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Causes of Death of Female Cooper's Hawks from an Urban Setting in New Mexico, USA

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ABSTRACT.—Knowledge of mortality factors affecting raptors is often based on opportunistically found carcasses. Some causes of mortality, however, are more likely to produce carcasses that will be discovered, thus opportunistic collections are biased. Studies of raptors tagged with transmitters can provide relatively unbiased cause-of-death information. We used data collected during 2011–2021 from 158 tagged female Cooper's Hawks (*Accipiter cooperii*) from an urban study area in New Mexico, USA to estimate the population-level effects of different causes of mortality. We used a multistate model to combine data from encounters of banded live and dead birds with data from transmitter-tagged hawks to estimate annual age-specific survival rates. Cause-of-death information from the subset of tagged individuals was used to estimate proportions of first year (FY) and older (AFY) hawks that died annually from different causes. Most mortalities were caused by anthropogenic factors, especially collisions with human structures (e.g., windows, vehicles), which accounted for 45% (credible interval = 31%–60%) of FY deaths and 32% (18%–45%) of AFY deaths annually. From July 2020 to June 2021, purposeful killing by humans accounted for deaths of 17 (6–33) female Cooper's Hawks out of an estimated starting population of 216 (184–254). For both age classes, the ultimate cause of most deaths in late winter and early spring appeared to be associated with securing a nesting territory and mate. To our knowledge, this is the first study to provide relatively unbiased information on the importance of different causes of mortality for an urban raptor population.

KEY WORDS: *mortality factors*; *mortality rates*; *multistate models*; *survival*; *urban.*

CAUSAS DE MORTALIDAD EN HEMBRAS DE *ACCIPITER COOPERII* EN UN ENTORNO URBANO DE NUEVO MÉXICO, EEUU

RESUMEN.—El conocimiento de los factores de mortalidad que afectan a las aves rapaces a menudo se basa en cadáveres encontrados de manera oportunista. Sin embargo, algunas causas de mortalidad son más propensas a producir cadáveres que serán descubiertos, por lo que las recolecciones oportunistas están sesgadas. Los estudios de rapaces seguidas con transmisores pueden proporcionar información relativamente imparcial sobre las causas de mortalidad. Utilizamos datos recolectados durante 2011–2021 de 158 hembras de *Accipiter cooperii* provenientes de un área de estudio urbana en Nuevo México, EEUU, para estimar los efectos a nivel poblacional de diferentes causas de mortalidad. Utilizamos un modelo de múltiples estados para combinar los datos de encuentros de aves anilladas vivas y muertas con los datos de aves seguidas por medio de transmisores para estimar tasas anuales de supervivencia específicas por edad. La información sobre la causa de mortalidad del subconjunto de individuos marcados con transmisores se

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utilizó para estimar las proporciones de *A. cooperii* del primer año (PA) y post primer año (PPA) que murieron anualmente por diferentes causas. La mayoría de las muertes fueron causadas por factores antropogénicos, especialmente colisiones con estructuras humanas (e.g., ventanas, vehículos), que representaron, anualmente, el 45% (31%–60%) de las muertes de PA y el 32% (18%–45%) de las muertes de PPA. Desde julio de 2020 a junio de 2021, la muerte intencional por parte de humanos representó la muerte de 17 (6–33) hembras de *A. cooperii* de una población inicial estimada en 216 (184–254) individuos. Para ambas clases de edad, la causa última de la mayoría de las muertes a fines del invierno y principios de la primavera pareció estar asociada con asegurar un territorio de nidificación y una pareja. Hasta donde sabemos, este es el primer estudio que proporciona información relativamente no sesgada sobre la importancia de diferentes causas de mortalidad para una población urbana de aves rapaces.

[Traducción del equipo editorial]

INTRODUCTION

Survival, particularly adult survival, is the demographic parameter that most strongly influences the population growth rate of most long-lived species of raptors (Newton et al. 2016). Knowledge of mortality factors and their relative frequency is therefore important for understanding mechanisms of population regulation. Information on causes of raptor mortality comes from a variety of sources, including determination of causes of injury or death for individuals that arrive at rehabilitation centers (Morishita et al. 1998, Wendell et al. 2002, Hernandez et al. 2018) or wildlife health laboratories (Russell and Franson 2014), and from recoveries of marked individuals (Schaub and Pradel 2004). These sources of information do not typically provide unbiased estimates of the frequencies of different mortality factors because the probability of detecting a raptor carcass is not the same for all causes of death (Schaub and Pradel 2004). Transmitter-tagged birds, however, can provide a relatively unbiased source of information on causes of death because detection is minimally affected by the cause of mortality (Kenward et al. 1993, Schaub and Pradel 2004, Millsap et al. 2022). Data from studies involving tagged raptors have the potential to provide unbiased information on population-level effects of different mortality factors, something that has been identified as a particular need for urban raptors (Hager 2009).

Recently, statistical models have been developed that produce estimates of survival along with relatively unbiased estimates of causes of mortality from birds tagged with VHF or GPS transmitters (hereafter, tags). The approach involves use of multistate survival models (White et al. 2006), modified to also account for the probabilities of death from various causes. We here apply the multistate survival model used by Millsap et al. (2022) to 12 yr of tagging data from females of an urban population of Cooper's Hawks (*Accipiter cooperii*) in northern New Mexico, USA. Our objectives were to describe for this population of hawks the: (1) true importance of the different sources of mortality for first year (FY, ages fledging through the first birthday) and after first year (AFY, ages >1 yr) age classes of females; and (2) seasonal timing of mortality of different causes by age class.

Although all our Cooper's Hawk banding and tagging occurred on an urban study area, each year about 50% of tagged hawks dispersed and settled outside of the urban area in surrounding exurban, rural, and wilderness landscapes (Millsap 2018), and some individuals migrated as far as central Mexico (B. Millsap unpubl. data). We continued to monitor tagged hawks to the extent possible wherever they settled. Consequently, our work is best characterized as a study of causes of death of Cooper's Hawks originating from an urban study area rather than a study of causes of death of urban Cooper's Hawks.

METHODS

Study Area and Data Collection. We conducted initial tagging of Cooper's Hawks on a 72-km^2 urban study area in northeastern Albuquerque, Bernalillo County, New Mexico (35.1107°N, 106.6100°W). Breeding adult and fledgling Cooper's Hawks were captured and tagged at nest sites during March through July 2011–2021. Tagged Cooper's Hawks dispersed widely to locations elsewhere in New Mexico and southern Colorado (B. Millsap, unpubl. data); during fall some individuals migrated southward up to 1600 km, as far as central Mexico. For a more thorough description and maps of the area see Lien et al. (2015), Millsap (2018), and Millsap et al. (2019).

Our terminology regarding nests and territories follows that in Millsap et al. (2015), and our data collection methods are described in detail in Lien et al. (2015), Millsap (2018), and Millsap et al. (2019). We briefly summarize these here. Each year during midwinter when deciduous trees were leafless we drove a network of roads on our study area to locate potential Cooper's Hawk nesting territories, as indicated by the presence of one or more stick nests. Although about 10% of Cooper's Hawk nests in our study area were in coniferous trees, in all cases there were alternate nest structures in nearby deciduous trees that were visible during the winter driving survey. Thus, the driving survey was an effective method for surveying the entire study area and locating previously potentially occupied nesting territories (Millsap 2018). We defined an occupied nesting territory as one in which a female Cooper's Hawk was observed in incubating position on a nest or adult behavior (e.g., nest defense, prey delivery) indicated a nest contained eggs or young. All potential nesting territories were visited to determine occupancy and nest status three to nine times each year during the breeding season (mid-March through early August). At each occupied nesting territory we examined breeding Cooper's Hawks for bands and to determine age; FY males and females were in juvenile plumage and thus were readily distinguished from AFY hawks (Millsap et al. 2019).

We captured unbanded breeders and fledged juvenile Cooper's Hawks at or near used nests each year, targeting nest sites that we had randomly selected from those occupied (see Millsap 2018 for details on capture methods). We banded the captured Cooper's Hawks with US Geological Survey and color alphanumeric-coded (ACRAFT Bird Bands, Edmonton, Alberta, Canada) leg bands. Annually during 2011–2021 we deployed an average of 14 tags including 12-g VHF tags (American Wildlife Enterprises Inc., Monticello, Florida, USA) and 10-g GPS tags (Ornitela, Vilnius, Lithuania) on FY female breeders and on recently fledged juveniles. Tags had a lifespan of up to 3 yr, but we recaptured most tagged hawks that survived that long and replaced their tags ($n = 21$). We monitored the tagged individuals for up to 7 yr; cumulatively we collected 296 bird-years of data from tagged hawks. We attached the tags by using backpack harnesses as described in Millsap et al. (2013) and Stewart and Millsap (2021). GPS tags provided location and status information roughly every 3 d via cellular downloads. We attempted to locate all VHF-tagged hawks weekly throughout the year regardless of where the birds moved. We conducted aerial searches by fixed-wing aircraft for VHF-tagged hawks that dispersed widely and were not detected during ground searches; once relocated, we resumed monitoring these hawks from the ground at least once per month. We obtained reports from the US Geological Survey Bird Banding Laboratory (BBL) for Cooper's Hawks we had banded that were found dead by others and reported to the BBL. Thus, data on survival, emigration, and return immigration of Cooper's Hawks came from the frequent relocations of tagged hawks, resightings of color-banded breeders at nests, and reports of dead hawks found by members of the public and reported to the BBL. We considered tagged or banded Cooper's Hawks that settled at nesting territories off the study area as emigrants; emigrants that subsequently returned and nested on the study area were considered immigrants in the year(s) of transition.

We placed particular emphasis on rapid recovery of the remains of tagged Cooper's Hawks that died. If a hawk's cause of death was not obvious when investigated in the field, we typically sent its remains to the Southeastern Cooperative Wildlife Disease Study, the US Fish and Wildlife Service Forensics Laboratory, or to a state wildlife health laboratory for necropsy. We confirmed some suspected gunshot deaths with X-rays performed by local veterinarians. To assign cause of death to a Cooper's Hawk that died in Mexico, we relied on observations and professional opinions conveyed by the officials who had recovered the hawk's remains.

Statistical Analyses. We used the multistate model described by Millsap et al. (2019) to analyze Cooper's Hawk capture histories, adding modifications from Millsap et al. (2022) to estimate probabilities of different causes of death. Our model contained 25 true (Fig. 1) and 25 observed (Fig. 2) states (Supplemental Material provides the full specifications of our model). The large numbers of states were necessary to account for differing probabilities of either encountering live Cooper's Hawks, or of recovering and receiving reports (hereafter recoveries) of dead Cooper's Hawks that either had been tagged or that wore only bands. Hawks with functioning tags that settled within 350 km of our study area had high live encounter and recovery probabilities. Hawks with only bands that settled at nesting territories on the study area also had relatively high live encounter probabilities. Hawks in all states had low but non-zero probabilities of being recovered dead and reported to the BBL. We assumed that the probability of receiving reports of dead recoveries by the public was the same for hawks wearing tags as for those with only bands, but we allowed the recovery rate to vary between FY and AFY hawks based on accumulating anecdotal evidence that these rates differ (Millsap et al. 2023).

Data were read into the model in the form of capture histories, with individuals in rows and time steps in columns. Capture histories provided the observed state of each individual at the start of each study year on 1 July, and survival and transition rates

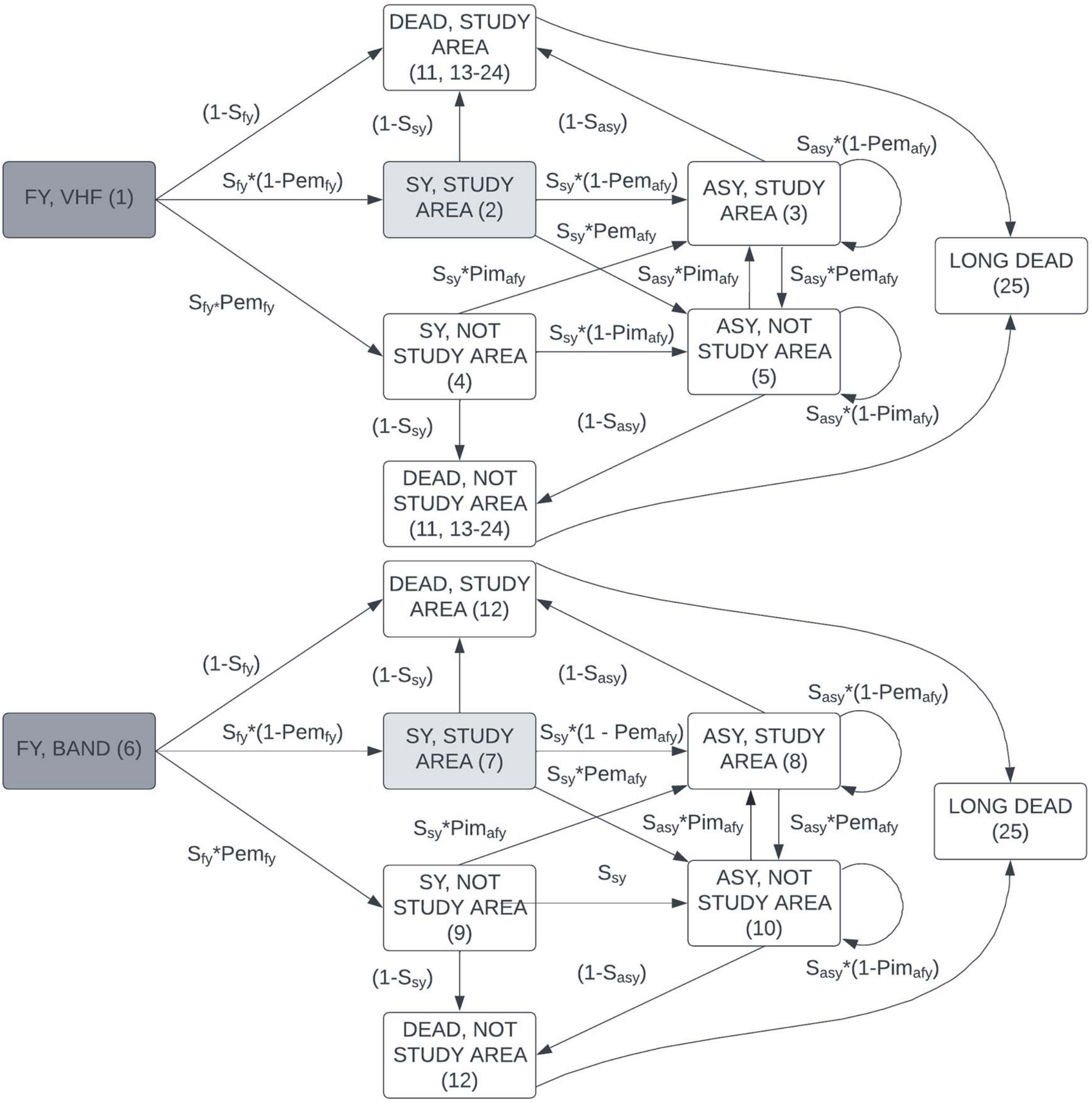

Figure 1. Graph of true states in the multistate survival model used to estimate survival rates and causes of death for female Cooper's Hawks from an urban area of New Mexico, 2011– 2021. Boxes denote true states (state numbers are in parentheses), and arrows denote transitions between states, with accompanying text specifying the transition probabilities. Long Dead (State 25) is the absorbing state; dead hawks transition into this state with a probability of 1 the year after they died. Shaded boxes indicate states in which Cooper's Hawks entered the capture history (dark gray are states where hawks only enter the history, light gray are states where hawks can enter or transition into). Abbreviations are FY = first year, SY = second year, ASY = after second year, VHF = hawks with VHF radio or GPS tags, BAND = hawks with only USGS and colored leg bands, Study Area = hawks occupying known nesting territories on the study area, Not Study Area = hawks not occupying known nesting territories on the study area, S_{fy} = first-year survival probability, S_{sy} = second-year survival probability, S_{asy} = after-second-year survival probability, Pem_{fy} = first-year emigration probability, Pem_{afy} = after-first-year emigration probability, Pim_{afy} = after-first-year immigration probability.

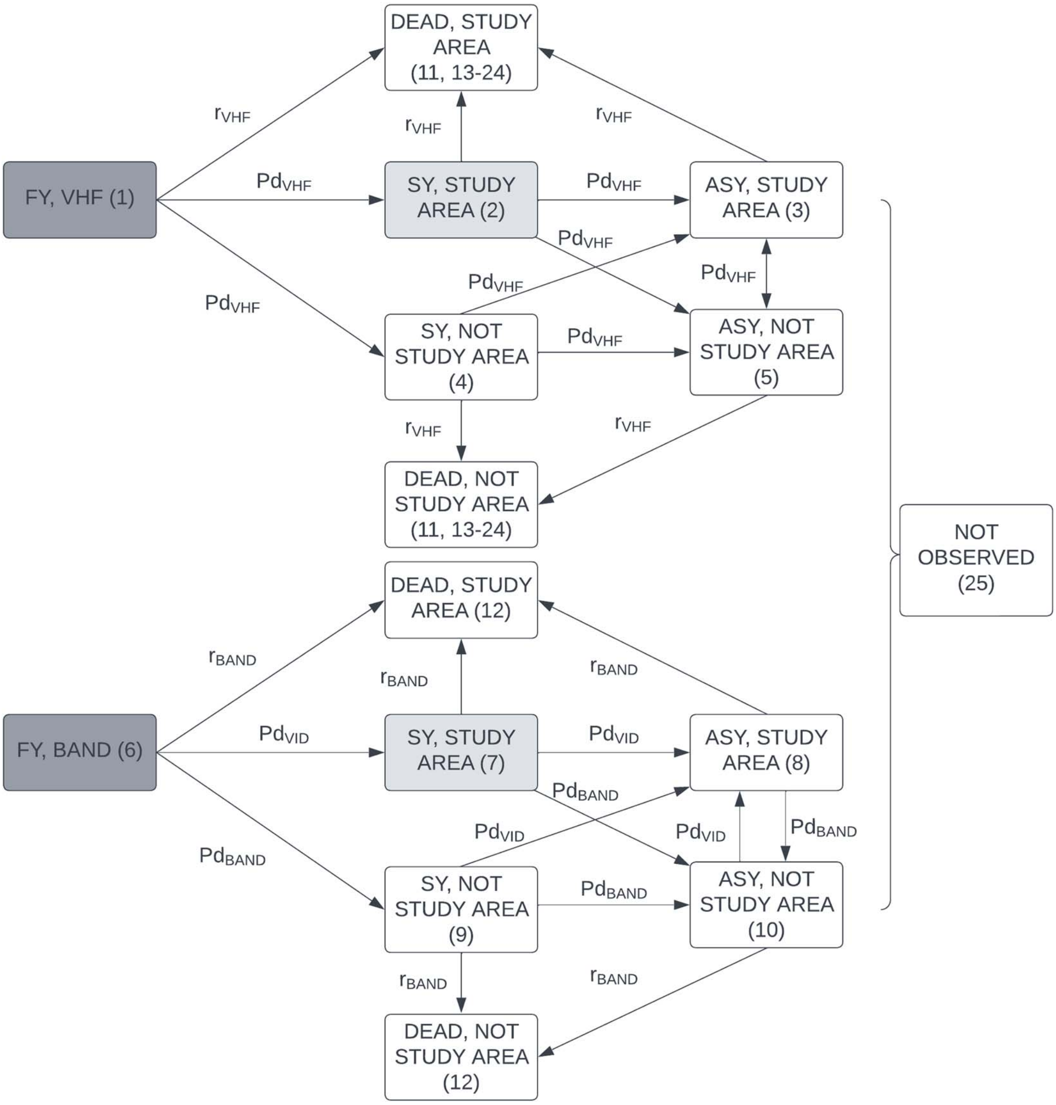

Figure 2. Graph of the observed states in the multistate survival model used to estimate survival rates and causes of death for female Cooper's Hawks from an urban area of New Mexico, 2011– 2021. Boxes denote observed states (state numbers are in parentheses), and arrows denote transitions between states, with accompanying text specifying the probabilities of observing each transition. Shaded boxes indicate states in which Cooper's hawks entered the capture history (dark gray are states where hawks only enter the history, light gray are states where hawks enter or can transition into). Abbreviations are FY first year, SY = second year, ASY = after second year, VHF = hawks with VHF radio or GPS tags, BAND = hawks with only USGS and colored leg bands, Study Area = hawks occupying known nesting territories on the study area, Not Study Area = hawks not occupying known nesting territories on the study area, Pd_{VHF} = live detection probability for hawks with functional VHF or GPS tags, Pd_{VID} = live detection probability for hawks by resighting color bands on the study area, Pd_{BAND} = live detection probability for hawks by resighting color bands off the study area, r_{VHF} = dead recovery probability for hawks wearing functioning VHF or GPS tags, and r_{BAND} = dead recovery and reporting probability for hawks based on USGS bands. Hawks that were not observed in a year entered the Not Observed state with the probability of 1 minus the relevant detection probability. Hawks that were observed to have died transitioned to the Not Observed state the year after death and each year thereafter with a probability of 1.

represented probabilities through June 30 of the next year. Time steps in the capture histories were years, and thus the parameters estimated by the model were annual probabilities (e.g., annual survival). We also provided a capture history that included known but unobserved latent states of individuals for years when they were not observed yet their status could be inferred with certainty based on subsequent encounters. For example, a banded hawk that entered the capture history in year t and that was next found newly dead in year $t + 2$ could be inferred to have been alive in year $t + 1$; that information was provided in the latent-state capture history.

We next read capture histories into our multistate model for analysis. The multistate model consisted of two matrices, one specifying the true probabilities of transitions between states between years, and the second with the probability of observing each transition. As recommended by Kéry and Schaub (2012), we included the probability of recovering and receiving reports of dead hawks in the state transition matrix. We estimated the following transition probabilities (i.e., ecological parameters) in the model: (1) annual and overall mean FY survival probabilities (S^{fy}_t and $S^{fy}_{.}$, respectively), SY survival probabilities (second-year; S^{sy}_t and $S^{sy}_{.}$), and ASY survival probabilities (after-second-year; S^{asy}_t and $S^{asy}_{.}$); (2) annual and overall mean FY emigration (Pem^{fy}_t and $Pem^{fy}_{.}$) and; (3) overall mean AFY emigration probabilities ($Pem^{afy}_{.}$), and the AFY immigration probability ($Pim^{afy}_{.}$). Parameters with the subscript "t" varied by year, whereas those estimated as constants had the subscript ".". We estimated the following probabilities of observing the transitions between ecological states: (1) the overall mean encounter probability for functioning tags ($Pd_{VHF.}$); (2) the overall mean live encounter probability for hawks with only bands that settled on nesting territories on the study area ($Pd_{VID.}$); (3) the overall mean live encounter probability for hawks with only bands that settled on nesting territories off the study area ($Pd_{BAND.}$); (4) the overall mean annual probability of failure of a tag ($\psi_{FAIL.}$); (5) the overall mean probability of recovering a dead Cooper's Hawk with a functioning tag ($r_{VHF.}$); and (6) the overall mean probability of obtaining a band recovery for a dead FY ($r^{fy}_{BAND.}$) or AFY ($r^{afy}_{BAND.}$) Cooper's Hawk. Cooper's Hawks that transitioned between ecological states between years also transitioned between corresponding detection states. For example, hawks with tags that failed, or that moved into areas where they could not be monitored transitioned into detection states for bands (i.e., $Pd_{VID.}$ if alive and occupying a known nesting territory on the study area, $Pd_{BAND.}$ if alive and off the study area, and $r^{fy}_{BAND.}$ or $r^{afy}_{BAND.}$ if dead).

In the state matrix, we specified the joint probability of individual hawks moving between ecological states between years. For example, the probability of a tagged FY hawk surviving from year t to year $t + 1$ with a functioning transmitter and settling at a nesting territory on the study area would be

$$S^{fy}_t \times (1 - \psi_{FAIL}) \times (1 - Pem^{fy}_t), \qquad (1)$$

and, in the observation matrix, we specified the probability of observing this transition as Pd_{VHF}. All tagged female Cooper's Hawks that fledged on our study area and survived until the following spring settled on nesting territories and attempted to breed in their first year and each year thereafter, so we treated the probability of breeding as 1.

Cooper's Hawks that died transitioned into a newly dead state in the model with the probability 1 – S (as indicated above, S was age- and year-specific). For Cooper's Hawks that died while wearing functioning tags, the probability of detection was high regardless of the cause of death, thus for these individuals we also estimated the overall mean transition probability to different causes of mortality for FY and AFY hawks. Causes of detected mortalities and their transition probability parameters were: (1) collision with a fence ($\psi_{FENCE.}$); (2) collision with an overhead electric distribution or other utility wire ($\psi_{WIRE.}$); (3) collision with a window ($\psi_{WINDOW.}$); (4) collision with a vehicle ($\psi_{CAR.}$); (5) electrocution ($\psi_{ELEC.}$); (6) entrapment in a structure ($\psi_{TRAPPED.}$); (7) intraspecific fighting ($\psi_{FIGHT.}$); (8) disease ($\psi_{SICK.}$); (9) poisoning ($\psi_{POIS.}$); (10) predation ($\psi_{PRED.}$); (11) illegal take (e.g., shot, or captured and killed, $\psi_{TAKE.}$); and (12) starvation ($\psi_{STARVED.}$) (Fig. 3). We also pooled probabilities of deaths from the various types of collisions to estimate the overall probability of death by collision ($\psi_{COLLISION}$). We included a state for tagged hawks that died and for which a cause of death could not be determined. Most hawks in this category died in places where we were denied access to recover them (e.g., sensitive Department of Defense or some Tribal lands). To ensure that the probabilities of known causes of death summed to 1, we included a parameter for the overall mean probability that cause of death of a tagged hawk was known ($\psi_{KNOWN.}$). We specified the transition probabilities from live states to dead states as the joint probabilities of the different parameters. Thus, for example, the probability an AFY Cooper's

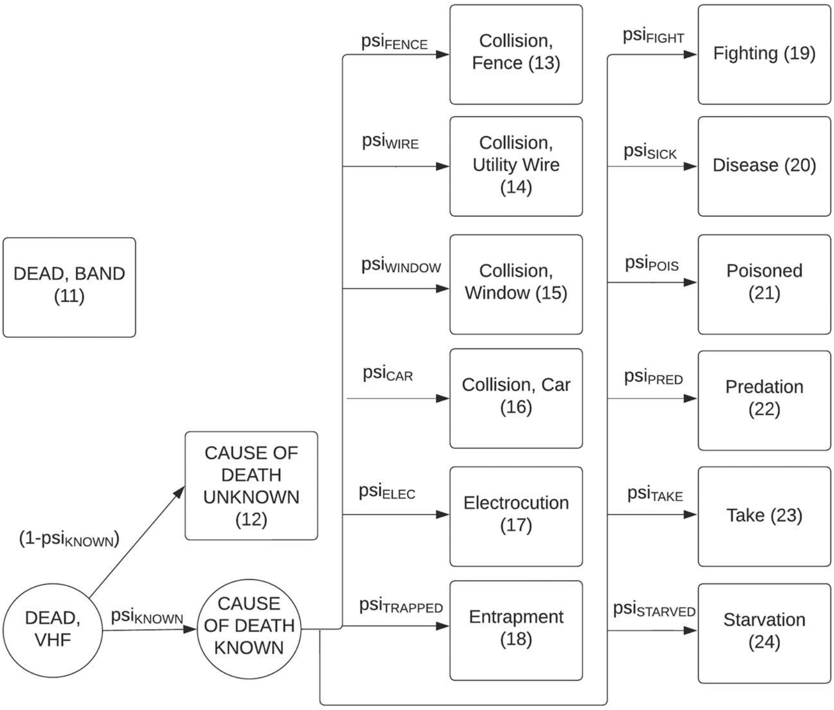

Figure 3. Cause-of-death component of the multistate survival model used to estimate survival rates and causes of death for female Cooper's Hawks from an urban area of New Mexico, 2011–2021. Squares denote true states in the model (state numbers are in parentheses), and circles denote intermediate conditions that contributed to determining a state. Transition probabilities between states, or between conditions and states, are denoted by arrows; the text denotes transition probability parameters. Probabilities of transition to each cause of death are estimated separately for FY and AFY hawks.

Hawk with a functioning tag dying in year t from a collision with a window and being recovered would be

$$\left(1 - S_t^{afy}\right) \times (1 - \psi_{FAIL}) \times \psi_{KNOWN} \times \psi_{WINDOW} \times r_{VHF}. \qquad (2)$$

As noted above, we included the probability of recovering dead hawks in the state transition matrices. Hawks wearing only bands were not included in the estimates of cause of death because of the inherent recovery bias, but they contributed to estimates of survival.

We acknowledge that tag loss associated with some forms of mortality might cause negative biases in our estimates of the probability of some causes of death (e.g., electrocution and vehicle collision, which could cause transmitters to fail). Tavecchia et al. (2012) developed a multistate cause-of-death model that accounts for such tag loss. However, to estimate the probabilities of tag failure associated with different causes of death, the model requires the recovery of some birds whose tags failed in association with a mortality event. In our study we observed no tag failure associated with any form of mortality, nor did we obtain any band recoveries of tagged hawks that had functioning tags at the time of their death. Given this, we had no data with which to implement the Tavecchia et al. (2012) model. We emphasize, however, that we had no direct evidence of a bias in recovery probability associated with any cause of death, therefore we do not believe mortality-related tag failure was a problem in our study.

Millsap et al. (2023) used a Bayesian integrated population model to generate estimates of age-specific population sizes of Cooper's Hawks on our study area immediately after fledging at the start of each year. We imported the posterior distributions of these estimates of age-specific population size for the year 2020 and then used estimates of annual survival and probabilities of different causes of death from this study to obtain joint estimates of the number of FY and AFY females that were alive on 1 July 2020 and died over the subsequent 12 mo from each cause of death. Thus, for example, the number of AFY female Cooper's Hawks that died from electrocution between 1 July 2020 and 30 June 2021 was given by

$$N^{afy}_{ELEC} = N^{afy}_{2020} \times \left(1 - S^{afy}_{2020}\right) \times \psi_{ELEC.} \qquad (3)$$

We employed Bayesian methods in most of our analyses; we fit Bayesian models with the *jagsUI* package (Kellner 2018) in R 4.1.2 (R Core Team 2021). We specified uninformative beta (1, 1) priors for all probability parameters except the cause of death transition probabilities, for which we used an uninformed Dirichlet distribution as the prior to ensure estimates across all causes of death summed to one (Kéry and Schaub 2012). For our final model run, we employed three chains of 50,000 iterations each, the first 25,000 of which were discarded as burn-in, and we used a thinning rate of 5, which provided 15,000 samples from the posterior distribution for inference regarding each parameter. We evaluated the performance of our model by using simulated data; in repeated runs, the probability density distribution of the posterior samples for parameter estimates from our model always included the parameter's true value. We assessed model convergence by examining $\hat{R}$ values (a measure of stability between chains of equal length in the Markov chain Monte Carlo output), visually inspecting posterior density plots from each chain, and by assessing autocorrelation plots and effective posterior sample sizes. We considered the model to have converged and produced adequate estimates when all $\hat{R}$ values were ≤ 1.1 (Gelman and Hill 2007), and when posterior density plots from all chains extensively overlapped and showed similar probability peaks. Throughout, we report parameter estimates as means and 95% credible intervals (0.025–0.975 quantiles; hereafter CRI). We considered parameter estimates to differ significantly if their 95% CRIs did not overlap, or if the 95% CRI of their differences did not include zero. We compared the observed monthly frequencies of fatalities against the expected uniform frequency using a χ^2-test, with P values estimated via Monte Carlo simulation (Hope 1968); we considered $P \leq 0.05$ statistically significant. We use N to denote values representative of the full population, in contrast to n for sample sizes.

RESULTS

From 2011 to 2021 we captured and banded 188 FY and 164 AFY female Cooper's Hawks on occupied nesting territories on our study area; 134 of the FY juveniles and 24 AFY breeders also were equipped with tags. Eighty-eight (55.7%) of the tagged individuals died and were recovered.

During our study, $S^{fy}_{\cdot} = 0.19$ (0.098–0.38), $S^{sy}_{\cdot} = 0.68$ (0.52–0.84), and $S^{afy}_{\cdot} = 0.75$ (0.70–0.80); annual survival rates varied among years but there was no apparent trend (Supplemental Material). As expected, live encounter probabilities were highest for hawks with tags ($Pd_{VHF.} = 0.98$ [0.94–1.0]), next highest for banded breeders at nesting territories on the study area ($Pd_{VID.} = 0.92$ [0.89–0.95]), and lowest for banded hawks not occupying breeding territories on the study area ($Pd_{BAND.} = 0.10$ [0.04–0.22]). Probabilities of band recoveries on dead birds differed as predicted between age classes, with no overlap in 95% CRIs ($r^{fy}_{BAND.} = 0.04$ [0.01–0.09] and $r^{afy}_{BAND.} = 0.22$ [0.15–0.29]).

Causes of death of the 88 tagged Cooper's Hawks that were recovered included (1) collision with fence ($n = 2$); (2) collision with overhead electric distribution line ($n = 6$); (3) collision with window ($n = 13$); (4) collision with vehicle ($n = 16$); (5) electrocution ($n = 8$); (6) entrapment in ductwork of buildings ($n = 2$); (7) intraspecific fighting ($n = 5$); (8) disease (trichomoniasis; $n = 2$); (9) poisoning ($n = 4$; all had high levels of Avitrol and Brodifacoum; death of one also may have been influenced by a high lead level); (10) predation ($n = 5$; one by domestic dogs [*Canus lupus familiaris*], one by a Great Horned Owl [*Bubo virginianus*], one by a bobcat [*Lynx rufus*], and two by unknown predator species); (11) killed by humans ($n = 8$; five were shot and three appeared to have been captured then bludgeoned); (12) probable starvation ($n = 3$); and (13) unknown cause ($n = 14$). The model-estimated probabilities of death by cause did not differ significantly between FY and AFY female Cooper's hawks (Fig. 4, Supplemental Material), although for all causes of death except overhead wire collision, poisoning, and disease, the point estimates were equal to or lower for AFY than FY hawks. Collisions overall accounted for the highest proportion of deaths regardless of age ($\psi^{fy}{}_{COLLISION.} = 0.45$ [0.31–0.60], $\psi^{afy}{}_{COLLISION.} = 0.32$ [0.18–0.50]). Collectively, anthropogenic causes of death (collisions, poisoning, shooting, entrapment, and electrocution) accounted for 73% [59–85%] of FY deaths and 68% (51–83%) of AFY deaths. Deaths attributable to predation all occurred

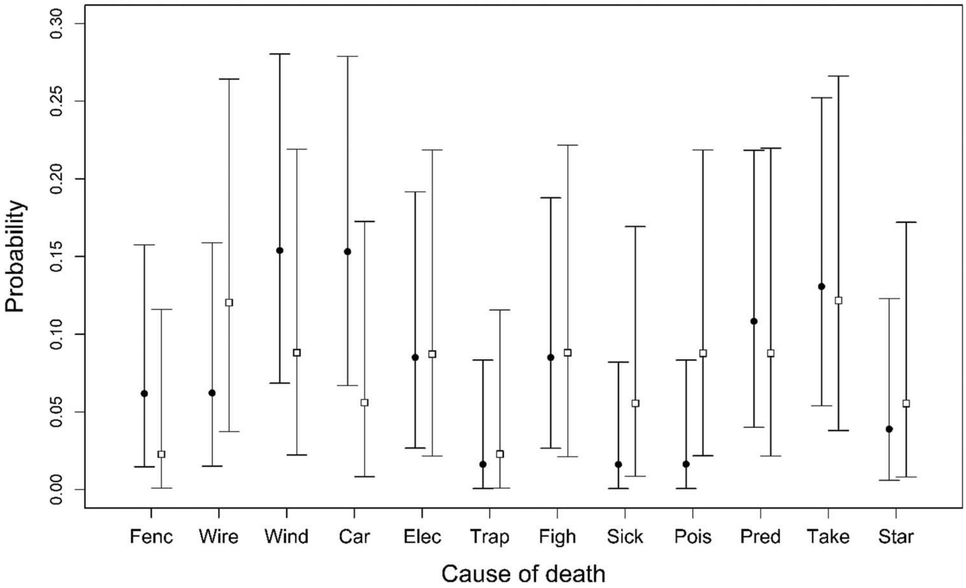

Figure 4. Model-estimated probabilities of causes of death of female Cooper's Hawks from an urban area in New Mexico, 2011–2021. Probabilities for first-year (FY) hawks are represented by closed circles, and for after-first-year (AFY) hawks by open squares. Abbreviations for causes of death are Fenc = collision with a fence, Wire = collision with an overhead electric wire, Wind = collision with a window, Car = collision with a vehicle, Elec = electrocuted, Trap = entrapped in a building, Figh = intraspecific fighting, Sick = disease, Pois = poisoned, Pred = predation, Take = illegal take, and Star = starvation. Error bars are 95% credible intervals.

off the study area and outside of the urban environment.

Deaths of FY female Cooper's Hawks were not evenly distributed across the year ($\chi^2 = 21.5$, $P = 0.02$), with frequencies highest during the first 4 mo after fledging (Fig. 5). After 31 October, the monthly frequency of mortalities dropped to a relatively steady rate that did not differ from uniform ($\chi^2 = 1$, $P = 0.99$). Deaths of AFY females did not differ from the expected uniform distribution ($\chi^2 = 11.8$, $P = 0.32$), though there was a discernable peak in February, attributable primarily to an increase in collisions. Most deaths from intraspecific fighting occurred among FY Cooper's Hawks during late winter or spring, whereas other causes of death seemed to occur at a relatively constant rate throughout the year.

Population-level consequences of the different causes of mortality reflected their respective relative frequencies (Table 1). We estimated that 126 (94–160) of 216 (184–254) female Cooper's Hawks alive on the study area on 1 July 2020 died over the subsequent year. Collisions were the most frequent cause of death (estimated $n = 54$ [18–112]) overall and the most frequent form of anthropogenic mortality, followed by illegal take ($n = 17$ [6–33]). Predation was the most frequent form of natural mortality ($n = 14$ [4–29]).

DISCUSSION

Although our understanding of causes of mortality among urban-dwelling raptors has increased greatly in recent years (Dwyer et al. 2018), biased recovery of carcasses remains a vexing problem in assessing population-level consequences of different forms of mortality (Hager 2009). The same applies to raptor populations in general (Newton et al. 1982, Kenward et al. 1993). Herein, we addressed this problem by using a known-fate sample of tagged female Cooper's Hawks originating from an urban study area to obtain relatively unbiased estimates of both the annual proportions and numbers that succumbed to different causes of death. As with several other studies of raptors in general, we found that anthropogenic factors accounted for most Cooper's Hawk deaths in our study population (De Pascalis et al. 2020, Millsap et al. 2022). We suggest this was because many hawks in our study largely spent their annual cycle

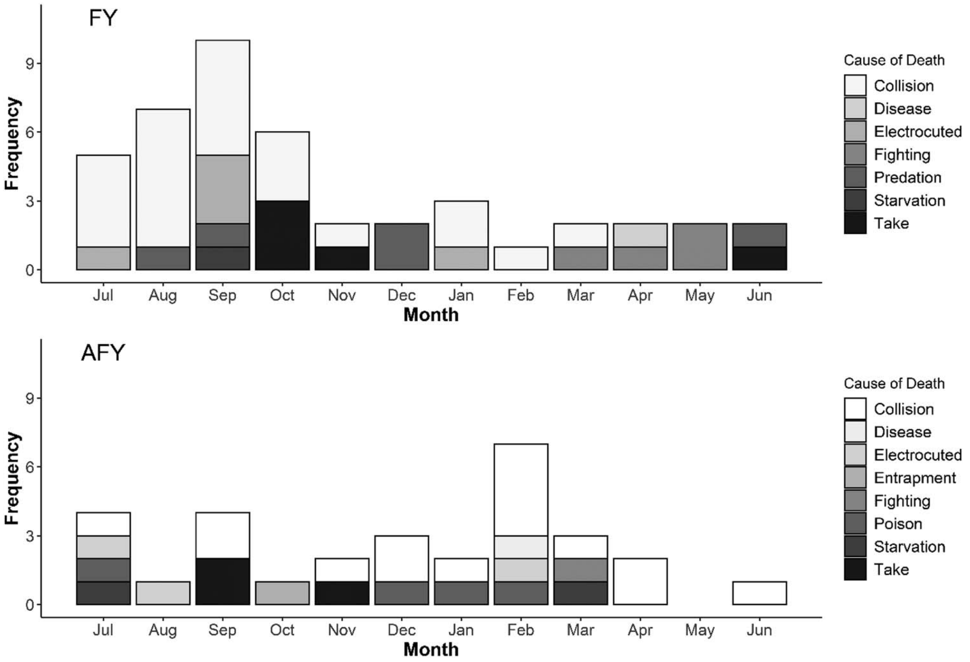

Figure 5. Frequency of observed deaths of VHF or GPS tagged female Cooper's Hawks from an urban area in New Mexico, 2011–2020 by month and cause of death. The plot labeled FY includes only Cooper's Hawks in their first year, whereas the plot labeled AFY includes only older Cooper's Hawks.

in an urban area, an environment where anthropogenic threats are widespread (Dwyer et al. 2018). Both Roth et al. (2005) and Millsap et al. (2013) reported predation as a frequent cause of Cooper's Hawk mortality in non-urban environments in Indiana and Florida, respectively. Although predation was not a leading cause of death in our study, all instances of predation we observed occurred outside the urban environment, suggesting that predation on Cooper's Hawks in New Mexico also occurs more frequently away from urban areas.

Traumatic injuries were the leading cause of death for Cooper's Hawks in our study population. Many previous retrospective studies identified such injuries as a leading cause of death in raptors as well (Morishita et al. 1998, Wendell et al. 2002, Hernandez et al. 2018, Panter et al. 2022), with collisions being a major cause of trauma (Roth et al. 2005, Dwyer et al. 2018). This was true in our study population, where collisions caused deaths of an estimated 47 of 131 FY and seven of 85 AFY female Cooper's Hawks in 2020. Collisions with windows and vehicles caused the greatest number of collision deaths, but their relative frequency dropped disproportionately after the first year of life, suggesting hawks may have learned to avoid these threats. Collisions with overhead wires, poisoning, and disease were the only types of mortality that increased proportionally with age. Higher rates of poisoning in older hawks may have resulted from bioaccumulation of both lead and anticoagulant rodenticides (Niedringhaus et al. 2021, Slabe et al. 2022).

We found that direct, purposeful take in the form of shooting or capture and bludgeoning also was a frequent cause of mortality for Cooper's Hawks in New Mexico. Killing of Cooper's Hawks is prohibited in the USA by the federal Migratory Bird Treaty Act and New Mexico state law unless authorized by permits (Millsap et al. 2007), and no instances of purposeful take that we observed were so authorized. Ours is at least the third recent published study to demonstrate that purposeful illegal killing remains a threat to raptors in the USA (Katzner et al. 2020, Millsap et al. 2022). Persecution, which could include many forms of take, is a pervasive risk to raptors worldwide (Madden et al. 2019). This may be lessening in parts of Europe (De Pascalis et al. 2020, but see Cianchetti-Benedetti et al. 2016), but apparently not in the USA despite enforcement of laws prohibiting take and widespread education

Table 1. Population-level impacts of different causes of mortality among female Cooper's Hawks from an urban area of New Mexico. Values are the number of female Cooper's Hawks in each age class estimated to be alive on 1 July 2020 and, for those that died by 30 June 2021, their estimated cause of death. Data on relative proportions of death by cause are based on information collected during 2011–2021, whereas population size information for 2020 is from Millsap et al. (2023). See Methods (formula 3) for more detail.

Bird Status or Mortality Cause	First Year			After First Year		
	Mean	SD	95% CRI[a]	Mean	SD	95% CRI[a]
Alive 1 July 2020	131	16	101–165	85	2	83–89
Alive 30 June 2021	27	7	14–43	63	3	58–70
Total Died	104	14	77–134	22	2	17–27
Cause of death						
Collision with fence	7	4	1–17	1	1	0–3
Collision with wire[b]	7	4	1–17	3	1	1–6
Collision with window	16	6	7–30	2	1	0–5
Collision with vehicle	17	6	7–31	1	1	0–4
Electrocution	9	5	3–21	2	1	0–5
Entrapped in building	2	2	0–9	1	1	0–3
Intraspecific fighting	9	5	3–20	2	1	0–5
Disease	2	2	0–9	1	1	0–4
Poisoning	2	2	0–8	2	1	0–5
Predation	12	5	4–24	2	1	0–5
Killed by human[c]	14	6	5–27	3	1	1–6
Starvation	5	3	1–13	1	1	0–4

[a] Credible interval.

[b] Overhead electric distribution lines.

[c] This category combines shooting and bludgeoning, both illegal forms of purposeful take.

efforts. There remains a need for novel, innovative conservation actions to curtail persecution of raptors by humans. To this end, Madden et al. (2019) recommended use of a multi-tiered strategy that could include economic incentives.

Trichomoniasis was rarely observed in our study and caused few deaths, but it was identified as a leading cause of mortality among fledglings in an urban population of Cooper's Hawks in Tucson, Arizona (Boal et al. 1998). This discrepancy is puzzling because main hosts of the protozoan that causes the disease, *Trichomonas gallinae*, are columbiform birds, which made up 78% of the diet of female Cooper's Hawks on our study area (Millsap 2018), and we know from the few hawks that were infected that the protozoan was present on our study area. We do not know why trichomoniasis was not more frequent among Cooper's Hawks in Albuquerque, but it is possible virulence varies geographically or temporally, or that the hotter and dryer conditions in Tucson led doves to congregate more at shared water sources, increasing opportunities for transmission (Hedlund 1998). This is an area where further research is warranted.

Annual survival rates of female Cooper's Hawks in our study were greater for AFY hawks than FY hawks, consistent with the trend typical of raptors (Newton et al. 2016). The AFY annual survival rate of 0.75 that we observed was comparable to AFY annual rates or approximations thereof from other studies across the species' range: 63–79% in eastern North America (Henny and Wight 1972), 66% and 81% apparent annual survival for SY and ASY individuals, respectively, in Arizona (Mannan et al. 2008); 84% in most years but as low as 36% in years of prey shortage in Florida (Millsap et al. 2013), and 75% apparent survival for breeding females in Wisconsin (Rosenfield et al. 2016). Fewer studies have reported annual survival rates for FY females, but the annual FY survival rate we observed was comparable to the 18–22% rate reported by Henny and Wight (1972) in eastern North America for 1925–1957, but much lower than the 64% apparent annual survival rate reported by Mannan et al. (2004) in Arizona. Cooper's Hawk population size increased during our study, resulting in a surplus of emigrant females in most years (Millsap 2018, Millsap et al. 2023). As such, the survival rates we observed were associated with positive population growth rates in most years.

Survival of AFY female Cooper's Hawks in our study population was relatively constant across a given year, as was the case in Florida (Millsap et al. 2013). FY female survival was not constant, however, with most deaths occurring during the first 4 mo after fledging as juvenile hawks transitioned to independence and undertook dispersal or, in some cases, migration. Although most initial FY deaths were due to collisions, most FY deaths later in the annual cycle (March–May) stemmed from intraspecific aggression during exploration for breeding opportunities. Aggressive encounters associated with breeding have also been reported for both sexes in other Cooper's Hawk populations (Boal 2001). Interestingly, we documented only one death of an AFY female from fighting, although the small peak in AFY mortality in February coincided with the initiation of annual pair-bonding on nesting territories (Millsap 2018). Females often engaged in vigorous chases with one another near nests early in the breeding season, which might explain the increase in collision mortality at this time. Thus, for both age classes, the ultimate cause of most deaths in late winter and early spring appeared to be associated with securing a nesting territory and mate.

We were unable to include male Cooper's Hawks in this analysis because males are not large enough to carry tags required for multi-year tracking. Elsewhere we analyzed and reported that male annual survival rates were similar to those of females (Millsap et al. 2019, 2023). Band recoveries of male Cooper's Hawks from our study ($n = 43$) suggest they are similarly susceptible to collisions and electrocution. Moreover, demographic modeling suggests male mortality rates increased with increasing density (Millsap et al. 2023), implying that as with females, intraspecific aggression may have been an important mortality factor. Males are the limiting sex in our study population (Millsap et al. 2019), thus mortality factors affecting that sex are of considerable interest. Consequently, replicating this study on male Cooper's Hawks once suitable tags are available would be an important direction for future research.

SUPPLEMENTAL MATERIAL (available online). R code and output from the multistate survival model used to estimate annual survival rates and causes of death of female Cooper's Hawks from an urban study area in New Mexico, 2011–2021.

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