Demographic consequences of sexual differences in age at first breeding in Cooper’s Hawks (Accipiter cooperii)

Brian A. Millsap,1,4,*, Kristin Madden,1 Robert K. Murphy,3 Mark Brennan,1 Joel E. Pagel,1 David Campbell,4 and Gary W. Roemer5

1 Division of Migratory Bird Management, U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA
2 Department of Biology, New Mexico State University, Las Cruces, New Mexico, USA
3 Eagle Environmental, Inc., Santa Fe, New Mexico, USA
4 Ecological Services, U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA
5 Department of Fish, Wildlife, and Conservation Ecology, New Mexico State University, Las Cruces, New Mexico, USA

* Corresponding author: brian_a_millsap@fws.gov

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ABSTRACT
Life-history theory predicts individuals should breed as soon as they are able to reproduce, but many long-lived birds delay breeding. In the Accipitriformes, delayed breeding is the norm, and age when breeding begins is influenced by competing selective pressures. In most Accipitriformes, the reproductive roles of males and females differ; males do most of the foraging and females tend eggs and young. Thus, sexual differences in age at first breeding might be expected, but these differences, possible causes, and implications for individual fitness have received little study. We investigated sexual differences in age at first breeding in a marked population of Cooper’s Hawks (Accipiter cooperii) from 2011 through 2018 in central New Mexico, USA. We hypothesized that males required more experience to pair and breed successfully than females, and we predicted: (1) a lower mean age at first breeding for females than males, and (2) that expected individual fitness of early-breeding males would be lower than for early-breeding females. We found that 79% more females than males bred in their first year (hatching year, HY), and expected individual fitness of HY-breeding females was 21% greater than for HY-breeding males. HY males that attempted to breed settled on nesting territories with exceptionally high prey abundance, nevertheless they experienced 37% lower second-year survival than males that delayed breeding. Females competed for mates based on male age. HY females that paired with relatively older males had 33% higher second-year survival and 16% higher expected individual fitness than HY females that initially paired with relatively younger males. The observed annual rate of growth ($\lambda$) of our study population was 1.08, closer to $\lambda$ predicted by male (1.02) than female (1.21) demographic models. Delayed breeding by males thus had important ramifications for $\lambda$, highlighting the need to consider sexual differences in age at first breeding in demographic analyses.

Keywords: Accipiter cooperii, delayed breeding, fitness, ideal preemptive distribution, intrasexual competition, mate choice, recruitment

Consecuencias demográficas de las diferencias sexuales en la edad al momento de la primera reproducción en Accipiter cooperii

RESUMEN
La teoría de historia de vida predice que los individuos deberían reproducirse tan pronto como puedan, pero muchas aves longevas retrasan la reproducción. En los Accipitriformes, el retraso en la reproducción es la norma, y la edad a la que comienzan a reproducirse está influenciada por presiones selectivas que compiten entre si. En la mayoría de los Accipitriformes, los roles reproductivos de los machos y las hembras son distintos; los machos realizan la mayor parte del forrajeo y las hembras atienden los huevos y los pichones. De este modo, se esperarían diferencias sexuales en la edad al momento de la primera reproducción, pero estas diferencias, las causas posibles y las implicancias para la adecuación biológica individual han sido poco estudiadas. Investigamos las diferencias sexuales en la edad al momento de la primera reproducción en una población marcada de Accipiter cooperii desde 2011 hasta 2018 en el centro de Nuevo México, EEUU. Hipotetizamos que los machos requieren más experiencia para ponerse en pareja y criar exitosamente que las hembras, y predijimos: (1) una menor edad promedio en la primera reproducción para las hembras que para los machos, y (2) que la adecuación biológica individual esperada de los machos reproductivos más jóvenes sería más baja que la de las hembras reproductivas más jóvenes. Encontramos que un 79% más de hembras que de machos se reproducen en su primer año (PA), y que la adecuación biológica individual esperada de las hembras del PA fue un 21% más alta que la de los machos reproductivos del PA. Los machos del PA que intentaron reproducirse se asentaron en territorios de
anidación con abundancias de presas excepcionalmente altas, a pesar de lo cual el segundo año experimentaron una supervivencia 37% menor que la de los machos que retrasaron la reproducción. Las hembras compitieron por parejas basándose en la edad del macho. Las hembras del PA que se pusieron en pareja con machos relativamente más viejos tuvieron una supervivencia 33% más alta en el segundo año y una adecuación biológica individual esperada 16% más alta que las hembras del PA que inicialmente se pusieron en pareja con machos relativamente más jóvenes. La tasa de crecimiento anual observada ($\lambda$) de nuestra población de estudio fue 1.08, más cercana a la tasa $\lambda$ predicha por los modelos demográficos para las hembras (1.21). Por ende, el retraso en la reproducción por parte de los machos tuvo ramificaciones importantes para la, subrayando la necesidad de considerar las diferencias sexuales de la edad al momento de la primera reproducción en los análisis demográficos.

Palabras clave: Accipiter cooperii, adecuación biológica, competencia intrasexual, distribución preventiva ideal, elección de la pareja, reclutamiento, reproducción retrasada

INTRODUCTION

Life-history theory predicts that to maximize lifetime reproductive success, individuals should breed as soon as they are physiologically capable of doing so (Smith 1978, Lande 1982, Williams 2008). In many species, however, mean age at first breeding is beyond the age when reproduction is first possible (Zack and Stutchbury 1992). Delayed breeding has long been recognized to profoundly affect both individual fitness (Prévote-Julliard et al. 1999, Brommer et al. 2002, Oli et al. 2002) and population regulation (Rodenhouse et al. 1997, Hunt 1998, 2015, Hunt and Law 2000), and as such is undoubtedly under strong selection pressure (Moreno 2016).

In the Accipitriformes—hawks, eagles, and kites—delayed breeding is the norm. Most species in this order go through 1 or more basic plumage cycles before attaining the definitive plumage (Clark and Pyle 2015), thus young usually differ markedly in appearance from adults. Newton (1979) postulated that such plumage cycles evolved in birds where individuals do not normally breed until attaining definitive plumage, and that in these species, breeding in predefinitive plumage should be rare. Multiple studies have demonstrated this to be the case (Newton 1979, Newton et al. 1981, Steenhof et al. 1983, Kenward et al. 1999, Newton and Rothery 2002, Rosenfield et al. 2013). In many populations of Accipitriformes, first breeding often occurs long after the definitive plumage is acquired, such that a portion of the adult population consists of nonbreeding adult floaters awaiting a chance to settle on a nesting territory (Newton and Marquiss 1991, Hunt 1998, Kenward et al. 2000, Penteriani et al. 2011). Moffat’s equilibrium theory predicts that such conditions should arise in populations where suitable breeding sites are limited, and under these conditions availability of suitable nesting territories may be the primary factor governing population size and structure (Hunt 1998, Hunt and Law 2015). Because greater age typically provides an advantage in acquiring a breeding slot (Newton et al. 1979, Ferrer and Bisson 2003, Lien et al. 2015), density-dependent age at first breeding is a predictable consequence of populations at Moffat’s equilibrium. There is ample evidence of such density dependence on age at first breeding in the Accipitriformes (Steenhof et al. 1983, Newton 1992, Ferrer et al. 2004, Krüger 2005, Balbontín and Ferrer 2008).

In contrast to the situation in stable populations where first breeding is often delayed, in increasing or declining hawk and eagle populations, individuals in predefinitive plumage are often observed breeding. This occurs, for example, when there is a high turnover of breeding adults (Ferrer et al. 2003, 2004), or in periods of rapid population growth (Margalida et al. 2008, Stout and Rosenfield 2010). However, even under these conditions, and despite the presence of young potential breeders and adult floaters, nesting territories may remain unused (Newton 1976, Newton and Marquiss 1991, Penteriani et al. 2011). Thus, there is likely a territory-quality component to suitability, such that below some variable threshold of quality, the cost of attempting to breed exceeds the benefits (Newton et al. 1979, Hunt 2015). Individual quality of a mate, including age, undoubtedly plays a role with respect to this territory suitability threshold (Newton et al. 1979, Zabala and Zuberoigotia 2014, Rosenfield 2017). The age at which a hawk or eagle begins breeding is thus under complex competing selective pressures; early breeding is advantageous, but only if a suitable breeding slot and mate can be obtained, and only then if the fitness benefit of attempting to breed exceeds the cost of not making the attempt. These tradeoffs vary greatly among and within species in different physical and demographic environments (Blas et al. 2009, Hunt 2015).

Sex is another factor that influences age at first breeding in some groups of birds with delayed breeding (e.g., Cathartiformes) (e.g., Blanco 1996, Sanz-Aguilar et al. 2017). In the Accipitriformes, males and females have different roles in reproduction. The male competes with other males for territories, courts females, and—perhaps most importantly—provides most of the food for the female and brood during the incubation and nesting periods (Newton 1979, 1986, Kenward 2006). The female competes with other females for territories and mates, does most of the incubation, broods and feeds the young, and performs the primary defense of the nest from predators (Newton 1979, 1986, Kenward 2006). The different roles the sexes play in reproduction would seemingly lead to differential selection
pressures on age at first breeding. For example, it has long been recognized that in many species of hawks and eagles, more females breed in predefinitive plumage than males (Newton 1979). This has been interpreted as evidence of earlier breeding by females than males, and attributed to the possibility that males either require more experience than females to breed successfully (Reynolds 1972, Boal 2001a, Tøttrup Nielsen and Drachmann 2003, Millsap 2018a), or because there are substantially greater fitness costs to males that breed early compared with females (Rosenfield et al. 2013). Despite this evidence and the potential significance of differences in age at first breeding between the sexes in the Accipitriformes, to our knowledge this topic has received little study. Four compelling questions, then, are, does age at first breeding in hawks and eagles vary with sex? If so, what are the differences, how does selection contribute to those disparities, and what are the demographic consequences of such differences?

We collected data on age at first breeding, along with other demographic information, from a sample of color-marked and radio-tagged Cooper’s Hawks (Accipiter cooperii; Figure 1). Cooper’s Hawks are well suited as a species for tests of hypotheses related to age at first breeding in the Accipitriformes. Both sexes of Cooper’s Hawks have a single first-cycle, juvenal plumage, and attain their definitive plumage in a molt that commences at about 1 yr of age (Curtis et al. 2006, Clark and Pyle 2015). Cooper’s Hawks are typically monogamous and have high fidelity to nesting territories once they have settled. Both sexes typically first breed at age 2 (Curtis et al. 2006), but in some areas comparatively large numbers of individuals breed as 1-yr olds (hereafter hatching year, or HY), while in juvenal plumage (Boal 2001a, Stout and Rosenfield 2010, Millsap et al. 2013). Sex ratios at fledging in Cooper’s Hawk broods in our study area are typically equal (Millsap 2018a).

We hypothesized that the comparative paucity of HY male breeders in many Cooper’s Hawk populations reflects a high fitness cost to males attempting to breed in their first year, as described above and as predicted by Rosenfield et al. (2013) (Table 1). Under this hypothesis, we predicted that the expected individual fitness of breeding HY males would be lower than that of males that delayed breeding. We also considered the alternative, but not mutually exclusive hypothesis, that breeding by young male Cooper’s Hawks was possible only when they were able to secure good nesting territories, as suggested by Newton (1976) for Eurasian Sparrowhawks (A. nisus). The most direct measure of territory quality in hawks and eagles is relative prey abundance (Newton 1979, Ferrer and Donazar 1996, Penteriani et al. 2013). Thus, under this alternative hypothesis, we predicted that male prey abundance on nesting territories occupied by HY males would be at least comparable with, if not higher than, prey populations on nesting territories occupied by after-hatching-year (AHY) males (we specify “male prey” here because male Cooper’s Hawks tend to capture smaller prey of different species than do the females [Millsap et al. 2013, Millsap 2018a]).

For female Cooper’s Hawks, we hypothesized that fitness costs of early breeding would be lower than those for males because females require less experience to breed successfully. Consequently, we predicted higher rates of first-year breeding for females than males, and higher expected individual fitness of HY females that bred compared with expected fitness of HY males that bred. We also hypothesized that under relaxed fitness constraints, intrasexual competition for available breeding opportunities would be the primary factor limiting breeding by HY females, as suggested by Lien et al. (2015). Under this hypothesis, we predicted that nesting territory acquisition by female Cooper’s Hawks would follow an ideal preemptive distribution model, where more competitive females acquire the best territories, and relegate less competitive females to lower-quality sites (Pulliam and Danielson 1991). Older hawks and eagles are typically more successful than younger...
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The primary factor limiting breeding by HY males is a high fitness cost to not delaying breeding until at least age 2

P1. Expected individual fitness of males that delay breeding will be greater than expected fitness of males that breed in their first year

H2. Breeding by younger males is more likely on nesting territories with high prey abundance

P2. Nesting territories occupied by relatively younger males will have comparable or higher mean prey abundance than those occupied by older males

H3. Fitness costs of breeding by HY males that breed in their first year are likely to be lower than for AHY males that breed in their first year

P3a. A higher proportion of HY females than AHY females will breed

P3b. Expected individual fitness of AHY females that initially settle on higher quality nesting territories will be greater than that of females that initially settle on less desirable nesting territories

H4. Intrasexual competition for nesting territories is the primary factor regulating early breeding by females

P4a. AHY females will settle at greater rates than HY females on nesting territories with higher male and female prey abundance, and with relatively older males

P4b. Larger HY females will settle at greater rates than smaller HY females on higher quality nesting territories

P4c. Expected individual fitness of HY females that initially settle on higher quality nesting territories will be greater than that of females that initially settle on less desirable nesting territories

H5. Differences in age at first breeding will affect the population finite rate of increase (λ)

P5. λ will be constrained by the sex that delays breeding to the greatest degree

TABLE 1. A summary of hypotheses and predictions tested regarding age at first breeding in a north central New Mexico Cooper’s Hawk population, 2011–2018. The term HY refers to individuals in the hatching year, therefore ≤1 yr old.

| Hypotheses | Prediction |
|-------------|------------|
| H1. The primary factor limiting breeding by HY males is a high fitness cost to not delaying breeding until at least age 2 | P1. Expected individual fitness of males that delay breeding will be greater than expected fitness of males that breed in their first year |
| H2. Breeding by younger males is more likely on territories with high prey abundance | P2. Nesting territories occupied by relatively younger males will have comparable or higher mean prey abundance than those occupied by older males |
| H3. Fitness costs of breeding by HY males that breed in their first year are likely to be lower than for AHY males that breed in their first year | P3a. A higher proportion of HY females than AHY females will breed |
| H4. Intrasexual competition for nesting territories is the primary factor regulating early breeding by females | P3b. Expected individual fitness of AHY females that initially settle on higher quality nesting territories will be greater than that of females that initially settle on less desirable nesting territories |
| H5. Differences in age at first breeding will affect the population finite rate of increase (λ) | P5. λ will be constrained by the sex that delays breeding to the greatest degree |

conspecifics in contests over territories (Newton et al. 1979, Ferrer and Bisson 2003, Margalida et al. 2008, Lien et al. 2015), so if the preemptive distribution hypothesis was supported, we predicted that most nesting territories occupied by AHY females would be of higher quality than those occupied by HY females. Another factor associated with greater competitive ability in females of several predatory birds is size: larger females are dominant over smaller ones (Olsen and Olsen 1987, Warkentin et al. 2016). Thus, we also predicted that larger HY females would more often acquire high-quality nesting territories than smaller HY females. Finally, we predicted that HY females that secured high-quality nesting territories would have greater expected individual fitness than those that settled on nesting territories of lesser quality. Assessing nesting territory quality for female Cooper’s Hawks is more complex than for males, because females do little foraging while breeding and instead rely heavily on food provided by males (Millsap et al. 2013, Lien et al. 2015). Thus, we surmised that male provisioning ability was likely an important indicator of nesting territory quality for a female, and one that could be affected by both the individual quality of the male and by the abundance of prey on the nesting territory. We used male age as the indicator of individual male quality, with older males generally being of higher quality and thus likely to be preferred by females, based on findings from previous work at our study area (Lien et al. 2015), and from work on several other hawk and eagle species (Penteriani et al. 2003, Murgatroyd et al. 2018). We also used male prey abundance as an alternative indicator of nesting territory quality, and we used the estimated abundance of female prey (the abundance of the larger avian prey preferred by females) within the nesting territory as a third potentially important indicator of nesting territory quality for females.

Finally, sexual differences in age at first breeding is a demographic consideration typically not included in population analyses. Yet, if males and females have similar life spans yet initiate breeding at different ages, the sex that delays breeding longer could become the limiting sex (Steifetten and Dale 2006). We hypothesized that this could be the case in hawks and eagles that display sexual differences in age at first breeding and in which the sexes have similar adult survival, as is the case with Cooper’s Hawks (Mannan et al. 2008, Millsap et al. 2013). Thus, we predicted that the population finite rate of increase (λ) of our study population would more closely match the expected individual fitness of the sex that delayed breeding to the greatest degree.

METHODS

Study Area

Our study was conducted from February 2011 through June 2018. Most data were collected on a 72 km² urban
study area in northeastern Albuquerque, a city of about 500,000 people in Bernalillo County, New Mexico, USA (35.1107°N, 106.6100°W). The urban study area was 49% residential, 37% industrial, and 14% parks and open space. Natal dispersal by Cooper’s Hawks from the urban study area ranged to 46 km, thus the extended study area for our analysis was the urban study area and surrounding urban and exurban areas within 46 km; for a more thorough description and maps of the area see Lien et al. (2015) and Millsap (2018a, 2018b).

Data Collection

We annually located potential Cooper’s Hawk nesting territories (terminology follows Millsap et al. 2015) on the urban study area by driving a network of roads over the entire area in winter to locate stick-nests when deciduous trees were leafless. Except for 2 pairs of American Crows (Corvus brachyrhynchos) and 2 pairs of Swainson’s Hawks (Buteo swainsoni), Cooper’s Hawks were the only bird or mammal species that constructed large stick nests on our study area. Thus, we were confident that the large nests we detected had been built by Cooper’s Hawks. Typically, Cooper’s Hawk nesting territories were occupied for several years and so they often contained many nests. We considered new nests further than the 10th quantile of the mean nearest-neighbor distance of simultaneously used nests as new potential nesting territories (see Millsap 2018a for additional details).

We monitored all previously known and new potential Cooper’s Hawk nesting territories each year to determine (1) whether they were occupied by a breeding pair of Cooper’s Hawks (confirmed by the presence of an incubating female, eggs in a nest, or fledged young); (2) whether the nest attempt was successful (>1 young survived to 24 d); and (3) if successful, the number of fledged young. Each year, all nesting territories were visited at least 3 times: once each during incubation, nestling, and predispersal periods; 50–60% were randomly selected to be visited 3 times during each period, for a total of 9 visits. We used playback calls (FoxPro Firestorm caller, FoxPro Inc., Lewiston, Pennsylvania, USA) to aid in the initial detection of occupied nesting territories (Mosher et al. 1990). Although playback calls occasionally attracted breeders from adjacent territories, we were able to confidently discern the status of each nesting territory through repeated visits. We counted the number of young seen on each post-fledging visit, and estimated age of fledglings based on plumage development (Madden et al. 2018).

We determined the age of breeders on each occupied nesting territory annually. We labeled hawks in their first full year of life (i.e. juveniles) as hatching-year (HY), hawks 1 to 2 yr-old as second-year (SY), and hawks older than 2 yr as after-second-year (ASY). For some analyses, we pooled SY and ASY individuals into an AHY age class. Note that we used a modified calendar-based age classification system to conform to the full annual cycle rather than adopting a molt-based system (Clark and Pyle 2015), because the former more closely matches the breeding cycle in Cooper’s Hawks.

Each year we captured and color-banded (ACRAFT Bird Bands, Edmonton, Alberta, Canada) as many breeding adults, fledged young, and overwintering HY female Cooper’s Hawks as possible using methods described in Millsap (2018b). Color bands had unique alpha-numeric codes readable from a distance with spotting scopes or binoculars. We identified all banded breeding Cooper’s Hawks each year by reading their color bands at nests. Cooper’s Hawks in juvenal plumage were known to be <1.25 yr-old, but individuals in definitive plumage could only be aged with certainty to >1.25 yr. Eye color in Cooper’s Hawks, however, provides a relative indication of age because iris color progresses predictably but somewhat irregularly from green at fledging, through yellow, orange, and eventually to red (Rosenfield et al. 1992). Rates of change in eye color vary geographically, between sexes, and among individuals (Rosenfield et al. 2003), thus eye color is not a direct determinant of age but can be used to distinguish between relatively younger and older individuals for a given population (Rosenfield et al. 2016). All male and female Cooper’s Hawks we captured were assigned an eye color score based on the predominate color of the iris in comparison to a standardized color chart (Palmer 1962). Following Rosenfield et al. (1992) and Rosenfield and Bielefeldt (1997), we recognized 5 eye-color categories among possible breeders: (1) yellow, (2) yellow-orange, (3) orange, (4) orange-red, and (5) red (see figure 2.1 in Millsap 2018b). We used eye color scores directly in some analyses, but to assess the role of individual male quality we grouped males into 2 age categories: (1) relatively younger males, those with yellow, yellow-orange, and orange irides; and (2) relatively older males, those with orange-red or red irides. Our categorization was supported by captures of known-age males on our study area: all of 13 SY males we recaptured had yellow-orange or orange irides, whereas all 8 known-age ASY males had orange-red or red irides.

To obtain data for size comparisons, we measured unflattened wing chord, tarsus length, and mass of each Cooper’s Hawk captured, as described in Millsap et al. (2013). We also recorded the fat score for each individual based on the extent of deposited fat visible in the underwing, following DeSante et al. (2016); scores ranged from 0 (no visible fat) to 6 (fat bulging). Nearly all fat scores were recorded by one individual (B.A.M.) to reduce sampling variation. We made a concerted effort during February through early April to capture or recapture HY females that were settling on nesting territories, along with their
prospective mates. We restricted comparisons of mass and fat scores to individuals captured in the February–April temporal window.

At randomly selected territories, we deployed 3 to 33 VHF radio transmitters (American Wildlife Enterprises Inc., Monticello, Florida, USA) on fledged female Cooper’s Hawks each year from 2011 to 2017 and on fledged males each year during 2015 to 2017 (see Appendix Table 5); we also deployed transmitters on 19 overwintering HY females trapped on the urban study area in autumn and winter. Transmitter attachment protocols followed Millsap et al. (2013), who showed there was no difference in survival rates or fecundity of Cooper’s Hawks radio-tagged under this protocol compared with those wearing only bands. Weight and battery life of transmitters on females and males were 13 g and 1,000 d, and 6 g and 300 d, respectively. We attempted to locate all radio-tagged hawks weekly throughout the study. When a radio-tagged hawk was found, we recorded its location, general behavior, and, if feeding, the species of prey. In autumn and spring of each year, we used fixed-wing aircraft equipped with receiving antennas to search for missing radio-tagged hawks throughout suitable habitat (Rio Grande River forest and nearby mountains) between Española in north central New Mexico (143 km north of our study area) to the USA–Mexico border (428 km south).

From 2013 to 2015, we estimated prey density with avian fixed-point counts at 67 systematic-random points distributed across the study area in April, the month in which most Cooper’s Hawks laid eggs. We conducted point counts following the Breeding Bird Survey protocol (Sauer and Link 2011), except that we conducted counts at each point for 5 as opposed to 3 min, and limited counts to birds detected by sight or sound within 100 m. We used a rangefinder (Nikon Laser 1200S, Nikon, Tokyo, Japan) to measure the distance to each bird detected during these surveys.

Analyses

For most analyses, we used Bayesian Markov chain Monte Carlo (MCMC) methods implemented in JAGS (Plummer 2017) or WinBUGS (Gimenez et al. 2009, Lunn et al. 2012) through Program R (R Core Team 2015) to estimate posterior distributions of parameters and unknown random variables. For most models, we ran 3 chains for 21,000 iterations each, and discarded the first 1,000 iterations as a burn-in; for the Poisson generalized linear mixed-models (GLMM), longer chains were necessary to attain convergence. We used R̃, a measure of stability between chains of equal length in MCMC output, to assess model convergence, with a value of R̃ < 1.1 indicating convergence (Gelman and Hill 2007). We also computed Bayesian P-values to assess model fit where appropriate (Kéry 2010).

We report the upper and lower 90% credible interval (CI) with parameter estimates except in the case of prey abundance, in which case we report 90% confidence intervals. Unless otherwise noted, we compared parameter estimates directly by determining differences between posterior distributions, and we report the probability that the difference differs from zero (P [x 0]).

Predictions regarding male fitness. Testing predictions regarding fitness consequences of male breeding alternatives required estimation of age-dependent survival and fecundity according to age of first breeding. We estimated the proportion of males that initiated breeding at each age, as well as age- and breeding age-dependent survival, using a live-dead, capture-recapture, multistate model in a state-space framework. We modified the basic multistate model described by Kéry and Schaub (2012) to estimate the age-specific transition probabilities to breeding status. The advantage of this model was the ability to combine information from band re-sightings, recoveries of dead individuals, and VHF radio-tracking into a joint estimate of survival; the model allowed us to account for the different detection probabilities within each of these types of data. We provide a full description of this model and its JAGS specification in Supplementary Material Appendix 1.

For fecundity of males, we estimated their mean brood size with a Poisson GLMM. Our model was

\[ y_i \sim \text{Poisson} \left( \lambda_i \right) \]

\[ \log \left( \lambda_i \right) = \beta_0 + \beta_{g1}HY_{b_i} + \beta_{g2}HY_{nb_i} + \beta_{g3}SY_{b_i} + \beta_{g4}SY_{nb_i} + \beta_{g5}ASY_{b_i} + \beta_{g6}ASY_{nb_i} + \varepsilon_i \]

where \( y \) was the maximum of 3 post-fledging brood counts; \( i \) denoted a given individual; \( \beta_0 \) was the intercept; \( \beta_{g1}, \beta_{g2}, \beta_{g3}, \beta_{g4}, \beta_{g5}, \beta_{g6} \) were breeding-age group coefficients; \( HY_{b_i}, \) \( SY_{b_i}, \) and \( ASY_{b_i} \) were dummy variables for males in each age group that initiated breeding their first year; \( HY_{nb_i}, \) \( SY_{nb_i}, \) and \( ASY_{nb_i} \) were dummy variables for males that delayed breeding (i.e. initiated breeding at 2- or 3-yr of age); and \( \varepsilon \) was a mean-zero random male effect. This approach incorporated nest success and probability of breeding directly into estimates of brood size because nest failures and nonbreeding years were recorded as zeros (i.e. \( y = 0 \)). Nest success of Cooper’s Hawks on our study area was relatively high, so we were not concerned with zero inflation in the brood count dataset.

We used estimates of \( \lambda \) for males in each group as our measure of expected individual fitness. Franklin et al. (2000) used this approach to explore the fitness consequences of habitat selection choices of spotted owls (Strix occidentalis), and Link et al. (2002) demonstrated formally the use of \( \lambda \) to describe expected individual fitness differences.
fitness. We used samples from the posterior distributions of age- and group-specific multistate survival and Poisson GLMM fecundity estimates as inputs for a 3-stage, Lefkovitch population projection matrix (Caswell 2001, Millsap 2018a, 2018b). Stage 1 consisted of HY individuals, stage 2 consisted of SY individuals, and stage 3 included all ASY Cooper’s Hawks. We used the Popbio package (Stubbenn et al. 2012) in Program R (R Core Team 2015) for the matrix analyses and to estimate $\lambda$, the dominant eigenvalue of the matrix. We used the symbol $\lambda_{annual}$ for expected individual fitness, to differentiate it from the population’s theoretical finite rate of increase ($\lambda$) or the observed finite rate of increase ($\lambda_{obs}$).

Predictions regarding male prey abundance. For tests of our predictions regarding differences in abundance of prey within territories of males that first bred at different ages, we needed estimates of male prey population size at the nest-territory level. We used Program DISTANCE 6.0 (Thomas et al. 2009) and avian point count data to estimate density of avian prey within Cooper’s Hawk nesting territories in April from 2013 to 2015. Many of the prey captured by males later in the nesting period were nesting birds (Lien et al. 2015), but we surmised that prebreeding abundance of adult prey in each territory provided a reliable indication of future nesting prey abundance as well. Primary prey species of female Cooper’s Hawks on the urban study area were medium-sized birds, especially Rock Pigeons (Columba livia) and White-winged Doves (Zenaida asiatica) (Millsap 2018a). Males fed on the same avian species, though much less frequently on pigeons and Eurasian Collared-Doves (Streptopelia decaocto); instead, males fed more frequently on sparrow-sized birds (Lien et al. 2015). We pooled Cooper’s Hawk prey species with similar detection probabilities to increase sample sizes for fitting detection functions in DISTANCE. Prey species groups were: (1) House Sparrow (Passer domesticus), Chipping Sparrow (Spizella passerina), and House Finch (Carpodacus mexicanus); (2) American Robin (Turdus migratorius) and European Starling (Sturnus vulgaris); (3) Mourning Dove (Zenaida macroura) and White-winged Dove; and (4) Eurasian Collared-Dove, Rock Pigeon, and Great-tailed Grackle (Quiscalus mexicanus). We 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). We calculated estimates of adult prey density for each group at each fixed point. We used the kriging tool in ArcGIS 10.2 (ESRI, Inc., Redlands, California, USA) to interpolate a prey-density surface for the study area from density estimates at sample points for each group each year following the approach described by Krivoruchko et al. (2011). We set kriging parameters to use the closest 4 fixed-point counts to each raster cell (usually within 0.8 km of the cell) for density estimation. We used the resulting raster dataset to estimate the mean prey density for each prey group for each year within 390 m of each nest used. We used 390 m because this was half of the mean distance between simultaneously used nests on our study area (Millsap 2018a); inter-nest distance is often used as a surrogate for territory size in raptors (birds in the orders Accipitriformes, Strigiformes, and Falconiformes) when direct estimates are lacking (Thorstrom 2001, Lien et al. 2015). We considered the area so circumscribed to likely include most of the foraging area of each resident male Cooper’s Hawk (Boal 2001b, Lien et al. 2015) because of the high nesting density and close nest spacing on our study area, and because of aggressive territorial defense by resident males towards trespassing males.

To assess the importance of variation in prey abundance within nesting territories of male Cooper’s Hawks, we first sought to determine if the males established nesting territories nonrandomly on the study area relative to male prey abundance. There was evidence of overdispersion in our sample, so we used a Poisson GLMM with an individual random-effects term to compare estimated male prey abundance within the 71 nesting territories occupied at least 1 yr during 2013 through 2015 with estimates of prey population size for an equal number of random points on the study area. We considered male prey to include all bird species in prey groups 1 through 3 as described previously; male prey abundance for this analysis was the sum of estimates of population size for all birds in these size classes within 390 m of each used nest or random point by year. Second, we tested our prediction that nesting territories used by younger males would have comparable or higher prey populations than those occupied by older males. For this analysis, we used a Poisson GLMM to estimate mean prey abundance on nesting territories occupied by relatively younger and relatively older males during 2013 through 2015.

Predictions regarding differences between sexes in age at first breeding. For comparative tests of age at first breeding, we required estimates of the rates of age of first breeding for male and female Cooper’s Hawks on the urban study area. For this, we separately estimated the proportion of males and females banded or radio-tagged as fledglings that initiated breeding at ages 1, 2, or 3 yr (no individuals first bred after 3 yr). For females, we estimated this parameter using data only from radio-tagged individuals, so age at first breeding was known with certainty and we were able to use a Bernoulli model to compute estimates. For males, most individuals had not begun breeding by the time their radio transmitters expired, so we combined band re-sight and radio-tracking data to compute the estimates as part of the male multistate model for estimating survival, as described previously.

Predictions regarding female individual fitness. To compare fitness of HY female breeders with that of HY
males that bred in their first year, we needed estimates of \( \lambda_{\text{ind}} \) for females to compare with those for males (described above). We also required these estimates according to the age of the male that a female initially paired with to test predictions regarding female fitness and male individual quality. Accordingly, for the female analyses we identified 2 pair-groups for estimates of vital rates: (1) HY females that initially paired with relatively younger males (young–young; YY) and (2) HY females that initially paired with relatively older males (young–old; YO). From 2011 to 2015, when we collected the data for these analyses, we observed no radio-tagged or color-marked AHY females that paired with younger males, or radio-tagged or color-marked HY females that failed to breed except under extenuating circumstances (see Results), hence the absence of these groups.

We estimated \( \lambda_{\text{ind}} \) for females in these 2 groups, and for females that settled on what were determined to be higher vs. lower quality nesting territories, much the same way as for males. For survival, we used the same live-dead, capture-recapture multistate model as for males, except that rates of initial settling with young vs. older males were estimated by the female transition probabilities (see Supplementary Material Appendix 2 for details of the female model). We used a Poisson GLMM to estimate mean brood size of females by pair-group. The female model was

\[
\log(\lambda_i) = \beta_0 + \beta_{y_1} H_{YY} + \beta_{y_2} H_{YO} + \beta_{y_3} S_{YY} + \beta_{y_4} S_{YO} + \beta_{y_5} A_{YY} + \beta_{y_6} A_{YO} + \varepsilon_i
\]

where \( y \) was the maximum of 3 post-fledging brood counts; \( i \) denoted a given individual; \( \beta \) was the intercept; \( \beta_{y_1} \) through \( \beta_{y_6} \) were the age-dependent pair-group coefficients; \( H_{YY} \), \( S_{YY} \), and \( A_{YY} \) were dummy variables for females that initiated breeding with younger males in their first year; \( H_{YO} \), \( S_{YO} \), and \( A_{YO} \) were dummy variables for females that settled with older males in their first year; and \( \varepsilon \) was a mean-zero random individual female effect. We used the posterior distributions of survival and fecundity in a matrix population model to obtain required estimates of \( \lambda_{\text{ind}} \) as described previously for males.

Predictions regarding female competition and nesting territory quality. For our assessment of female competition for nesting territories, we first wanted to determine whether there was evidence that females competed for multiple nesting opportunities. For this analysis, we counted the number of nesting territories visited by radio-tagged HY females while prospecting for nesting sites prior to settling on a nesting territory. We also monitored all the nesting territories visited by the prospecting HY females to confirm their eventual occupancy status. For each such territory, we determined the age (HY or AHY) of the male in residence, and the age of the female that settled on the territory if it was eventually occupied. We estimated the proportion of nesting territories visited that were eventually occupied using a Bernoulli model.

For the main analysis, we used a Bernoulli generalize linear model (GLM) to test our predictions regarding the roles of male prey abundance, female prey abundance, and relative male age on the attractiveness of nesting territories to female Cooper’s Hawks. We limited this analysis to the years 2013 through 2015, the period when we collected prey abundance data and focused our efforts on monitoring settling behavior of radio-tagged female Cooper’s Hawks. Two complications with this analysis were the potential for pseudoreplication and for a confounding influence of philopatry if we included all nesting territories each year. To address this, we used only new pairings (i.e. newly occupied nesting territories or nesting territories where the previous year’s female did not return) of individual male and female Cooper’s Hawks for these analyses. We considered that by limiting the analysis in this way we might be using a biased subset of nesting territories for the analysis, but felt this was unlikely because all known female settling opportunities were included in each year. Given the latter, our response variable was the probability that an available breeding opportunity on nesting territory \( i \) in year \( t \) would be filled by an AHY female (\( \rho_{\text{ahy}} \)). We included 3 predictor variables specific to each nesting territory and year in the global model: (1) male prey abundance (estimated number of individuals in prey groups 1 through 3 within a 390 m radius of the nest used); (2) female prey abundance (estimated number of individuals in prey groups 3 and 4 within a 390 m radius of the nest used); and (3) male eye color score (categorical values from 1 to 5, for the eye colors yellow to red). Variable inflation factors for predictor variables were all <3.0, thus we did not regard multicollinearity as a major concern (Zurr et al. 2010). Our global model was thus

\[
y_{it} \sim \text{Bernoulli} (\rho_{\text{ahy}_{it}})
\]

\[
\logit (\rho_{\text{ahy}_{it}}) = \beta_0 + \beta_{\text{male}} \times M_{\text{prey}_{it}} + \beta_{\text{female}} \times F_{\text{prey}_{it}} + \beta_{\text{eye}} \times \text{eye}_{it}
\]

where \( y_{it} \) was the age (0 = HY, 1 = AHY) of the female, \( \beta_0 \) was the intercept, \( \beta_{\text{male}} \) was the male prey coefficient and \( M_{\text{prey}_{it}} \) the male prey abundance, \( \beta_{\text{female}} \) was the female prey coefficient and \( F_{\text{prey}_{it}} \) the female prey abundance, and \( \beta_{\text{eye}} \) was the male eye color score coefficient and \( \text{eye}_{it} \) was the eye-color score of the resident male, all indexed by territory (\( t \)) and year (\( i \)). We used Bayesian model averaging to compare coefficients derived from models with all 8 combinations of subsets of the explanatory variables. Bayesian model averaging is conceptually like model averaging under the information-theoretic approach, which uses frequentist
maximum likelihood methods (Burnham and Anderson 1998, Anderson and Burnham 2002, Burnham et al. 2011, Hobbs and Hooten 2015). However, there is not full agreement on which measures of model probability are best suited for model ranking or model averaging in the Bayesian framework. Hoeting et al. (1999) and Hooten and Hobbs (2015) reviewed current approaches in Bayesian model selection and model averaging and, based on their reviews, we selected the Watanabe-Akaike information criterion (WAIC) for our purposes. The WAIC’s advantage is that it is derived from the full posterior predictive distribution as opposed to being conditioned on a point estimate, and is therefore a fully Bayesian form of model selection (Gelman et al. 2014, Hooten and Hobbs 2015). We calculated estimates of WAIC for each model by using the WAIC method in the R package BLMECO (Korner-Nievergelt et al. 2015). We estimated model probabilities for all 8 models as described by Burnham et al. (2011), and we computed model-averaged estimates of predictor variables as described in Burnham and Anderson (1998). To further aid in interpreting contributions of predictor variables, we calculated the odds ratio, importance measure, model-averaged t-value (Kuhn and Johnson 2013), and model-averaged coefficients for each variable (see Supplementary Material Appendix 3 for more details on our predictor-variable evaluation methods). We used Bayesian separate variance t-tests to compare wing chord, tarsus length, and mass between HY females that settled on nesting territories determined to be of higher quality to those that settled on lower quality nesting territories (Kéry 2010).

Predictions regarding population growth rates. For this analysis we were interested in comparing sex-specific, model-based estimates of \( \lambda \) with the observed rate of population growth derived from annual counts of occupied nesting territories \( (\lambda_{\text{obs}}) \) on the study area from 2011 through 2018. We compared differences in posterior distributions of the different estimates of \( \lambda \) directly. Additionally, we simulated and plotted annual estimates of the number of occupied nesting territories and 90% credible intervals under each model, starting from the count of occupied nesting territories on the study area in 2011, to assess how each compared with the observed population trajectory. Again, we used posterior distributions of the annual estimates of the number of occupied nesting territories for these comparisons.

RESULTS

Male Expected Individual Fitness
We captured and radio-tagged 199 male Cooper’s Hawks on the urban study area between 2011 and 2017; 121 were of known age when captured (all HY), including 30 HY males we radio-tagged from 2015 through 2017 (Appendix Table 5). The multistate survival model estimated that: (1) dead recovery rates were 0.11 for bands (0.07–0.15) and 0.83 (0.56–0.99) for radio-tags, and (2) band re-sighting probabilities were 0.61 (0.42–0.80) prior to settling on a nesting territory and 0.92 (0.88–0.97) after settling. The second-year annual survival rate of males that bred in their first year was 37% (13–59%) lower than for males that delayed breeding until at least year 2, but survival of older males was comparable between the 2 groups (Figure 2, Appendix Table 6). Expected productivity of males that bred in their first year and survived was greater than that of males that delayed breeding until their second or third year, such that over the first 3 yr of life, HY male breeders produced 3.5 (–1.8 to 8.1) more fledglings than males that delayed breeding. Despite this, the point estimate of \( \lambda_{\text{ind}} \), was 6% (–18 to 45%) higher for males that delayed breeding, though the uncertainty around this estimate was large (\( P \{ \neq 0 \} = 0.59 \)). Elasticity values from the transition matrix indicated that survival was the most important demographic parameter relative to \( \lambda_{\text{ind}} \) (0.82 [0.79–0.86]), so the difference in SY survival had a greater impact on \( \lambda_{\text{ind}} \) of males than did the higher overall fecundity of early breeders.

Prey Abundance and Male Age
Mean April abundance of male prey on Cooper’s Hawk nesting territories was 1,940 (1,813–2,072) individuals compared with 1,332 (1,247–1,427) at random points on the study area, a difference of 608 (448–766) more male prey on nesting territories (\( P \{ \neq 0 \} > 0.99 \)) (Figure 3). We concluded that Cooper’s Hawk nesting territories were not located randomly with respect to male prey abundance. The 3 nesting territories occupied by HY male Cooper’s Hawks between 2013 and 2015 had a mean prey abundance of 2,819 (2,150–3,593) compared with 1,889 (1,815–1,975) for 133 AHY male nesting territories, a difference of 929 (251–1,702; \( P \{ \neq 0 \} > 0.99 \)).

Rates of Early Breeding
We were certain of the age of first breeding for 20 male Cooper’s Hawks first banded as fledglings; 14% (4–31%) first bred at age 1 yr, 71% (55–88%) at age 2 yr, and 15% (5–30%) at age 3 yr. We were certain of the age of first breeding for 37 female Cooper’s Hawks; 93% (73–99%) first bred at age 1 yr, and only 1 female injured in a skirmish over a nesting territory in her first year delayed breeding until age 2 yr. Thus, 79% (56–92%) more females initiated breeding at age 1 yr than males (\( P \{ \neq 0 \} = 0.99 \)). No females or males were observed to skip breeding after they settled on a nesting territory.

Expected Individual Fitness of Early Breeders
We captured and marked 168 female Cooper’s Hawks of known age (HY or SY) on the study area between 2011 and
Cooper’s Hawk age at first breeding

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2017, 113 of which were radio-tagged. Forty-one of the radio-tagged females had transmitters that still functioned when the hawks began exploring nesting territories the subsequent March, at ~10 mo old. All 41 of these females attempted to recruit on breeding territories, and 37 were successful. The unsuccessful prospective recruits included the 1 female injured in a territorial skirmish in 2012, and 3 females that died from collisions in 2015 while they were known to be aggressively competing for breeding opportunities.

Based on this sample, we estimated that for female Cooper’s Hawks: (1) dead recovery rates were 0.11 for bands (0.05–0.18) and 0.97 (0.90–1.0) for radio-tags, (2) band re-sighting probability after settling on a nesting territory was 0.77 (0.57–0.98), (3) HY annual survival rate was 0.24 (0.15–0.33), (4) SY annual survival rate was 0.75 (0.65–0.85), and (5) ASY annual survival rate was 0.91 (0.85–0.96). HY females fledged a mean of 2.5 (2.1–2.9) young per breeding attempt, SY females that bred in their first year fledged a mean of 2.6 (2.0–3.2) young in their second year, and ASY females that bred in their first year fledged a mean of 3.3 (2.6–3.9) young per year after their second year. Expected $\lambda_{ad}$ for female Cooper’s hawks with these demographic rates was 1.2 (1.1–1.3), which was 0.21 (~0.05 to 0.54) greater than for males that bred in their first year ($P [\neq 0] = 0.90$).

**FIGURE 2.** Box plots of annual survival rates (A), fecundity (B), and expected individual fitness (C) of male Cooper’s Hawks in central New Mexico, USA, 2011–2018, based on the relative age of first breeding. Early individuals are those that initiated breeding in their first year, whereas delayed individuals postponed first breeding until at least year 2. Dark bars are medians, gray boxes are interquartile ranges, whiskers are 1.5 times the interquartile range, and dots are outliers.
Figure 3. Estimated density (number per km²) of Cooper’s Hawk avian prey in April, averaged over the years 2013–2015, on our study area in Albuquerque, New Mexico, USA. (A) Group 1 (sparrow-sized) prey, (B) group 2 (American Robin-sized) prey, (C) group 3 (dove-sized) prey, and (D) group 4 (Rock Pigeon-sized prey). Cooper’s Hawk nesting territories are depicted by hollow circles, and the black outline is the urban study area boundary.
Female Competition for Nesting Territories

HY females were observed to visit between 1 and 5 (mean = 2.0 [1.5–2.4]) nesting territories before settling. All but 1 of the 39 nesting territories known to have been visited by a radio-tagged HY female during the intensive monitoring period from 2011 to 2015 were eventually occupied by a pair; the probability of occupancy of nesting territories visited was 0.96 (0.89–0.99). We also observed numerous instances of aggression among HY females attempting to settle on nesting territories, including the aforementioned 3 that died and 1 that was injured in skirmishes during the settling process.

We captured the breeding male in 52 initial Cooper’s Hawk pairings while concurrently completing 603 fixed-point avian counts during this study. Sixty-nine percent of breeding males had orange-red or red eyes, indicative of older individuals. Density of avian prey varied widely across the study area (Figure 3). Rock Pigeons, Eurasian Collared-Doves, House Sparrows, House Finches, and White-winged Doves all attained estimated densities >1,000 individuals per km² locally on the study area, although only House Sparrows, House Finches, and White-winged Doves reached these densities over more than a few Cooper’s Hawk nesting territories. Male eye color differed between nesting territories occupied by HY and AHY female Cooper’s Hawks, and was the strongest predictor of occupancy by an AHY female (Tables 2 and 3). The latter relationship was positive, indicating AHY females tended to pair with males with darker eyes (i.e. relatively older males). Among HY females, those that paired with older males were heavier than those that paired with younger males (Table 4). However, the 2 groups of HY females did not differ in other traits, including the body fat score.

Female Expected Individual Fitness

There was little difference in the proportion of HY female Cooper's Hawks that initially paired with younger (0.54 [0.31–0.76]) compared with older 0.46 [0.24–0.69] males. Second-year survival rates of females that recruited with older males averaged 33% (11–55%) higher than second-year survival of females that recruited with younger males ($P \neq 0 \leq 0.99$) (Figure 4, Appendix Table 7). Of 8 females that paired initially with younger males, and which subsequently died from known causes in their second year, 6 died from collisions with vehicles or power distribution lines, and 2 were due to starvation or disease. These deaths occurred when the females were no longer being provisioned by or interacting with their prior year’s mate, shortly after these females transitioned back to hunting for themselves. Females that recruited with younger males and survived their second year of life had higher productivity in their second breeding attempt than did females that initially recruited with older males; in subsequent years productivity was similar between the pair groups. Using these demographic values, $\lambda_{\text{cont}} = 0.16 (0.08–0.33)$ higher for females that initially paired with older males ($P \neq 0 \leq 0.96$).

Population Growth Rate

The number of occupied Cooper's Hawk nesting territories observed on the study area increased from 52 in 2011 to 89 in 2018 (Appendix Table 5), yielding an estimate for $\lambda_{\text{obs}} = 1.08 (0.94–1.20)$. This was closer to the estimate of $\lambda_{\text{ind}}$ from the male-based demographic model (1.02 [0.93–1.13]) than $\lambda_{\text{ind}}$ from the female-based model (1.21 [1.09–1.34]). Over the 8 yr duration of our study, a female-based demographic model overpredicted the number of occupied nesting territories by 122 (93–149), whereas a male-based model underpredicted by 27 (20–34) nesting territories (Figure 5).

DISCUSSION

Variation in the age at first breeding has been recognized as an important demographic parameter across a wide range of plant and animal taxa (Langvatn et al. 1996, Gaillard et al. 1998, Caswell 2001, Tavecchia et al. 2001, Tsitrone et al. 2003). Our study demonstrates that differences between the sexes in age at first breeding, a factor not considered in most demographic analyses, can have important implications for both individual fitness and population regulation in the Accipitriformes. Most importantly

| Model | $K$ | $D$ | $\Delta$WAIC | $\omega$ |
|-------|-----|-----|--------------|--------|
| Male eye | 2 | 8.64 | 0.00 | 0.28 |
| Male eye + male prey | 3 | 8.48 | 0.83 | 0.19 |
| Male eye + female prey | 3 | 8.52 | 1.02 | 0.17 |
| Intercept only | 1 | 9.47 | 1.72 | 0.12 |
| Female prey | 2 | 9.21 | 2.23 | 0.09 |
| Male eye + male prey + female prey | 4 | 8.47 | 2.89 | 0.07 |
| Male eye + female prey | 2 | 9.31 | 3.42 | 0.05 |
| Male prey + female prey | 3 | 9.20 | 4.62 | 0.03 |

*Male eye = male eye color score, surrogate for male age; male prey = abundance of male Cooper's Hawk prey on the nesting territory; and female prey = abundance of female Cooper's Hawk prey on the nesting territory.

* Significant difference in WAIC value between the indicated model and the model with the lowest WAIC value.
in this regard, our results supported the hypothesis that in some species with sexual differences in age at first breeding, the operational sex ratio is affected such that the sex that delays breeding to the greatest degree becomes the limiting sex (sensu Emlen and Oring 1977). Despite essentially equal sex ratios at fledging in our Cooper’s Hawk study population (Millsap 2018a), delayed breeding by males but not females resulted in an imbalance in the operational sex ratio in favor of females. Although polygyny has been reported in Cooper’s Hawks (Rosenfield et al. 2007), including in our study population (3 instances by the same male in 558 nesting attempts, B.A.M. and K.M. personal observation), it appears to be rare and thus not a plausible mechanism to offset this imbalance at this time.

A consequence of the imbalanced operational sex ratio was that \( \lambda_{obs} \) of our study population was 13% lower than that predicted solely by the female-based demographic model. We suspect this may not be uncommon in the Accipitriformes, as well as in other orders of raptors with similar selection pressures on age at first breeding (e.g., Hunt et al. 2013). Typically, researchers employ female-based demographic models in population studies of raptors (Lahaye et al. 1994, Katzner et al. 2006, Ortega et al. 2009, Krüger et al. 2010, Hernández-Matías et al. 2013, Monzón and Friedenberg 2018). Our findings, and those of Reynolds et al. (2017) for the Northern Goshawk (A. gentilis), suggest this choice is not trivial, and that careful consideration should be given to possible sexual differences in demographic rates, including age at first breeding, when modeling demographic parameters and population trajectories of raptor populations. Additionally, sexual differences in age at first breeding can have implications for population regulation and persistence in the Accipitriformes, where the ability for younger individuals to acquire nesting territories and reproduce when competition is relaxed is thought to be an important mechanism that bolsters the probability of persistence at low population sizes (Ferrer et al. 2004, Margalida et al. 2008).

Consistent with the hypothesis that early breeding is costlier to male than female Cooper’s Hawks, we found that males more often delayed breeding than did females, estimated individual fitness of early-breeding males was lower than that of early-breeding females, and early-breeding males experienced higher second-year mortality than males that delayed breeding. Despite these costs, early-breeding males that survived attained substantially higher overall fecundity, at least through 3 yr of age, than males that delayed breeding. Thus, fitness of early-breeding males was enhanced under some conditions. We found that the few nesting territories occupied by HY males had an average of 1.5 times more male prey than nesting territories occupied by older males. We regard this as tentative support for the hypothesis that first-year breeding by male Cooper’s Hawks was more likely on nesting territories with high prey abundance, as previously reported for the Eurasian Sparrowhawk (Newton 1976). Overall, these results suggest a major factor favoring delayed breeding in male Cooper’s Hawks is strong selection pressure against early breeding in most situations because of low post-breeding, second-year survival. However, we cannot rule out that HY males were also ineffective at securing mates. Male age was an important factor in selection of a

### Table 3.

| Variable | \( \beta_{ma} \) | SE(\( \beta_{ma} \)) | Importance | Odds ratio | \( t_{ma} \) |
|----------|----------------|---------------------|------------|------------|------------|
| Male eye | 0.58           | 0.31                | 0.70       | 2.42       | 1.88       |
| Male prey | -0.34        | 0.47                | 0.33       | 0.50       | 0.73       |
| Female prey | -0.13        | 0.27                | 0.36       | 0.50       | 0.50       |

*Male eye = male eye color score, surrogate for male age; male prey = abundance of male Cooper’s Hawk prey on the nesting territory; and female prey = abundance of female Cooper’s Hawk prey on the nesting territory.

### Table 4.

| Variable pair-type | Mean | 90% credible interval (difference ≠ 0) | \( P \) |
|--------------------|------|--------------------------------------|------|
| Wing chord (mm)    |      |                                      |      |
| Young ♀ Young ♂     | 258.4| 254.6–257.5                           | 0.09 |
| Young ♀ Old ♂       | 254.9| 251.2–257.6                           | 0.49 |
| Tarsus length (mm) |      |                                      |      |
| Young ♀ Young ♂     | 78.8 | 75.3–82.2                             | 0.56 |
| Young ♀ Old ♂       | 78.5 | 77.0–80.0                             |      |
| Mass (g)            |      |                                      |      |
| Young ♀ Young ♂     | 469.5| 463.5–475.6                           | 0.99 |
| Young ♀ Old ♂       | 482.7| 478.5–486.8                           |      |
| Fat score*          |      |                                      |      |
| Young ♀ Young ♂     | 4.6  | 3.5–5.7                               | 0.62 |
| Young ♀ Old ♂       | 4.9  | 4.1–5.6                               |      |

*Fat score reflected the extent of visible deposited fat in the underwing, scored from 0 (no visible fat) to 6 (fat bulging).

b Probability that the difference between the parameter estimates for the 2 pair groups is zero.
nesting territory by female Cooper’s Hawks, likely because older males were more experienced and therefore better providers (Lien et al. 2015).

The lack of delayed breeding by females in our study population was possible because urban female Cooper’s Hawks that did not migrate from our study area for winter could settle on nesting territories before migrant females returned in the spring; the former thus avoided much potential competition for nest sites. Prospective female recruits filled nesting territories within the urban area first, but ~30% emigrated and settled on exurban nesting territories, where most females were migratory (Millsap 2018a).

Many HY male Cooper’s Hawks were also residents, but we suspect fewer exurban males than females migrated. Thus, we surmise there was less opportunity for HY males to usurp nesting territories from exurban migrants. This outcome demonstrates that when intrasexual competition is relaxed, female Cooper’s Hawks do not delay breeding. We interpret this as consistent with the hypothesis that intrasexual competition is the most important factor regulating early breeding among female Cooper’s Hawks.

The outcome of competition among female Cooper’s Hawks for nesting territories was consistent with the ideal preemptive distribution model. Females preferentially

FIGURE 4. Box plots of annual survival rates (A), fecundity (B), and expected individual fitness (C) of female Cooper’s Hawks in central New Mexico, USA, 2011–2018, based on the relative age of the male on the initial recruitment nesting territory. YY refers to females that recruited with relatively young males, and YO refers to females that recruited with relatively older males. HY = hatching year, SY = second year, and ASY = after-second year. Dark bars are medians, gray boxes are interquartile ranges, whiskers are 1.5 times the interquartile range, and dots are outliers.
High-quality males are likely the direct result of intrasexual competition for nesting territory, greatest for AHY females, intermediate for younger males, and, among HY females, those of greater body mass. The cost of early breeding for female Cooper’s Hawks occurred immediately before and after breeding. Before breeding, primary risks were injury or death in fights to secure a nesting territory, whereas post-breeding risk was associated with starvation or accidents that occurred when the females resumed foraging for themselves. These deaths occurred primarily among SY females that had paired with younger males. Lien et al. (2015) reported that male prey delivery rates on Cooper’s Hawk nesting territories with HY females were lower than those in nesting territories with AHY females on our study area. We hypothesize that many females that paired with younger males were in lower body condition when they transitioned to foraging for themselves after breeding than females that paired with more experienced males, and consequently may have been more prone to starvation and disease or to taking risks while hunting.

In summary, our study provides evidence that costs of early breeding, and mechanisms that regulate it, differ between male and female Cooper’s Hawks. For males, early breeding was attempted only when individuals could secure nesting territories with abundant prey, and even in these situations there was high post-breeding mortality such that mean \( \lambda_{\text{ind}} \) of early breeders did not exceed replacement (i.e. 1.0). Thus, there was strong selection pressure against early breeding by males. Conversely, all HY female Cooper’s Hawks attempted to settle on nesting territories and breed in their first year, and intrasexual competition among females of all ages was likely the primary mechanism that regulated their distribution among
available breeding opportunities. Importantly, however, \( \lambda_{ind} \) of breeding HY females substantially exceeded 1.0 regardless of the quality of nesting territory and mate. These sexual differences in costs resulted in predictable differences in the frequency of early breeding between the sexes, which in turn affected the operational sex ratio of our study population in favor of females. Consequently, males were the limiting sex, and their demographic rates had a strong effect on the overall population growth rate of our study population.

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**Author contributions:** B.A.M., R.K.M., and K.M. conceived the idea and designed the study; G.W.R., M.B., J.E.P., and D.C. contributed to the design as the study progressed. B.A.M., K.M., R.K.M., M.B., D.C., J.E.P., and G.W.R. collected the data. B.A.M. performed the analyses and wrote the manuscript. All authors edited the manuscript.

**Data repository:** All data used in the analyses are available from the Zenodo digital repository at https://doi.org/10.5281/zenodo.1745386.

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APPENDIX TABLE 5. Annual counts of occupied nesting territories, computed estimates of $\lambda_{\text{obs}}$ (the observed population rate of increase) from those counts, and sizes of samples of banded and radio-tagged Cooper’s Hawks by year on the urban study area in Albuquerque, New Mexico, USA.

| Year | Occupied nesting territories | $\lambda_{\text{obs}}$ | Radio-tagged HY females | Radio-tagged HY males | Band-only HY females | Band-only HY males | Band-only AHy females | Band-only AHy males |
|------|-------------------------------|------------------------|------------------------|----------------------|---------------------|-------------------|---------------------|---------------------|
| 2011 | 52                            | –                      | 3                      | 1                    | 10                  | 9                 | 10                  | 9                   |
| 2012 | 53                            | 1.02                   | 16                     | 1                    | 23                  | 16                | 13                  | 14                  |
| 2013 | 69                            | 1.30                   | 23                     | –                    | –                   | 13                | 13                  | 11                  |
| 2014 | 74                            | 1.07                   | 33                     | –                    | 10                  | 7                 | 9                   | 11                  |
| 2015 | 72                            | 0.97                   | 6                      | –                    | 16                  | 13                | 3                   | 10                  |
| 2016 | 67                            | 0.93                   | 18                     | –                    | 8                   | 16                | 8                   | –                   |
| 2017 | 82                            | 1.22                   | 14                     | –                    | 6                   | 16                | 11                  | –                   |
| 2018 | 89                            | 1.09                   | –                      | –                    | –                   | –                 | –                   | –                   |

APPENDIX TABLE 6. Demographic rates of 121 marked and radio-tagged known-age male Cooper’s Hawks according to the age at which they initiated breeding in central New Mexico, USA, 2011–2018. Delayed breeders did not breed until at least year 2.

| Parameter | HY breeders | Delayed breeders | $P$ (difference ≠ 0) |
|-----------|-------------|------------------|----------------------|
| HY $\bar{x}$ number fledged | 2.32 (1.59–3.17) | 0 | 1.00 |
| SY $\bar{x}$ number fledged | 3.53 (2.31–5.24) | 2.23 (2.20–5.10) | 0.98 |
| ASY $\bar{x}$ number fledged | 2.93 (1.58–4.65) | 3.48 (2.65–4.39) | 0.72 |
| HY $\bar{x}$ survival | 0.25 (0.17–0.34) | 0.25 (0.17–0.34) | – |
| SY $\bar{x}$ survival | 0.42 (0.20–0.66) | 0.71 (0.50–0.90) | 0.99 |
| ASY $\bar{x}$ survival | 0.75 (0.36–0.98) | 0.79 (0.74–0.83) | 0.50 |
| Expected individual fitness | 0.98 (0.69–1.30) | 1.04 (0.95–1.13) | 0.59 |
**APPENDIX TABLE 7.** Demographic rates of 170 known-age marked and radio-tagged female Cooper’s Hawks according to the relative age of the male they first paired with in central New Mexico, USA, 2011–2018.

| Parameter                  | Mean (90% CI) | Females initially paired with younger males | Females initially paired with older males | \( P \) (difference \( \neq 0 \)) |
|----------------------------|---------------|----------------------------------------------|------------------------------------------|----------------------------------|
| HY \( \bar{x} \) number fledged | 2.29 (1.75–4.30) | 2.61 (2.11–3.27) | 0.76 |
| SY \( \bar{x} \) number fledged | 3.50 (2.31–5.24) | 2.23 (1.64–3.04) | 0.94 |
| ASY \( \bar{x} \) number fledged | 3.03 (1.97–4.62) | 3.36 (2.61–4.41) | 0.76 |
| HY \( \bar{x} \) survival       | 0.24 (0.15–0.33) | 0.24 (0.15–0.33) | -     |
| SY \( \bar{x} \) survival       | 0.56 (0.37–0.77) | 0.90 (0.78–0.98) | 0.99  |
| ASY \( \bar{x} \) survival       | 0.84 (0.69–0.95) | 0.92 (0.84–0.98) | 0.82  |
| Expected individual fitness  | 1.09 (0.92–1.26) | 1.26 (1.12–1.40) | 0.94  |