

Do wing moult and egg size in yearling female Cooper's Hawks reveal age-dependent intrinsic liabilities when breeding?

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Abstract: Prompted by possible age-dependent, eco-physiological influences on the reproductive ecology of Cooper's Hawks (*Accipiter cooperii*) on southeastern Vancouver Island, British Columbia, Canada (1995–2011) and southern Wisconsin, United States (1980–2022), we found that compared to after second year (ASY) (*i.e.*, those ≥ 2 year old) females in both study sites, second year (SY) (*i.e.*, those 1 year old) females were moulting to a greater extent and laid smaller eggs. Rather than extrinsic factors such as habitat or territory quality, we suggest that intrinsic physiological factors associated with age of breeders likely foster trade-offs in energy allocations that are manifest in reproductive attributes, such as smaller eggs, and reduced clutch (and hence brood) sizes in first-time breeding (SY) female Cooper's Hawks.

Key words: yearling, moult, egg size, age-dependent, energy trade-off, eco-physiology, Cooper's Hawk, *Accipiter cooperii*, British Columbia, Wisconsin

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Introduction

Several studies have suggested and/or demonstrated that one-year-old breeding raptors, including Cooper's Hawks, are under different selective pressures than older, experienced birds in part because life history trade-offs render yearlings competitively inferior, and hence of lower quality, compared to older breeders in several aspects of reproduction (*e.g.*, Curio 1983; Lieski *et al.* 1997; Koons *et al.* 2008; Rosenfield *et al.* 2013, 2020b; Lien *et al.* 2015). Moore and Henny (1984) reported that yearling, second year (SY) female Cooper's Hawks in brown plumage typically produced fewer eggs and young than blue-grey plumaged, ≥ 2 -year-old, after second year (ASY) females in Oregon. They speculated that age-dependent disparities in reproductive output could be due to greater energetic costs of production for inexperienced birds, and/or that SY females may be nesting in suboptimal habitat; they called for more research to elucidate the role of these factors.

Some researchers have suggested that the trade-off in resource allocation for moult versus reproduction is a mechanism by which the costs of reproduction are higher in yearling birds compared to older individuals (Dawson

et al. 2000, Rosenfield *et al.* 2013). Indeed, breeding SY male Cooper's Hawks were moulting more extensively than nesting ASY males in Wisconsin (Wis.), which may in part have reduced their productivity and shortened their longevity compared to that of breeding ASY males (Rosenfield *et al.* 2013). Henny *et al.* (1985) mentioned that yearling female Cooper's Hawks breeding in Oregon were moulting "slightly ahead" of older females. Similarly, we observed that SY breeding female Cooper's Hawks in both British Columbia (B.C.) and Wis. appear to be moulting to a greater extent than are nesting ASY birds (RNR, WES, ACS, pers. obs.); and we have shown that reproductive output, including clutch sizes in Wis., is lower for SY versus ASY females (Rosenfield *et al.* 2015, 2020a). Further, we have observed that eggs in nests of SY female Cooper's Hawks in B.C. appear smaller than those in nests of ASY females (ACS and RNR, pers. obs). In his review of the determinants of egg size in birds, Christians (2002) suggested that physiological characteristics (*e.g.*, endogenous protein reserves) of the female might influence egg size, and that larger eggs might increase the chances of survival early in the chick-rearing period. Similarly, Martin (1987) reported that within avian species, hatching success, growth rate, weight, and survival of young from large eggs are typically greater than from small eggs.

In their ecological studies of breeding Cooper's Hawks in Albuquerque, New Mexico, Lien *et al.* (2015) "doubted" that, compared to ASY females, yearling female Cooper's Hawks had a lower innate reproductive potential that physiologically constrained them such that they produced smaller average brood sizes compared to ASY females. Indeed, they believed that brood provisioning rates and "hence the quality of the territories or mates of females of the two age classes," was a more tenable explanation for the disparity in brood sizes (via counts of fledglings) between these two age cohorts. Interestingly, they presented no comparative data on egg size, clutch counts, hatchling mortality rates, nestling brood sizes, parental care, or moult for these two age cohorts; nor did they report the prey delivery rates by males to female mates during the pre-incubation period, of which food resources would certainly influence female endogenous reserves in preparation for egg production and hence annual reproductive potential. Notably, Moore and Henny (1984) stated that the role of age (in behaviour and physiology) versus the role of habitat in age-related disparity in female Cooper's Hawk reproduction was an intriguing subject for future ecological research.

Here we present novel comparative data and inferential analyses on wing moult and egg size between SY and ASY female breeding Cooper's Hawks in B.C. and Wis. Additionally, we discuss other select aspects of the comparative breeding biology of SY versus ASY female Cooper's Hawks among different breeding populations. Combined, these factors support the premise that contrary to the casts by Lien *et al.* (2015), intrinsic physiological factors of SY females limit their reproduction versus that of older counterparts. We emphasize that age structure is a major element in key theories about population and life-history biology (Lack 1968), and the mechanisms underlying the role of maternal age as a factor influencing avian reproduction are unclear (Christians 2002; Rutz *et al.* 2006; Koons *et al.* 2008; Rosenfield *et al.* 2015).

Methods

Our two study sites spanned ~2,660 km across the northern part of Cooper's Hawk's breeding range (42–48°N). The study area on south Vancouver Island, B.C. (48° N, 123° W) included urban and rural areas in and around Victoria, which has a temperate coastal climate (Rosenfield *et al.* 2010), consisting of conifer dominated (*Pseudotsuga menziesii* and *Abies grandis*) rural forests and sparsely to heavily wooded urban habitat in parks, golf courses, other landscaped areas, or undeveloped areas (Stewart *et al.* 1996).

The Wis. study area (43° N, 88° W) occurred in both rural and urban sites consisting of mixed coniferous (*Pinus strobus*, *P. banksiana*) and deciduous (*Quercus* spp., *Populus* spp., *Acer* spp.) forests and small woodlands in and

around Stevens Point in the central part of the state, as well as pine plantations (*P. strobus*, *P. resinosa*) and oak forests in the Kettle Moraine State Forest-South Unit (Rosenfield 2018), and urban developed and undeveloped areas of the metropolitan Milwaukee area in southeastern Wis. (Stout *et al.* 2007). Wisconsin has a highly seasonal, mid-continental climate (Rosenfield *et al.* 2010).

We trapped and individually marked adult breeding Cooper's Hawks with U.S. Geological Survey aluminum leg bands at both study sites, 1995–2011 (B.C.) and 1980–2022 (Wis.). Cooper's Hawks were caught in mist nets near nests with nestlings (Rosenfield *et al.* 2010). Age of breeding females was determined by plumage colour: SY birds were brown-plumaged, whereas grey-plumaged breeders were ASY hens, following Rosenfield *et al.* (2020b).

An index to the extent of moult in breeding females in B.C. and Wis. was determined by recording the loci of the farthest extent of moult in the primary feathers of the wing. Cooper's Hawks have 10 primaries in each wing, which are conventionally numbered from innermost to most distal as LP (left wing) or RP (right wing) 1 through 10 (Figure 1). Plumage moult in breeding Cooper's Hawks begins simultaneously in each wing during the mid-incubation stage with LP and RP 1; primary moult proceeds simultaneously and sequentially in each wing to the most distal primary (Rosenfield *et al.* 2020b). In both age cohorts, we thus tallied each individual by its most distal locus of moult in its primaries, at which location an old primary was either missing (*i.e.*, feather 'dropped') or a new feather was in partial growth (Figure 1). For a tenable comparison of moult of these cohorts, we used moult data from breeding females caught from the last 11 days of June and the first 6 days of July when nestlings in all years were about 2–3 weeks of age on both study areas. Our pool of ASY females used in our moult analyses for both study areas did not include any of the individuals that initially bred in their second year. We highlight that moult of primary feathers in both SY and ASY females coincides with the overall body moult (*i.e.*, other flight [wing and tail] and non-flight feathers), and regardless of age, breeding Cooper's Hawks of both sexes do not complete entire plumage moult until after the breeding season in both study areas (Rosenfield *et al.* 2020b).

During our nest visits to count and band nestlings in our B.C. study area, 1995–2011, we opportunistically measured length and breadth of unhatched eggs (one unhatched egg per nest [choosing at random a single egg when >1 unhatched egg present]). Analyses of these egg dimensions from nests of differently marked tending females revealed a significantly smaller breadth of eggs in nests of SY versus ASY hens. To explore this comparative phenomenon in Wis., we collected the same egg dimensions at 7 and 8 nests of SY and ASY females, respectively, in the mid-incubation period during 2022 (note, we measured all eggs per nest except that in one case, due to inclement weather, we randomly [eggs closest to the observer when initially reaching the



Figure 1. Primary moult in a yearling, second year (SY) breeding female in Wisconsin. Note the blue grey colour of new feathers and the faded brown in old plumage. Molt starts simultaneously in each wing with the dropping and replacement of primary number 1 (or RP and LP 1); these dynamics proceed sequentially through primary 10. This bird was tallied by her most distal locus of moult, which was primary number 8 (RP 8 missing here).

nest] obtained measurements of 2 of 5 total eggs at one ASY female's nest). Egg volume was determined using Hoyt's (1979) length-breadth formula: $\text{Volume} = 0.51 \times \text{LB}^2$, where L is length and B is breadth (maximum diameter).

We used chi-square (χ^2) statistical tests to determine if extent of primary moult differed significantly between SY and ASY female cohorts in both study areas, and t-tests in cohort comparisons of egg dimensions and egg volume in B.C. nests. We measured eggs from 7 SY female nests and 8 ASY female nests in Wis. The small sample size of nests and the lack of independence for combined egg dimensions from Wis. nests precluded tenable use of inferential statistical tests for comparisons of eggs between the age cohorts; we thus report descriptive statistics to interpret obvious cohort disparities in Wis. egg dimensions congruent with B.C. results. Statistical procedures follow Whitlock and Schluter (2009); we accepted significance at $P < 0.05$.

Results

Moult

The most distal moult in the 10 primary feathers of the wing of breeding females at our B.C. and Wis. study sites ranged from the 4th to the 8th primary in both SY and ASY females, with considerable overlap of moult at certain loci, especially at primary 6 (Table 1). However, SY breeders with nestlings 2–3 weeks of age in both B.C. and Wis. exhibited a significantly greater extent of moult versus that of ASY hens with similar aged young ($\chi^2 = 26.34$, $df = 3$, $P < 0.0005$ and $\chi^2 = 49.76$, $df = 3$, $P < 0.0005$ for B.C. and Wis., respectively).

The maximum extent of moult during the nestling stage reached primary numbered 6 or 7 in 80% and 93% of SY breeders in B.C. and Wis., respectively. The maximum extent of moult included primary 5 or 6 in 82% and 95% of ASY females in B.C. and Wis., respectively (Table 1). Additionally, a few yearling females in both B.C. and Wis. exhibited moult reaching the 8th primary, while no yearlings exhibited most distal moult at the 4th primary. By contrast, no moult in ASY females at either study area reached the 8th primary, and several of these older females in both study sites exhibited their most distal moult at only the 4th primary (Table 1).

Egg dimensions

Mean values of egg length were identical (48 mm) in nests of both SY and ASY females in our independent samples of unhatched eggs in our B.C. study area. We found a lower mean breadth in eggs at nests of SY females (37.1 mm) versus that in nests of ASY females (37.8 mm). Egg volume in SY females was about 5% lower than in ASY females. There was no significant difference in mean egg length ($t = -0.062$, $df = 74$, $P = 0.95$), but there were significant differences in means for egg breadth ($t = 2.36$, $df = 74$, $P = 0.02$) and egg volume ($t = -2.4$, $df = 74$, $P = 0.02$) between SY and ASY female cohorts in B.C.

Congruent with significant differences in egg metrics between age cohorts in B.C., there were smaller mean values for both egg breadth and egg volume in SY versus the ASY cohort in non-independent Wis. samples (Table 2, Figure 2). Additionally, and similar to B.C. results, the smallest minimum values for egg breadth occurred in the SY cohort in Wis. (Table 2). Thus, egg dimension metrics suggest that eggs are smaller at nests of SY versus ASY females for both our B.C. and Wis. study areas.

Table 1. Percent frequency of most distal moult loci in primaries of yearling, second year (SY) and ≥ 2 -year-old, after second year (ASY) female Cooper's Hawks with 2–3-week-old nestlings in British Columbia (B.C.) and Wisconsin (Wis.), 1995–2011 and 1980–2022, respectively. Note that the maximum extent of moult in both B.C. and Wis. yearling females typically reached primary numbered 6 or 7, whereas the greatest extent of moult in older, ASY females typically reached primary numbered 5 or 6. See Methods and Figure 1 for description and recording of primary moult.

Site	Age	Primary Feather				
		4	5	6	7	8
B.C.	SY (n = 44)	0	18	48	32	2
	ASY (n = 49)	12	51	31	6	0
Wis.	SY (n = 29)	0	3	45	48	3
	ASY (n = 90)	3	46	49	2	0

Discussion

Our study, prompted by possible age-dependent, eco-physiological influences on reproductive ecology, represents to our knowledge the first analysis of the comparative metrics in wing moult and egg size in SY versus ASY female breeding Cooper's Hawks. We found that compared to ASY females in both B.C. and Wis. study sites, SY females were moulting to a greater extent and laid smaller eggs.

It is well reported across North America that yearling female Cooper's Hawks produce smaller clutch and/or brood sizes compared to ASY females (Moore and Henny 1984; Lien *et al.* 2015; Rosenfield *et al.* 2015, 2020b). SY females in brown plumage possibly produce fewer young than blue-grey

plumaged ASY females, in part because energetic costs of production may be greater for the younger birds, and/or that yearlings breed in suboptimal habitat (*e.g.*, Moore and Henny 1984; Koons *et al.* 2008; Lien *et al.* 2015; Rosenfield *et al.* 2013, 2020a,b). That said, despite detecting SY and ASY females on territory at the same calendric timing during the pre-incubation period on our study sites (ACS and RNR, unpubl. data), SY females generally take longer than ASY females to initiate egg laying possibly in part because yearlings—who on average weigh less than older birds—require more time to attain resources/mass requisite for breeding (Rosenfield *et al.* 2015, 2020a,b; RNR and ACS, unpubl. data). Henny *et al.* (1985) and Lien *et al.* (2015) also noted that SY females take longer than ASY females to initiate incubation.

Table 2. Means \pm SD and range of physical measurements of Cooper's Hawk eggs in yearling, second year (SY) and ≥ 2 -year-old, after second year (ASY) female Cooper's Hawks in British Columbia (B.C.) and Wisconsin (Wis.), 1995–2011 and 2022, respectively. Metrics of egg dimensions were independent (one unhatched egg per nest at nestling stage) in B.C. samples; whereas in Wis., egg metrics were non-independent because we measured multiple eggs at 7 and 8 nests for SY and ASY females, respectively, during the incubation period.

Site	Age	Length (mm)	Breadth (mm)	Volume (ml)
B.C.	SY (n = 32)	48.0 \pm 1.58	37.1 \pm 1.22	33.5 \pm 3.32
		42.6 – 49.0	34.7 – 40.0	26.2 – 43.4
	ASY (n = 43)	48.0 \pm 2.45	37.8 \pm 1.22	35.1 \pm 2.78
		45.1 – 51.3	35.1 – 40.3	28.3 – 41.9
Wis.	SY (n = 27)	47.5 \pm 1.78	38.0 \pm 0.87	35.3 \pm 2.77
		43.2 – 49.8	36.3 – 39.8	29.0 – 40.6
	ASY (n=39)	49.1 \pm 1.72	40.0 \pm 1.28	40.0 \pm 3.42
		46.4 – 53.7	36.8 – 42.3	32.0 – 47.5



Figure 2. Disparate size and shape in a set of Wisconsin Cooper's Hawk eggs: a pyriform shaped, smaller egg of a yearling, second year (SY) female on the left; and the larger, elliptical shaped egg of an older, after second year (ASY) female, right. Irrespective of age of the female, most Cooper's Hawk eggs are elliptical in our study sites. L = egg length, B = egg breadth.

Some researchers have suggested that the trade-off in resource allocation to moult versus reproductive output is a mechanism by which the costs of reproduction are higher in yearling birds than in older individuals (Dawson *et al.* 2000, Rosenfield *et al.* 2013). Indeed, breeding SY male Cooper's Hawks were moulting more extensively than nesting ASY males in Wis. Intrinsic, costly physiology incurred when breeding as yearlings, may in part have reduced their reproductive output and shortened their longevity compared to those males that first bred as ≥ 2 -year-olds (Rosenfield *et al.* 2013; Zuberogoitia *et al.* 2018). Similarly, we speculate that compared to ASY females, yearling females on our B.C. and Wis. study sites incurred greater physiological costs associated with moulting more feathers while breeding (*sensu* Zuberogoitia *et al.* 2018).

In contrast, New Mexico researchers indicated that because two SY female Cooper's Hawks produced the maximum brood sizes (5 fledglings) on their Albuquerque study site, they implied that all, or that SY females in general, have the potential to produce broods as large as ASY females (Lien *et al.* 2015). They therefore doubted that compared to ASY females, yearling female Cooper's Hawks had a lower innate reproductive potential that physiologically constrained them such that they produced smaller average brood sizes compared to ASY females. In fact, and based in part on varying prey numbers among breeding territories, they believed that brood provisioning rates and "hence the quality of the territories or mates of females of the two age classes" (p. 867, Lien *et al.* 2015) was a more tenable explanation for the disparity in brood sizes (via counts of fledglings) between these two age cohorts. However, they presented no comparative data on egg size, clutch counts, hatchling

mortality rates, nestling brood sizes, parental care, or moult for these two age cohorts. Nor did they report the prey delivery rates by males to female mates during the month-long pre-incubation period. Such food resources (upon which a female depends) certainly would influence the endogenous protein reserves in preparation for egg production and hence the annual reproductive potential (Rosenfield *et al.* 2020b). Further, we challenge their unstated assumption that food supplies alone could overcome the likely default liabilities of being an inexperienced first-time breeder; indeed, no amount of food can tenably confer upon an individual the benefits that experience bestows. For example, improvement in food provisioning of chicks via increased age of parents, especially in first-time breeders versus experienced individuals, has been reported in the congeneric Northern Goshawk (*A. gentilis*; Byholm *et al.* 2011) and other birds (*e.g.*, Limmer and Becker 2009). Moreover, we suggest that rather than extrinsic factors associated with habitat or territory quality, intrinsic physiological factors associated with age more likely foster trade-offs in energy allocations that become manifest (or restraining) in reproductive attributes, such as the smaller size of eggs and reduced production in SY female breeding Cooper's Hawks.

Similarly, there is recent evidence that the physiology of first-year Cooper's Hawks and other raptors, including the physiology of feather growth in Cooper's Hawks among widely spaced North American populations, varies with that of older individuals (*e.g.*, Meehan *et al.* 2003; Urban and Mannan 2014; Zuberogoitia *et al.* 2018). Notably, we recently predicted and found that compared to ASY hens, breeding SY female Cooper's Hawks in Wis.—where reproductive output regardless of age is unrelated to habitat variation or putative territory quality (Rosenfield 2018; Rosenfield *et al.* 2020a)—tended to produce more male than female nestlings. We reasoned males, being much smaller than females in this species, were physiologically easier (cheaper) for yearling females to produce because they were physiologically restrained more so than older hens (we note that sex ratio adjustment occurred at conception; Rosenfield *et al.* 2015). Similarly, in a study of Booted Eagles (*Aquila pennata*) the sex ratio in broods was affected by age of breeders and not by territory quality: that is, younger breeders raised more male offspring, the smaller and less expensive sex (Morandini *et al.* 2020). Our findings of concordant, comparative differences in extent of moult and size of eggs in SY versus ASY female Cooper's Hawks in two widely spaced, and genetically different populations (Sonsthagen *et al.* 2012), seem to underscore these recent discoveries that apparently highlight the effects of intrinsic factors in the breeding life-histories of Cooper's Hawks and other raptors.

Lastly, we recognize that given the import of adequate resources, or the physiological 'threshold' required for successful breeding, it would seem maladaptive for yearling females with nestlings to be moulting as many, let alone more feathers than older breeders with similar-aged young.

However, there conceivably is selective pressure for yearlings to 'hasten' out of their first plumage because their juvenile feathers are likely weaker and looser in texture and ergo lack the integrity of adult feathers (Zuberogoitia *et al.* 2018). We encourage further research on the eco-physiological dynamics of the comparative age-dependent biology we addressed herein to better elucidate the poorly understood mechanisms influencing the role (and life-history trade-offs) of maternal age on the breeding biology of birds.

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