Do British Columbia Cooper's Hawks Have Big Feet?

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Abstract: Our investigations of the morphology of live breeding Cooper's Hawks (*Accipiter cooperii*) in southeastern Vancouver Island, British Columbia, Canada, and central and southeastern Wisconsin, United States, 2005-2009, revealed small differences in absolute toe lengths in birds between study sites, but that relative to body size (mass) in both sexes, smaller British Columbia hawks had longer middle-toes than did larger Wisconsin hawks. Our findings support a predator-prey principle that the smaller size of British Columbia hawks reflects selection for an optimum body size that enhances agility when pursuing their dominant prey, small to mid-sized songbirds. Further, relatively longer toes may impart a longer reach that enhances capture of agile avian prey. Less agile mammalian prey are more prevalent in the diet of Wisconsin birds, which may suggest less selective pressure for longer toes in this eastern population.

Key words: morphology, Cooper's Hawk, *Accipiter cooperii*, intraspecific geographic variation, middle-toe length, body mass, predator-prey relationships, British Columbia, Wisconsin.

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Introduction

Researchers have indicated that patterns of intraspecific, geographic variation in morphology of North American birds of prey, or raptors, is not adequately documented (*e.g.* Whaley and White 1994, Andersen *et al.* 2004, Rosenfield *et al.* 2010). This is concerning because research of intraspecific variation in traits helps reveal population structure, and this research is requisite to understanding how a species, especially those which exhibit wide geographic distributions, is adapted to local habitat (Rosenfield 2018, Hull *et al.* 2010).

The Cooper's Hawk (*Accipiter cooperii*) is broadly distributed across North America, breeding from both coasts into southern Canada and south into central Mexico (Rosenfield 2018). Our investigations of several breeding populations, including British Columbia (BC) and Wisconsin (WI), have demonstrated important relationships between morphological and environmental or life history variables among these populations (Rosenfield *et al.* 2007, 2010, Sonsthagen *et al.* 2012). For example, BC birds of both sexes are significantly smaller in body mass or size than counterparts in WI (Rosenfield *et al.* 2010). We suggested that intraspecific variation in body size between these two study populations was in accord with a hypothesis that body size was influenced by selective pressure of different size and agility of the Cooper's Hawk prey. Thus, smaller predator body mass is associated with smaller, more agile prey (Andersson and Norberg 1981). Indeed, small to mid-sized birds (25-80 g, especially Passeriformes, including House Sparrow, *Passer domesticus*, American Robin, *Turdus migratorius*, and European Starling, *Sturnus vulgaris*) comprised 96% of prey by frequency of occurrence and about 85% by biomass in Victoria, BC (Cava *et al.* 2012). Whereas in WI, small to mid-sized Passerines, including House Sparrow, American Robin, and Blue Jay (*Cyanocitta cristata*), made up about 60% of diet by frequency of occurrence, but only about 43% by biomass; mammalian prey made up about 57% of prey by biomass in WI (Bielefeldt *et al.* 1992). The Eastern Chipmunk (*Tamias striatus*), which is larger (~ 100 g) and presumably less agile than birds was, by biomass, the predominant prey of larger WI Cooper's Hawks (Nicewander and Rosenfield 2006, Bielefeldt *et al.* 1992).

Figure 1. Measuring middle-toe length in adult breeding Cooper's Hawk

Wattel (1973) stated that long toes, as indexed by middle-toe length, were characteristic of accipiter species that catch tender-skinned avian prey in mid-air (*i.e.* longer toes enhance reaching for agile prey), whereas hawks with short toes were adapted to taking larger, less agile, relatively tough-skinned ground prey such as mammals. Whaley and White (1994) reported that eastern breeding Cooper's Hawks had longer toes relative to body size in comparison to western breeding populations. However, their important studies were based on museum specimens often of unknown breeding status and geographic (and population) origin. Further, their specimens spanned over a 100-year period and thus likely experienced shrinkage (Greenwood 1979); and their study did not account for possible temporal variation in morphology, which has been reported for the genus *Accipiter* (Tornberg *et al.* 1999, Rosenfield *et al.* 2010). Further, most older museum specimens lack any data on body mass, precluding any adjustment for measurements as a function of mass (size); body mass is considered by many to be the most accurate univariate measure of body size in birds (*e.g.* Cade 1960, Mueller 1986, Dunning 2008). Lastly, Whaley and White (1984) also reported, contrary to our diet findings of BC vs. WI Cooper's Hawks, that a greater percentage of birds are taken by eastern Cooper's Hawks.

Our objective here is to investigate if, relative to body mass or size, western Cooper's Hawks breeding in BC, whose primary prey are small, agile songbirds, have longer toes than those of WI Cooper's Hawks whose nesting diet commonly consists of presumably less agile, mammalian prey. Our study uses morphological data from live birds across five concurrent study years.

Methods

Our two study sites spanned ~ 2660 km across the northern part of Cooper's Hawk's breeding range (42–48° N). The BC study area in 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 (*Pseudotsuga menziesii* and *Abies grandis*)-dominated rural forests and sparsely to heavily wooded urban habitat in parks, golf courses, other landscaped areas, or undeveloped areas (Stewart *et al.* 1996).

The study area in central and southeastern WI (43° N, 88° W) included 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. We also trapped hawks in southeastern Wisconsin, primarily at nests in rural pine plantations (*P. Strobus, P. resinosa*) and oak forests in the Kettle Moraine State Forest-South Unit (Rosenfield 2018), and at urban nests in parks, lawns, or undeveloped areas of metropolitan Milwaukee County (Stout *et al.*

Table 1. Means ± SE (n) and ranges of body mass and middle-toe length of male and female Cooper's Hawks in breeding populations in southern Vancouver Island, British Columbia (BC) and central and southeastern Wisconsin (WI). Differences among geographic sites were analyzed by *t*-tests for body mass and by ANCOVA and Tukey multiple-range test for middle-toe length.

		BC	WI
Males	Body Mass (g)	296.4 ± 1.78 (44)[a] 272–321	329.3 ± 2.93 (47)[a] 286–369
	Toe Length (mm)	37.0 ± 0.20 (44)[b] 33.8–39.4	37.6 ± 0.22 (47)[b] 34.2–40.6
Females	Body Mass (g)	510.8 ± 4.42 (39)[a] 452–565	588.7 ± 5.84 (47)[a] 462–678
	Toe Length (mm)	40.7 ± 0.27 (39)[b] 37.1–43.9	41.5 ± 0.24 (47)[b] 37.3–45.7

[a] There was a statistical difference between study sites in mean mass for males (t = -9.45, df = 89, P < 0.0005) and females (t = -2.12, df = 84, P = 0.03).
[b] There was no statistical difference between study sites in mean middle-toe length in males (F = 0.03, df = 1, 88, P = 0.87) and females (F = 0.09, df = 1, 83, P = 0.76).

2007). WI 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, 2005–2009. Cooper's Hawks were caught in both sites in mist nets near nests when their nestlings were about 2–3 weeks of age. In these analyses, we used data only from grey-plumaged birds (≥2 years old; Rosenfield 2018).

In all hawks we determined body mass to the nearest 1 g with a balance-beam scale, and we measured linear length of the middle-toe (minus the talon; Fig. 1) to the nearest 0.1 mm following Wattel (1973) and Whaley and White (1994). RNR measured all toe-lengths in WI birds and either measured or field-verified > 90% of toe-lengths in BC hawks. We estimated the mass of food in the crop and subtracted it from the total mass; fewer than 10% of hawks had detectable food in their crop. We report means ± standard error (SE).

We used a *t*-test to determine if the mean mass of Cooper's Hawks differed significantly by study area. Because this test revealed significant difference in average mass by site for both sexes, and because other mensural characters may be attributable to body mass (which is a reliable index to body size in birds generally [Askenmo 1982, Dunning 2008], including Cooper's Hawks specifically [Rosenfield and Bielefeldt 1999, Rosenfield *et al.* 2010, Sonsthagen *et al.* 2012]), we tested for differences in middle-toe length between our two study sites as a function of mass (*i.e.* did birds of the same mass differ significantly by site in toe length). In our analysis of co-variance (ANCOVA) the treatment was the study site, the dependent variable was toe length, and the covariate was mass. We used a Tukey multiple-range test to determine differences in middle-toe length by study site. Tests of homogeneity of slope for toe length indicated no significant interaction (P > 0.05) between covariate (mass) and treatment (study sites), thus validating the assumption of homogeneity of slope for the use of ANCOVA. Our use of ANCOVA for analyzing intraspecific morphology of breeding Cooper's Hawks in BC vs. WI populations follow the morphological analyses by Rosenfield *et al.* (2010) for Cooper's Hawks in the same study sites. Invocation of similar techniques for analyzing intraspecific variation in morphology facilitates a tenable discussion of results among studies (Whitlock and Schluter 2009). In our analyses we used SYSTAT (Wilkinson 1992) and accepted significance at $P \leq 0.05$).

Results

Mean values for mass of male and female Cooper's Hawks in WI were significantly greater than these metrics by sex in BC counterparts (Table 1). Middle-toe length in WI birds of both sexes were on average < 1 mm longer than the corresponding metrics by sex for BC hawks; mean values for toe length were not statistically different between sites (Table 1). Thus, relative to body mass in both sexes, smaller BC Cooper's Hawks had relatively longer toes vs. toe length of larger WI hawks.

Discussion

This study represents the first analysis of comparative metrics in toe lengths of live breeding Cooper's Hawks between different populations across this species' broad continental distribution. Further, to our knowledge, there are no published descriptive statistics of toe length in live breeding Cooper's Hawks. Toe length in accipiter hawks has been hypothesized to accord with prey capture dynamics: longer toes should occur in those populations that predominately hunt agile, small avian prey (Wattel 1973, Whaley and White 1994). Our investigations in 2005–2009 in BC and WI revealed that relative to body size (mass) in both sexes, smaller breeding BC birds had longer middle-toes than did WI hawks.

Our results are contrary to those of Whaley and White (1994) who reported that relative to body size eastern Cooper's Hawks had longer toes than western Cooper's Hawks. They suggested a basis for their findings: eastern Cooper's Hawks had a greater percentage of birds in their diet compared to their western counterparts. In contrast, our diet studies in BC and WI indicated that western breeding BC birds took more avian prey than did eastern WI hawks. WI birds commonly took mammalian prey, and the Eastern chipmunk, which was larger (weighing about 100 g) than the smaller (30–70 g) avian prey of BC hawks, constituted the greatest biomass in WI breeding birds (Bielefeldt *et al.* 1992). Thus, our diet findings support our earlier suggestion (Rosenfield *et al.* 2010) that the smaller size of BC hawks represents selection for an optimum body size that enhances agility when pursuing small and agile avian prey. And that relatively longer toes that impart a longer reach may further enhance capture of avian prey by Cooper's Hawks in BC.

We do not know why our results regarding toe length relative to body size for BC vs. WI birds do not concord with the findings of Whaley and White (1994). However, these authors did indicate that their diet data, and hence the ecological relation between morphology and diet, may have been compromised in two ways: 1) the lower percentage of avian prey in the diet of western Cooper's Hawks did not appear to hold for all western localities, and 2) some differences in percentages of food types in diets may reflect different methods in gathering and analyzing food data. Whaley and White (1994) admitted that they had relatively poor sample sizes of Cooper's Hawk specimens from western provinces of Canada, and that they may have included in their analyses some migrant, non-breeding birds of unknown geographic origin (Rosenfield *et al.* 2010). Regarding their second point, it is well known that there are significant biases in methods of sampling food habits data in Cooper's Hawks (*e.g.* collection of prey remains near nests can overestimate the proportion of avian items because avian pluckings are larger, often more colourful, and hence more conspicuous than mammalian remains). We have comprehensively reviewed and rendered suggestions for minimizing these biases in diet studies of Cooper's Hawk (*e.g.* Rosenfield 2018, Bielefeldt *et al.* 1992), and note that these biases did not influence the food habits data we collected at our BC and WI study sites (Bielefeldt *et al.* 1992, Cava *et al.* 2012).

Breeding Cooper's Hawks are principally avivores throughout North America (Rosenfield 2018, Millsap *et al.* 2013), as is true of our BC and WI study sites. But our novel findings on toe length relative to body size strengthen and expand our earlier suggestion (Rosenfield *et al.* 2010) that the proportionate make-up of prey of varying agility and/or size in this bird's diet may influence the morphology of a breeding population. Further, the Eastern Chipmunk appears to be an important prey species in frequency and/or biomass in breeding Cooper's Hawks in several areas of eastern North America (*e.g.* Meng 1959, Janik and Mosher 1982). Because of the mobility and evasiveness of prey species (or lack thereof), wings, bills, toes, and talons of raptors are likely subject to strict canalizing influences (Whaley and White 1994). We thus urge further investigation of the possible relation between diet and intraspecific geographic variation in the morphology of the Cooper's Hawk, including these types of dietary studies in non-breeding seasons, which latter ecology is relatively poorly documented (Bielefeldt *et al.* 1992, Rosenfield 2018). Such research will help us better understand the variation in predator biology, population structure, and evolutionary adaptations of this continentally distributed species.

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