras urbanas de *A. cooperii* a lo largo de todo el año, mientras que casi todas las hembras suburbanas migraron. Las hembras residentes urbanas que emigraron se establecieron en territorios de anidación suburbanos antes del regreso de los migrantes, y por ende no tuvieron competencia directa de su parte. Los modelos metapoblacionales previos no incorporan el concepto de que diferencias en el comportamiento de dispersión entre subpoblaciones pueden ocasionar dinámicas de dispersión en una metapoblación. Estos hallazgos brindan evidencia adicional de que la dinámica de parches en una metapoblación puede ser compleja y puede estar gobernada por otros factores que no sean solo las tasas demográficas y la conectividad.

Palabras clave: Accipiter cooperii, dinámica metapoblacional, modelo de dispersión balanceada, modelo fuente-sumidero, modelo poblacional integrado bayesiano, vida silvestre urbana

INTRODUCTION

Metapopulation theory predicts that, in heterogeneous landscapes, individuals are distributed among habitat patches of varying quality, and that the population dynamics of a species is determined by the demographic characteristics of, and interaction among, the subpopulations occupying the various patches (Hanski 1998, Donahue et al. 2003). Two general models have been proposed to describe the demographic relationships among subpopulations (Diffendorfer 1998). The source–sink model presumes subpopulations occupying high-quality habitat patches function as sources while those in low-quality habitats become sinks or traps, with the overall outcome that sinks are maintained by immigrants from sources (Pulliam 1988). The balanced dispersal model presumes immigration is proportional to carrying capacity between subpopulations, such that no patches are sources or sinks (McPeek and Holt 1994, Doncaster et al. 1997). Urban areas and surrounding rural lands constitute a stark example of heterogeneous habitats where differences in demographic rates and carrying capacity might be expected, and as such, offer an ideal opportunity to test between the source–sink and balanced dispersal hypotheses.

Urban habitats can be sources or sinks (Harris and Smith 1987, Vierling 2000, Balogh et al. 2011). One group of birds that does well in urban habitats are raptors, especially avivores (Sodhi et al. 1992, Kauffman et al. 2003, Millsap et al. 2004, Mannan et al. 2008, Rutz 2008, Kunca and Yosef 2016). Despite much study of birds in urban ecosystems, little is known about the metapopulation dynamics of urban and surrounding exurban populations for any avian species (Marzluff et al. 2001). Urban avivores represent an ideal study system to explore such metapopulation dynamics.

If natal dispersal from urban subpopulations follows the balanced dispersal model, immigration and emigration rates into and out of urban subpopulations should be equal (Doncaster et al. 1997, Diffendorfer 1998, Tattersall et al. 2004). Under this model annual rates of population change (λ) would be explained by a combination of philopatry and an equal contribution and debit of immigrants and emigrants. Under the source–sink model, λ for the urban subpopulation would reflect the contribution of philopatry and an unbalanced combination of immigration and emigration, with more immigrants than emigrants if the urban subpopulation was a net importer (i.e. a sink), and more emigrants than immigrants if it was a net exporter (i.e. a source).

Testing source–sink and balanced dispersal models has proven difficult because few studies have estimates of all relevant demographic rates (Diffendorfer 1998). Here, I use data for female Cooper's Hawks (*Accipiter cooperii*) in and around Albuquerque, New Mexico, USA, to estimate which model best explains interactions between an urban and surrounding mostly exurban subpopulations. Diffendorfer (1998) predicted that vagile species with the capacity to assess the quality of many habitat patches should exhibit balanced dispersal. Cooper's Hawks are highly mobile, thus based on Diffendorfer's (1998) prediction they should demonstrate metapopulation dynamics consistent with balanced dispersal. Conversely, given the potential for rapid population growth by many urban avivores, it is plausible Cooper's Hawks exhibit source–sink dynamics, as suggested by Mannan et al. (2008).

I used analytical methods of Abadi et al. (2010a,b) and data from this study to parameterize an integrated population model (IPM) from which I computed (1) differences between annual and pooled estimates of the number of emigrants and immigrants for the urban study area, and (2) the per capita contribution of breeding urban females to the metapopulation following Runge et al. (2006). Under the balanced dispersal model, I expected an equal number of emigrants and immigrants, and a per capita contribution to the metapopulation of $\sim$1 per breeding urban female; under the source–sink model I expected a positive difference in the number of emigrants versus immigrants in the urban subpopulation, and a per capita contribution to the metapopulation of $>$1 per breeding urban female.

METHODS

Study Area

My primary study area was 72 km^2 of the urban zone of northeast Albuquerque, Bernalillo County, New Mexico, USA (35.1107°N, 106.6100°W; Lien et al. 2015). The urban study area was 49% residential, 37% industrial, and 14%

parks and open space. This urban study area was within the Albuquerque subpopulation of the regional Cooper's Hawk metapopulation (Figure 1). Other Cooper's Hawk subpopulations within the natal dispersal range of the Albuquerque subpopulation were (1) riparian forest and associated agricultural fields and orchards along the Rio Grande; (2) conifer woodland in the Sandia, Manzanita, and Manzano mountains; and (3) suburban parts of western Albuquerque and Rio Rancho. I refer to these as the Rio Grande, Mountain, and Rio Rancho subpopulations, respectively (Figure 2).

Data Collection

I conducted this study from February 2011 through August 2015. Each winter I drove the entire urban study area when trees were bare to locate stick-nests in trees, which represented potential Cooper's Hawk nesting territories (terminology follows Millsap et al. 2015). In 2011, the driving survey provided the initial count of nesting territories on the urban study area, whereas in subsequent years it revealed previously overlooked nests that may have been occupied nesting territories the preceding year. In 2011–2014, a random subset of the urban study area was searched independently by another trained observer following a double-observer survey protocol (Nichols et al. 2000) so that I could adjust potential nesting territory counts for imperfect detection.

Each year, 50–60% of the known potential nesting territories were randomly selected to be visited by myself or a colleague 3 times each during incubation, nestling, and pre-dispersal periods. All other potential nesting territories were visited at least once during each period. On each visit, we determined whether the nesting territory was occupied, using playback calls (FoxPro Firestorm caller, FoxPro Inc., Lewiston, Pennsylvania, USA) to aid in detection (Mosher et al. 1990). We determined the age of breeders based on plumage, classifying individuals $\leq$1.25 yr old as juveniles, and those in definitive plumage as adults. We counted the number of young seen on each post-fledging visit, and estimated age of fledglings based on plumage development. In 2012–2015, we determined the sex of fledglings whenever possible on each brood count, but we were unable to obtain sex-specific counts at all nesting territories. Cooper's Hawks can be reliably sexed by measurements (Pyle 2008), and females on the urban study area averaged 1.5 times heavier than males (B. A. Millsap personal observation), thus sexes were usually distinguishable by visual size differences.

I captured and color-banded (ACRAFT Band and Tag, Edmonton, Alberta, Canada) as many breeding adults, fledged young, and overwintering juvenile female Cooper's Hawks as possible. Breeding adults were trapped at nests using a non-releasable Great Horned Owl (*Bubo virginianus*) behind a mist net. Fledged young and overwintering juveniles were trapped using bal-chatri traps with non-protected birds as lures (Bloom et al. 2007). Each year I deployed 15–30 backpack-mounted 1,000-day battery-life VHF radio transmitters (American Wildlife Enterprises Inc., Monticello, Florida, USA) on fledged female Cooper's Hawks from the randomly selected nesting territories; transmitter attachment protocols followed Millsap et al. (2013). I also deployed transmitters on overwintering juveniles trapped on the urban study area. Colleagues and I identified all banded breeding Cooper's Hawks each year. We attempted to locate all radio-tagged hawks once weekly throughout the study. In fall and spring of each year we searched for missing radio-tagged hawks throughout the metapopulation and along the Rio Grande north to Espanola, New Mexico, and south to the Mexican border by aircraft. In 2012 and 2013 we searched north to Taos, New Mexico, and in the Jemez Mountains, but we detected no hawks in these areas and dropped them from subsequent surveys. When a radio-tagged hawk was found, we recorded the location, information on behavior, and, if feeding, the species of prey. Radio-tagged hawks that overwintered outside of the natal dispersal range (46 km) of the urban study area were considered migrants.

I used the information on prey captures by radio-tagged female Cooper's Hawks to determine prey species, as in Millsap et al. (2013). White-winged Doves (*Zenaida asiatica*) were the major prey of Cooper's Hawks during the breeding season (Lien et al. 2015), so I estimated their abundance each April (when most Cooper's Hawks began nesting) at 67 systematic-random points distributed across the urban study area. I used the Breeding Bird Survey protocol (Sauer and Link 2011), except I conducted counts for 5 min, limited counts to birds detected within 100 m of the point, and used a range finder (Nikon Laser 1200S, Nikon, Tokyo, Japan) to measure the distance from the fixed point to each bird detected. In January 2015, I conducted counts of all avian prey species at the 67 urban points as well as at 32 randomly placed points in exurban areas frequented by emigrant radio-tagged female Cooper's Hawks.

Analyses

I conducted analyses using Bayesian methods to facilitate estimating joint likelihoods while fully accounting for uncertainty (Kéry 2010, Hooten and Hobbs 2015). I used the Markov chain Monte Carlo (MCMC) method implemented in WinBUGS (Lunn et al. 2009) through Program R (R Core Team 2015) to estimate posterior distributions of parameters and unknown random variables. For all models, I ran 3 chains for 60,000 iterations each, used the first 10,000 iterations for a burn-in, and after thinning made inferences using 25,002 iterations. I used $\hat{R}$, a measure of stability between chains of equal length in MCMC output, to assess model convergence, with value of

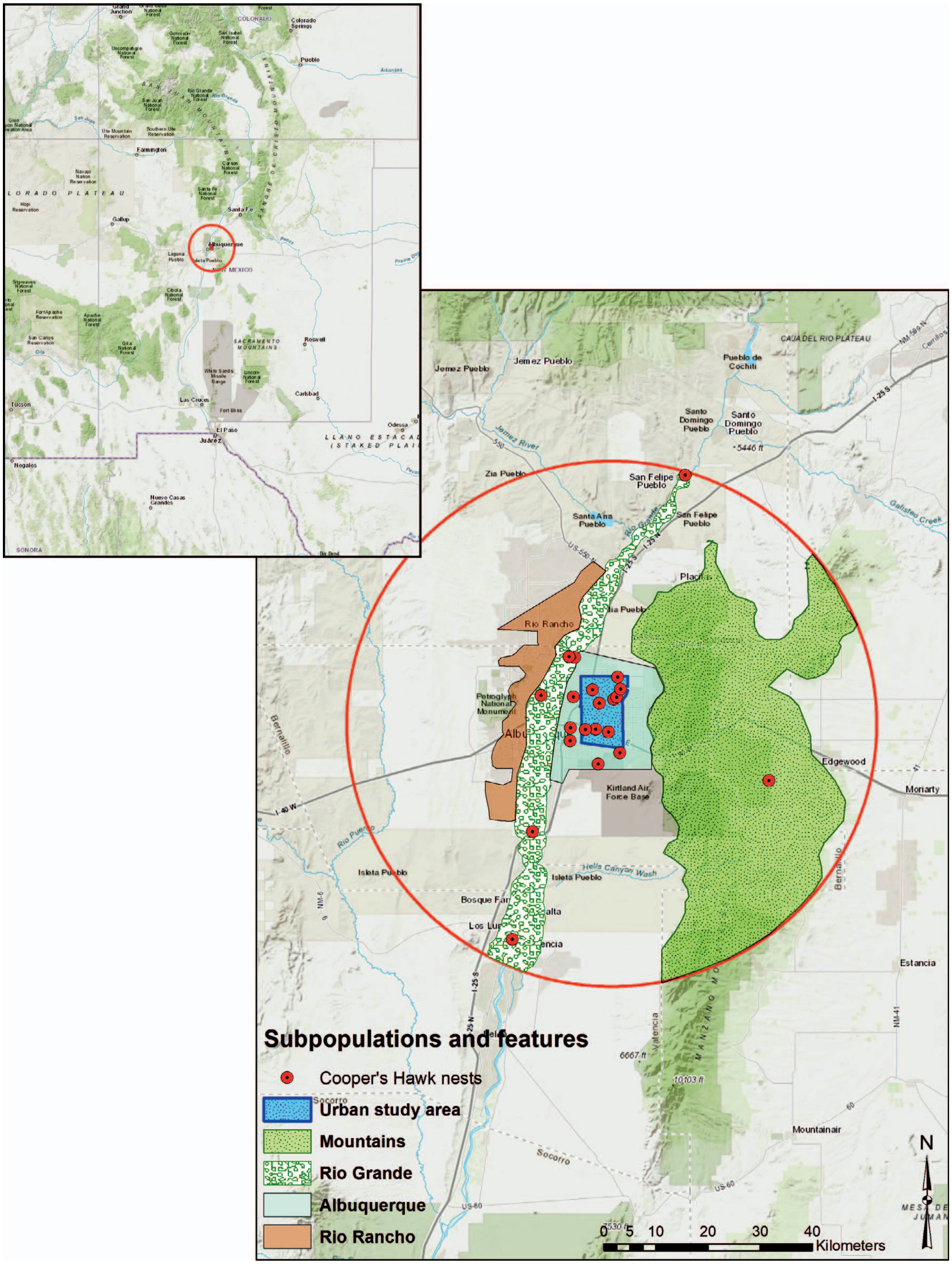

FIGURE 1. Map of Cooper's Hawk subpopulations comprising the central New Mexico, USA, metapopulation. Red dots are nesting territories used by radio-tagged females; the large red circle denotes the maximum natal dispersal distance (46 km). Inset shows the location of the study area relative to the western United States and Mexico. Areas not shaded are grassland and desert scrub not used by Cooper's Hawks for nesting.

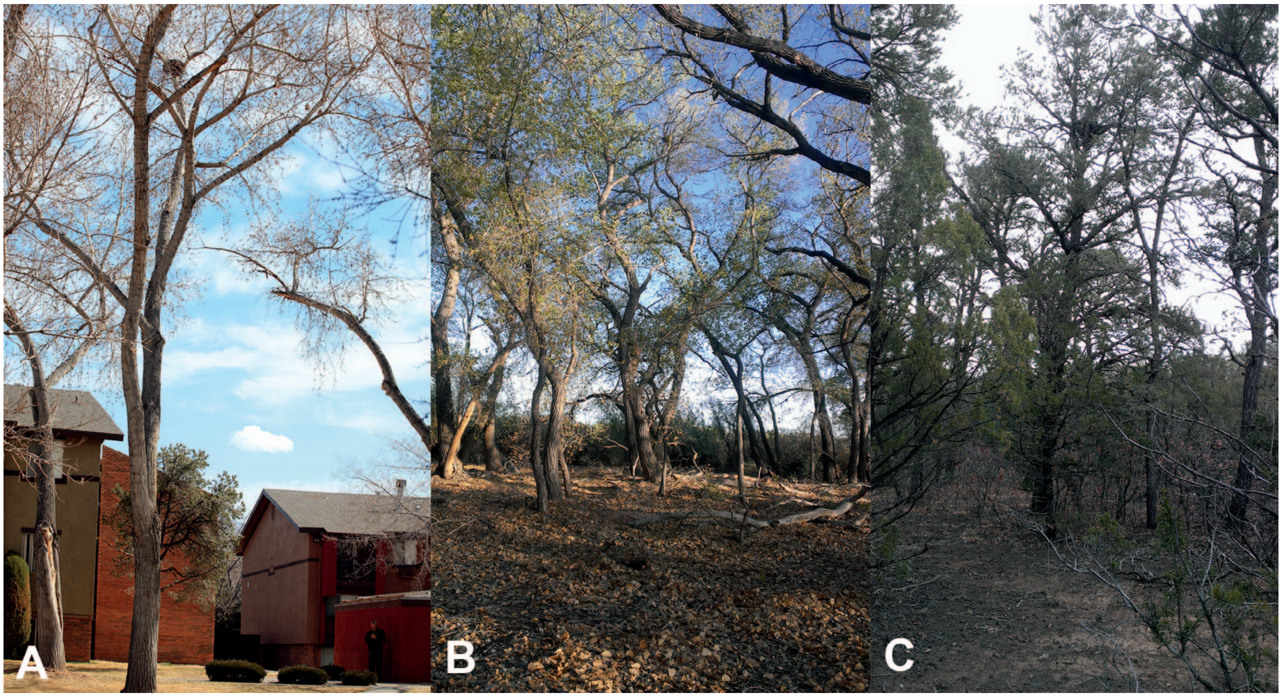

FIGURE 2. Nests used by radio-tagged female Cooper's Hawks in the Central New Mexico Cooper's Hawk metapopulation: (**A**) urban Albuquerque subpopulation, (**B**) riparian forest in the Rio Grande subpopulation, and (**C**) conifer woodland in the mountain subpopulation.

$\hat{R} \leq 1.1$ indicating convergence (Gelman and Hill 2007). I report the upper and lower 90% credible interval (CI) with parameter estimates throughout this paper; where I compare parameter estimates I report the probability the difference differs from zero ($P\ [\neq 0]$).

I used data collected to parameterize an IPM for female Cooper's Hawks fledged on the urban study area. IPMs combine the information from population counts and estimates of vital rates in a formal manner to derive joint insights into population dynamics (Besbeas and Freeman 2006, Schaub and Abadi 2011, Kéry and Schaub 2012). I followed the general IPM approach described in Kéry and Schaub (2012) to reduce problems associated with a lack of independence in the count and demographic data. I used uninformative priors for most models; in such cases the median of the posterior probability distribution approximates the maximum likelihood solution, except the posterior distribution integrates to 1 and is thus a true probability distribution (Kéry 2010, Hooten and Hobbs 2015).

I used the estimated number of occupied Cooper's Hawk nesting territories ($Nocc_t$) as the basis for the count of pre-breeding females on the urban study area in year t. I estimated total population size ($Ntot$) as

$$Ntot_t = Nocc_t^{\frac{1}{\kappa}}$$

where κ was the probability of breeding for a breeding-age female. Expansion by $1/\kappa$ accounted for nonbreeding females, so that $Ntot$ included all breeding-age females (Nad). I estimated κ with a Bernoulli model using data pooled over years based on the breeding status of radio-tagged females, and I assumed the breeding rate of radio-tagged females was representative of all breeding-age females in the population.

The structure of the likelihood model for estimating $Nocc$ was

$$Nocc_t = \left(Nk_t + Nnew_{t+1}^{\frac{1}{p(Nnew)}} \right) p(occ)_t$$

Nk_t was the number of previously known nesting territories in year t, $Nnew_{t+1}$ was the number of potential nesting territories overlooked in year t detected on the winter survey in year $t + 1$, $p(Nnew)$ was my probability of detecting a potential new nesting territory derived from the double-observer data (Nichols et al. 2000) and pooled over years, and $p(occ)_t$ was the occupancy probability for nesting territories in year t. I considered new nests further than the 10^{th} quantile of the mean nearest-neighbor distance of simultaneously used nests as new potential nesting territories. I used the state-space formulation of a dynamic site-occupancy model to estimate $p(occ)$ as described in MacKenzie et al. (2003) and Royle and Kéry (2007). Repeated visits to nesting territories in each year were used to estimate the probability of detecting occupancy. Note that I used the average probability of detecting potential missed territories to adjust the winter counts of missed territories, and I used the time-dependent estimate of the probability of detecting an occupied nesting territory to adjust the count of occupied nesting territories. Here, and elsewhere, I pooled detection probabilities for years when I had insufficient data for annual estimates.

I selected a pre-breeding, female-based, 2-stage Lefkovitch population projection matrix (Caswell 2001) with age-at-first-breeding of 1 yr for the underlying population model. Stage 1 consisted of juveniles and stage 2 included all older hawks. I used time-dependent parameter estimates for most parameters. I described the number of breeders (philopatric adults, *Nad*, and 1-yr-old juveniles, *Nj*) as:

$$Nad_{t+1} \sim \text{Binomial}\left(Nj_t^{\frac{1}{\kappa}} + Nad_t^{\frac{1}{\kappa}} + N\omega_t, \phi_{ad_t}\right)$$

and

$$Nj_{t+1} \sim \text{Poisson}\Big(\Big((Nj_t\kappa) + (Nad_t\kappa) + N\omega_t\Big) \times \phi_{j_t}(1-\zeta_t)\eta_t\nu_t\Big),$$

where ϕ_{j_t} and ϕ_{ad_t} were apparent survival of juveniles and adults, respectively, from year t to year $t+1$; η_t was the number of young fledged per breeding-age female in year t; v_t was the proportion of females in broods in year t; ζ_t was the estimated juvenile female emigration rate in year t, and κ was the probability of breeding pooled over years. Immigration also contributed to *Nad*, but I accounted for the number of immigrants ($N\omega$) separately as described below. For adults, ϕ_{ad} theoretically included emigration, but I did not observe any radio-tagged females emigrating as adults so I suspect such movements were rare.

I estimated productivity in year t using the formula

$$\eta_t = \phi_{nest_t} brood_t \kappa,$$

where ϕ_{nest_t} was the probability an occupied nesting territory fledged ≥ 1 young in year t and $brood_t$ was the mean post-fledging brood size at successful nesting territories in year t. I included κ as an expansion factor so that η accounted for all breeding-age females, not just those occupying nesting territories. I estimated daily probability of survival of occupied nesting territories using a hierarchical daily nest survival model (Royle and Dorazio 2008, Schmidt et al. 2010); ϕ_{nest_t} was the daily survival rate expanded to the 54-d nesting period. I used a binomial mixture model to estimate brood. This model consisted of a time-dependent Poisson generalized linear mixed-model (GLMM) to estimate brood size, and a constant binomial model to estimate the probability of detecting a fledged juvenile in a brood based on the repeated counts of fledged young at intensively monitored nesting territories (Kéry and Schaub 2012). I used a common detection probability for both sexes as there was no evidence of a sexual difference in detection probability. I included a random nesting territory effect to account for overdispersion from repeated measures at the same nesting territories. I estimated the brood sex ratio as a derived parameter in the binomial mixture model for 2012–2015; for 2011, I used the mean sex ratio for the period 2012–2015 because I did not obtain separate counts of male and female fledglings that year.

I used a state-space formulation of the Cormack–Jolly–Seber (CJS) capture–recapture model to estimate ϕ_j and ϕ_{ad} (Royle and Dorazio 2008, Kéry and Schaub 2012). I allowed for time-dependence on both resighting probability (p_s) and apparent survival in all models, and I allowed for an effect of the radio-transmitter on p_s. I did not allow for a transmitter effect on ϕ because previous work with the same transmitter protocol on Cooper's Hawks showed no such effect (Millsap et al. 2013). I allowed for only 2 age classes because I could not assign unknown-age females captured in definitive plumage to finer age categories. I estimated emigration probability for radio-tagged Cooper's Hawks from the data using a Bernoulli model, and I used a binomial generalized linear model to estimate the overall rate of emigration to each subpopulation.

I estimated the joint likelihood of the IPM as the product of the likelihoods, with parameters conditioned on the data (Figure 3). Annual immigration rate (ω_t) was estimated by including priors for ω_t and its variance in the IPM without likelihoods, because no data on immigration were available. I modeled the number of immigrants in year t as

$$N\omega_t \sim \text{Poisson}(Ntot_t\omega_t)$$

In this formulation, the IPM treated immigration as a random variable to be estimated as part of the state-space observation model. This approach could not distinguish immigrants from the Albuquerque subpopulation outside the urban study area with immigrants from other subpopulations and thus likely overestimated the true subpopulation-level immigration rate. I estimated the per capita contribution of each female in the urban study population (C^r) to the metapopulation as described in Runge et al. (2006), using annual estimates of relevant parameters from the data. Values of $C^r>1$ indicate subpopulation r was a source, whereas $C^r<1$ indicated a sink.

I used R package popbio (Stubben and Milligan 2007) to estimate potential population growth rates (λ_{pot}) and other population attributes from the population projec-

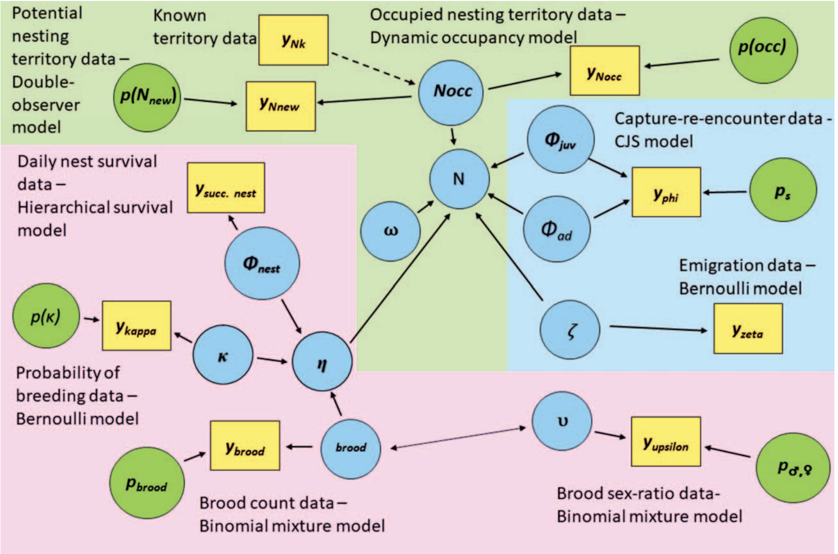

FIGURE 3. Graph of the integrated population model for female Cooper's Hawks in Albuquerque, New Mexico, USA. Blue circles are parameters of interest estimated with the model, orange boxes are data, and green circles are nuisance parameters estimated with the model. The pink background denotes data and parameters related to fecundity. Blue background denotes data and parameters related to debits (survival, emigration). Green background denotes data and parameters related to counts and the state-space models used to relate count data to *N*, total female population size. See text for more details on parameters and model structure.

tion matrix using the full posterior parameter distributions; the resulting estimates were in the form of joint probability density functions. I also separately computed estimates of λ_{pot} and related statistics for emigrant Cooper's Hawks. For the latter, I computed estimates of ϕ directly from the sample of radio-tagged emigrants, and I used information on subpopulation-specific fecundity from the literature (Hawks Aloft 2016). I calculated the observed population growth rate (λ_{obs}) for the urban study area and for the single exurban subpopulation for which there were data in the literature from trends in annual estimates or counts of occupied nesting territories.

I suspected urban and exurban Cooper's Hawks differed in their probability of migrating, and that these differences affected nesting chronology. I tested whether migrants and residents differed in (1) first-year migration probability using a Bernoulli model, (2) the first date detected with a potential mate at a nest using a Bayesian one-way ANOVA, and (3) the probability of breeding dispersal as a 2-yr-old using a Bernoulli model.

I estimated the proportion of each prey species in the diet of radio-tagged females using a binomial GLM. I used Program DISTANCE (Thomas et al. 2010) and avian prey count data to estimate density of White-winged Doves on the urban study area in April 2013–2015. I used the half-normal function with a cosine expansion to fit prey detection functions; this model adequately fit the data judging from the chi-square goodness of fit statistics ($P > 0.1$ in all cases). I did not have enough samples to adequately fit distance detection functions to the count data for the exurban winter samples, so for both urban and exurban winter samples I used the raw counts with a Poisson GLM to model and compare relative prey abundance. In the urban study area prey density estimates were strongly correlated with raw counts ($r = 0.84$), so I believe the winter prey indices were acceptable for this analysis.

RESULTS

Population Size and Fecundity

I located and determined occupancy at up to 80 potential Cooper's Hawk nesting territories on the urban study area each year (Figure 4). Occupied Cooper's Hawk nesting territories increased from ~52 in 2011 to ~74 in 2014, then possibly declined slightly in 2015 (Figures 4 and 5; see Appendix Table 3 for estimates and credible intervals for all parameters). The decline in occupied nesting territories in 2015 was coincident with a decline in abundance of White-winged Doves (2013 = 33,560 [25,031–44,996], 2014 = 31,656 [23,611–42,443], 2015 = 22,611 [16,865–30,316]). I monitored 211 occupied nesting territories to determine nest success, which ranged from 92% to 98% across years, and paralleled trends in the number of occupied nesting territories (Figure 5). Post-fledging brood size ranged from 1 to 5, averaging 3.2 (2.8–3.4, $n = 171$; Figure 6). Fledgling sex ratio was 58% (54–63%, $n = 10$ broods) females in 2012,

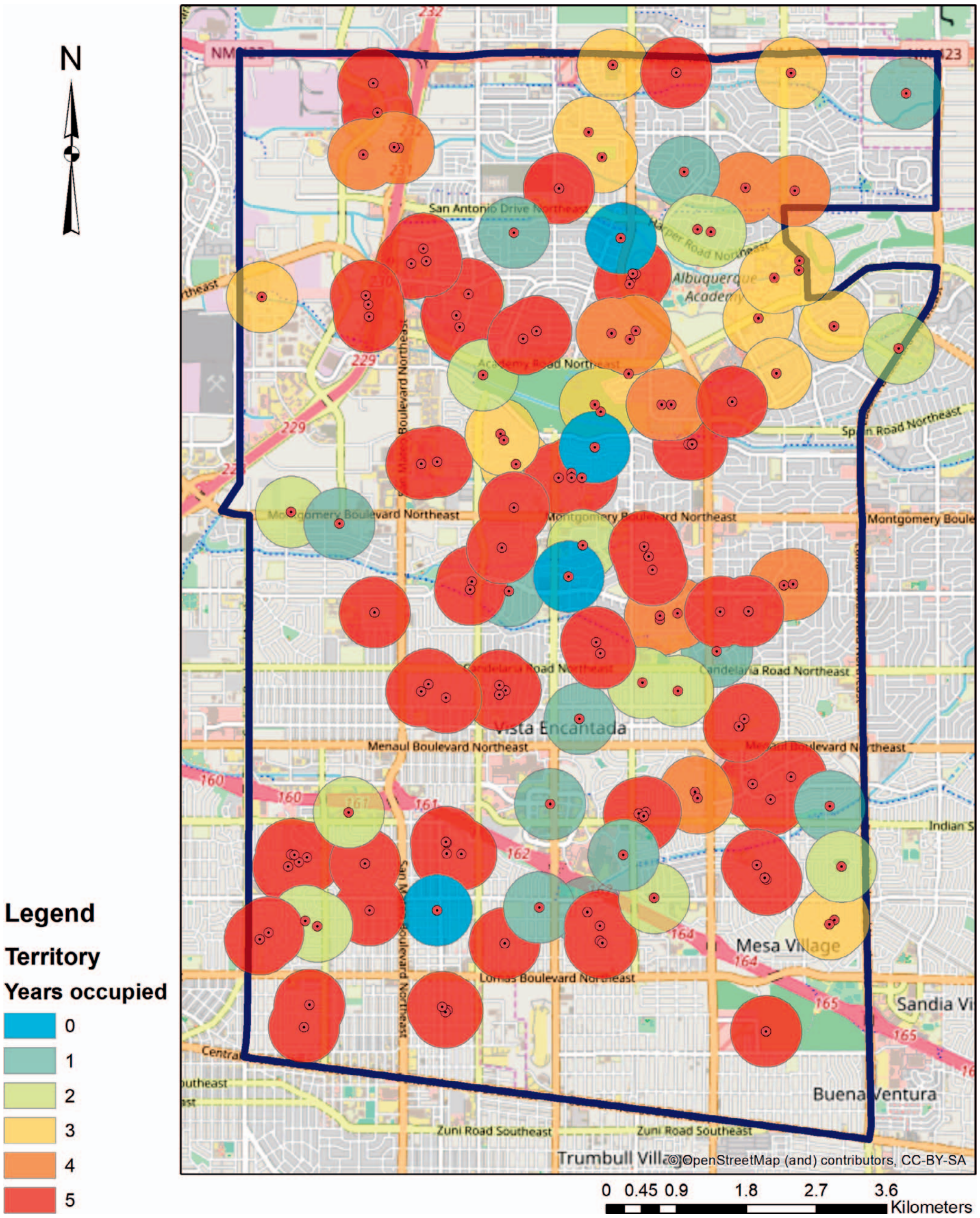

FIGURE 4. Map of used Cooper's Hawk nests (red dots) and associated occupied nesting territories (larger circles) from 2011 to 2015 on the 72 km^2 core study area, Albuquerque, New Mexico, USA.

but otherwise sexes fledged in approximately equal numbers (2013 = 53% [47–59%, $n = 7$], 2014 = 51% [46–55%, $n = 15$], 2015 = 50% [46–55%, $n = 21$]). These data indicate 127–216 Cooper's Hawks fledged per year, and 76–112 fledglings were females. These estimates were predicated on the potential nesting territory detection model, which estimated my detection probability as 0.88 (0.79–0.94, $n = 45$).

Survival and Migration

I marked 166 female Cooper's Hawks (96 juveniles, 70 adults) and 165 males (83 juveniles, 82 adults); 85 juvenile females were also equipped with radio transmitters. Annual apparent survival rates ranged from 27% to 38% for juveniles, and from 82% to 88% for adults. Reencounter probability was 42% (11–84%) for juveniles with bands, 86% (78–94%) for juveniles with radio tags,

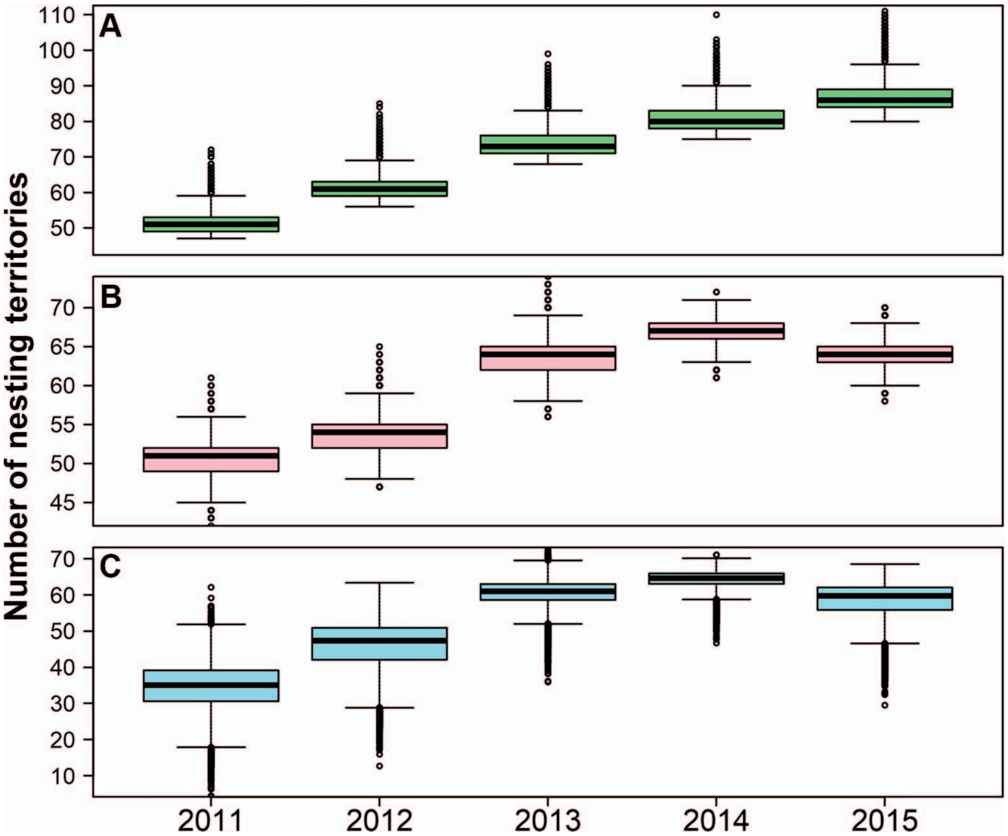

FIGURE 5. Boxplots of posterior distributions for the number of (**A**) potential (green), (**B**) occupied (pink), and (**C**) successful (blue) Cooper's Hawk nesting territories on the urban study area, Albuquerque, New Mexico, USA. Dark bars are medians, colored boxes are interquartile ranges, whiskers are 1.5 times the interquartile range, and dots are outliers.

91% (75–99%) for adults with bands, and 94% (83–100%) for adults with radio tags.

Only 0.3% (0–2%) of females that initially settled in the urban subpopulation migrated compared to 93% (80–100%) of females that settled in an exurban subpopulation ($P [\neq 0] > 0.99$, $n = 43$). The mean date resident juveniles began settling on nesting territories was 22 March (ordinal date 81.1 [76.9–85.2]) compared to 12 April (ordinal date

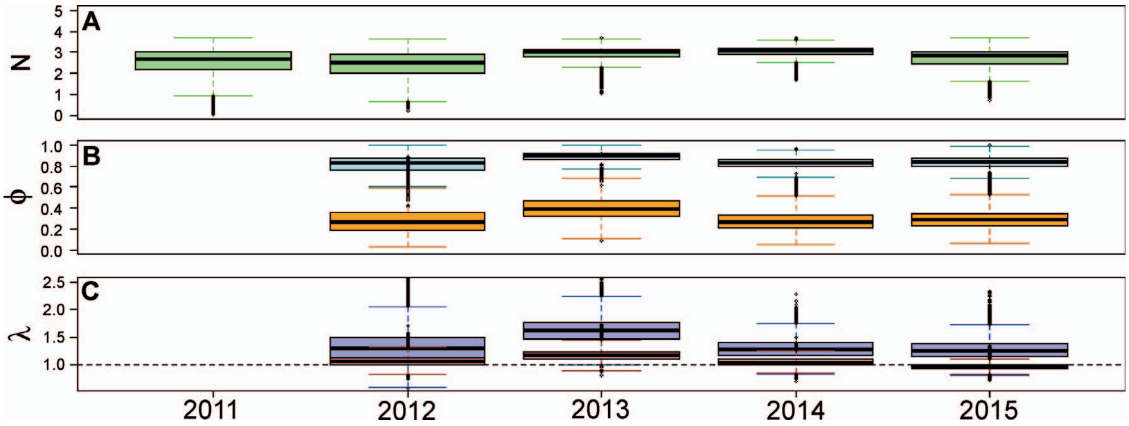

FIGURE 6. Boxplots of posterior distributions for (**A**) brood size (green), (**B**) adult (blue) and juvenile (orange) annual apparent survival rates, and (**C**) observed (rose) and potential (lavender) rates of population change on the urban study area, Albuquerque, New Mexico, USA. Dark bars are medians, colored boxes are interquartile ranges, whiskers are 1.5 times the interquartile range, and dots are outliers.

TABLE 1. Diet of female Cooper's Hawks radio-tagged in urban Albuquerque, New Mexico, USA, 2011–2015. Only prey items observed being consumed by radio-tagged hawks are included. Prey during the breeding season not known to have been captured by a radio-tagged female are excluded.

Prey	*n*	Estimated proportion in diet (90% CI)
Reptilia	1	0.01 (0–0.02)
Lacertilia	1	0.01 (0–0.02)
Unidentified lizard	1	0.01 (0–0.02)
Aves	120	0.96 (0.64–1.00)
Galliformes	7	0.06 (0.01–0.13)
Scaled Quail (*Callipepla squamata*)	3	0.02 (0.01–0.05)
Gambel's Quail (*C. gambelii*)	2	0.02 (0–0.04)
Domestic chicken (*Gallus gallus*)	2	0.02 (0–0.04)
Columbiformes	98	0.78 (0.60–0.99)
Rock Pigeon (*Columba livia*)	59	0.47 (0.40–0.55)
Eurasian Collared-Dove (*Streptopelia decaocto*)	14	0.11 (0.07–0.16)
White-winged Dove (*Zenaida asiatica*)	21	0.17 (0.12–0.23)
Unknown dove	4	0.03 (0.01–0.06)
Passeriformes	15	0.12 (0.04–0.21)
Woodhouse's Scrub-Jay (*Aphelocoma woodhouseii*)	2	0.02 (0–0.04)
American Robin (*Turdus migratorius*)	8	0.06 (0.03–0.10)
House Sparrow (*Passer domesticus*)	3	0.02 (0–0.04)
House Finch (*Haemorhous mexicanus*)	1	0.01 (0–0.02)
Great-tailed Grackle (*Quiscalus mexicanus*)	1	0.01 (0–0.02)
Mammalia	4	0.03 (0.01–0.06)
Leporidae	4	0.03 (0.01–0.06)
Desert cottontail (*Sylvilagus audubonii*)	4	0.03 (0.01–0.06)
Total	125	

102.0 [95.1–101.0]) for migrants, a difference of 20.9 (12.7–29.0) days ($P\ [\neq 0] > 0.99$, $n = 31$). Resident juveniles began nesting 11.7 (4.5–18.9, $n = 31$) days earlier than migrants on average. At 2 yr of age, 97% (82–100%) of migrants undertook breeding dispersal compared to 16% (5–31%) of residents ($P\ [\neq 0] > 0.99$, $n = 21$). Three radio-tagged females that were migrants survived into their second breeding season, and all were replaced on their previous-year's nesting territory by the time they returned in their second spring. One of these females survived into her third breeding season, and she was also replaced by the time she returned in her third year. Two of the replacements were known to be residents; the other two were unmarked females of unknown status.

Age at First Breeding

Thirty-four radio-tagged female Cooper's Hawks survived their first year, and all but one injured female settled on a nesting territory and laid eggs, thus the probability of breeding by age 1 was 0.96 (0.91–0.99). Thirty-three of 305 (11%) breeding females on the urban study area were juveniles compared to 3 juveniles among 305 (1%) breeding males. Age-at-first-breeding for 6 males banded as fledglings was 2 yr, whereas the age-at-first-breeding for 24 of 25 females banded as fledglings was 1 yr. All radio-tagged females $\geq$2 yr old also settled on a nesting territory and laid eggs. The estimated annual average number of nonbreeding urban female floaters in all age classes was 0.35 (0.24–2.3).

Diet

Female Cooper's Hawks were observed with at least 14 species of prey, 96% (64–100%, $n = 125$) of which were birds (Table 1). The most important prey were 4 species of Columbidae and American Robins (*Turdus migratorius*). Winter relative abundance of these prey in 2015 was 8.0 (7.5–8.6) individuals per sample point in urban areas compared to 2.3 (1.9–2.8) in exurban areas, thus female Cooper's Hawk prey were 3.5 (3.1–4.0) times more abundant in urban than exurban areas in winter 2015 ($P\ [\neq 0] > 0.99$, $n = 99$).

Population Growth and Structure

Elasticities of the female Cooper's Hawk population projection matrix showed survival accounted for 66% (55–77%) of annual variation in λ; adult survival was most important, accounting for 44% (34–59%) of variation. The overall median generation time for female Cooper's Hawks was 5.8 (4.9–7.3) yr, and the stable age distribution (assuming equilibrium) consisted of 60% (57–64%) juveniles. The annual proportion of occupied nesting territories on the urban study area attended by juvenile females ranged from 7% to 25%, with the greatest proportion in 2013. The value of λ_{pot} averaged over all years was 1.29, and the lowest value in any year was 1.28 in 2015. The observed growth rate on the urban study area was well below the potential growth rate, averaging 1.08 (1.02–1.16).

Emigration and Immigration

Emigration likely accounted for the difference between λ_{pot} and λ_{obs}. Juvenile female emigration averaged 57% (22–100%), with 46% (24–68%) of emigrants settling off the urban study area but within the Albuquerque subpopulation, 46% (24–68%) in the Rio Grande subpopulation, 8% (0.4–22%) in the mountain subpopulation, and 0.1% (0.01–4%) in the Rio Rancho subpopulation ($n = 31$).

The average estimated annual immigration rate into the urban study area was 1% (0–21%); this amounted to fewer than 4 females immigrating into the urban study population in most years compared to 15–27 (4–47) emigrants (Figure 7). C^r ranged from 1.07 (0.88–1.32) in

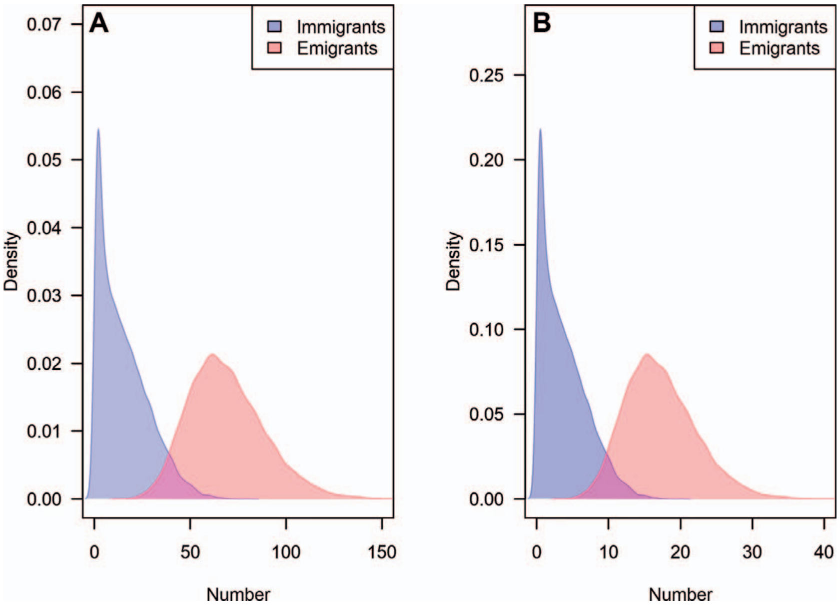

FIGURE 7. Posterior probability distributions for the (**A**) cumulative total (sum) and (**B**) mean annual number (mean) of female Cooper's Hawks that emigrated, and the number that immigrated into, the urban study area, Albuquerque, New Mexico, USA, 2012–2015.

2012 to 1.84 (1.10–2.85) in 2015, and the probability that emigration exceeded immigration on the urban study area was $\geq$90% in each year for which I had estimates. I documented 3 immigrants during the study, all of which had been banded as breeders off the urban study area but in the Albuquerque subpopulation. This suggests that many immigrants on the urban study area likely arose from elsewhere in Albuquerque rather than from exurban subpopulations.

Demographic data on other Cooper's Hawk subpopulations was scarce, but fortunately the primary subpopulation of concern, the Rio Grande, has been monitored since 2004 (Table 2). These data suggest that density of occupied nesting territories was higher, fecundity and survival lower, and λ likely lower and more variable than for the urban Albuquerque subpopulation. From 2004 to 2013, λ_{obs} based on annual counts of occupied nesting territories in the Rio Grande subpopulation averaged 1.03, and from 2011 to 2013 λ_{pot} for radio-tagged emigrant females from the urban study area that settled in the Rio Grande subpopulation averaged 1.03 (0.67–1.38, $n = 13$). Extrapolation using the subpopulation-specific emigration rates and population estimates from the IPM suggested that, on average, 7.3 (2.2–19.0) emigrant females from the urban study area settled in the Rio Grande subpopulation annually.

DISCUSSION

These results indicate that the urban study area, and thus the Albuquerque subpopulation, was a source subpopulation for the Cooper's Hawk metapopulation in north-central New Mexico, with an emigration rate ~30 times the immigration rate. This rules out balanced dispersal as a tenable dispersal model for this metapopulation. Opportunities for recruitment by female Cooper's Hawks on the urban study area occurred when breeding females died (an average of 15% annually) or when new nesting territories

TABLE 2. Status of the primary central New Mexico, USA, Cooper's Hawk subpopulations considered in this study.

Parameter	**Albuquerque**	**Rio Grande**
Period of observations	2011–2015	2004–2013
$\bar{x}$ annual nesting territory density (N per km^2)	1.01	3.04
Range in $\bar{x}$ number fledged per occupied nesting territory (n)	2.42–3.13 (305)	2.07–2.30 (488)
Juvenile female ϕ(90% CI)	65% (33–95%)	34% (18–32%)
Adult female ϕ (90% CI)	85% (73–93%)	61% (40–81%)
Observed λ (range in λ between years)	1.08 (0.96–1.18)	1.03 (0.58–1.48)
Source	This study	ϕ from this study, others from Hawks Aloft (2016)

were colonized (8% on average annually). Most radio-tagged 1-yr-old females initially attempted to settle within the Albuquerque subpopulation; 69% were successful, but that percentage varied annually. Remaining recruits emigrated and secured breeding slots in other subpopulations, primarily the Rio Grande. Thus, annual production from the urban study area was sufficient to support both modest growth in Albuquerque as well as provide recruits for exurban subpopulations. Although other studies have suggested sources and sinks within urban areas (Mannan et al. 2008, Björklund et al. 2009), this Cooper's Hawk metapopulation shows an urban area to be a significant source for surrounding exurban areas, based on accounting for both emigration and immigration.

Cooper's Hawks typically exhibit delayed reproduction, with members of both sexes usually breeding for the first time in their third year (age 2; Curtis et al. 2006). Although no quantitative estimates of age-at-first-breeding are available for Cooper's Hawks, for the larger Northern Goshawk (*A. gentilis*) previous studies estimated between zero (Kenward et al. 1999) and 42% (Krüger 2005) of 1-yr-old females bred, whereas for the smaller Eurasian Sparrowhawk (*A. nisus*) one study estimated that 18% of 1-yr-old females bred (Newton 1985). It was therefore notable that essentially all 1-yr-old female Cooper's Hawks from the urban study area settled on nesting territories rather than spending the first year as nonbreeding floaters (Hunt 1998, Hunt and Law 2000, Penteriani et al. 2011, Hunt 2015). Floaters are generally believed to comprise a substantial proportion of the adult component of healthy raptor populations (Franklin 1992, Millsap and Allen 2006, Penteriani et al. 2011), but their cryptic nature makes detection and quantification difficult (Katzner et al. 2011). I could estimate accurately the probability of breeding for females in this study and thus show that there were few if any floater females originating from the urban study population. Conversely, juvenile males seldom bred on the urban study area. Given the relatively even sex ratio at fledging, and assuming similar first-year survival, this implies there was a pool of floating 1-yr-old males comparable in number to the cohort of breeding juvenile females. That female raptors breed at younger ages in higher proportions than males is well known, which is hypothesized to be because the female's role of egg production, incubation, and nestling care does not require as much experience as does the male's role of providing prey for nesting females and young (Newton 1979, Newton et al. 1981, Newton and Marquiss 1984, Krüger 2005). Age-related increases in breeding performance by males in other *Accipiter* species have been reported (Newton and Rothery 2002, Tøttrup Nielsen and Drachmann 2003), and Lien et al. (2015) speculated that proficiency of male Cooper's Hawks increased with age in Albuquerque. I suspect most 1-yr-old male Cooper's Hawks were unable to provision females sufficiently to attract and hold a mate.

Discussions with knowledgeable residents (falconers, birdwatchers) suggested colonization of urban Albuquerque by breeding Cooper's Hawks likely began in the 1980s. Although Cooper's Hawks were probably always present and breeding in riparian forest along the Rio Grande, in the 1980s migratory White-winged Doves expanded their range into central New Mexico and soon thereafter became abundant residents in urban areas like Albuquerque (Schwertner et al. 2002). Given the importance of White-winged Doves in the diet of urban Cooper's Hawks today, it is tenable to hypothesize that their establishment in Albuquerque contributed to the hawk's expansion into urban habitats at that time. Assuming the rate of Cooper's Hawk population growth has been relatively constant, colonization in the 1980s is consistent with a population doubling time of 9 yr, the rate associated with λ_{obs} of 1.08 (Mills 2012). The generally positive population growth rate I observed suggests Cooper's Hawks were still expanding across urban Albuquerque, and that sufficient resources existed to support additional population growth. Thus, given the disparity in age at first breeding between Cooper's Hawk sexes, the availability of new males to colonize nesting territories was likely the key factor limiting the rate of population growth in the Albuquerque subpopulation, and likely contributed to the high emigration rate among females. In this context, this study provides further direct evidence that sex-specific factors may affect the proclivity for floating as a strategy, which in turn likely leads to different selection pressures acting on the sexes with respect to breeding and dispersal behavior (Moreno 2016).

Although these results comport most closely with the source–sink model, the findings suggest the most important recipient subpopulation was not a demographic sink. Immigration from the Albuquerque subpopulation certainly contributed to a stable or increasing λ in the Rio Grande, but estimated demographic rates for that subpopulation indicate continued immigration was not necessary to maintain a positive population trajectory. Thus, a major question that emerges from this study is why urban female emigrants were universally successful at securing nesting territories in a self-sustaining exurban subpopulation. Competition among females for nesting territories was intense (Lien et al. 2015), thus this outcome implies that female emigrants from the urban study area had a competitive advantage in exurban areas. A key behavioral difference between females in urban and exurban subpopulations was the high rate of migration among the latter. Kennedy (1991) noted that breeding female Cooper's Hawks from her exurban northern New Mexico study area were migratory, as were 93% of radio-tagged females in this study that settled after initial dispersal in exurban subpopulations. In contrast, all radio-tagged females from this study that initially settled in the Albuquerque subpopulation were residents. Cooper's Hawks have a well-described seasonal migration in western North America (DeLong and Hoffman 1999), but clearly migratory behavior, at least at more southern latitudes, is facultative. Although based on only 1 yr of data, prey counts indicated avian prey were considerably more abundant in urban than exurban habits in winter, which likely explained the discrepancy in migratory behavior. Increased residency associated with colonization of urban habitats has been detected in other species (Plowright et al. 2011), including the closely related Sharp-shinned Hawk (*A. striatus*) in eastern North America, where increased residency at northern latitudes is associated with increases in prey due to recreational bird feeding (Viverette et al. 1996).

At least 2 factors associated with migration could lead to a competitive advantage for resident female Cooper's Hawks. First, if migrant females in the Rio Grande subpopulation experienced higher mortality than their mates, it could lead to a shortage of breeding females and greater opportunities for immigrants. Second, resident female Cooper's Hawks began settling on nesting territories before migrants returned, and thus may have had a temporal advantage with respect to acquiring mates. Although I cannot rule out the possibility of higher mortality in adult females than adult males in the Rio Grande subpopulation, I obtained direct evidence in support of a temporal advantage to residency in securing a nesting territory: (1) first-year residents acquired nesting territories an average of 21 d earlier than migrants, (2) second-year migrants were 81% more likely than second-year residents to undertake breeding dispersal, and (3) breeding dispersal by migrants often appeared to be the result of having been displaced. These factors strongly support the idea that the nonmigratory juvenile emigrants from the Albuquerque subpopulation found and secured breeding slots in the Rio Grande and perhaps other exurban subpopulations before philopatric migrants returned.

Changes in migratory behavior that lead to temporal segregation and assortative mating can have profound population effects, including sympatric speciation (Bearhop et al. 2005). Moreno (2016) contends that traits that reduce the propensity for floating, and consequently decrease age at first breeding, will be under strong positive selection pressure. This is highly relevant for Cooper's Hawks, whose overall fitness is correlated with the number of breeding attempts in a lifetime (Rosenfield et al. 2009). In this metapopulation, if attributes leading to a competitive advantage in securing an initial urban settling area, such as large size or aggressiveness (Rosenfield et al. 2016, Warkentin et al. 2016), are heritable, natural selection should favor individuals that possess those heritable traits and they should increase in frequency. Conversely, female Cooper's Hawks that initially settled in exurban subpopulations typically migrated, and thus likely had lower recruitment rates; heritable features associated with this dispersal behavior should decrease in frequency. It is also possible that selection in urban Cooper's Hawks could lead to the evolution of traits that are less adaptive in exurban habitats, counteracting, over time, the advantages of residency.

The metapopulation dynamics of central New Mexico Cooper's Hawks during the time of this study did not conform fully to predictions under either the source–sink or the balanced dispersal models. In part, this may have been because this system was not in equilibrium. The urban Cooper's Hawk subpopulation was growing, attributable partly to the aforementioned increase in numbers and residency of White-winged Doves. More generally, however, Cooper's Hawks across most of North America have been increasing since the mid-1970s as the species recovered from declines associated with DDT use from the 1940s until 1972 (Farmer et al. 2008). Several lesser-known dispersal models have been proposed to explain dispersal dynamics under nonequilibrium conditions, including unbalanced dispersal (Lin and Batzli 2001), sources and pools (Senar et al. 2002), and reciprocating dispersal (Morris and Diffendorfer 2004). Unbalanced dispersal is characterized by positive in situ recruitment in all subpopulations, but with higher movement rates from low- to high-quality subpopulations than from high to low (Lin and Batzli 2001). The sources and pools model is similarly characterized by net positive movement from lower- to higher-quality subpopulations within the metapopulation, but without regard to in situ recruitment potential within the subpopulations (Senar et al. 2002). The reciprocating dispersal model predicts higher dispersal rates from high- to low-quality subpopulations during periods of positive population growth, with the reverse being true during periods of population decline, such that over time and with enough environmental fluctuation net dispersal can be balanced (Morris and Diffendorfer 2004). Based on demographic rates in this study, individual fitness was likely higher in the urban Albuquerque subpopulation than in the Rio Grande, thus net movement was from a higher- to a lower-quality subpopulation, which is only consistent with predictions under the reciprocating dispersal model. None of these models, however, explicitly incorporate the concept of behavioral differences among subpopulations interacting with dispersal and influencing movement within the metapopulation to the degree reported here. Without the joint propensity for residency among urban and migration among exurban Cooper's Hawks, dispersal dynamics in the central New Mexico Cooper's Hawk metapopulation would likely have been much different, potentially conforming to any one of the other nonequilibrium dispersal models. I suggest in systems such as this, the term "behavior-modified dispersal" is an appropriate label because it acknowledges that the behavior, in this case migration, modifies the underlying dispersal dynamic.

Urban breeding by Cooper's Hawks is not unique to Albuquerque. Coincident with rapid population growth during the recovery from the effects of DDT, Cooper's Hawks expanded or were absorbed into urban areas throughout their range; long-term studies of urban Cooper's Hawks have been conducted in Arizona (Boal and Mannan 1999, Mannan et al. 2008), British Columbia (Stewart et al. 2007), North Dakota (Rosenfield et al. 2007), Wisconsin (Stout and Rosenfield 2010), California (Chiang et al. 2012), and Washington (Deal et al. 2017). None of these studies examined metapopulation relationships between the urban and surrounding exurban subpopulations, but they do provide evidence that demographic rates are not consistently higher in urban compared to exurban habitats (Rosenfield et al. 2016). Given the spatial heterogeneity in relative quality of urban habitat to Cooper's Hawks, and likely differences in migration biology across the range, it seems plausible that multiple forms of dispersal characterize the metapopulation dynamics of this hawk, as suggested as a general rule by Morris and Diffendorfer (2004). Conversely, the form of dispersal dynamics reported here could explain metapopulation relationships in other urban raptors in some situations, such as that described for Peregrine Falcons (*Falco peregrinus*) in California (Kauffman et al. 2003).

In summary, I present data that shows the Albuquerque Cooper's Hawk subpopulation functioned as a source because it occupied an adaptive peak in the metapopulation's fitness landscape. This competitive advantage accrued because high nonmigratory avian prey populations in the urban area supported year-long residency, and residents secured breeding slots before, and thus without direct competition from, migrants. These findings support the idea that patch dynamics in a metapopulation can be governed by factors other than just demographic rates and connectivity (Doebeli and Ruxton 1997, Figueira 2009). Although differences in reproductive timing have been identified previously as a factor compromising successful dispersal between metapopulation patches (Carson et al. 2010), these findings are novel in that they suggest landscape changes that affect migratory behavior can alter the patch dynamics of metapopulations. This study also provides support for theoretical models of Guo et al. (2005) that suggest the equilibria of metapopulations could be disrupted by changes in dispersal and migration associated with climate change and landscape disturbances. In this context, these results illustrate that urban populations of a widespread species may serve as important reservoirs of diversity during times of rapid ecological change.

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Ethics statement: All work was conducted in compliance with the Guidelines to the Use of Wild Birds in Research under an approved IACUC protocol through New Mexico State University.

Data deposits: All data used in the analyses are available from the Zenodo digital repository at https://zenodo.org/deposit/802292.

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APPENDIX TABLE 3. Population and demographic parameter estimates from a female-based integrated Cooper's Hawk population model and associated submodels, Albuquerque, New Mexico, USA, 2011–2015. Values are medians over 90% credible intervals.

Parameter	2011	2012	2013	2014	2015
Number of occupied nesting territories (Nad)[a]	52 43–63	53 45–62	69 59–79	74 63–85	72 61–84
Number of female recruits (Nj)[b]	-	6 1–14	18 8–29	12 3–23	6 1–15
Annual juvenile female apparent survival (Φ_j)	-	0.29 0.12–0.53	0.38 0.23–0.56	0.27 0.15–0.42	0.29 0.16–0.45
Annual adult female apparent survival (Φ_{ad})	-	0.83 0.69–0.93	0.88 0.80–0.95	0.82 0.74–0.90	0.84 0.74–0.92
Proportion of occupied nesting territories successful (Φ_{nest})	0.92 0.64–0.99	0.91 0.60–0.99	0.97 0.86–0.99	0.98 0.90–0.99	0.94 0.74–0.99
Young fledged per occupied nesting territory	2.4 1.5–3.3	2.9 1.9–3.7	3.1 2.6–3.6	3.1 2.6–3.6	3 2.6–3.5
Young fledged per successful occupied nesting territory ($brood$)[c]	2.8 2.0–3.4	3.4 2.8–4.0	3.3 2.8–3.9	3.3 2.9–3.8	3 2.6–3.5
Proportion of females in broods (ν)	0.51 0.48–0.55	0.58 0.54–0.63	0.53 0.47–0.59	0.51 0.46–0.55	0.5 0.46–0.54
Probability of breeding (κ)[d]	0.96 0.91–0.99	0.96 0.91–0.99	0.96 0.91–0.99	0.96 0.91–0.99	0.96 0.91–0.99
Female emigration rate (ζ)[e]	-	0.66 0.34–0.91	0.44 0.20–0.70	0.6 0.33–0.82	0.82 0.55–0.98
Female immigration rate (ω)[f]	-	0.06 0–0.26	0.06 0–0.24	0.06 0–0.24	0.05 0–0.22
Observed growth rate (λ_{obs})[g]	-	1.02 0.81–1.26	1.3 1.07–1.58	1.08 0.90–1.30	0.98 0.90–1.30
Potential growth rate (λ_{pot})[h]	-	1.33 0.92–1.83	1.62 1.27–2.03	1.29 1.03–1.60	1.28 1.02–1.60
Probability emigration exceeded immigration[i]	-	0.9	0.93	0.91	0.98
Probability of migration–urban[d]	-	0.003 0–0.021	0.003 0–0.021	0.003 0–0.021	0.003 0–0.021
Probability of migration–exurban[d]	-	0.93 0.81–1.0	0.93 0.81–1.0	0.93 0.81–1.0	0.93 0.81–1.0
Probability of detection–potential nesting territory ($p(N_{new})$)[d]	0.88 0.79–0.94	0.88 0.79–0.94	0.88 0.79–0.94	0.88 0.79–0.94	0.88 0.79–0.94
Probability of detection–occupied nesting territory ($p(occ)$)	0.95 0.91–0.97	0.87 0.84–0.90	0.89 0.86–0.92	0.93 0.90–0.95	0.84 0.81–0.87
Probability of detection–fledged young in brood counts[d]	0.88 0.79–0.94	0.88 0.79–0.94	0.88 0.79–0.94	0.88 0.79–0.94	0.88 0.79–0.94

[a] Synonymous with the number of breeding females.

[b] Number of females fledged from nesting territories on the urban study area in year t that survived and settled on nesting territories in the urban study area in year $t + 1$.

[c] A successful nesting territory was an occupied nesting territory in which at least 1 young survived to fledging age (24 d).

[d] Estimates are pooled over years.

[e] Number of females fledged from nesting territories on urban study area in year t that survived and settled on nesting territories off the urban study area in year $t + 1$.

[f] Number of females estimated to have immigrated and settled on nesting territories in the urban study area in year t.

[g] λ estimated from observed changes in the number of occupied nesting territories between years.

[h] λ estimated from demographic rates ignoring emigration.

[i] Probability that the number of emigrants exceeded the number of immigrants in year t.