

LIFE-HISTORY TRADE-OFFS OF BREEDING IN ONE-YEAR-OLD MALE COOPER'S HAWKS

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Abstract. Life-history theory suggests that delayed maturation is beneficial to birds when costs of breeding early in life are high. We compared selected aspects of the biology of male Cooper's Hawks (*Accipiter cooperii*) that began breeding at 1 year of age (SY males) vs. males that began breeding ≥ 2 years of age (ASY males) in an effort to elucidate what renders breeding of SY males rare. Of the 732 males of known age whose breeding we studied over 32 years (1980–2011) 13 (2%) were SY and 719 (98%) were ASY. During this period, the incidence of breeding of SY males changed markedly, as 12 of the instances of breeding of SY males were recorded in the first half of our study, only 1 in the latter half. We suggest that SY males could acquire nest sites more readily in the first half of the study when the breeding population of ASY males was apparently lower. Males breeding in their second year were on average similar in size to ASY males but were molting more extensively than were ASY males. ASY males lived longer than males breeding in their second year, and maximum lifetime production of young was greater, so SY males may have sacrificed greater longevity for breeding early. A strategy of facultative breeding in response to the constraints of higher numbers of older breeding males and restraints of trade-offs in energy allocation may explain why SY male Cooper's Hawks rarely breed.

Key words: *Accipiter cooperii*, life-history trade-offs, age at first breeding, life-history evolution, Cooper's Hawk, molt, lifetime reproduction.

Soluciones de Costo-Beneficio de la Reproducción de Individuos de un Año de Edad de *Accipiter cooperii*

Resumen. La teoría de la historia de vida sugiere que un retraso en la maduración es beneficioso para las aves cuando los costos de criar temprano en la vida son altos. Comparamos aspectos seleccionados de la biología de los machos de *Accipiter cooperii* que comienzan a reproducirse al año de edad (machos PA) vs. machos que comienzan a reproducirse con >2 años de edad (machos SA) para dilucidar qué es lo que hace rara la reproducción de los machos PA. De los 732 machos de edad conocida cuyos periodos reproductivos estudiamos a lo largo de 32 años (1980–2011), 13 (2%) fueron PA y 719 (98%) fueron SA. Durante este periodo, la incidencia de cría de los machos PA cambió marcadamente, ya que 12 de las instancias de cría de los machos PA fueron registradas en la primera mitad de nuestro estudio y sólo una en la segunda mitad. Sugerimos que los machos PA podrían haber adquirido sitios de anidación más fácilmente en la primera mitad del estudio cuando la población reproductiva de machos SA fue aparentemente más baja. Los machos PA fueron en promedio similares en tamaño a los machos SA, pero mudaron más extensamente que los machos SA. Los machos SA vivieron más tiempo que los machos PA y la producción máxima de por vida de juveniles fue mayor, de modo que los machos PA pueden haber sacrificado una mayor longevidad a cambio de reproducirse más temprano. Una estrategia de reproducción facultativa en respuesta a las limitaciones de una mayor densidad de machos reproductivos más viejos y a las restricciones de soluciones costo-beneficio en la asignación energética puede explicar por qué raramente crían los machos PA de *A. cooperii*.

INTRODUCTION

Delayed maturation is common among many bird species, particularly birds of prey (Newton 1979, Millon et al. 2010). Costs associated with early reproduction therefore must be

large to make delayed reproduction evolutionarily beneficial (Koons et al. 2008). It is generally theorized that the experience of older individuals allows them to be competitively superior to younger individuals in both procuring breeding sites and in reproductive output (Lack 1968, Lieske et al. 1997).

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Much empirical evidence matches life-history predictions and suggests that individuals indeed face a strong evolutionary trade-off between early and late investment in reproduction (Millon et al. 2010).

Many investigations have documented the nesting of 1-year-old raptors in subadult plumage, otherwise known as second-year or SY birds (e.g., Newton 1979, Moore and Henny 1984, Boal 2001, Rutz 2008). In many species of raptors, including Cooper's Hawk, it is typically females that nest in their second year, which is likely related to the marked division of nest duties between the sexes (Newton 1979, Rosenfield and Bielefeldt 1993, Boal 2001). In the majority of raptors it is the male that acquires the breeding territory and is the sole provider of food to himself, his mate, and his nestlings (Thiollay 1994, Rosenfield and Bielefeldt 1991a). Hence his ability to forage influences the fitness of both sexes greatly (Krüger 2005). Male raptors are believed to take longer than females to gain experience sufficient to reach a reproductive state and are generally reported to begin breeding at ages >1 year (Bildstein 1992, Krüger 2005). This may explain why researchers infrequently detect breeding by SY males and hence why, despite the oft-touted significance of the age at first breeding to life-history evolution, limited ecological understanding of these birds constrains investigation of their life-history trade-offs (Stearns 1992, Millon et al. 2010).

Temporal variation in the frequency and proportion of 1-year-old birds in breeding populations, especially from long-term datasets, may provide insight into the trajectory and pace of population flux. In several raptors, including Cooper's Hawk, investigators have shown that a higher proportion of 1-year-old individuals occurs in populations colonizing novel habitats such as cities; these populations can grow rapidly despite the typically lower production of these young breeders (e.g., Rutz 2008, Oliphant and Haug 1985, Tordoff and Redig 1997, Stout and Rosenfield 2010, Stout et al. 2007). Furthermore, empirical data allowing comparison of breeding of 1-year-old males and older males may help identify the selective pressures and trade-off costs between early and late investment in reproduction.

Since 1980, we have conducted cross-generational, mark-recapture studies of breeding Cooper's Hawks in a variety of habitats in Wisconsin and have shown that males maintain lifetime fidelity to a nesting area (Rosenfield and Bielefeldt 1996, Rosenfield et al. 2009) and that age of adult males appears unrelated to brood size (Rosenfield and Bielefeldt 1997). Other aspects of reproduction, including brood size, are correlated with body mass (a reliable index of body size) in male and female Cooper's Hawks. Mating is nonrandom by body mass, birds of similar size being more likely to pair (Rosenfield and Bielefeldt 1999). Our long-term data sets have allowed elucidation of selective pressures that influence the fitness of Cooper's Hawks. For example, males' lifetime production is strongly related to longevity, whereas longevity and its effects on lifetime reproduction are unrelated to body mass or breeding

habitat (Rosenfield et al. 2009). These investigations were based mostly on data from after-second-year (ASY), gray-plumaged birds (Rosenfield et al. 2003, 2009; RNR, unpubl. data). We have examined few ecological contexts regarding our data on males breeding in their second year.

We used a 32-year data set to (1) report the occurrence and overall proportion of breeding by SY male Cooper's Hawks in Wisconsin by year, (2) examine the body mass (or size) of SY breeding males, (3) report the age and size of females paired to SY breeding males, (4) compare the extent of wing and tail molt of SY and ASY breeding males, (5) compare the reproduction of SY males to that of ASY males, and (6) determine if there is a difference in lifetime breeding longevity (hence lifetime longevity) of males that began breeding at 1 year of age and males that began breeding at ≥ 2 years of age. We were particularly interested in examining how some of our findings might relate to trade-off costs associated with males breeding at 1 year of age.

METHODS

STUDY SITES

We investigated breeding male Cooper's Hawks at two principal study areas in central and southeastern Wisconsin described by Murphy et al. (1988), Rosenfield et al. (1995), and Rosenfield and Bielefeldt (1996). Our central Wisconsin area included rural landscapes and the abutting municipalities of Stevens Point, Whiting, and Plover with a predominately urban human population of ~38,000. Our southeastern Wisconsin area involved rural environs of the Kettle Moraine State Forest, South Unit. These study sites were chosen without preconceptions about their suitability for nesting Cooper's Hawks (Trexel et al. 1999, Bielefeldt et al. 1998, Rosenfield and Bielefeldt 1996).

FIELD PROCEDURES AND ANALYSES

From 1980 to 2011, we located a minimum of 16 and a maximum of 44 (mean = 28) Cooper's Hawk nests each year from a total of 911 nests within 110 nesting areas, with each yearly total number of nests divided about equally between our two study areas. We did not check all known nesting areas each year.

We defined a nesting area as an area 800 m in diameter that was occupied by a breeding adult male in 1 or more years; we considered it reoccupied when we found a new nest in a subsequent year within 400 m of the original nest (Rosenfield and Bielefeldt 1996). Each year we found most nests (>90%) before egg laying by listening for dawn vocalizations (Rosenfield and Bielefeldt 1991b) or by searching for partially constructed nests during the pre-incubation stage, about mid-March through late April in Wisconsin (Bielefeldt et al. 1998).

In later years we trapped and recaptured (or remotely identified via color marks) birds near their nests, occasionally during the pre-incubation or incubation stages but mostly

during the nestling stage, with a variety of techniques (Rosenfield and Bielefeldt 1993, 1999, Rosenfield et al. 2007a). Following Rosenfield and Bielefeldt (1997), we classified the age of breeding Cooper's Hawks at initial capture as 1 year old (SY birds in brown plumage), or ≥ 2 years of age (ASY birds in gray plumage). Breeding adults were banded with U.S. Geological Survey lock-on aluminum leg bands as well as colored, alphanumericly coded leg bands (Rosenfield and Bielefeldt 1996). We measured body mass of breeding birds to the nearest 1 g with a balance-beam scale. Body mass of breeding male and female Cooper's Hawks at the nestling stage varies negligibly by year and is a reliable index to size (Rosenfield and Bielefeldt 1999, Sonsthagen et al. 2012).

We also recorded the molt of the wing and tail of captured hawks by noting loci of missing feathers or extent of growth (scored as 1, 2, 3, etc., tenths grown) of new feathers, which if fully grown were identified by their obvious unfaded blue color. Molt of breeding males varies by nesting stage (Rosenfield and Bielefeldt 1993; RNR, TLB, and JB, unpubl. data). For a tenable comparison of molt of these cohorts, we used molt data from 8 SY and 94 ASY males caught from the last 7 days of June through the first 12 days of July, when nestlings were about 2–3 weeks of age. The pool of 94 ASY males did not include any of the individuals that initially bred in their second year. We tallied a bird as being in arrested molt when no flight feathers (of 10 primaries and 10 secondaries per wing and the total of 12 rectrices) were missing or growing. In this paper we emphasize molt of primaries and tail feathers because these are the flight feather tracts in which adults, especially males, typically exhibit the most molt during the nestling stage of breeding (Rosenfield and Bielefeldt 1993; RNR, TLB, and JB, unpubl. data). Molt of primaries of breeding adult Cooper's Hawks begins with the innermost primary and proceeds sequentially outward with wings in symmetry (Rosenfield and Bielefeldt 1993). Tail molt begins with the innermost rectrix and proceeds outward in symmetry; during the nestling stage, breeding males are typically molting only the innermost pair of rectrices (Rosenfield and Bielefeldt 1993). Molt of secondaries is variable and often begins after 3–5 primaries have been replaced, then proceeds symmetrically. During the nestling stage usually no more than two secondaries are in molt simultaneously. For comparison we report the proportion of SY and ASY males molting secondaries.

We aged birds not captured by noting their plumage color through binoculars and/or a spotting scope. We frequently obtained very close (1–5 m) and unobstructed views of breeding males near our traps. We were unable to age all birds each year. Sexing of birds not captured was facilitated by the species' pronounced sexual size dimorphism and observations of behaviors (e.g., copulations, prey deliveries; Rosenfield and Bielefeldt 1991b). Except for SY males and ASY males in the first year of our study, the total number of *aged males* in any given year does not necessarily represent different males each

year because some males breed in an area they used in a previous year. Unless specified otherwise, we treat a detection of an ASY male at any nest as an independent event each year.

In Wisconsin, male Cooper's Hawks maintain lifetime fidelity to a nesting area, so a new male in a nesting area or failure of a color-marked male to reoccupy a nesting area indicated death of the previous occupant; we thus documented many replacement (new) males in their first year of breeding (Rosenfield and Bielefeldt 1996, Rosenfield et al. 2009). We determined duration (years) of lifetime breeding in 8 SY males for which we had complete temporal information by noting the time between the year (inclusive) of each bird's first detection as a breeder through the last year we detected it breeding in its nesting area. We excluded 5 of the 13 total SY males from most of the analyses of duration of lifetime breeding because we did not search their nesting areas in the year after we first detected them. That said, we discuss the maximum duration of breeding of these 5 SY males and their lifetime production, assuming they had produced the average brood size annually (Rosenfield et al. 2007b, c), because, from timing of appearance of new males in these 5 males' nesting areas, none of these 5 could have bred for more than 2 years. To facilitate a comparison of duration of lifetime breeding of males that began breeding at an age of 1 year with that of males that began breeding at an age of ≥ 2 years, we calculated the duration of lifetime breeding for 64 males that began breeding at ≥ 2 years of age on the basis of data in Rosenfield et al. (2009) and unpublished data (RNR and JB).

We made at least two visits to nests to assess reproduction of individual adult males and/or the presence of hatchlings <1 week old (or to document nest failure). We later climbed to nests when nestlings were 16–19 days of age, or about 70% of fledging age, to ascertain brood size and band young (Rosenfield and Bielefeldt 2006). This schedule avoided the criterion of 80% of fledging age Steenhof and Newton (2007) suggested for other raptor species, an age at which visits could result in premature fledging of some nestlings and/or inaccurate counts of young (Rosenfield et al. 2007a). We compare reproduction of SY and ASY males in the following ways: annual production is the number of young of bandable age per successful nest for males in their first year of breeding, and lifetime reproduction is the number of nestlings that survived to about 18 days of age during the total number of years in which a male was known to be breeding, until that male was not found on its nesting area and so inferred to be dead (Rosenfield et al. 2009). We assumed that a male in a given nesting area was the father of the young in that area. We used lifetime reproduction of ASY males analyzed by Rosenfield et al. (2009) and others whose data is not previously published (RNR and JB). In comparisons of reproduction by age cohort, an SY male is one that began breeding at 1 year of age, an ASY bird is one that began breeding at ≥ 2 years of age. A successful nest was one in which at least one young reached bandable age (~18 days).

We report the number and proportion of SY males to all aged males across all years of the study to facilitate comparisons of such metrics conventionally calculated by other researchers (Rosenfield and Bielefeldt 1993). We also report the temporal incidence of ASY males detected in their first year of breeding (these first-time breeding males are a subsample of the total number of males aged as ASY). We used a Fisher's exact test to determine if the proportion of SY to ASY males nesting in the first 16 years was significantly different from the same proportion in the second 16 years of the study. This inferential analysis assures statistical independence of the temporal incidence of SY vs. ASY birds by avoiding pseudoreplicative counts of ASY birds that presumably were or known to be returning breeders.

In other comparisons of data on SY and ASY males we deemed inferential statistical tests untenable in part because of the likely risk of type II errors in analysis of very small samples of SY males (and their mates; Zar 1999). These small samples likely reflect the very low frequency of breeding by SY male Cooper's Hawks (see Discussion). There are, however, obvious patterns of disparity and/or similarity between our objectively obtained sample data for SY and ASY birds,

so we believe that our analytical and biological interpretations of our data are logical and reasonable.

All statistical procedures follow Zar (1999). We calculated probability with StatXact Turbo (Mehta and Patel 1992) and accepted significance at $P \leq 0.05$.

RESULTS

Over 32 years (1980–2011), we detected 13 (2%) SY and 719 (98%) ASY males among 732 aged breeding male Cooper's Hawks. The mean numbers of aged males and males not aged per year over the entire study are 23 and 5, respectively. Seventy ASY males in their first year of breeding were detected in 25 (78%) of the 32 years, whereas SY males were detected in only 11 (34%) of the 32 (Fig. 1). The average and median numbers of SY breeding males detected per year over the 32 years were 0.4 and 0, respectively. The maximum percentage of SY males of all aged males within a year when at least one SY male was detected was 13% (mean = 6%). The frequency of occurrence of SY birds changed markedly during the study, as 12 (92%) and 1 (8%) of the total 13 SY males were detected in the first and second 16 years of our study, respectively (Fisher

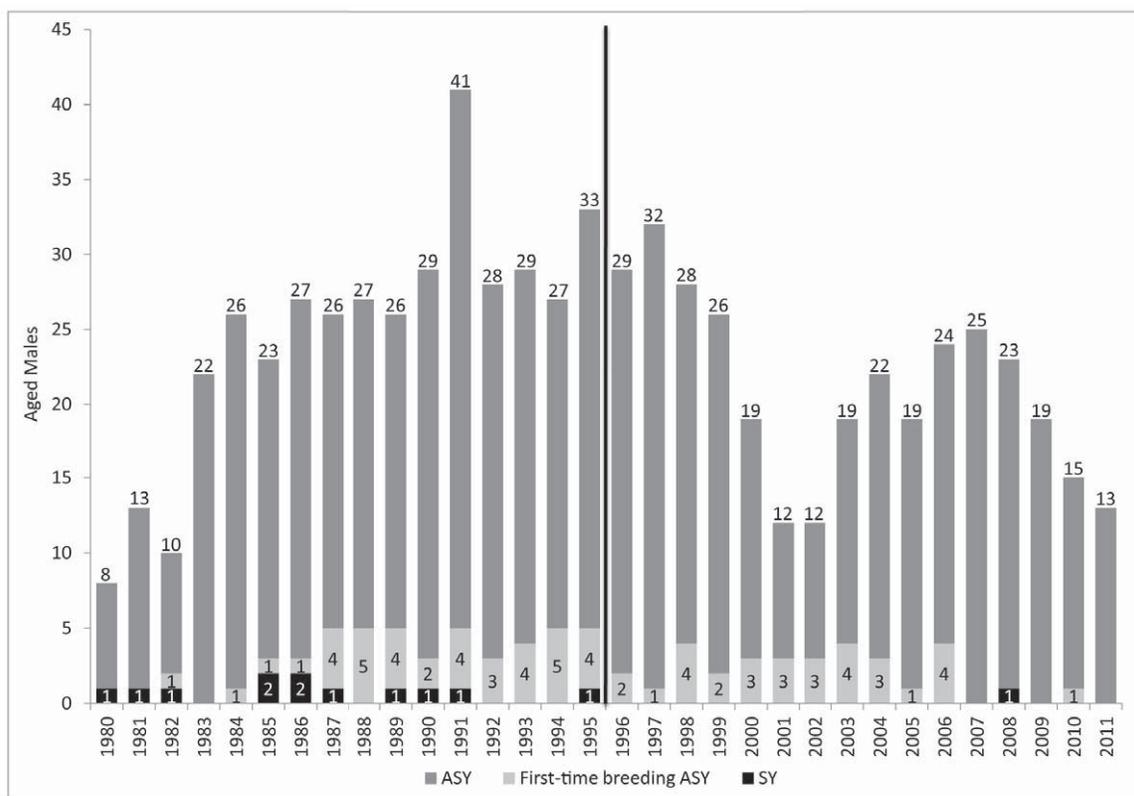


FIGURE 1. The incidence and number of nestings of one-year-old (SY) males, of ≥ 2 -year-old (ASY) males breeding for the first time, and of other ASY male Cooper's Hawks in Wisconsin, 1980–2011. Number atop each bar is the total number of aged males detected each year. Numbers within blackened and light gray portions of a bar are the number of SY males and ASY males breeding for the first time, respectively. Bold vertical line separates the first 16 years of the study from the second 16 years.

TABLE 1. Selected attributes of reproduction of male Cooper's Hawks first breeding at an age of 1 year (SY) and ≥ 2 years (ASY) in Wisconsin.

	SY				ASY			
	Mean \pm SE	Median	Range	<i>n</i>	Mean \pm SE	Median	Range	<i>n</i>
Mass (g) ^a	336 \pm 7.3	327.0	308–375	10	332 \pm 1.8 327 \pm 1.9	329.8 327.0	274–397 ^b 275–366	159 ^b 69 ^c
Annual production	2.9 \pm 0.3	3.0	1–4	12	3.6 \pm 0.1	4.0	1–6	70 ^d
Breeding longevity (years)	2.6 \pm 0.5	2.0	1–6	8	2.7 \pm 0.3	2.0	1–9	64
Lifetime production	8.8 \pm 2.3	8.0	1–23	8	8.7 \pm 0.9	7.0	0–32	64

^aMass at nestling stage.

^bData from Rosenfield and Bielefeldt (1999; maximum mass was incorrectly reported as 421 g).

^cData from Rosenfield et al. (2010).

^dMales first breeding at age ≥ 2 years.

statistic = 6.5, *df* = 1, *P* = 0.01). Furthermore, breeding by SY males was relatively consistent early in our investigation, as we did not detect it in only three (1983, 1984, and 1988) of the first 12 years of our investigation (Fig. 1). Six (46%) and 7 (54%) of the 13 total SY males were detected at our central and southeastern Wisconsin study sites, respectively.

The average sizes of the SY and ASY males were similar (Table 1). Metrics for the ASY cohort are from two independent samples of different breeding males caught at the nestling stage at the same study sites in Wisconsin where SY males occurred, 1980–2007 (Table 1).

Twelve (92%) of the 13 SY males were paired with ASY females; one SY male was paired with an SY female. The ASY females paired with SY males were on average smaller than the average of other breeding ASY females in Wisconsin. The mean \pm SE, median, and range of masses at the nestling stage of 11 ASY females paired with SY males were 561 \pm 14.9 g, 564 g, and 473–626 g, respectively. We earlier reported mean masses of 582 \pm 3.0 g (455–722 g) and 580 \pm 5.1 g (482–667 g) for two independent samples of 210 (Rosenfield and Bielefeldt 1999) and 58 (Rosenfield et al. 2010) different ASY females caught at the nestling stage at the same study sites where we caught the SY males, 1980–2007, respectively.

Eight SY and 94 ASY males were molting their flight feathers, but the extent of that molt was greater in SY males than in ASY males caught at a similar stage of nesting and comparable calendar date of molting. Arrested molt occurred in none of the 8 SY birds but it did in 15 (16%) of the 94 ASY males. Wing molt had reached the fifth primary in 7 (88%) of the 8 SY males but in only 8 (9%) of 94 ASY males. All 8 SY males were molting the innermost pair of rectrices, where annual tail molt begins; in 7 (88%) of these 8 birds the feathers were at least half grown. All other tail feathers of these 8 males were old. Only 21 (22%) of the 94 ASY males were molting the central rectrices, and in only 12 (57%) of these 21 males were these feathers at least half grown. As in the SY males, all other tail feathers in these ASY males were old.

Five (63%) of 8 SY but only 23 (24%) of 94 ASY males were molting secondaries. The median masses of the SY and ASY males used in this molt analysis were 324 g (*n* = 8) and 327 g (*n* = 94), respectively. A generalized composite depiction of these molt metrics for SY vs. ASY males is in Figure 2.

Annual production of young by SY males was lower than that by ASY males, by an average of about 1 fewer young per successful nest (Table 1). The mean and median duration of lifetime occupancy of a nesting area by SY males were similar to those of ASY males at our Wisconsin study sites (Table 1). There was, however, a notable difference in the duration of lifetime breeding between males that began breeding at an age of 1 year or at an age of ≥ 2 years: only 1 (8%) of 13 SY males bred ≥ 4 years (a 6-year-old), whereas 18 (28%) of 64 ASY males bred ≥ 4 years (2 individuals bred for the maximum of 9 years).

Mean and median values of lifetime production for SY males were similar to those for ASY males (Table 1). We note that 5 (63%) of 8 SY males produced at or above the median number of nestlings produced by SY birds, and these five

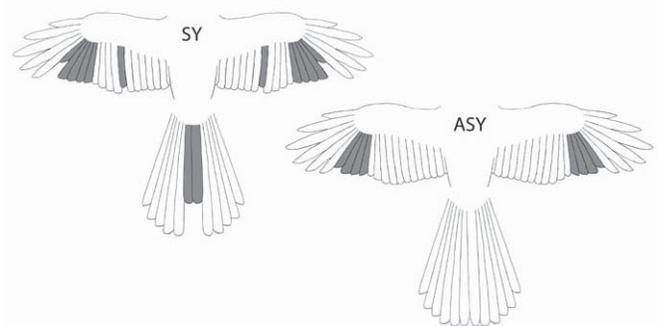


FIGURE 2. Generalized pattern of flight feather molt at the nestling stage of one-year-old (SY) and ≥ 2 -year-old (ASY) male Cooper's Hawks breeding in Wisconsin. White, old flight feathers; gray, new flight feathers.

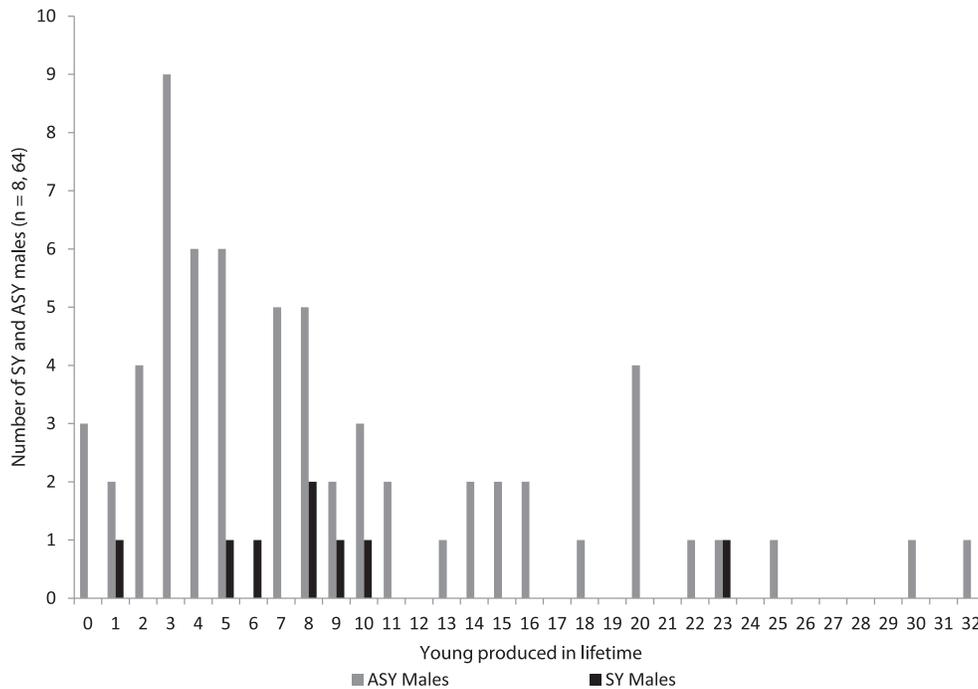


FIGURE 3. Total young produced in the lifetime of individual male Cooper's Hawks first breeding at the age of one year (SY) and ≥ 2 years (ASY) in Wisconsin.

birds produced 58 (83%) of the 70 total nestlings raised by SY males. Similarly, the majority, or 33 (52%) of 64 ASY males, produced at or above the median number of nestlings produced by ASY males, and these 33 birds produced 465 (83%) of the 558 total nestlings produced by ASY males. The two categories differed, however, in lifetime production. Two (15%) of 13 SY males produced ≥ 10 nestlings (maximum was 23 young), whereas 22 (34%) of 64 ASY males produced ≥ 10 young, and 9 of these 22 males produced ≥ 20 young in their lifetimes (maximum was 32 young; Fig. 3).

DISCUSSION

Theory and much empirical evidence suggest that delayed maturation is beneficial in birds when the costs of breeding early in life are high. Most studies have for practical reasons focused on the costs of reproduction for females, yet these costs may be higher for males, especially male birds of prey. Male raptors generally do not begin breeding at an age of 1 year because it is believed that it takes more time for them to acquire the skills needed to obtain a territory and become the principal provider of food to himself, his mate, and his young. Over our 32 years of study in Wisconsin, we found a very low frequency of breeding by SY male Cooper's Hawks, but that frequency was greater in the first half than in the latter half of our study. Despite our small sample size of nesting SY males, there were obvious similarities and differences in various aspects of reproduction

between males that began breeding at 1 or at ≥ 2 years of age. We suggest that a strategy of facultative breeding in response to the constraints of a greater abundance of older breeding males and the constraints of trade-offs in energy allocation explains why SY male Cooper's Hawks rarely breed in our population.

Across Cooper's Hawk's broad continental distribution, breeding by SY males appear to be nonexistent, rare, or uncommon. No breeding of SY males has been detected in multi-year (maximum of 6 years) studies of Cooper's Hawk in Florida (B. A. Millsap, unpubl. data), New York (Meng 1951), Oregon (Reynolds and Wight 1978, Henny et al. 1985), Arizona (Millsap 1981), Utah (Hennessy 1978), California (Asay 1987), North Dakota (Rosenfield et al. 2007c; T. C. Driscoll, unpubl. data), and Minnesota (T. C. Driscoll, unpubl. data). Boal (2001) reported that SY males constituted 7% of all nesting males ($n = 184$) in Tucson, Arizona, but he did not indicate the proportion of SY males breeding by year. In a 17-year study in British Columbia, A. C. Stewart (unpubl. data) detected only one (0.2%) SY male among 579 breeding pairs of Cooper's Hawks. Six of 123 (4.8%) aged males in Milwaukee, Wisconsin, were SY birds (Stout et al. 2007). In the Milwaukee study, there was no temporal trend across years in the percentage of SY males among all breeding males (the proportion of SY females breeding declined as this pioneer population increased; Stout et al. 2007, Stout and Rosenfield 2010). To our knowledge ours is the first study to show a statistically significant temporal trend in the frequency of breeding by SY male Cooper's Hawks.

Over our entire study, SY males were rarely detected as breeding birds (mean = 0.4 year⁻¹); however, they made up a maximum of 13% (1 of 8) of aged males in the first year of the study. Early in the study, breeding by SY males was relatively consistent, recorded in 9 of the first 12 years of the study. Conversely, males' rate of breeding for the first time at an age of ≥ 2 years was relatively consistent throughout the study. Relatively similar levels of sampling each year throughout most of the 32-year study (covering about 5 generations of breeding birds; Rosenfield et al. 1995), with the similar number of detections of SY males in central and southeastern Wisconsin, suggest that SY male Cooper's Hawks bred comparatively more often from 1980 to the early 1990s than later. This remark excludes the still growing urban population in Milwaukee, which Cooper's Hawks apparently colonized in 1993, 14 years after the start of this study and after we had documented a stable breeding population at our southeast study site from 1986 through 1992 (Rosenfield et al. 1995, Stout et al. 2007, Stout and Rosenfield 2010, W. E. Stout and RNR, unpubl. data).

A number of investigations of several raptor species, including Cooper's Hawk, have documented a disproportionately greater number of 1-year-old individuals breeding initially in colonizing and/or recolonizing (and growing) populations (e.g., Newton 1979, Stout et al. 2007). When such populations increased, the proportion of inexperienced breeders declined as older, more experienced birds became more prevalent (e.g., Rutz 2008, Oliphant and Haug 1985, Tordoff and Redig 1997, Stout et al. 2007). Implicit in this scenario is that SY birds generally cannot successfully compete for nesting places with older, more experienced breeders when the older birds are more abundant. That is, SY birds are more constrained from breeding in a larger than in a smaller population perhaps because of the greater risk of engaging in territorial disputes with older, experienced, and perhaps competitively superior breeders, aggravated by the physiological costs of reproduction as an inexperienced first-time breeder (Williams 1966, Curio 1983, Lieske et al. 1997, Hunt 1998; but see below). Such constraint would likely be greater for male rather than for female raptors because the male is principally responsible for establishing territories and for procuring prey for himself, his mate, and their young (Bildstein 1992, Lieske et al. 1997, Krüger 2005).

SY males may, however, be relaxed from this constraint in an area lacking breeders because of a lower frequency of territorial contests (e.g., Tordoff and Redig 1997). Our study was initiated in 1980 following the listing of the Cooper's Hawk by the state of Wisconsin as a threatened species in 1979 (Bielefeldt et al. 1998). Curiously, there were no population data to indicate a low or declining statewide population of Cooper's Hawk prior to or at the time of its listing (Bielefeldt et al. 1998). We did, however, receive anecdotes and opinions from many birders and several avian ecologists (e.g., J. J. Hickey and F. N. and F. Hamerstrom) at the inception of our study supporting the premise that in the 1960s and

1970s the Wisconsin population of Cooper's Hawk had declined, was low, or was extirpated (pers. comm.; Hamerstrom 1972). It is possible that the higher prevalence of SY males in the earlier than in the later years of our study reflected temporarily reduced costs for breeding 1-year-old males, which could more likely obtain unoccupied nesting places in a then smaller breeding population. The Wisconsin population was likely growing during the 1980s, on the basis of significantly increasing counts of migratory Cooper's Hawks at Great Lakes and Wisconsin watch sites (Farmer et al. 2008, Mueller et al. 2001), high indices of annual productivity statewide, and high rates of annual survival of breeding males during that decade (Bielefeldt et al. 1998, Rosenfield et al. 2009), and the removal of the Cooper's Hawk from Wisconsin's list of threatened species in 1989 (Bielefeldt et al. 1998). Furthermore, the increase in Great Lakes and Wisconsin migration counts began to slow and/or had stabilized from the 1990s through 2010 (Farmer et al. 2008, Mueller et al. 2011). We believe that, outside Milwaukee (see above), these stabilized counts reflect a larger population of probably older breeding males in Wisconsin since the 1990s, which could thus explain why we detected fewer SY breeding males since the 1990s. We reiterate that from 1986 through 1992 the population of Cooper's Hawks (all breeding males ≥ 2 years old) at our southeastern study site was stable (Rosenfield et al. 1995, RNR and JB, unpubl. data).

It is also possible that male Cooper's Hawks do not typically breed at 1 year of age because they trade survival for breeding early, exercising "restraint" from breeding at 1 year of age so that they can live longer and produce more young (Curio 1983). Our data support this premise in part. The average numbers of years of breeding by males first breeding at 1 and ≥ 2 years were similar, but because in our study population this duration terminates in death, males first breeding at 1 year generally do not live as long as those first breeding at ≥ 2 years. In their first year of breeding SY males also produced fewer young (on average about 1 fewer) per successful nest than males first breeding at ≥ 2 years. By contrast, in the congeneric Eurasian Sparrowhawk (*A. nisus*), the greater experience of older females does not enable them to raise more young at their first attempt than younger birds, including SY females (Newton 1986). Indeed, considering survivorship, there is an advantage for female Eurasian Sparrowhawks to begin breeding as early in life as possible, and to not exercise restraint (Newton 1986). It could be hypothesized that male Cooper's Hawks that breed at 1 year of age are individuals with the poorest prospects for survival and opt for a "best-of-a-bad-job" strategy (Millon et al. 2010). We think that this scenario is unlikely in our population because under it these bet-hedging SY males should have occurred throughout our long-term study with no temporal variation.

The specific mechanisms that cause production by SY males to be lower than that of ASY males are not known. In a 1-year-old first-time breeder that must forage for a family of

hawks besides himself over several months, inexperience likely increases the costs of reproduction over those for experienced birds, which in turn could result in lower reproduction in SY males (sensu Newton 1979). Additionally, the trade-off in resource allocation to molt vs. reproduction (e.g., Dawson et al. 2000, Millon et al. 2010) may be a mechanism by which the cost of reproduction is aggravated in SY males more than in ASY males. SY males were molting wing and tail feathers to a greater extent than were ASY males, and we conjecture that the increased needs of energy for feather replacement, concomitant with a flight efficiency of SY males perhaps less than that of ASY males, could at least result in a greater energetic struggle for production of young by SY males than by ASY males.

Average lifetime production of SY and ASY males was similar, but *maximum* lifetime production of these two cohorts differed. The disparity in maximum lifetime production between the cohorts is related to the strong positive correlation between lifetime production of young and longevity of breeding males in our study areas and the consequent disproportionate production by the longest-lived individuals (Rosenfield et al. 2009). The maximum duration of breeding by any of the 13 SY males was 6 years ($n = 1$), and no other SY male bred ≥ 4 years. Four of the oldest individuals that began breeding at ≥ 2 years of age, two that bred for 7 years and two for 9 years, collectively produced 110 young, 40 more than the 70 all 8 SY males produced in their lifetimes. Indeed, these four individuals most likely, given the aforementioned average values of annual production by SY and ASY males, collectively produced more young than all 13 SY males collectively produced in their lifetimes. Although lifetime production of some SY males was greater than that of some ASY males, the key point is that maximum lifetime production of the ASY cohort was greater. Similarly, it took fewer individuals (52%) of the ASY cohort than of the SY cohort (63%) to produce 83% of the respective totals of lifetime output of young. Moreover, none of the 13 SY males we observed can be assumed to be alive, but several older males that began breeding at age ≥ 2 years were alive in the last year of this study, and their production to date over 6–11 years accentuates (and increases) the greater maxima in lifetime production of ASY males (RNR, unpubl. data). We suggest that males that begin breeding at 1 year of age in our study areas sacrifice extended longevity and hence maximum lifetime reproductive output. Consequently, it is possible that males that begin breeding at 1 year of age produce fewer recruits; the mean and median duration of lifetime breeding by males that produced recruits that we detected in our study is 5.4 and 6 years, respectively (RNR and JB, unpubl. data). The maximum number of recruits produced by a breeding male in our study was three, and our unpublished data suggest that males that live ≥ 6 years and produce ≥ 15 young are more likely to contribute detectable recruits. We detected only one recruit from a male that began breeding at 1 year of age, and that male that bred for 6 years, producing the

maximum number of young ($n = 23$) of any SY bird. Notably, he was the largest of the SY males we weighed and the fourth largest among 237 ASY males breeding in our study areas.

Despite the aforementioned constraints of temporal variation in numbers of older males, and the restraints of energy-allocation trade-offs, it is possible that the nesting SY males we encountered had intrinsic qualities that enhanced their ability to become breeders. We previously documented that the size of Cooper's Hawks in breeding Wisconsin is related to brood size, recruitment, and mate selection (Rosenfield and Bielefeldt 1999). SY males were on average similar in size to average-sized ASY males. Perhaps smaller SY males are not as successful at attracting mates and/or these males cannot endure the physiological costs of breeding over several months as well as larger SY males. Newton (1986) found that SY female Eurasian Sparrowhawks that bred were larger than those that did not breed. Twelve of the 13 (92%) SY males in our study were paired with ASY females, and these females were smaller than most breeding ASY females in our study population. Their smaller size may have contributed to the smaller sizes of their broods and of their SY male mates, as in our population brood size is positively correlated with size of the female (Rosenfield and Bielefeldt 1999). That said, most SY males were able to pair with possibly experienced breeders, rather than with inexperienced SY females (who were detected as breeders in most years in our long-term study; Rosenfield and Bielefeldt 1993; RNR and JB, unpubl. data). In Arizona, by contrast, Boal (2001) found that 7 of 9 (78%) SY breeding males were paired with SY females, and he suggested that experienced females likely favored more experienced ASY males over SY males for mates. We note that the average size of broods of our SY males was greater than that of all SY male pairings and even greater than production by ASY males paired with SY females reported by Boal (2001); he did not report data on the size or molt of his SY breeding males or of the size of their mates.

It is difficult to identify mechanisms that influence the breeding, or lack thereof, by SY male Cooper's Hawks because they rarely breed. Despite this hurdle our long-term data on several aspects of the species' nesting ecology suggest that a facultative breeding strategy in response to both the constraints of varying abundance of older males and the restraints of trade-offs in energy allocation explains why in our population SY male Cooper's Hawks rarely breed.

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