

**COMPARATIVE MORPHOLOGY AMONG THREE NORTHERN  
POPULATIONS OF BREEDING COOPER'S HAWKS**

by

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A Thesis

submitted in partial fulfillment of the  
requirements for the degree

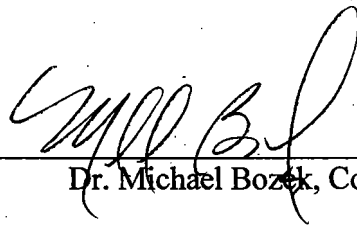
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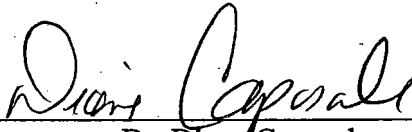
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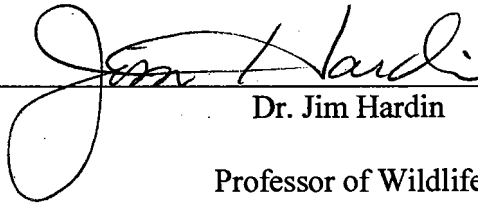
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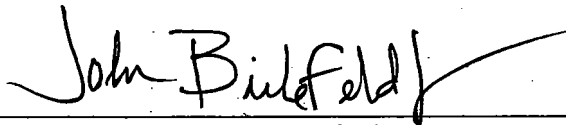
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## *Abstract*

The Cooper's Hawk (*Accipiter cooperii*) is designated as threatened, rare, or species of concern by several state and provincial governments in the United States and Canada. However, informed management of this species across its broad North American range is hampered by a paucity of data on its nesting biology and biogeographic distribution. Conservation agencies currently cannot identify individual populations or understand the extent of eco-variation in phenotypes that may exist in different Cooper's Hawk breeding populations across the continent. I studied differences in morphological characteristics of nesting Cooper's Hawks in the eastern deciduous forests of Wisconsin, isolated drainage woodlands in short grass prairies of North Dakota, and the coniferous forests of British Columbia, Canada; a longitudinal span of 2700 km. I measured body mass, wing chord, tail length, tarsus diameter, hallux length, and culmen length in captured nesting adults. In this study, Cooper's Hawk populations exhibited significant variation in several of these morphological across sites including body mass; when body mass was used as a covariate in ANCOVA several morphological characteristics still differed among study sites. These data suggest that there is little gene flow among populations so discernable morphological differences appear to persist. I speculate that these differences are adaptive and, in part, the result of geographic isolation, where diets, migratory behavior, and/or structural characteristics of nesting habitats vary across landscape types.

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## LITERATURE REVIEW

The Cooper's Hawk is a Crow (*Corvus brachyrhynchos*)-sized woodland raptor that breeds throughout much of North America, including most of the United States, parts of southern Canada, and northwestern and northcentral Mexico (Rosenfield and Bielefeldt 1993a). These hawks have short, rounded wings and a relatively long tail adapted for maneuverability in relatively dense cover. Female Cooper's Hawks are about one-third larger than males, and indeed this species shows among the greatest reversed-size dimorphism of any of the world's hawks. The Cooper's Hawks breed in a variety of habitat including extensive forests and smaller woodlots of deciduous, coniferous, and mixed pine-hardwoods, as well as in pine plantations and suburban habitats. This raptor captures a variety of prey items but mostly small to medium-sized birds such as House Sparrows (*Passer domesticus*), Blue Jays (*Cyanocitta cristata*), American Robins (*Turdus migratorius*), and Mourning Doves (*Zenaidura macroura*); they also take small mammals such as the Eastern Chipmunk (*Tamias striatus*) (Rosenfield and Bielefeldt 1993a). The breeding season for Cooper's Hawks generally begins in February/March, with egg laying during April-May and tending of young by parents during late May through mid-August. Nests are built in many species of coniferous or deciduous trees. The average nest height is between 8-20 m above ground; nest structures consists of sticks with a cup that is lined with bark flakes. Nests are typically placed in a main crotch or against the tree trunk on horizontal limbs. Female Cooper's hawks lay from 1-7 eggs, but generally, clutches consist of 3-5 eggs (Rosenfield and Bielefeldt 1993a).

Raptors have gained much attention from conservation and management agencies throughout North America. The Cooper's hawk in particular is federally (U.S.) protected under the Migratory Bird Treaty Act. Some eastern populations of Cooper's Hawks declined significantly in the mid-1900s, probably due to shooting, pesticide (DDT) contamination, and habitat/forest fragmentation; although recent evidence suggests that breeding populations have recovered in many areas (Rosenfield and Bielfeldt 1993a). To stabilize or increase Cooper's Hawk populations, recent management suggestions in Arizona include livestock exclosure and reforestation to improve riparian nesting habitat (Millsap 1981) whereas in Wisconsin, suggestions include scheduling timber harvests during nonbreeding season months (Rosenfield and Bielefeldt 1993a).

Because of their high trophic position, Cooper's Hawks, like other raptors, are used as a bio-indicator species to gauge the integrity of ecosystems. Most raptor species use large, diverse habitats and thus act as links among habitats, connecting ecosystems across the landscape (Fuller 1996). As a result, not only do raptors require conservation planning on a landscape scale (Fuller 1996) but some also serve as indicators of specific environmental perturbations (e.g. Henny 1977). Despite this attention, the geographic ranges and abundance levels of hawks are often poorly known (Fuller 1996, Whaley and White 1994). This is particularly true for forest dwelling species, including the Cooper's Hawk, that are less-readily observed and/or surveyed (Fuller 1996, Rosenfield et al. 1991, Kirk and Hyslop 1998). For example, the Peterson Field Guide to Hawks (Clark and Wheeler 1987) along with a photographic guide to identification of raptors (Clark and Wheeler 2003), reports that the Great Plains of North America is not included in the Cooper's Hawk's (*Accipiter cooperii*) breeding range. Another popular text, the Peterson

Field Guide to Eastern Birds (Peterson 1980), states that the Cooper's Hawk is "now seldom found nesting in much of its range." Mackenzie (1986) even suggests that the Cooper's Hawk is extirpated from all of eastern North America. These statements regarding Cooper's Hawk range and population status are inaccurate; rather this raptor exhibits high nesting densities in these areas (Rosenfield et al. 1996, Bielefeldt et al. 1998, Nenneman et al. 2002). Yet, in some parts of its range the Cooper's Hawk is still perceived to be in peril (usually without support of demographic data) and as such, is variously designated as threatened, rare, or species of concern by several state and provincial governments in the United States and Canada (Rosenfield and Bielefeldt 1993a, Kirk and Hyslop 1998, Nenneman et al. 2003). Thus, conservation assessment and informed management of this species is clearly hampered by the inadequate and/or inaccurate information on its nesting biology (Rosenfield and Bielefeldt 1993a, Kirk and Hyslop 1998).

Currently, conservation agencies do not have adequate information on general distribution and also have not identified individual breeding populations that may exist across the continent. Geographic variation (e.g., morphological, behavioral, dietary) among Cooper's Hawks suggests that different populations may exist. Geographic variation has been defined by Mayr (1963) as "the occurrence of differences among spatially segregated populations of a species." For instance, White (1993) detailed differences in plumage and morphology attributes of separable falcon populations, and Peregrine Falcons (*Falco peregrinus*), in particular exhibit considerable geographic variation in morphology (White and Boyce 1988). As a result, at least 19 subspecies of Peregrine Falcons are recognized worldwide (Johansson et al. 1998). This morphological

variation presumably results from differences in prey, geographic location, migratory habits, and degree of isolation (White and Boyce 1988). However, for birds of prey in particular, there have been relatively few attempts to make detailed analyses of large-scale trends in the size and shape of individuals of a given species relative to geographic distribution (Whaley and White 1994).

Inadequacies in our knowledge of the Cooper's Hawk biology are exacerbated, in part, by clear east-west differences in morphology (i.e., size) among populations (Jones 1979, Smith 1988, Brown and Amadon 1968, Clark and Wheeler 1987, Whaley and White 1994, Henny et al. 1985). Reports of intraspecific size differences (see Henny et al. 1985) have led to debate among taxonomists; in the late 1800s, an eastern race, *A. c. cooperii*, a western race, *A. c. mexicanus* (Swainson), and a Cuban race, *A. c. gundlachi* (Swann) frequently were acknowledged (Friedman 1950). Cuban birds currently are given full species recognition as Gundlach's Hawk (*A. gundlachi*) (Lawrence) by most authorities (Brown and Amadon 1968, Stressman and Amadon 1979, American Ornithologists' Union 1983). The two other races were primarily differentiated by color variation in plumage and by size. The eastern race, *A. c. cooperii*, was considered the largest and ranged from the east coast of North America to the Rocky Mountains. The western race, *A. c. mexicanus*, inhabited the area west of the Rocky Mountains to the Pacific Coast. Today, however there are no subspecies classifications for *Accipiter cooperii* (American Ornithologists' Union 1998, Rosenfield and Bielfeldt 1993a).

The concept of subspecies and the value of designating them formally is still debated (e.g. Whaley and White 1994) despite the fact that subspecies classification is commonly used in Class Aves (American Ornithologists' Union 1982). For example,

within the Falconiformes, the Merlin (*Falco columbarius*) has three subspecific forms associated with regional environments (American Ornithologists' Union 1998): *F. c. columbarius* (taiga), *F. c. richardsonii* (prairie), and *F. c. suckleyi* (Pacific northwest forests). Similarly, a close relative of the Cooper's Hawk, the Northern Goshawk (*Accipiter gentilis*) has three subspecific forms based on morphological differences across different regional habitats (American Ornithologists' Union 1998): *A. g. laingi* (Pacific), *A. g. apache* (Southwest U.S.), and *A. c. atricapillus* (continental). Some disagreement for subspecies descriptions revolves around whether distinctive populations are truly isolated or more or less separated by steep clines (see Haffer and Fitzpatrick 1985, White and Boyce 1988). The most recent checklist for birds of North America by the American Ornithologists' Union (1998) states that "the Committee strongly and unanimously continues to endorse the biological reality and practical utility of subspecies. Subspecies names denote geographic segments of species' populations that differ abruptly and discretely in morphology or coloration; these differences often correspond with differences in behavior and habitat." Further, the recognition of subspecies allows scientists to address many questions not easily answered otherwise, ranging from dispersal and migration, to local selection and adaptation, and ultimately management practices (Patten and Unitt 2002).

Understanding geographic variation is an important goal in raptor ecology, which should endeavor to describe the patterns of morphological variation over much or all of a species' range, and not to necessarily emphasize naming new subspecies (Storer 1982, Zusi 1982, Haffer and Fitzpatrick 1985). For example, Storer (1952) examined the geographic variation present in resident Sharp-shinned Hawks (*Accipiter striatus*) in

Mexico to help elucidate these previously poorly documented differences. Storer (1952) found differences in size (wing chord and tail length), color, and markings among these Mexican hawks. McGillivray (1989) examined the geographic variation in seven subspecies of the Great Horned Owl (*Bubo virginianus virginianus*), *B. v. occidentalis*, *B. v. wapacuthu [subarcticus]*, *B. v. pallescens*, *B. v. pacificus*, *B. v. saturatus*, and *B. v. lagophonus*. McGillivray (1989) found there were significant differences in size (18 skeletal features) among these subspecies. These past studies, and recent similar ones, may play a role in the ongoing debate over the nature of a species.

Comparative analyses are potentially one of the most powerful tools in ecology and evolution (Ricklefs as cited by Kruger 2000). Comparative data from different populations of widespread species can help to document morphological differences which identify and help explain the selective pressures that produce phenotypic variation (Kroodsma and James 1994). However, from its inception the study of geographic variation in morphology has principally been a collection-based, museum discipline (Baker 1985). In investigations of geographic variation in the Cooper's Hawk, Whaley and White (1994) examined and documented trends using museum specimens from various locations across North America. However, in this study and others, there are numerous problems associated with using museum specimens in studies of geographic variation. First, rarely is there an extensive enough collection to fulfill minimum suitable criteria for statistical analyses (Baker 1985). For example, Whaley and White (1994) have a sample size of fewer than 7 birds (for each sex) in many regions of North America. It is also not uncommon to come across misidentified and mis-sexed specimens in museum collections (Storer 1966, Smith 1988, McGillivray 1989). In morphological

assessments, shrinkage is a factor on preserved specimens (Greenwood 1979, Fjeldsa 1980, Smith 1988), and often there are not enough breeding season specimens of adult birds (Whaley and White 1994). For instance, Whaley and White (1994) found “less than optimal numbers of breeding season Cooper’s Hawk museum specimens” available. Whaley and White (1994) also admit to having gaps in regions of their breeding range, including northern and central plains states. Errors in documenting specific collection sites for specimens also exist in other previous studies (e. g. Wood 1992, McGillivray 1989). Indeed, some museum specimens of adult Cooper’s Hawk in Whaley and White’s (1994) study probably came from collection of migrant individuals, and thus the origin of their breeding locations and population affinities were unknown. Despite these methodological flaws, the limited, previous knowledge on geographic variation of Cooper’s Hawks indeed required the use of museum specimens (Wattel 1973, Whaley and White 1994).

Population boundaries in birds are not necessarily associated with obvious geographical barriers to dispersal. Further, morphological differences among populations may be cryptic or complex and thus not include plumage differences that are easily observed but difficult to describe (Buerkle 2000, Avise and Nelson 1989, Rising and Avise 1993). For example, Bardwell et al. (2001) compared beak characteristics (size and shape) of Western Scrub-Jays (*Aphelocoma californica*) occupying different habitats. These discrete differences (e.g., curvature of beak culmen, and length, width, and depth of beak) are not readily discerned by observers.

Relations between climate and color or morphology are known in a variety of avian species (Rensch 1959); several rules have been promulgated regarding morphology

and environmental relations (Welty 1982). **Bergman's Rule** states that birds in colder climates (more northerly latitudes) have larger bodies. Black-faced Sheathbills (*Chionis minor*) for example, residing in higher latitudes are larger and heavier following Bergman's Rule (Bried and Jouventin 1997). **Allen's Rule** states that birds living in colder regions have shorter beaks, legs, and wings than relatives in warmer regions. Red-billed Choughs (*Pyrrhocorax pyrrhocorax*), for example, have longer extremities of the body (bill and tarsus) in warmer areas following Allen's Rule (Laiolo and Rolando 2001). **Gloger's Rule** states that races of birds that live in warm/ humid regions have darker pigmentation than races of the same species that live in cool/dry regions. The Suirir Flycatchers (*Suiriri suiriri*), for example, exhibit lighter plumage characteristics in drier/cooler regions than those found in warmer/wetter climates (Hayes 2001).

In nature, form and function are generally closely associated; form is often a response to environmental factors and specific life history requisites (Thompson 1942, Frazzetta 1975, Calder 1984, Leisler and Winkler 1985, Johansson et al. 1998). For instance, migratory populations are known to have longer, narrower wings than their sedentary counterparts. Such wing shape apparently reduces energy expenditures during long distance flights (e.g. Welty 1982, Whaley and White 1994). Across their geographic range, beak variation in bird species may reflect adaptive pressure exerted by diet or dietary niches (e.g. Bierregaard 1978, Hull 1993, Hertel 1995, Jenkins 1995). Longer tails may enable better maneuverability (e.g. Hamilton 1961, Mueller et al. 1981). Size may also be influenced by other adaptive forces, such as how prey size influences predator body size (Whaley and White 1994). For Accipiter hawks that predominantly prey upon birds, Andersson and Norberg (1981) argued that because their avian prey is



extremely agile, there should be strong selection toward an optimal body size relative to their prey size, thus allowing them maximum maneuverability relative to prey maneuverability. Andersson and Norberg (1981) further argued that because of a putative optimal prey size, raptors should hunt most effectively within a narrow size range centered near the size of the prey.

A variety of environmental factors across geographic areas likely produce varying optimum body sizes across a species' entire geographic range. Thus, different populations in different environments may exhibit different suites of morphological features (Blackburn and Gaston 1996). Further, given the diversity of lifestyles, habitats, and selective forces acting on a species, a single optimum size seems unlikely (Blackburn and Gaston 1996). Size should reflect prey base and the environment in a manner that optimizes fitness. Moreover, climate differences may affect migration behavior, and habitat composition where hawks breed and nest should influence wing length and tail length. Identifying these morphological differences among geographic regions should allow conservation agencies to target specific management strategies adjusted to specific populations (Fuller 1996).

Cooper's Hawks occur across North America in a variety of differing habitat types. For instance, Cooper's Hawks occupy habitat ranging from the humid, temperate, old growth coniferous forests of the Pacific Northwest, to the relatively dry, sparse deciduous/juniper woodlands of the Great Plains of North America, to the temperate, mixed deciduous forests of Eastern North America (Rosenfield and Bielefeldt 1993a, Nenneman et al. 2003). Because these environments and potential prey species for

Cooper's Hawks are considerably different, morphological differences may exist as local adaptations.

## INTRODUCTION

There have been few large-scale studies of intraspecific variation in morphological characteristics among potentially different populations of woodland nesting hawks in the genus *Accipiter* (Handford 1983, Smith 1988, Whaley and White 1994). The Cooper's Hawk (*Accipiter cooperii*), a Crow-sized accipiter that exhibits a broad North American distribution, has a well-documented natural history in mid-western and south-western states (Rosenfield and Bielefeldt 1993a). But inadequacies in knowledge of Cooper's Hawk biology pertain in part to east-west morphological differences among potentially different breeding populations (Jones 1979, Smith 1988, Brown and Amadon 1968, Clark and Wheeler 1987, Whaley and White 1994, Henny et al. 1985). In the late 1800s, an eastern subspecies, *A.c. cooperii*, a western subspecies, *A.c. mexicanus*, and a Cuban subspecies, *A.c. gundlachi* were often acknowledged (Friedman 1950). Cuban birds currently are given full species recognition as Gundlach's Hawk (*A. gundlachi*) by most authorities (American Ornithologists' Union 1983, Brown and Adadon 1968, Stressman and Amadon 1979). The eastern continental subspecies, *A.c. cooperii*, was considered the largest and supposedly ranged from the east coast of North America to the Rocky Mountains. Allegedly, *A.c. mexicanus* occupied the area west of the Rocky Mountains to the Pacific Coast. However, there are currently no recognized subspecies classifications for continental Cooper's Hawks (American Ornithologists' Union 1998).

Recent approaches to studies of geographic variation in morphology have often stressed the patterns of variation throughout a species' range rather than focusing on

arbitrary subspecific delineations (Storer 1982, Zusi 1982, Ricklefs 1996, Haffer and Fitzpatrick 1985). However, from its beginning the study of geographic variation in morphology has been principally a collection-based museum discipline (Baker 1985). In fact, previous studies on geographic variation in breeding Cooper's Hawks have used only museum specimens (Wattel 1973, Whaley and White 1994), with the largest North American study particularly lacking in specimens from northern and central plains states and western Canada (Whaley and White 1994, McGillivray 1995). Numerous problems arise in using museum specimens in studies of geographic variation (e.g. Greenwood 1979, Fjeldsa 1980, Smith 1988, McGillivray 1989, Wood 1992). There is rarely an extensive-enough collection to fulfill criteria for statistical analyses (Baker 1985, McGillivray 1995), and it is not uncommon to find misidentified and mis-sexed specimens (Storer 1966, Smith 1988, Wood 1992). Other limitations include shrinkage (Greenwood 1979, Fjeldsa 1980), extreme feather wear and damaged parts (Whaley and White 1994), a relative scarcity of known breeding season specimens (Whaley and White 1994), and incomplete coverage of a species' distribution (Whaley and White 1994, McGillivray 1989, 1995). Additionally, collection dates for museum specimens of Cooper's Hawks in Whaley and White's study (1994) covered a period of more than 100 years precluding any account for temporal variation in morphology. Temporal variation in bird morphology can be detected over relatively short periods of time: e.g., 50 years in the Fox Sparrow, *Passerella iliaca* (Zink 1983), 10 years in the Song Sparrow, *Melospiza melodia* (Marshall 1948), and within the genus *Accipiter*, 30 years (Tornberg et al. 1999). Lastly, data on body masses are also absent on most museum specimens, thus precluding any adjustment for morphological measurements as a function of mass (i.e., size) in birds

(Askenmo 1982, Zink and Remsen 1986, Johansson et al. 1998, McGillivray 1987). For theoretical and empirical reasons, mass is considered to be the most accurate univariate measure of body size in birds in comparative studies (Cade 1960, Mueller 1986, McGillivray 1987, Marti 1990, Dunning 1993). Body mass has been used extensively as an index to size in intra-specific, morphological investigations of raptors (e.g. Mueller 1986, Snyder and Wiley 1976), and body mass was a reliable index to, and a heritable attribute of, body size in breeding adult Cooper's Hawks in Wisconsin (Rosenfield and Bielefeldt 1999).

Geographic affinities and morphological similarities within cross-continental populations of a species, such as the Cooper's Hawk, are not necessarily associated with obvious geographic barriers to dispersal; morphological variation may also be cryptic or complex and thus not include plumage differences that are easily observed but difficult to describe (Buerkle 2000, Avise and Nelson 1989, Rising and Avise 1993). In the absence of genetic data, morphology can provide "surrogate genetic" information to studies of geographic variation (Avise 1994). Although the use of morphological characters requires consideration of environmental influences on development, morphological variation may reflect underlying genetic variation (Boag 1983, James 1983, Buerkle 2000). However, genetic studies frequently reveal variation not reflected in avian morphology; conversely, morphological studies frequently reveal variation not reflected in genetic studies of birds (Patten and Unitt 2002). For Cooper's Hawks in particular, little is known about morphological variation among known breeding populations.

The objective of this study was to compare, using an inferential statistical approach (Zink and Remsen 1986), the morphology of breeding Cooper's Hawks in

southern Vancouver Island, British Columbia, northwestern and northcentral North Dakota, and central and southeastern Wisconsin. I also speculate in accord with hypotheses made by others (e.g., Wattle 1973, Whaley and White 1994) on how different environmental attributes and varied life history events may influence morphological characteristics among these separable populations of nesting Cooper's Hawks.

## STUDY AREAS

From 1999-2003, I trapped and individually marked adult breeding Cooper's Hawks at nests in three study localities at similar latitudes (44-49°N): south Vancouver Island, British Columbia, Canada (n = 46 females; n = 53 males), northwestern and northcentral North Dakota (n = 38 females; n = 42 males) and central and southeastern Wisconsin (n = 58 females; n = 60 males) (Figure 1). The British Columbia (BC) study area (49°32'N; 123°10'W) included rural and urban areas in and around "greater" Victoria, BC. Rural sites were forested tracts and urban sites were small (1-12 ha), coniferous woodlands (*Pseudotsuga menziesii* and *Abies grandis*) in or around parks, golf courses, institutional grounds, or undeveloped areas (Stewart et al. 1996). Southern Vancouver Island exhibits a temperate, coastal climate (average temperature of 4.9 °C in January and 16.3° C in July; average precipitation of 137.7 mm in January and 16.9 mm in July).

The rural North Dakota (ND) study area (48°37'N; 102°27'W) lies in northwestern parts of the state in areas of shortgrass prairie (*Stipa viridula*, *S. coma*, *Agropyron*, spp. *Poa pratensis*) interspersed with wetland basins, and with isolated clumps of relatively small deciduous trees (*Populus tremuloides*, *Acer negundo*, *Fraxinus pennsylvanicus*) in drainage corridors (Murphy 1993). The ND study area experiences highly seasonal, mid-continental climate (average temperature of -14.8 °C in January and 19.7 °C in July; average precipitation of 11.5 mm in January and 65.6 mm in July).

The central Wisconsin (WI) study area in Portage County (44°32'N; 89°31'W) includes both rural and urban sites consisting of mixed coniferous (*Pinus strobus*, *P.*

*banksiana*) and deciduous (*Quercus* spp., *Populus* spp., *Acer* spp.) woodlands. The southeastern WI rural nests in Waukesha and Jefferson Counties (42°52'; 88°30' W) include pine plantations (*P. strobus*, *P. resinosa*) and oak forests in the Kettle Moraine State Forest - South Unit (Rosenfield and Bielefeldt 1996, Bielefeldt et al. 1998). Wisconsin also experiences a highly seasonal, mid-continental climate (average temperature of -8.8 °C in January and 22.4 °C in July; average precipitation of 35.5 mm in January and 88.2 mm in July).



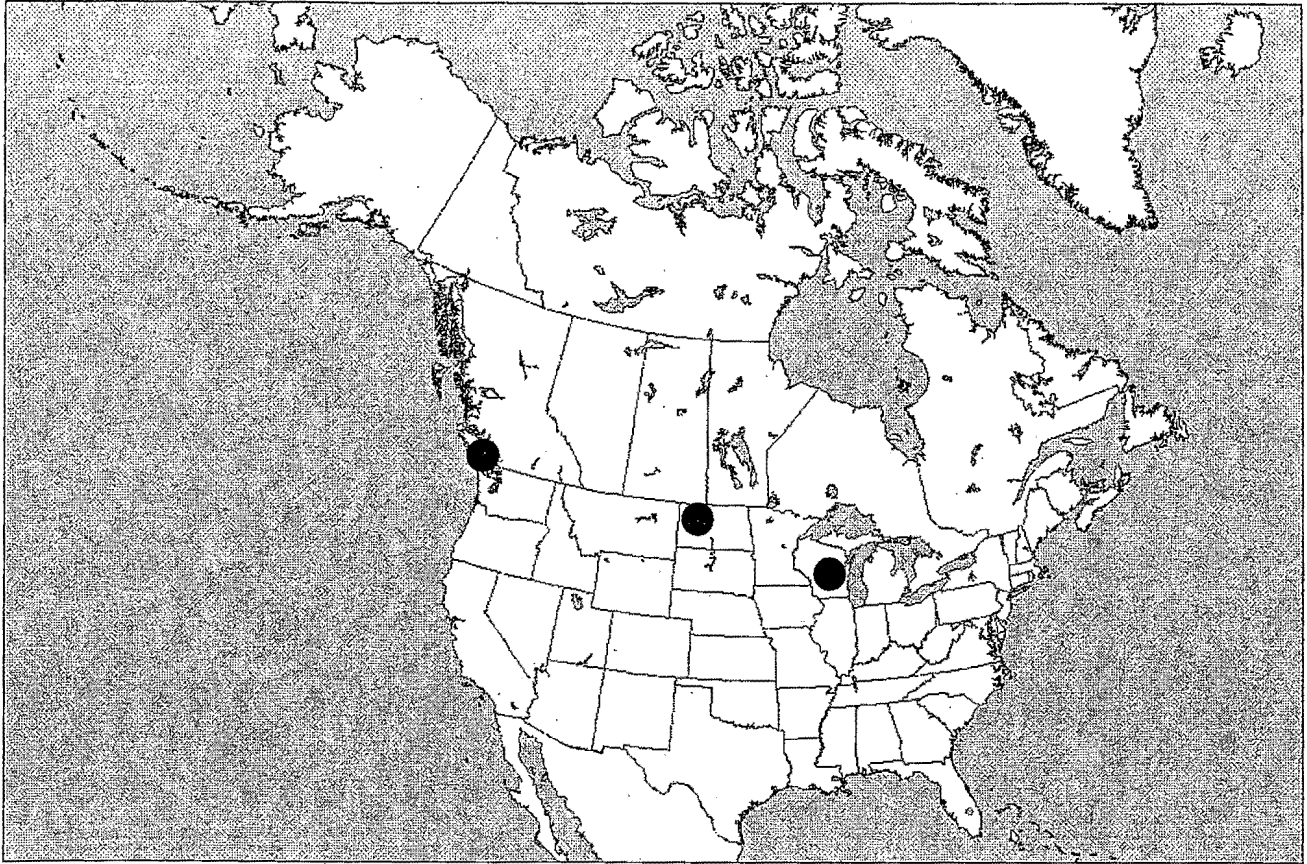


Figure 1. Study site locations for assessing morphological differences among populations of Cooper's Hawks across North America from west to east: British Columbia, North Dakota and Wisconsin.

## METHODS

Morphological data from breeding Cooper's Hawks were collected between late May and early July from 1999 – 2003 from Wisconsin (WI), North Dakota (ND) and British Columbia (BC). Only gray-plumaged, adult birds ( $\geq 2$  years) were used in these analyses. To sample birds, Cooper's Hawk nests were discovered through searches of either potential nest areas and/or by checking historic nesting areas. Nests were located through intensive ground searches of potential nest sites when: 1) colleagues or the general public not associated with this project informed me or my collaborators of potential Cooper's Hawks during the breeding season and 2) through intensive repetitive ground searches of historic nesting areas and by checking for re-occupancy of nesting areas on randomly located quadrats. A nesting area was defined as an area within 400 m radius around a tree that previously held a nest (Rosenfield and Bielefeldt 1992). In other nest searches, quadrats were objectively delineated and ground-searched completely regardless of their perceived suitability for nesting and without foreknowledge of current or historical nest sites on these areas. A detailed description was reported by Bielefeldt et al. (1998), Stewart et al. (1996; A. C. Stewart pers. comm.), and Nenneman et al. (2002, 2003).

Breeding Cooper's Hawks on all study areas were trapped during the mid-to-later stages of the nesting cycle (i.e., when nestlings were 2-3 weeks of age). During this study, median hatch dates were 7 June in WI and BC, and 24 June in ND. Age of nestlings was determined by climbing to nests and noting plumage development as described by Palmer (1988). Hawks were trapped near the nest using a live Great Horned

Owl (*Bubo virginiana*) (Bloom et al. 1992, Rosenfield and Bielefeldt 1993b). The decoy owl was tethered near a mist net by a swivel and leash to a perch within 0.5 m of the ground and within 1.5 m of the net. This system was set up at variable distances from the nest, typically  $\leq 50$  m away. Male and female Cooper's Hawks that made attempts to drive the owl away by stooping at it were captured in the mist net, removed, processed, and released.

Previous studies on morphological variation in birds have used between 6-15 characteristics that can be measured with high precision (Baker 1985). Measurements of a large number of characteristics are highly correlated, thus giving redundant information on characteristics that are part of the same functional complex (e.g. culmen depth and culmen width) (Baker 1985). Six anatomically distinct characteristics that are readily and conventionally measured in birds were chosen: body mass, unflattened wing chord, standard tail length, tarsus length, hallux claw length, and exposed culmen length (Wattel 1973, Pyle 1997). Unflattened wing chord, standard tail length, tarsus (leg) diameter, hallux (hind claw) length, and culmen (beak) length was measured to the nearest 1.0 mm. Body mass of adults was rounded to the nearest 1.0 g with a balance-beam scale. When necessary, an estimate of mass of food in the crop was subtracted from total mass as described in Rosenfield and Bielefeldt (1993b, 1999). Less than 10% of birds had detectable food in their crops, and no adult had more than one-quarter of its crop full.

For adult birds, I ran ANOVA to determine if there was a significant difference in mass among sites, and a Tukey multiple-range test to determine which specific sites were different from others. Because ANOVA revealed a difference in mass among sites for both sexes and because other mensural characters may be attributable to body mass or

size (Askenmo 1982, Dunning 1993, Rosenfield and Bielefeldt 1999, Johansson et al. 1998), each morphological metric was tested using Analysis of Covariance (ANCOVA) to evaluate if differences in morphology exist among geographic regions as a function of mass (i.e., did birds of the same mass differ significantly in other attributes among sites). In ANCOVA the treatment was the geographic region; the dependent variables were the morphological characters, and the covariate was mass. Homogeneity of slope tests for each dependant variable indicated that there was no significant interaction ( $P \geq 0.05$ ) between covariate (mass) and treatment (geographic regions), thus validating the homogeneity of slope assumption for the use of ANCOVA (Wilkinson 1992). Pairwise comparisons were then evaluated among sites to determine which populations were distinct. Analyses were performed using SYSTAT (Wilkinson 1992). The alpha level used in all statistical tests was  $\leq 0.05$ .

## RESULTS

Cooper's Hawks clearly showed morphological differences among geographic regions for both males and females, but the magnitude of individual metrics was not concordant with relative differences in mass. For males, WI birds were on average the largest in mass (325.0 g), ND birds were intermediate (301.5 g) but similar to BC birds, which were smallest (295.8 g) (Tables 1, 2). WI birds also had the longest mean wing chord (237.4 mm), ND birds were intermediate (232.6 mm), and BC birds had the shortest wing chord (227.0 mm). WI males also had the longest tails (185.2 mm), with BC birds intermediate (182.9 mm) and ND birds the shortest (180.6 mm). WI birds had the largest tarsus (6.4 mm), ND males were the same (6.4 mm) and BC birds had the smallest (6.1 mm), and also the longest hallux (19.7 mm), with BC birds intermediate (19.2 mm) and ND birds the shortest (19.1 mm). WI males had the longest mean culmen lengths (16.6 mm), with BC birds intermediate (16.3 mm), and ND birds shortest (16.1 mm).

As with males, females in WI were on average the largest in mass (580.3 g), but in contrast to males, BC females were intermediate (525.5 g) and ND birds were smallest (514.3 g) (Tables 3, 4), though ND and BC females, like their male counterparts, were more similar to each other in mean mass than either group was to WI females. WI birds also had the longest wing chord (267.1 mm), and as with males, ND birds were intermediate (264.3 mm) and BC females shortest on average (256.8 mm). WI females had on average the longest tails (210.3 mm); and again, as with males, BC birds were intermediate (208.6 mm), and ND birds the shortest (206.3 mm). WI females had the largest tarsus (8.3 mm), with ND birds intermediate (7.9 mm), and BC birds smallest (7.6

mm). BC females had the longest mean hallux (24.2 mm), with WI birds intermediate (23.8 mm), and ND birds the shortest (23.2 mm). The longest culmens (19.3mm) were in both WI and BC females, while ND birds had the shortest (18.8 mm) culmens.

There was a statistically significant difference in mean body mass among study sites for males ( $P < 0.0005$ ) and for females ( $P < 0.0005$ ). In both sexes BC and ND masses did not differ ( $P = 0.154$  males,  $P = 0.342$  females). However, body masses between WI and ND and WI and BC were significantly different ( $P < 0.0005$  for both sexes; Tables 1, 3). For wing chord, WI and ND males ( $P = 0.066$ ) and WI and ND females ( $P = 0.398$ ) were not different, but both sexes in WI differed significantly from BC birds ( $P < 0.0005$  for both comparisons). Regarding mean tail lengths, WI and BC males ( $P = 0.969$ ) were not different from each other, but both were different from ND birds ( $P < 0.0005$  in both comparisons). In females pairwise comparisons revealed no significant differences in mean tail lengths between BC and ND ( $P = 0.269$ ), BC and WI ( $P = 0.592$ ), or ND and WI ( $P = 0.071$ ). Regarding tarsus, mean widths between WI and ND ( $P = 0.610$ ) and WI and BC ( $P = 0.168$ ) males were not different. However, BC and ND males were significantly different ( $P < 0.0005$ ) although WI and ND females were not different in tarsus width ( $P = 0.199$ ), comparisons between BC and ND ( $P = 0.021$ ) and between BC and WI ( $P < 0.0005$ ) revealed birds being significantly different. Regarding hallux, BC and ND males were not significantly different ( $P = 0.964$ ), but both were different from WI males ( $P = 0.040$  and  $P = 0.024$ , respectively). Mean hallux lengths of BC and WI females were not different ( $P = 0.114$ ), nor were lengths for WI and ND females ( $P = 0.964$ ), but BC and ND females were different ( $P = 0.028$ ). Finally, there were no significant differences in mean culmen lengths among any of the study

Table 1. Mean  $\pm$  SE (n) and range values of morphological characteristics of male Cooper's Hawks among three breeding populations in North America. BC = southern Vancouver Island, British Columbia, ND = northwest and north central North Dakota, and WI = central and southeastern Wisconsin. Differences among geographic regions were analyzed using ANOVA/Tukey Multiple Range Test for mass and ANCOVA for other characteristics. Superscripts **a**, **b**, and **c** indicate significant differences. Alpha was set at  $P \leq 0.05$ .

Character	WI	ND	BC	F	P
Mass (g)	325.0 $\pm$ 2.26(60) <sup>a</sup> 275.0-358.0	301.5 $\pm$ 2.24(42) <sup>b</sup> 275.0-329.0	295.8 $\pm$ 1.47(53) <sup>b</sup> 275.0-316.0	62.379	<0.005
Wing chord (mm)	237.4 $\pm$ 0.71(59) <sup>a</sup> 226.0-252.0	232.6 $\pm$ 0.81(42) <sup>a</sup> 224.0-246.0	227.0 $\pm$ 0.58(53) <sup>b</sup> 217.0-236.0	23.093	<0.005
Tail (mm)	185.2 $\pm$ 0.75(59) <sup>a</sup> 172.0-200.0	180.6 $\pm$ 0.94(42) <sup>b</sup> 169.0-192.0	182.9 $\pm$ 0.62(53) <sup>a</sup> 172.0-191.0	3.999	0.020
Tarsus (mm)	6.4 $\pm$ 0.06(28) <sup>a,b</sup> 5.8-7.0	6.4 $\pm$ 0.06(27) <sup>a</sup> 5.8-7.0	6.1 $\pm$ 0.04(41) <sup>b</sup> 5.3-6.7	7.333	0.001
Hallux (mm)	19.7 $\pm$ 0.17(29) <sup>a</sup> 17.8-21.7	19.1 $\pm$ 0.11(27) <sup>b</sup> 18.1-20.3	19.2 $\pm$ 0.10(42) <sup>b</sup> 17.1-20.3	3.852	0.025
Culmen (mm)	16.6 $\pm$ 0.15(28) <sup>a</sup> 14.9-18.3	16.1 $\pm$ 0.22(27) <sup>a</sup> 11.7-17.5	16.3 $\pm$ 0.08(41) <sup>a</sup> 15.2-17.3	1.515	0.225

Table 2. Results of ANCOVA interaction tests for male morphological characteristics by region. Significant results are shown in **bold**.

Variable	Effect	df	MSE	F	P
Wing chord	Covariate*Region	2	30.343	1.316	0.271
	Covariate (Mass)	1	296.522	12.808	<b>0.000</b>
	Region (Location)	2	534.626	23.093	<b>0.000</b>
	Error	150	23.151		

Parameter Estimates

	n	Estimate	SE	LS Means
Intercept	59	203.005	0.763	235.834
Covariate (Mass)		0.763		
Region (Location)	ND 42	0.824	0.766	233.263
	BC 53	-0.4218	0.741	228.22

Variable	Effect	df	MSE	F	P
Tail	Covariate*Region	2	72.438	2.576	0.080
	Covariate (Mass)	1	157.665	5.490	<b>0.020</b>
	Region (Location)	2	114.835	3.999	<b>0.020</b>
	Error	150	28.716		

Parameter Estimates

	n	Estimate	SE	LS Means
Intercept	59	161.534	0.849	184.102
Covariate (Mass)		0.070		
Region (Location)	ND 42	-1.891	0.853	181.106
	BC 53	0.786	0.826	183.783

Variable	Effect	df	MSE	F	P
Tarsus	Covariate*Region	2	0.001	0.013	0.987
	Covariate (Mass)	1	0.153	1.824	0.180
	Region (Location)	2	0.616	7.333	<b>0.001</b>
	Error	91	0.084		



Table 2 Cont.

Parameter Estimates					
		n	Estimate	SE	LS Means
Intercept		28	5.301	0.073	6.292
Covariate (Mass)			0.003		
Region (Location)	ND	26	0.125	0.058	6.388
	BC	41	-0.155	0.051	6.108

Variable	Effect	df	MSE	F	P
Hallux	Covariate*Region	2	0.031	0.059	0.943
	Covariate (Mass)	1	0.258	0.491	0.485
	Region (Location)	2	2.026	3.852	<b>0.025</b>
	Error	93	0.526		

Parameter Estimates					
		n	Estimate	SE	LS Means
Intercept		29	20.546	0.180	19.736
Covariate (Mass)			-0.004		
Region (Location)	ND	26	-0.238	0.147	19.068
	BC	42	-0.191	0.127	19.114

Variable	Effect	df	MSE	F	P
Culmen	Covariate*Region	2	0.163	0.247	0.782
	Covariate(Mass)	1	1.065	1.640	0.225
	Region (Location)	2	0.984	1.515	0.225
	Error	91	0.649		

Parameter Estimates					
		n	Estimate	SE	LS Means
Intercept		28	13.720	0.206	16.422
Covariate (Mass)			0.008		
Region (Location)	ND	26	-0.226	0.162	16.055
	BC	41	0.084	0.145	16.365

Table 3. Mean  $\pm$  SE (n) and range values of morphological characteristics of female Cooper's Hawks among three breeding populations in North America. BC = southern Vancouver Island, British Columbia, ND = northwest and north central North Dakota, and WI = central and southeastern Wisconsin. Differences among geographic regions were analyzed using ANOVA/Tukey Multiple Range Test for mass and ANCOVA for other characteristics. Superscripts a, b, and c indicate significant differences. Alpha was set at  $P \leq 0.05$ .

Character	WI	ND	BC	F	P
Mass (g)	580.3 $\pm$ 5.11(57) <sup>a</sup> 482.0-667.0	514.3 $\pm$ 7.22(38) <sup>b</sup> 444.0-618.0	525.5 $\pm$ 3.76(46) <sup>b</sup> 480.0-577.0	46.338	<0.005
Wing chord (mm)	267.1 $\pm$ 0.84(56) <sup>a</sup> 254.0-278.0	264.3 $\pm$ 0.90(38) <sup>a</sup> 251.0-276.0	256.8 $\pm$ 0.80(45) <sup>b</sup> 247.0-268.0	36.365	<0.005
Tail (mm)	210.3 $\pm$ 0.84(57) <sup>a</sup> 196.0-225.0	206.3 $\pm$ 1.20(38) <sup>a</sup> 187.0-220.0	208.6 $\pm$ 0.94(46) <sup>a</sup> 195.0-221.0	2.525	0.084
Tarsus (mm)	8.3 $\pm$ 0.09(28) <sup>a</sup> 7.3-9.2	7.9 $\pm$ 0.07(26) <sup>a</sup> 7.0-8.4	7.6 $\pm$ 0.10(35) <sup>b</sup> 6.2-9.2	11.532	<0.005
Hallux (mm)	23.8 $\pm$ 0.16(29) <sup>a,b</sup> 22.6-25.9	23.2 $\pm$ 0.29(26) <sup>b</sup> 19.3-26.0	24.2 $\pm$ 0.16(35) <sup>a</sup> 22.2-26.7	2.773	0.014
Culmen (mm)	19.3 $\pm$ 0.15(29) <sup>a</sup> 17.9-21.0	18.8 $\pm$ 0.21(26) <sup>a</sup> 17.5-23.0	19.3 $\pm$ 0.12(35) <sup>a</sup> 17.8-20.8	1.515	0.068

Table 4. Results of ANCOVA interaction tests for female morphological characteristics by region. Significant results are shown in **bold**.

Variable	Effect	df	MSE	F	P
Wing chord	Covariate*Region	2	22.027	0.772	0.464
	Covariate (Mass)	1	40.143	1.411	0.237
	Region(Location)	2	1034.611	36.365	<b>0.000</b>
	Error	136	28.937		

Parameter Estimates				
	n	Estimate	SE	LS Means
Intercept	57	251.317	0.823	266.124
Covariate (Mass)		0.021		
Region(Location)	ND 38	2.181	0.941	264.906
	BC 45	-5.580	0.832	257.145

Variable	Effect	df	MSE	F	P
Tail	Covariate*Region	2	1.420	0.031	0.969
	Covariate (Mass)	1	1.392	0.031	0.860
	Region(Location)	2	113.272	2.525	0.084
	Error	138	44.639		

Parameter Estimates				
	n	Estimate	SE	LS Means
Intercept	58	208.280	1.014	210.353
Covariate (Mass)		0.000		
Region(Location)	ND 38	-2.124	1.171	206.297
	BC 46	0.192	1.023	208.614

Variable	Effect	df	MSE	F	P
Tarsus	Covariate*Region	2	0.026	0.108	0.898
	Covariate (Mass)	1	0.128	0.534	0.467
	Region(Location)	2	2.757	11.532	<b>0.000</b>
	Error	82	0.239		

Table 4 cont.

Parameter Estimates					
		n	Estimate	SE	LS Means
Intercept		26	7.337	0.115	8.285
Covariate (Mass)			0.001		
Region (Location)	ND	25	0.019	0.108	7.981
	BC	35	-0.341	0.084	7.622

Variable	Effect	df	MSE	F	P
Hallux	Covariate*Region	2	0.667	0.535	0.588
	Covariate (Mass)	1	3.332	2.704	2.704
	Region (Location)	2	5.543	4.499	<b>0.014</b>
	Error	82	1.232		

Parameter Estimates					
		n	Estimate	SE	LS Means
Intercept		26	20.528	0.261	23.533
Covariate (Mass)			0.006		
Region (Location)	ND	25	-0.295	0.245	23.430
	BC	35	0.488	0.190	24.213

Variable	Effect	df	MSE	F	P
Culmen	Covariate*Region	2	0.623	0.947	0.392
	Covariate (Mass)	1	2.862	4.357	<b>0.040</b>
	Region (Location)	2	1.821	2.773	0.068
	Error	82	0.657		

Parameter Estimates					
		n	Estimate	SE	LS Means
Intercept		26	16.150	0.190	18.993
Covariate (Mass)			0.006		
Region (Location)	ND	25	-0.160	0.179	18.954
	BC	35	0.281	0.139	19.395

## DISCUSSION

I found statistically significant morphological differences in body mass and body structure among breeding populations of Cooper's Hawks in British Columbia, North Dakota, and Wisconsin. These differences held true for both breeding males and females, suggesting that regional differences may result from geographic segregation/isolation. Four of six characters in females and five of six characters in males -- body mass, wing chord, tail, tarsus, hallux, and/or culmen -- differed among two or more of these three populations. Some differences among these three populations were attributable to mass while other differences were attributable to other metrics even after considering body mass as a covariate (Tables 1 - 4). However, differences were not uniform, i.e., birds of larger mass did not necessarily have larger metrics for wing chord, tail, etc. In addition, these three populations also revealed age- and sex-related differences in pace of eye color change (Rosenfield et al. 2003).

While morphological characteristics are highly heritable in most organisms (Zink 1986, Zink and Remsen 1986), in passerines they are also subject to strong non-genetic environmental influences (James 1983). For example, James (1970) found a relationship between intraspecific size variation and topographic features in several species of birds. This link between size and topographic features may be adaptations to minor climate gradients (James 1970). Environmental attributes and varied life history events may also influence phenotypes and provide insights into ecomorphology. For example, migratory populations within a species usually have longer wings than their less migratory

counterparts (Storer 1952, Wattel 1973, Welty 1982, Winkler and Leisler 1992). Longer wings have been shown to provide more efficient flight (more power at a lower energetic cost) (e.g. Kerlinger 1989, Winkler and Leisler 1992). Based on band recoveries and re-sightings of marked birds, the adult Cooper's Hawk population in BC is for the most part a resident population (A. C. Stewart pers. comm.), while breeding populations in ND and WI are migratory and partially migratory, respectively (Meehan et al. 2003). After adjusting for differences in body mass among populations, I found significantly longer wing chords in both male and female Cooper's Hawks from the migratory or semi-migratory populations in ND and WI compared to sedentary Cooper's Hawks in BC, in accord with the aforementioned principles.

Another morphological characteristic that may vary based on local environmental features is tail length. Longer tails are alleged to allow better maneuverability of birds occupying forested habitats (Hamilton 1961, Wattel 1973, Mueller et al. 1981). For instance, Wattel (1973) states "the denser the vegetation in which the prey has to be pursued, the more important it is that the predator be very maneuverable." BC and WI habitats consist of relatively large and more densely forested tracts versus ND, where birds nest in smaller woodlands (e.g. drainage basins, coulees, and shelterbelts) surrounded by short grass prairie and cropland (Murphy 1993, Nenneman et al. 2003). My results concur with Hamilton (1961) and others, tails of ND Cooper's Hawks were significantly shorter in males than in BC or WI. In females, ND Cooper's Hawk tails were significantly shorter than those in WI birds.

It has been suggested that raptors evolved toward an optimum body size, such that a predator should be close to the size of its prey (Wattell 1973, Gittleman 1985, Kruger 2000, Andersson and Norberg 1981, Whaley and White 1994). In this study, body mass, a good index to body size in birds (Askenmo 1982, Mueller 1986, Dunning 1993, Rosenfield and Bielefeldt 1999), was significantly different among the three populations. I speculate that body mass may be influenced by other ecological forces and selective pressures, such as the presumably different prey bases among the three study sites. For those accipiter hawks that predominantly prey upon birds, Andersson and Norberg (1981) argued that because their avian prey is extremely agile, there should be strong selection toward an optimal body size relative to prey size, thus allowing them maximum maneuverability relative to prey agility. Andersson and Norberg (1981) further argued that because of a putative optimal prey size, raptors should hunt most effectively within a narrow size range of prey sizes. Wisconsin males and females were significantly larger than those in BC or ND in apparent accord with the above speculations about prey and predator size: in BC and ND small mid-sized birds (25-80 g, especially from the Order Passeriformes) make up a majority of the prey of nesting Cooper's Hawks (Peterson and Murphy 1992 [ND], A. C. Stewart pers. comm. [BC]). In contrast, the Eastern Chipmunk, which is larger (ca. 100 g) than the avian prey used by Cooper's Hawks in BC and ND, predominated in terms of biomass as prey of breeding Cooper's Hawks in one Wisconsin study (Bielefeldt et al. 1992).

The other morphological characteristics I studied may also be adaptations to the character of prey hunted and/or taken by Cooper's Hawks. Indeed, bill and leg sizes may be more influenced by feeding ecology than homologous elements in mammals because

of birds' lack of grasping forelimbs and teeth for food manipulation (Zink and Remsen 1986). Small beaks, long middle toes, and short hind claws are said to be characteristic of accipiter hawks that catch avian prey (Wattel 1973), whereas short toes and long hind claws are characteristic of those that prey upon mammals (tougher-skinned prey and ground-dwelling prey). Short and sturdy tarsi and the heavy talons may have evolved as adaptations to capturing heavy prey by pouncing on it (Wattel 1973). Thick tarsi should enable Cooper's Hawks to avoid damage to their legs when they contact prey and the ground (Smith 1988). Tarsus and hallux dimensions were significantly different among BC, ND, and/or WI populations in both males and females after controlling for body mass. For example, in accord with Wattel (1973), breeding male Cooper's hawks in WI, where mammalian prey is commonly taken (Bielefeldt et al. 1992), had a significantly longer hallux claw ( $P < 0.040$ ,  $P < 0.024$ ) than males in BC and ND, respectively, where avian prey appears to predominate in the diet of breeding hawks (Peterson and Murphy 1992, A.C. Stewart pers. comm.).

Morphological variation among these three study populations across a 2700 km longitudinal distribution may provide insights about the degree of evolutionary isolation, and the development of conservation tools. Discovery and further study of morphologically and genetically distinguishable populations provide the opportunity to enhance an understanding of gene flow, speciation, migration, dispersal, geographic variation, and local selection (Patten and Unitt 2002). At present, there is no evidence of movement of breeding adults among the three populations I studied: the sedentary adult BC population (Campbell et al. 1990, A.C. Stewart pers. comm.), the highly migratory population in ND (Meehan et al. 2003), or the partially-migratory population in WI



(Rosenfield and Bielefeldt 1993). Band recoveries have shown that migrational and/or dispersal movements of Cooper's Hawks are generally on north-south axes for eastern, Great Plains, and western parts of North America (Hoffman and Smith 2003 [western U.S. and Canada], A. C. Stewart pers. comm. [BC], R. K. Murphy pers. comm. [ND], R. N. Rosenfield and H. C. Mueller pers. comm. [WI]).

Morphological clines among the three breeding populations of Cooper's Hawk are not evident at this time. Moreover, there appears to be no evident physical environmental barrier that would inhibit gene flow between ND and WI populations. Even so, these two populations separated by less than 850 km differ markedly in mass and other morphological respects. Despite the presence of possible barriers to gene flow (e.g. Rocky Mountains), I found that ND and BC populations are more similar to each other in body mass and other respects than either is to the WI population (Tables 1,3). In another study, age- and sex- related differences in eye color were also more similar to each other in these two western populations than either were to Cooper's Hawks in WI (Rosenfield et al. 2003). Using museum specimens from across all of North America, Whaley and White (1994) found east to west differences in size of Cooper's Hawks (based on wing chord) and they also reported that the smallest birds were in the Pacific Northwest region of the breeding range. Whaley and White (1994) also suggested that the largest individuals were found in the southwestern United States (largest male and female wing chords = 245 mm and 278 mm, respectively, which figures for wing chord are not greater than those I recorded for male and female Cooper's Hawks [252 mm and 278 mm] in WI). However, it is possible that shrinkage influenced their metrics on wing chord, and they had a relatively poor sample size from the northern Great Plains and western Canada, and

they may have included some migrant non-breeding birds in their analyses of museum specimens (see Introduction). In contrast, my study with relatively large sample sizes is composed exclusively of live, breeding Cooper's Hawks, including the first morphological data for known nesting birds in the Great Plains of ND. If clinal variation does exist between the ND and WI populations of breeding birds, the cline(s) must be abrupt.

It is possible that differing selective pressures may operate upon morphological features of smaller male versus much larger female Cooper's Hawks in the breeding season in western, mid-continental, and eastern populations, as noted by Whaley and White (1994). Cooper's Hawks exhibit one of the highest degrees of reversed sexual-sized dimorphism among the world's raptors, and nesting duties differ markedly between the sexes with males providing the bulk of prey resources to the females and nestlings in early- to mid-stages of breeding (Rosenfield and Bielefeldt 1993). Intersexual selective forces may also differ among males and females in the mainly resident, partially migratory, and mostly migratory populations in BC, WI, and ND, respectively. Such intersexual selective pressures may explain why some character differences between the genders (e.g., tail length, Tables 1, 3) within these three populations may not always show similarly significant differences across the entire suite of the six morphological features examined in this study. Therefore geographic differences for sexual-size dimorphism between males and females could be present among our populations. Research on this topic is ongoing in the BC, ND, and WI study sites (R. N. Rosenfield pers. comm.).

Clark et al. (2004) have called for studies that address population dynamics and conservation actions at spatial scales that may span entire continents. The extensive continental distribution and identification of morphologically separable populations of Cooper's Hawks make it highly suitable for an examination of the genetic structure of bird species, now a burgeoning field of avian conservation (Fleischer 1998). My discovery of morphologically separable breeding populations also may warrant a re-examination of the lack of subspecific classification for *Accipiter cooperii*.

My study provides substantial evidence of morphological variation in body structure in breeding Cooper's Hawks across North America and clearly demonstrates population differences. In conservation terms, potential management plans for these three morphologically and geographically separable populations should take into account their differences in habitat use, landscape mosaics, and prey availability. Because these populations differ significantly in several morphological attributes that are presumably the result of different selective pressures of varying environments, it seems unlikely that one management scheme would apply equally well throughout the broad North American range of the Cooper's Hawk. However, despite my speculations, the causative factors responsible for the morphological variations are still unknown. Therefore, I recommend that biologists and conservationists investigate the relation(s) between fitness (e.g. reproductive success) and various aspects (e.g. nest-site habitat structure, prey use, etc.) of the breeding habitat of my study populations. This effort should help to identify important selective pressures of environments managed by wildlife biologists.

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