Morphological and molecular variation in four species of migratory raptors from North America

Elise Vernon Schmidt

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MORPHOLOGICAL AND MOLECULAR VARIATION
IN FOUR SPECIES OF MIGRATORY RAPTORS
FROM NORTH AMERICA

by

Elise Vernon Schmidt

A dissertation submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Biological Science

Department of Biological Sciences
University of Nevada, Las Vegas
December 1996
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University of Nevada, Las Vegas
December 1996
ABSTRACT

Population structure and ecological morphology of four species of raptors were studied in three migratory populations. Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks (*A. cooperi*), Red-tailed Hawks (*Buteo jamaicensis*), and American Kestrels (*Falco sparverius*) all migrate through three major flyways in North America: the Goshute Mountains of Nevada, the Manzano Mountains of New Mexico, and Cape May Point in New Jersey. Restriction fragment analysis of mitochondrial DNA was used to elucidate population structure, and analyses of morphological characteristics provided information on ecomorphology of raptors. Geographic population structure was found only in Red-tailed Hawks with Cape May individuals having a different haplotype than western individuals. The other three species did not exhibit obvious phylogeographic population structure with most individuals of these three species having one common haplotype. All four species exhibited size and shape differences consistent with predictions of morphological variation related to migration distance and/or habitat. Those individuals migrating through western flyways had longer wings and tails and lower body weights than eastern individuals; autumn flights being much longer in the west than in the east. I predicted that individuals from the Manzano Mountains would be capturing more mammalian and ground-dwelling prey on the breeding grounds than individuals from the other flyways. Male Cooper's Hawks and female Sharp-shinned Hawks from the Manzano Mountains differed significantly from those in other flyways for characteristics, such as short, stout tarsi, related to hunting ground-dwelling prey. Red-tailed Hawks and American Kestrels exhibited no significant differences between flyways for morphological
characteristics related to hunting. In spite of low or non-existent levels of phylogeographic structure, raptors exhibit morphological variation across flyways consistent with predicted adaptations unique to different flight or predatory habits on the breeding grounds. Natural selection of wing and tail length as a response to migratory distance could account for variation across flyways in all four species. Response to selection may be through rapid morphological evolution or through phenotypic plasticity.
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ACKNOWLEDGEMENTS

Daniel Thompson and Brett Riddle contributed significantly to my development as a scientist. Charles Douglas provided unfailing support on many fronts, and Clayton White and Donald Baepler were a source of experience, encouragement and assistance. Steve Hoffman, Phil Magasich, Bob Straub, John Delong, Bill Clark, Chris Schultz and Paul Napier provided generous assistance in gathering data. Many banders gladly cooperated in this project and contributed time and space in small, busy blinds during trapping seasons.

Financial and logistical support was generously provided by the following UNLV organizations, the National Biological Service CPSU, the Marjorie Barrick Museum, the Department of Biological Sciences and the Graduate Student Association. Financial assistance was also provided by a National Science Foundation Doctoral Dissertation Improvement Grant (DEB-9321656), the Raptor Research Foundation Stephen Tully Grant, and the Arizona-Nevada Academy of Sciences.

I would like to thank Dorothy Crowe without whom field trips would not have been nearly as productive or enjoyable and office mates Jef Jaeger, Kathy Longshore, Don Ebert, and Darren Divine for many hours of serious and not-so-serious discussion. Lab associates Kim Hunter and David Orange were always available to dispense advise and sympathy. Most of all I appreciate my family for reminding me of life's priorities and making sure I had a life outside of graduate school.
CHAPTER 1

INTRODUCTION

It is a fairly simple exercise to map the extent of occurrence of a species, however, within that distribution local populations may vary in their relative genetic isolation and in exposure to different environmental conditions. A dynamic relationship potentially exists between populations with respect to migration, extinction and recolonization and varying levels of movement of individuals are to be expected from population to population. The degree of isolation, and thus genetic uniqueness, of a population depends on these parameters. Additionally, environmental or habitat variables relating to food habits, foraging patterns, temperature, humidity, nest site location and many other parameters may vary widely within a species range. Evolutionary responses to natural selection associated with this environmental variation may consist of population-level genetic divergence, where differences are genetically determined, or phenotypic plasticity, where individuals may be genetically similar but differences between populations arise in response to environmental cues that affect behavior or morphology. Thus, populations within a species may exhibit behavior and morphology that reflect a range of environmental conditions to which the species as a whole is exposed. How a population evolves in response to varying local conditions depends in large part on population
limits genetic differentiation among populations and local adaptation but enhances the evolution of phenotypic plasticity.

The study of ecomorphology investigates the relationship between population-specific morphology and the environment. Population structure can be assayed through variation in neutral genes such as mitochondrial DNA (Moore et al. 1991, Hare and Shields 1992, Avise et al. 1992). A study with both components, ecomorphology and neutral molecular characters, explicitly compares geographical variation in characters that may be subject to natural selection with geographic variation in neutral characters and provides “an extremely useful approach to the problem of inferring process given pattern” (Barrowclough 1983, p. 245).

Superficially similar species sharing geographic space may each exhibit unique population structure and morphological responses to environmental variables. For example, if species differ with regard to foraging, response to climate, or migration requirements then different morphological patterns may evolve for each species. Alternatively, if an environmental parameter affects these different species in a similar fashion, morphological responses may exhibit a common trajectory (Aldrich and James 1991). If there are no morphological differences among populations under conditions of environmental heterogeneity, natural selection may not differ among environments or some species may exhibit phylogenetic constraints that prevent local adaptation in particular characters. Through phylogenetic constraints, the trajectory of morphological change may be limited or influenced by the evolutionary history of a taxon. This may reduce the potential direction and magnitude of change in characters such as maximum or
minimum body size, wing shape, or leg proportions. Correlation of within-species morphological variation with environmental parameters and comparison between species can provide support for hypotheses of evolution in response to the environment. However, differences between populations may arise through adaptation and selection but without a selective basis for the adaptations (Gould and Lewontin 1979). Populations may arrive at different solutions to the same problem or may inhabit slightly different adaptive peaks, all equally fit yet unique. It is important to remember that "(t)he mere existence of a good fit between organism and environment is insufficient evidence for inferring the action of natural selection" (Gould and Lewontin 1979, 593).

If a population is responding to the environment in a characteristic way, it is important to determine what role natural selection might play in the relationship between morphology and environment. For natural selection to occur, it is necessary that individuals within a population possess heritable traits and that the differential expression of these traits affects individual fitness (Endler 1986). Endler (1992) further refines this definition to include three variables indicative of natural selection within a population, a) phenotypic variation, b) variation in fitness in which there is a consistent relationship between a particular trait and some measure of fitness and c) inheritance or the consistent relationship for a particular trait between parents and offspring. This relationship must be independent of environmental effects. Alternatively, differences may be due to genetic drift and not be reflective of local natural selection or natural selection may be acting on some character not measured.

Presence or absence of population structure determines the ability of a species to
respond to a varying environment. If populations experience little or no gene flow then they are able to adapt uniquely to their local environment. Gene flow between populations, on the other hand, acts as a constraint to local adaption (Endler 1986, Singh and Long 1992). However, Slatkin (1987) reports that “Natural selection for locally important adaptations could cause substantial differences at a few loci, with other loci that are neutral or only weakly selected being relatively uniform throughout a species’ range. In terms of the relative strengths of evolutionary forces, gene flow might be weaker than selection at some loci yet much stronger than genetic drift at other loci.” The response of a population to local natural selection depends on 1) the strength of the natural selection, 2) heritability of the selected trait, 3) gene flow and isolation of the population from other populations and 4) predictability or uniformity of the natural selection. With different combinations of the above factors, a species may exhibit no variation in geographic populations or, with low gene flow, and/or strong, disparate natural selection, variable populations may arise with unique, genetically-determined characters that reflect local habitat.

Morphological variation in response to local natural selection may be through genetic divergence, as described above, or adaptive phenotypic plasticity (James 1983, 1991, Via and Lande 1985, and Bull 1987). Populations within a species that are undifferentiated genetically but that respond characteristically to a given environment are exhibiting phenotypic plasticity in response to local habitats (Nager and van Noordwijk 1995). These populations, when exposed to different environments, exhibit morphological variation consistent with some environmental cue producing a ‘norm of reaction’ (Bull
1987, Schlichting 1989, and van Noordwijk 1990). Phenotypic plasticity is most likely to evolve where there is disparate natural selection and high gene flow (Via and Lande 1985). Thus, it may be a response to heterogeneous environments within the range of a species (Via and Lande 1985, Schlichting 1989, and Zhivotovsky et al. 1996).

Local natural selection or environmental induction has been shown to affect morphology in ways that do not reflect the evolutionary history of populations. For example, rapid evolution of phenotypes, recency of dispersal, phenotypic plasticity and stochasticity of lineage sorting often produces mtDNA phylogeographic structure that is not congruent with morphological variation or subspecies designations in birds (Ball et al. 1988, Degnan and Moritz 1992, Gill et al. 1993, Zink et al. 1991, Zink and Dittman 1993).

Phenotypes may also be the target of several different types of natural selection. Natural selection of flight ability may tend to produce long wings and tail along with low body weight. However, cool, arid climates may cause the evolution of large body size. Thus, long-distance migrants from a cool climate may represent a compromise morphology resulting from opposing natural selection of body weight.

Avian studies have used geographic variation to infer the action of natural selection upon characters within populations. Populations that show consistent morphological variation that is correlated with some environmental variable such as flight, climate or food availability are assumed to be responding to natural selection for that character (however, see Zink and Remsen 1986). Some studies have investigated clinal patterns of ecogeographical variation in species such as: Robins (Turdus migratorius; Aldrich and James 1991), Acorn Woodpeckers (Melanerpes formicivorus; Benitez-Diaz

Wing length and shape can be variable between populations of birds and longer, more pointed wings are found in highly migratory populations (Temple 1972, Wiedenfeld 1991, Winkler and Leisler 1992, Senar et al. 1994, and Monkkonen 1995). Wing shape is also correlated with foraging habits (Norberg 1986) and relative openness of habitat (Aldrich 1984). Forest-dwelling hawks generally have short wings and long tails whereas those inhabiting open areas have long, broad wings (Bierregaard 1978, Burton and Alford 1994). Altitude has also been shown to influence wing length with birds from high altitudes having longer wings (Moreau 1960 and Hamilton 1961).

Leg, foot and beak morphology have been shown to be correlated with feeding and
foraging habits in birds (Wattel 1973, Schluter and Smith 1986, Leisler et al. 1989, Grant and Grant 1989, Burton and Alford 1994, and Herdl 1995). In a variable landscape the abundance and type of prey available can differ between geographic areas or through time. Population-level phenotypic change in beak morphology appears to occur rapidly in some species, especially passerines, in response to very strong natural selection. Disruptive natural selection of beak morphology that occurred during an extreme drought resulted in significantly different beak sizes in populations of the large cactus finch (Geospiza conirostris) (Grant and Grant 1989). Geographic variation in avian morphology is correlated with climate, habitat and ecology. Consequently, populations of widespread species are expected to show variation in morphology consistent with environmental heterogeneity within their range if they are responding to natural selection of characters under study.

Research Objectives

Species of raptors that are widespread across North America encounter a variety of habitats and prey types. In this study I examine patterns of geographic variation in morphology and variation of neutral molecular markers within species to determine the degree to which different species of raptors exhibit concordant patterns of adaptive morphological variation. Natural selection of characters favorable within local environments may produce similar patterns in migratory populations of different species from similar habitats. I sampled four species of migratory raptors to investigate morphological variation in wing, body, foot, and beak size and shape as it may relate to
environmental conditions such as altitude and climate and ecological attributes such as vegetation type and prey type across North America. The Sharp-shinned Hawk (*Accipiter striatus*), Cooper's Hawk (*A. cooperii*), Red-tailed Hawk (*Buteo jamaicensis*) and American Kestrel (*Falco sparverius*) are all found throughout North America and migrate south from the northern part of their range each autumn. Individuals from three migratory routes were studied, two routes from western North America and one from the east. Adaptive predictions were formulated based on general knowledge of morphological characteristics for populations in varying climates that migrate different distances, breed in open or forested habitat, and utilize different types of prey. Phylogeographic structure, the geographic pattern of genetic diversity among populations, was also investigated for a portion of the mitochondrial genome. Analysis of haplotype variation was studied as an indication of the presence or absence of gene flow between raptors using different flyways.

**Life Histories**

**Sharp-shinned Hawk**

The Sharp-shinned Hawk is a forest-dwelling hawk of North and perhaps South America (Brown and Amadon 1968). Species status of those in Central and South America is still debated (del Hoyo et al. 1994). It has the broad, rounded wings, long tail and long legs typical of its genus. Wattel (1973) classifies the Sharp-shinned Hawk as one of the most morphologically adapted for a diet of primarily birds. Usually 90% or more of the diet consists of birds and seldom includes other animals such as mammals, reptiles, amphibians and insects (Sherrod 1978 and Palmer 1988). Migration occurs within the
northern hemisphere from August through October with young of the year migrating first and adult migration peaking about the time that migration of hatch-year birds tapers off (Palmer 1988). Non-breeding grounds for most birds can be anywhere from the southern United States to Costa Rica. First year males tend to spend the boreal winter further north than first year females, and adults winter north of young birds of corresponding sex with broad overlap in all categories (Brown and Amadon 1968, Palmer 1988). There is no overlap in size and virtually none in weight between the sexes, with the male being the smallest of the two. Of all the accipiters, the Sharp-shinned Hawk has the longest middle toe relative to body mass and the largest eye proportional to head size (Palmer 1988). In comparison with other accipiters, they also have relatively long, slender legs and toes and short hallux and beak, the wings are medium length and rounded and the tail is rather long (Wattel 1973).

Cooper's Hawk

Cooper's Hawks are larger than Sharp-shinned Hawks. They are also strongly dimorphic; fewer than 5% of individuals show overlap between the sexes (Palmer 1988). The Cooper's Hawk is confined to North America in distribution and does not breed as far north nor south as the Sharp-shinned Hawk. The Cooper's Hawk seems to prefer discontinuous wooded areas and has benefited in many areas from forestry practices. A recent range extension northward into Canada east of the Rockies may be a result of forest alteration (Brown and Amadon 1968 and Palmer 1988). Like the Sharp-shinned Hawk, the Cooper's Hawk includes mammals and reptiles as a significant portion of the diet.
However, in some areas it is known to specialize on certain types of prey, such as lizards in California and chipmunks and squirrels in Massachusetts (Sherrod 1978, Rosenfeld and Bielefeldt 1993). Of partially migratory habits, the Cooper's Hawk will remain as far north as central New York or fly as far south as Costa Rica or Columbia for the winter. In comparison with other accipiters, the tarsus and toes are long and heavy, claws are heavy and bill is moderate. Their wings are medium length and rounded and the tail is very long (Wattel 1973). This combination of traits, intermediate between the bird-specialist Sharp-shinned Hawks and the larger Goshawk (Accipiter gentilis), which utilizes a large proportion of ground-dwelling prey, supports the observations that prey items tend to be larger and composed more of mammals and reptiles (Wattel 1973).

**Red-tailed Hawk**

The Red-tailed Hawk is one of the most variable North American raptors in terms of plumage. A number of races are described based on plumage "morphs" across North America, five of which occur in the northern portion of the continent and are probably migratory (Preston and Beane 1993). Because of its adaptability in both habitat and prey use it is considered to have the widest ecological tolerance of any buteonine hawk in North America (Brown and Amadon 1968). Red-tailed Hawks usually prefer to hunt mammals but are known to concentrate on birds and reptiles on occasion, depending on availability. Forty-one percent of the diet in Red-tailed Hawks from Washington was comprised of snakes (Knight and Erickson 1976). Males and females of the species are indistinguishable based on either mass or wing chord because of broad overlap of
measurements, but females tend to be larger than males. Migration is variable within and between geographic areas. Many northern birds will migrate south and winter within the range of southern resident birds while others from the same area will remain on established territories all year. Northern birds are known to migrate as far as the Gulf coast and Nicaragua (Brown and Amadon 1968, Palmer 1988). Red-tailed Hawks possess the typical buteonine morphology of long, rounded wings and medium length tail adapted for soaring. Their legs and feet are typically stout and strong with short tarsus and toes.

American Kestrel

The American Kestrel is a small falcon that is slightly sexually dimorphic in body size and distinctly dimorphic in coloring. This bird can be found throughout North and South America from almost tree line in Alaska south into Tierra del Fuego (Brown and Amadon 1968). Open areas are preferred habitat, from desert to the edges of groves, and it thrives in many different temperature and climate regimes. Insects generally comprise a large part of the diet of a typical American Kestrel but they will also take mammals, birds, reptiles and amphibians. It appears that individuals tend to develop a search image and concentrate on a particular species or group as prey (Sherrod 1978, Palmer 1988). Migration patterns parallel those of the Red-tailed Hawk in which northerly populations are migratory, intermediate populations are a mixture of migratory and non-migratory individuals and southern populations are year-round residents (Palmer 1988). A typical falcon, American Kestrels have medium length pointed wings and a fairly long tail.
Migratory Flyways

There are a number of major migratory routes for raptors in North America that are generally influenced by topographical "leading lines" such as coastlines, ridge lines and peninsulas (Kerlinger 1989). The Goshute Mountains of Nevada and the Manzano Mountains of New Mexico are monitoring points along major raptor flyways in the west, and Cape May Point in New Jersey is situated on a major eastern flyway (Fig. 1). The Goshute and Manzano Mountains are both ridge systems and the migrants generally follow the Rocky Mountains to the south. Cape May Point is a coastal flyway and migratory individuals build up along the coastline and funnel along the southern New Jersey peninsula to cross the ocean at the point. Breeding grounds are generally north of the western flyways (Smith et al. 1990, Hoffman 1992, 1993 and 1995) and north and east of the eastern flyway (Clark 1985 for Sharp-shinned Hawk breeding grounds and W. S. Clark, pers. com.)

Goshutes migrants travel each fall to wintering grounds in central and western Mexico, a distance much farther than eastern migrants in this study (Smith et al.1990, Clark 1985, and W. S. Clark, pers. com.). The Manzano Mountains of New Mexico also funnel migratory raptors coming from the northwest, although the numbers of raptors using this route tends to be lower than migrants through the Goshutes. Manzano migrants are generally found wintering in the same geographic areas as Goshutes migrants. As is true with Goshutes migrants, Manzano migrants probably travel much greater distances than eastern migrants and are predicted to have relatively longer, wider wings and longer tails. Both western flyways entail migration at high altitudes in relatively arid climates.
Figure 1. A map of North America illustrating the relative position of flyways in this study. Arrows originate from the general area of breeding grounds. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Migration along these routes is likely to require more efficiency than along low-lying, humid coastal flyways.

Migrants through Cape May are concentrated in great numbers as they travel down the coastline of northeastern North America. These individuals originate in the northeastern United States and eastern Canada and winter in the southeastern United States (Clark 1985, W. S. Clark, pers. com.). Migratory flights are thus much shorter for these migrants than for western individuals.

Adaptive Predictions

The following predictions are derived from the hypothesis that natural selection associated with environmental variables has resulted in the evolution of geographic variation in morphology. Environmental factors such as climate and migration distance vary on a large scale and variation resulting from natural selection related to these environmental parameters is expected to produce the same pattern in all four species. With respect to predation, raptor taxa are expected to exhibit different morphological responses to unique prey assemblages. Predictions made relative to prey selection and predatory characters should differ for Accipiters and the other two species (Table 1). Sharp-shinned Hawks, and to a lesser extent Cooper’s Hawks, are bird specialists and populations of these species that prey in high percentage on mammals may experience strong natural selection of mammalian predatory characters (Snyder and Wiley 1976). Other taxa that are classed as generalists may possess predatory morphology that is appropriate for a variety of prey items. The generalist morphology and a tendency to
capture a variety of prey items may result in predatory characters that do not experience strong natural selection in a particular direction (Snyder and Wiley 1976).

Table 1. Adaptive predictions of morphological size in avian characters related to variation in migration and habitat flight of raptors and local availability of prey types. Predictions for each character are made for size relative to the alternative selective environment. All four species in the study are predicted to vary in the same manner for characteristics related to flight. Specific predictions relative to predatory habits are made only for the genus *Accipiter*.

### Predictions for flight characteristics (all species)

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<th>Decreased Flight</th>
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<tr>
<td>Wing</td>
<td>longer</td>
</tr>
<tr>
<td>Tail</td>
<td>longer</td>
</tr>
<tr>
<td>Leg, foot and bill</td>
<td>smaller</td>
</tr>
</tbody>
</table>

### Predictions for predatory characteristics (genus *Accipiter* only)

<table>
<thead>
<tr>
<th>Ground-dwelling Prey</th>
<th>Aerial Prey</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tarsus length</td>
<td>shorter</td>
</tr>
<tr>
<td>Tarsus width</td>
<td>wider</td>
</tr>
<tr>
<td>Hallux</td>
<td>shorter</td>
</tr>
<tr>
<td>Culmen</td>
<td>longer-mammals</td>
</tr>
</tbody>
</table>

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Climate

Climate often correlates with body size in some bird species. James (1991) found that birds from cool, dry climates tend to be large while those from warm, humid climates tend to be small as predicted by Bergmann's rule. In some birds the tarsus has been thought to be an effective way to regulate temperature (e.g. the American Kestrel, Bartholomew and Cade 1957). If these predictions hold true, western migrants that inhabit relatively dry habitat at high altitudes would be larger than individuals from the east. However, large body size would increase overall weight, an evolutionary response that could oppose natural selection of flight ability since, for a given wing area, large body weight increases wing-loading and makes flight more costly. Tarsus length is expected to be long in individuals faced with the potential for extreme summer heat such as those from the west.

Flight

As soaring and gliding flight are important for the four migrant species considered in this study (Kerlinger 1984, Kerlinger 1989, Kerlinger and Gauthreaux 1984 and Smith et al. 1990), a consideration of the role of both wing area and tail area are important. Increased flight surface, indicated in this study by longer wings, imparts a lower wing-loading which enables birds to fly more slowly and turn more sharply in order to take advantage of thermals (Pennycuick 1975). Soaring, or circling in thermals, was observed in a majority of migrating Sharp-shinned Hawks at Cape May in New Jersey. Time spent soaring averaged 44.6% before 0900 EST and 60.7% between the hours of 0900 and
1100 EST. Gliding speed between thermals is then regulated by flexing of the wing and folding of the tail for maximum lift to drag ratio and maximum speed (Tucker and Parrott 1970, McGahan 1974, Mueller et al. 1981, and Kerlinger 1989). Tail length is a vital component of flight surface, especially when lift is important (Thomas and Balmford 1995). Wing-loading in raptors is reduced by from 19.7% in Red-tailed Hawks to 29.3% in Sharp-shinned Hawks by spreading the tail (Kerlinger 1989).

Migration distance

Increased flight surface enhances a raptor's ability to utilize even weak thermal updrafts (Mueller et al. 1981). Surface area is a function of length and width and wing area increases proportionally as a square of wing span in wings of similar shape (Tucker and Parrott 1970, Pennycuick 1975). Within a species, wing shape is not expected to change greatly, thus wing area may increase isometrically with wing length. If this is true, long wings and tail should be an advantage for long-distance migrants that utilize soaring as part of their migration strategy. Because raptors migrating through the Goshutes and Manzanos have the greatest distance to travel (Smith et al. 1990), natural selection of wings and tail in these individuals should result in increased flight surfaces. Atmospheric conditions such as high altitude and low humidity in western flyways may also influence natural selection of flight efficiency with the response again being greater flight surface than eastern individuals. Morphological characters that add weight would create an energetic disadvantage in flight and are predicted to be reduced as a result of natural selection pertaining only to flight ability. Leg, feet and beak dimensions are predicted to
be reduced in individuals that fly long distances, such as the western migrants. However, because these characters (leg, foot and bill) are important in obtaining prey this pattern may be counteracted by natural selection related to hunting ability.

**Habitat Flight**

Natural selection of wing and tail length may also occur in response to local, hunting flights and differences may be observed if particular flyways are consistently gathering individuals from open habitat while others draw from forested habitat. Habitat flight may include flights between perches, soaring in search of food, or flying between suitable hunting patches. I predict that western individuals inhabit relatively more open areas (Carter and Mather 1966, Aldrich 1984, Walter 1985, and Smith et al. 1990) and that natural selection of flight efficiency is greater here than in eastern population of raptors. Western individuals, especially those from the open areas east of the Rockies migrating along the Manzano flyway, are predicted to have longer wings and tail than individuals from the other flyways.

**Predatory Habits**

In raptors, there are characteristic shapes associated with particular diet and hunting methods. Within the genus *Accipiter*, avivores generally have a long, thin tarsus with large feet while mammalivores tend to have short, thick tarsi and small feet (Wattel 1973, Newton 1986, Burton and Alford 1994). However, Bierregaard (1978) found that avivores from a wide range of taxa tend to have short legs and long toes. According to Snyder and Wiley (1976) bird specialists have long thin toes that may be vulnerable to the
sharp teeth of mammalian prey. They go on to state that "(i)t is not likely that species adapted to take birds might take mammals as efficiently in times of food stress and vice versa. Raptors adapted to take both sorts of prey are presumably not optimally adapted for either." Bill shape may also reflect diet with avivores having a short culmen (Hertl 1995).

Relatively open habitat seemingly supports a greater proportion of ground-dwelling prey than forested areas whereas the opposite is true of avian prey. However, food studies of the four species of raptors do not show clear differences between eastern and western populations (see citations in Table 2). Variation seems to be more likely to occur on geographic or local rather than landscape scales. Also, raptors have a well-known tendency to exhibit individual hunting preferences which may confound overall patterns (Newton 1986, Palmer 1988). However, there may be a general pattern that relates to relative abundance of local habitat characteristics in the east and west. In conjunction with hypothesized openness of habitat in breeding grounds of western individuals, ground-dwelling prey may form the bulk of the diet. Natural selection of mammalivore characters is predicted for individuals from open habitats in the west, particularly the Manzanos. If there is a difference in prey selection between populations using different flyways, natural selection of tarsus, foot and bill characters may influence leg and bill shape. Accipiters from the Goshutes and Cape May are predicted to specialize more frequently on avian prey and to have a long, thin tarsus. Manzano accipiters are predicted to have short, thick tarsi if these populations are originating in breeding grounds that are relatively more open than either the Goshutes or Cape May. Toe length is an

1 percent stomachs containing prey (percentages total more than 100)

### Sharp-shinned Hawks

<table>
<thead>
<tr>
<th>Western:</th>
<th>Birds</th>
<th>Mammals</th>
<th>Reptiles</th>
<th>Invertebrates</th>
<th>Source</th>
</tr>
</thead>
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<td>9</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
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<td>6.5</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>Oregon</td>
<td>&gt;95</td>
<td>&lt;5</td>
<td>-</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td>Arizona/New Mexico</td>
<td>97.1</td>
<td>0</td>
<td>2.9</td>
<td>-</td>
<td>10</td>
</tr>
<tr>
<td>Throughout the range</td>
<td>85</td>
<td>6</td>
<td>2</td>
<td>16</td>
<td>11³</td>
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### Cooper's Hawks

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<td>63</td>
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<td>26</td>
<td>5</td>
<td>69</td>
<td>-</td>
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<td>-</td>
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<tr>
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<td>-</td>
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<td>16</td>
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<td>18</td>
<td>-</td>
<td>-</td>
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## Red-tailed Hawks

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<th>Reptiles</th>
<th>Invertebrates</th>
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<tr>
<td>Utah</td>
<td>9</td>
<td>89</td>
<td>-</td>
<td>-</td>
<td>9</td>
</tr>
<tr>
<td>Washington</td>
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<td>41.3</td>
<td>-</td>
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<td>4</td>
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<tr>
<td>Oregon</td>
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<td>73.3</td>
<td>13.3</td>
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<td>-</td>
<td>-</td>
<td>13, 14</td>
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<tr>
<td>Alberta</td>
<td>34.5</td>
<td>65.5</td>
<td>-</td>
<td>-</td>
<td>18</td>
</tr>
</tbody>
</table>

### Eastern:

| Arkansas      | 92    | 3      | -        | -             | 5      |
| Pennsylvania  | 11    | 69     | 8        | -             | 8      |
| Wisconsin     | 13    | 84     | -        | -             | 8      |
| Wisconsin     | 58    | 38     | -        | -             | 8      |
| Michigan      | 14.8  | 66.7   | 18.5     | -             | 15     |
| Michigan      | 27    | 73     | -        | -             | 8      |
| Oklahoma      | 7     | 88     | 5        | -             | 8      |
| Ontario       | 16.2  | 79.2   | 4.7      | 0             | 16     |

## American Kestrel

<table>
<thead>
<tr>
<th>Western:</th>
<th>Birds</th>
<th>Mammals</th>
<th>Reptiles</th>
<th>Invertebrates</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>UT</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>99</td>
<td>8</td>
</tr>
<tr>
<td>UT</td>
<td>16</td>
<td>27</td>
<td>-</td>
<td>52</td>
<td>9</td>
</tr>
</tbody>
</table>

### Eastern:

| Pennsylvania | 14    | 54      | -        | 32            | 8      |
| Ontario      | 21    | 3       | -        | 76            | 8      |
| Ontario      | 21.5  | 41      | 1.5      | 36            | 17     |
important character for avivores, however this was not measured and cannot be assessed relative to flyways. The generalist species, Red-tailed Hawks and American Kestrels, are not predicted to exhibit variation for the characters measured.

**Alternative Hypotheses**

**Genetic Drift**

Natural selection may not be influencing size and shape variation in the morphological characters under study. Geographic variation could be caused by genetic drift and thus may be unpredictable in relationship to habitat variables. Genetic drift implies genetic differentiation between populations which is due to chance events rather than specific responses to habitat. Under this scenario, variation in characters between flyways would be random and unrelated to environment on the breeding grounds or ecology of the four species. Because any pattern of geographic variation could arise from genetic drift, this serves as the null hypothesis of evolutionary change.

**Gene Flow**

If there is extensive gene flow among flyways for any of the species, populations will not vary in morphology even if natural selection may be occurring. In spite of a general tendency towards natal philopatry, dispersal is known to occur regularly in young raptors (Newton 1979). If there is no divergence in morphological characters in response to environmental variation, it may be due to regular gene flow between populations using the three flyways. Alternatively, random morphological variation may seem to be
organized as a result of gene flow between adjacent populations.

Natural Selection on Winter Habitat

Migratory individuals spend a large portion of the year in non-breeding habitat. It is likely that natural selection influences the same morphological characters in response to similar environmental variables in this alternate environment. In some cases, this may alter predictions. For example, from distributions of the four species on non-breeding habitat, Bergmann's rule would actually predict the largest individuals to be from the eastern flyway as they winter north of western migrants. Food habits and flight requirements may also be different.

Population Genetic Structure

Although migratory birds travel long distances and experience mixing of individuals from different areas on the wintering grounds, in some cases breeding populations remain distinct (Quinn 1992 and Wennick et al. 1993 and 1996). In raptors, which generally exhibit natal philopatry (Newton 1979), morphological divergence among different habitats or biogeographical areas might result from genetic differentiation between distinct populations. Alternatively, if there is gene flow, phenotypic plasticity may be the means by which populations respond to natural selection associated with differences in breeding grounds.

The mitochondrial genome is maternally inherited, quickly evolving, non-recombining and essentially neutral in character (Shields and Helm-Bychowski 1988, Ball and Avise 1992, Hare and Shields 1992, and Zink 1996). These attributes make it an
appropriate genetic marker for studies of within-species, population-level genetic processes (Moore et al. 1991, Hare and Shields 1992, and Avise et al. 1992). A neutral marker such as mitochondrial DNA can provide evidence of population structure and depth of historical separation of populations that can be compared to morphological response to environment. A study that combines molecular methods with morphological characters can thus investigate genetic characters that are neutral and phylogenetically informative as well as morphological characteristics of a population that are responsive to local habitat.

If migratory raptors are maintaining distinct populations by returning to known breeding grounds every spring, these differences should result in separation of mtDNA lineages such that it would be possible to demonstrate among population differences in molecular characteristics. A study of Lesser Snow Geese (Quinn 1992) indicated the presence of two distinct mitochondrial clades within the species range; of 21 variable sites seven were fixed differences between the two clades. Geographic structuring was apparent in one major clade but not in the other (Quinn 1992). Dunlins exhibit geographically structured haplotypes in spite of migratory habits (Wennick et al. 1993; 1996). It should be possible to isolate population-specific haplotypes if sufficient time has elapsed (e.g. about 2Nf; Hartl and Clark 1989) for lineage sorting and mutation to result in population specific haplotypes. Genetic differences may not exist if migratory individuals are not maintaining distinct populations, if they have a recent history of colonization in the north, or if there has been a recent bottleneck in the populations (e.g. chickadees, Gill et al. 1993).
Five co-distributed species of birds demonstrated differing levels of phylogeographic structure with three species exhibiting no structure and two species with structure (Zink 1996). The two phylogeographically structured species, however, showed no similarity in haplotype diversity relative to geography. Although the five species currently occur in the same habitat, different phylogeographic patterns were attributed to different long-term histories. Additionally, although seven Australian species of rainforest birds showed lack of overall congruence of phylogeographic structure to their populations, subsets of the species demonstrated congruent patterns (Joseph and Moritz 1994). Even similar organisms with similar distributions may not exhibit the same level of population structure. The four species in this study will provide additional insight into large-scale phylogeographic structure in North American avifauna.

Methods

Morphological

Measurements using a balance, dial calipers, metric ruler and wing chord ruler were taken on seven morphological characters. Weight (Wt), length of central retrix (T), wing chord (W), tarsus length (Tl), tarsus width at the narrowest point (Tw), culmen length (Cn, from cere to tip) and hallux length (Hx) (Fig. 2) were measured along each of three migratory flyways as birds were trapped for banding between September and November from 1991 to 1994. These measurements were made by me or experienced banders; where possible measurements were compared with mine. The assumption was made that error resulting from different measurers would be evenly distributed around the
Figure 2. A generalized drawing of an accipitrine hawk illustrating the morphological measurements used in this study. \( W \) = wing length, \( T \) = tail length, \( Tl \) = tarsus length, \( Tw \) = tarsus width, \( Hx \) = hallux length, and \( Cn \) = culmen length.

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true measurement and not biased in any one direction. All persons making measurements had experience banding and measuring large numbers of raptors. Experience significantly reduces measurement error (Yezerinac et al. 1992). Any birds with a noticeable crop were removed from analyses involving body mass. Sharp-shinned Hawks, Cooper's Hawks and American Kestrels were placed into groups by sex and age because of sexual dimorphism and differential growth of feathers. Results are reported for hatch-year birds only.

All measurements were log-transformed and compared character by character using StatGraphics (Manguistics 1992) multiple analysis of variance. A multivariate analysis was also performed to remove possible allometric relationships and to investigate morphological shape variables. Data for this analysis were log-transformed to conform to a multi-variate normal distribution. Principal component scores were determined from a data set in which all three flyways were pooled for each species and then scores were assigned to individuals. For the principal components analysis, weight was eliminated from analyses of size and shape because it can be highly variable and may reflect conditioning of migrants rather than absolute mass. I used ANOVA to test for significant differences between flyways for each component score. Principal component weights were plotted as bar graphs for visualization of shape variables and comparison of means between flyways. To determine the relevance of shape variables to the second and third principal component, a "shape" ratio (Mosimann and James 1979) was plotted against
each principal component score. In this study the shape ratio was composed of the two most important, or heavily weighted, characters that were of opposite sign for a particular principal component. A visual inspection of the pattern and correlation analysis indicated relevance of the shape variables. Wing-loading was estimated as weight divided by wing chord. Although this is not the measure generally used in the literature it provided a good indication of relative wing-loading between flyways for the same species. This is because wing surface area is known to increase linearly with wingspan (Tucker and Parrott 1970, Kerlinger 1989).

Molecular

Blood samples were taken from individual birds during migration in the fall of 1993-1995 on each of the three flyways. These were frozen or preserved in a lysis buffer (100 mM Tris - HCL, pH 8.0, 100 mM EDTA, 10 mM NaCl, 0.5% SDS) for later use in the lab and DNA was isolated using a standard phenol-chloroform extraction. The gene region of interest included the ND2 gene, five tRNA gene and part of the COI gene (about 2150 base pairs, Fig. 3). Samples were amplified by PCR using primers from Riddle et al. (1993) and general PCR protocols. These samples were digested with an array of 4-, 5- and 6-base restriction enzymes. Samples were electrophoresed through 1.2% agarose gel and fragments were visualized with ethidium bromide. Resultant restriction digest fragments were sized relative to a standard molecular weight marker. Fragment patterns were used to infer restriction sites (Dowling et al. 1990). Fragments resulting from digestion with a single restriction enzyme were assumed to result from cleavage at
Figure 3. A general representation of avian mtDNA based on sequence data from chickens (Desjardins and Morais 1990).
identical sites if the fragments were of equal size. Gain of a restriction site resulted in two fragments, the sum of their sizes equal to a missing fragment. Loss of a restriction site resulted in a large fragment, equal in size to the sum of two missing fragments. Individuals of the same haplotype possessed identical fragments patterns for all restriction enzymes. Gain or loss of a site, resulting in fragments of differing lengths, resulted in an individual being classified as an alternate haplotype. The composite haplotype for each individual was recorded using a different letter for distinct patterns for each restriction endonuclease. Approval for all animal protocols was obtained from the University of Nevada, Las Vegas Institutional Animal Care and Use Committee October 27, 1993.
CHAPTER 2

RESULTS

Sharp-shinned Hawk Univariate Results

Male hatch-year Sharp-shinned Hawks weigh more in the east than in the west (Table 3) and western migrants of both sexes have significantly longer wings and tail. Sharp-shinned Hawks from the Goshutes also have longer, thinner tarsi than eastern individuals but the culmen in eastern hawks is larger. The hallux is significantly shorter in males from Cape May but not significantly different for females.

Weight was not strongly correlated with other morphological characters in males but was correlated with tarsus width, hallux and culmen in females (Table 4). Wing length was strongly correlated with tail length and tarsus length was most strongly correlated with wing length in both sexes. Tail length was strongly correlated only with wing length in females but also with hallux in males. Tarsus width was most strongly correlated with weight in males and females. Culmen and hallux were correlated in females and culmen was correlated with weight in males. Wing-loading was estimated by weight divided by wing length as stated in methods. There were significant differences between eastern and western flyways. Wingloading average for male Sharp-shinned Hawks were 0.57 (± 0.003) in the Goshutes, 0.56 (± 0.010) in the Manzanos and 0.62 (± 0.009) in Cape
May, Cape May migrants were significantly different (ANOVA, p < 0.001). For female Sharp-shinned Hawks averages were 0.81 (± 0.006) in the Goshutes, 0.84 (± 0.02) in the Manzanos and 0.87 (± 0.01) in Cape May, Cape May migrants were significantly different (ANOVA, p < 0.001).

**Cooper’s Hawk Univariate Results**

Hatch-year Cooper’s Hawks were significantly heavier in the east than in the west but western birds did not have significantly longer wings and tails (Table 5). Male Cooper’s Hawks from the Manzanos had significantly longer tails; tail length was not significantly different for females. Goshutes migrants had significantly shorter wings than Manzanos and Cape May migrants. The tarsus was significantly thinner in Cooper’s Hawks from the Goshutes than other migrants and significantly longer in both sexes migrating through Cape May. Female Cooper’s Hawks from the Manzanos had significantly shorter tarsi than the other flyways.

Weight was highly correlated with tail length, tarsus length, and hallux in both sexes (Tables 6 and 7). Weight was also positively correlated with tarsus width and culmen in females. Wing and tail were the most highly correlated. Tarsus length was correlated with hallux in males and with hallux and culmen in females. Wing-loading was determined as described for Sharp-shinned Hawks. Males from the Goshutes had a wing-loading of 1.15 (± 0.01), from the Manzanos 1.18 (± 0.16) and Cape May 1.49 (± 0.03). Individuals from Cape May were significantly different (p < 0.001). Females from the Goshutes had a wing-loading of 1.49 (± 0.02), Manzanos were 1.57 (± 0.02) and Cape
Table 3. Results of multiple analysis of variance for significant differences in mean morphological characters of male and female Sharp-shinned Hawks in three flyways. Significant differences are represented by unique letters for flyways (p < 0.05). Standard deviation is in parentheses. Coefficient of variation values indicate absolute variation for the character and are in square parentheses [ ]. Weight is given in grams and linear measurements in millimeters.

<table>
<thead>
<tr>
<th>Character</th>
<th>Goshutes</th>
<th>Manzanos</th>
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<tr>
<td></td>
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<td>N = 24</td>
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<td>[6.2]</td>
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<th>Character</th>
<th>Goshutes</th>
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<th>Manzanos</th>
<th>N = 9</th>
<th>Cape May</th>
<th>N = 38</th>
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<tbody>
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<td>Weight</td>
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<td>170.6(15.5)*</td>
<td>170.9(16.1)*</td>
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<tr>
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<tr>
<td>Tail</td>
<td>162.7(4.7)*</td>
<td>160.0(6.3)*</td>
<td>154.1(5.3)*</td>
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<tr>
<td>Wing</td>
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<td>202.4(4.5)*</td>
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<td>[3.0]</td>
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<td>[6.1]</td>
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<td>14.3(0.6)*</td>
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<td>Culmen</td>
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<td>11.9(0.2)*</td>
<td>12.2(0.5)*</td>
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Table 4. Correlation analysis of principal component scores, morphological characters and 'shape' ratios for Sharp-shinned Hawks. Correlations were performed on log-transformed measurements. PCI = first principal component, PC2 = second principal component, PC3 = third principal component, Wt = weight, T = tail, W = wing, Tl = tarsus length, Tw = tarsus width, Hx = hallux, Cn = culmen. Principal component scores were derived from all morphological characters excluding weight. Females are the top of the diagonal, males are the bottom.

<table>
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<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>Wt</th>
<th>T</th>
<th>W</th>
<th>Tl</th>
<th>Tw</th>
<th>Hx</th>
<th>Cn</th>
<th>Cn/T</th>
<th>Tw/Tl</th>
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<tbody>
<tr>
<td>PCI</td>
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<td>0.451</td>
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<td>-0.416</td>
<td>-0.248</td>
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<td>0.003</td>
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<td>-0.148</td>
<td>0.095</td>
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<td>0.687</td>
<td>0.863</td>
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<td>-0.237</td>
<td>-0.016</td>
<td>-0.142</td>
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<td>0.272</td>
<td>0.269</td>
<td>0.001</td>
<td>0.040</td>
<td>0.153</td>
<td>0.326</td>
<td>0.371</td>
<td>0.286</td>
<td>0.241</td>
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<td>-0.023</td>
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<td>-0.130</td>
<td>0.226</td>
<td>-0.073</td>
<td>-0.540</td>
<td>-0.149</td>
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<td>0.268</td>
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<td>-0.093</td>
<td>-0.447</td>
<td>-0.059</td>
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<td>-0.145</td>
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<td>0.338</td>
<td>-0.149</td>
<td>0.254</td>
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<td>-0.060</td>
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<td>-0.076</td>
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<td>0.200</td>
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<td>0.117</td>
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<td>0.340</td>
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<td>0.066</td>
<td>-0.086</td>
<td>0.933</td>
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<tr>
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<td>-0.148</td>
<td>-0.007</td>
<td>-0.206</td>
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</table>
Table 5. Results of analysis of variance for significant difference in morphological characters between flyways for male and female Cooper's Hawks. Significant differences are represented by unique letters for flyways (p < 0.05). Standard deviations are in parentheses. Coefficient of variation values are in []. Weight was measured in grams and linear measurements in millimeters.

<table>
<thead>
<tr>
<th>Character</th>
<th>Goshutes (N = 38)</th>
<th>Manzanos (N = 40)</th>
<th>Cape May (N = 37)</th>
</tr>
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<td>Weight</td>
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<td>266.6(24.6)b</td>
<td>339.2(38.7)c</td>
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<tr>
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<td>[11.4]</td>
</tr>
<tr>
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<td>191.0(5.6)*</td>
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<tr>
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<td>228.0(4.9)b</td>
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</tr>
<tr>
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<td>61.6(1.5)*</td>
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<td>[3.0]</td>
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<td>[2.8]</td>
</tr>
<tr>
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<tr>
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<td>[9.2]</td>
</tr>
<tr>
<td>Hallux</td>
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<td>18.8(0.6)*</td>
<td>19.7(0.6)b</td>
</tr>
<tr>
<td></td>
<td>[3.4]</td>
<td>[3.2]</td>
<td>[3.2]</td>
</tr>
<tr>
<td>Culmen</td>
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<td>14.7(1.1)*</td>
<td>14.9(2.0)*</td>
</tr>
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<td>[3.7]</td>
<td>[7.6]</td>
<td>[13.3]</td>
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<table>
<thead>
<tr>
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<th>Female Cooper's Hawks (N = 28)</th>
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<th>N = 21</th>
</tr>
</thead>
<tbody>
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<td>401.3(35.9)b</td>
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<tr>
<td>Tail</td>
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<tr>
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<td>[3.0]</td>
<td>[3.5]</td>
</tr>
<tr>
<td>Wing</td>
<td>252.0(4.8)b</td>
<td>255.4(6.0)b</td>
<td>260.2(6.6)c</td>
</tr>
<tr>
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<td>[2.5]</td>
</tr>
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<td>Tarsus Length</td>
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<td>67.3(2.3)b</td>
<td>73.2(1.8)c</td>
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<tr>
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<td>[2.4]</td>
</tr>
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<td>7.1(0.4)b</td>
<td>7.4(0.4)c</td>
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<td>[5.2]</td>
<td>[6.1]</td>
</tr>
<tr>
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<td>22.3(0.8)a</td>
<td>22.2(0.7)a</td>
<td>23.7(1.7)b</td>
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<td>[7.1]</td>
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<td>17.0(1.5)a</td>
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Table 6. Correlation analysis of principal component scores, morphological characters and 'shape' ratios for male Cooper's Hawks. Correlations were performed on log-transformed measurements. PCI = first principal component, PC2 = second principal component, PC3 = third principal component, Wt = weight, T = tail, W = wing, Ti = tarsus length, Tw = tarsus width, Hx = hallux, Cn = culmen. Principal component scores were derived from all morphological characters excluding weight.

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>Wt</th>
<th>T</th>
<th>W</th>
<th>Ti</th>
<th>Tw</th>
<th>Hx</th>
<th>Cn</th>
<th>Cn/T</th>
<th>Cn/Ti</th>
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</thead>
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<tr>
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<td>0.150</td>
<td>-0.437</td>
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<td>-0.445</td>
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<td>0.666</td>
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<tr>
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</table>
Table 7. Correlation analysis of principal component scores, morphological characters and 'shape' ratios for female Cooper’s Hawks. Correlations were performed on log-transformed measurements. PCI = first principal component, PC2 = second principal component, PC3 = third principal component, Wt = weight, T = tail, W = wing, Tl = tarsus length, Tw = tarsus width, Hx = hallux, Cn = culmen. Principal component scores were derived from all morphological characters excluding weight.

<table>
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<th>PC2</th>
<th>PC3</th>
<th>Wt</th>
<th>T</th>
<th>W</th>
<th>Tl</th>
<th>Tw</th>
<th>Hx</th>
<th>Cn</th>
<th>Cn/T</th>
<th>Tw/Hx</th>
</tr>
</thead>
<tbody>
<tr>
<td>PCI</td>
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May 2.02 (± 0.03). Averages from all flyways were significantly different (p < 0.001).

**Sharp-shinned Hawk and Cooper’s Hawk**

**Multivariate Results**

**General Patterns**

In a principal components analysis of the six morphological characters (excluding weight) in each species, the first three principal components explained between 70 and 80% of morphological variation in both sexes. Principal components one, two, and three accounted for 30-48%, 17-21% and 13-16% of the variation, respectively. There were significant differences between flyways for all three components in both species (Figs. 4-7). The relative weighting and sign of eigenvector loadings were interpreted for information on the importance of each character in either the size or shape variables (Manly 1986). From interpretation of eigenvector loadings, there appeared to be a general size component in Cooper’s Hawks and a flight shape component and predatory component in both species. Interpretation of components varies between species and sexes and will be treated separately for each group. There were, however, some strong patterns that appeared for all species and sex groupings that will be addressed in the discussion.

**Sharp-shinned Hawks**

The first principal component for both sexes is absolute size of the tail and wing with some information on tarsus length and hallux (Figs. 4 and 5). Flyway averages
Figure 4. Principal component weightings for six morphological variables (T = tail length, W = wing length, Tl = tarsus length, Tw = tarsus width, Hx = hallux length, and Cn = culmen length) for male Sharp-shinned Hawks are presented as bar graphs in the upper panels. Principal component scores were assigned to individuals and significant differences between flyways were determined by ANOVA. Significantly different means (p < 0.05) for flyways (GS = Goshutes, MZ = Manzanos, and CM = Cape May) are indicated by unique letters in the bottom panel.
Figure 5. Principal component weightings for six morphological variables (T = tail length, W = wing length, Tl = tarsus length, Tw = tarsus width, Hx = hallux length, and Cn = culmen length) for female Sharp-shinned Hawks are presented as bar graphs in the upper panels. Principal component scores were assigned to individuals and significant differences between flyways were determined by ANOVA. Significantly different means (p < 0.05) for flyways (GS = Goshutes, MZ = Manzanos, and CM = Cape May) are indicated by unique letters in the bottom panel.
Figure 6. Principal component weightings for six morphological variables (T = tail length, W = wing length, Ti = tarsus length, Tw = tarsus width, Hx = hallux length, and Cn = culmen length) for male Cooper's Hawks are presented as bar graphs in the upper panels. Principal component scores were assigned to individuals and significant differences between flyways were determined by ANOVA. Significantly different means (p < 0.05) for flyways (GS = Goshutes, MZ = Manzanos, and CM = Cape May) are indicated by unique letters in the bottom panel.
Figure 7. Principal component weightings for six morphological variables (T = tail length, W = wing length, Tl = tarsus length, Tw = tarsus width, Hx = hallux length, and Cn = culmen length) for female Cooper's Hawks are presented as bar graphs in the upper panels. Principal component scores were assigned to individuals and significant differences between flyways were determined by ANOVA. Significantly different means (p < 0.05) for flyways (GS = Goshutes, MZ = Manzanos, and CM = Cape May) are indicated by unique letters in the bottom panel.
from the west are different from the east for this component and average wing and tail length are significantly greater in the west. Average wing and tail length was significantly shorter in the east in spite of significantly greater weight. The lack of an overall size component, positive loading of all variables in the principal components analysis, indicates that variation in tail and wing is decoupled from variation in other characters. This can also be seen in the high positive correlation of PC1 with wing and tail and lower correlations with tarsus length and hallux. Variation between flyways for this character was consistent with predictions for selection on migratory and breeding ground flight.

The second principal component was mainly absolute culmen size with some residual tarsus length in males. Culmen did not contribute to PC1 so the variation for culmen is explained here. There were significant differences between flyways with Cape May individuals having the longest average culmen. Males migrating through Cape May had the longest average culmen, but tarsus width and hallux covaried more with culmen in females. Males migrating through the Manzanos had significantly shorter culmen length than other flyways. These results are consistent with the univariate analysis for culmen length. Some information about flight shape is also contained in PC2 for males and females, a graph of PC2 against a “flight ratio” consisting of culmen divided by tail length indicates a non-random relationship (see Figs. 8 and 9).

Male and female Sharp-shinned Hawks differed in the loading of the third principal component. In males, PC3 was mainly related to absolute tarsus width. Manzanos and Cape May migrants had significantly positive scores for this component indicating wider tarsus than Goshutes migrants. This pattern is also seen in analysis of tarsus width as a
univariate character. Principal component three was a shape component in female Sharp-shinned Hawks with tarsus width loading opposite tarsus length. The Manzano average for this component was significantly positive indicating a have short, thick tarsus whereas Goshutes and Cape May averages indicated long, thin tarsi in these flyways. For female Sharp-shinned Hawks, PC3 indicated shape and size consistent with predictions of differences in predatory habits related to openness of habitat. Male Sharp-shinned Hawks had a wider tarsus in the Manzanos and Cape May than Goshutes; these differences do not completely match adaptive predictions. Graphs of shape ratios and PC2 and PC3 indicate the relevance of the components for information on shape (Figs. 10 and 11). Overall, Cape May birds are most divergent from the other two flyways in terms of PC1 and PC2 (Figs. 12 and 13).

Cooper’s Hawks

Principal component one was a fairly good indicator of overall size for both sexes as reflected by the generally positive loadings of all variables (Figs. 6 and 7). Cape May migrants were significantly positive for this component indicating larger overall size. This component was positively correlated with all morphological characters (Tables 6 and 7). These results are consistent with those from the univariate analysis and consistent with predictions from the hypothesis that western migrants, which fly the farthest, will have a lighter weight than eastern migrants. The results did not match adaptive predictions for climate on the breeding grounds and it may be that natural selection, if it occurs, of these characters is stronger on the non-breeding grounds.
Both sexes showed similar patterns for PC2 that was interpreted as a shape component related to flight efficiency. Tail and wing loaded opposite to other weight-adding characters. A flight shape ratio, culmen divided by tail length, when plotted against scores for PC2 showed a non-random relationship (Figs. 14 and 15). Manzano migrants were significantly negative for this component, indicating that they had longer wings and tails than migrants from other flyways. Results from this analysis were consistent with predictions from flight habits, that raptors migrating through the Manzanos breed in the most open habitat and would have longest wings and tail. This was slightly different from results of univariate analyses. Results were not consistent with predictions of migratory distance.

Principal component three was a shape component and was interpreted to relate to hunting characters. In male Cooper’s Hawks culmen length and tarsus width loaded opposite of tarsus length and Manzano migrants were significantly positive for this component. Male Cooper’s Hawks migrating through the Manzanos have a long culmen and a short, wide tarsus (Fig. 13) while Goshutes and Cape May migrants have relatively long, thin tarsi and short culmens (Fig. 14). Female Cooper’s Hawks have opposite loadings of tarsus width and hallux length. Goshutes Cooper’s Hawks are significantly different for this component and have a long hallux and narrow tarsus. Manzano and Cape May females tend to have wide tarsus and short hallux. Tarsus shape variation between flyways was consistent with predictions of feeding habits on the breeding grounds for male Cooper’s Hawks. Morphological variation between flyways in female Cooper’s Hawks did not support predictions relative to predatory habits. Plots of PC3 and
predatory shape variables illustrate the non-random relationship (Figs. 16 and 17). A plot of PC1 vs PC2 (Figs. 18 and 19) indicates the relative position of each population in multivariate space.

**Red-tailed Hawk**

**Univariate Results**

Hatch-year Red-tailed Hawks weigh significantly more in the east than in the west. Other characters that might reflective overall size were also larger in the east, with the exception of wing and tail length (Table 8). Tarsi in eastern birds do not differ in average length from western birds but are significantly wider in the east than the west. Eastern birds also have significantly longer culmen and hallux than do western birds. Wing length was significantly different between the Manzanos and the other flyways with birds migrating through the Manzanos having the longest wings. Correlations between all characters tended to be positive (Table 9). Wing-loading was significantly different ($p < 0.001$) between eastern and western Red-tailed Hawks, Goshutes migrants had a wing-loading of 2.34 (± 0.03), Manzanos migrants 2.35 (± 0.03) and Cape May migrants 2.92 (± 0.08).

Weight was positively correlated with all other characters. Tail length was most highly correlated with wing length whereas wing length was also highly correlated with weight, tarsus width and hallux. Tarsus length was most highly correlated with weight. Tarsus width was positively correlated with all characters. Tail length and tarsus length exhibited the lowest correlation. Hallux exhibited generally positive correlations and

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Figure 8. Scatterplot of PC2 and a shape ratio, culmen divided by tail length, for male Sharp-shinned Hawks. Flyways are represented by different symbols. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 9. Scatterplot of PC2 and a shape ratio, culmen divided by tail length, for female Sharp-shinned Hawks. Flyways are represented by different symbols. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 10. Scatterplot of PC3 and a shape ratio, tarsus width divided by tarsus length, for male Sharp-shinned Hawks. Flyways are represented by different symbols. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 11. Scatterplot of PC3 and a shape ratio, tarsus width divided by tarsus length, for female Sharp-shinned Hawks. Flyways are represented by different symbols. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 12. Plot of PC1 against PC2 for male Sharp-shinned Hawks. Individual principal component scores are represented by open symbols, flyway means are solid symbols with standard deviation bars. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 13. Plot of PC1 against PC2 for female Sharp-shinned Hawks. Individual principal component scores are represented by open symbols, flyway means are solid symbols with standard deviation bars. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 14. Scatterplot of PC2 and a shape ratio, culmen divided by tail length, for male Cooper's Hawks. Flyways are represented by different symbols. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 15. Scatterplot of PC2 and a shape ratio, culmen divided by tail length, for female Cooper's Hawks. Flyways are represented by different symbols. Gs = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 16. Scatterplot of PC3 and a shape ratio, culmen divided by tarsus length, for male Cooper's Hawks. Flyways are represented by different symbols. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 17. Scatterplot of PC3 and a shape ratio, tarsus width divided by hallux, for female Cooper's Hawks. Flyways are represented by different symbols. GS = Goshutes, MZ = Manzanos, and CM = Cape May.

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Figure 18. Plot of PC1 against PC2 for male Cooper's Hawks. Individual principal component scores are represented by open symbols, flyway means are solid symbols with standard deviation bars. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 19. Plot of PC1 against PC2 for female Cooper's Hawks. Individual principal components scores are represented by open symbols, flyway means are solid symbols with standard deviation bars. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
culmen correlated most highly with weight, tarsus width and hallux.

Multivariate Results

In a principal components analysis of the six morphological characters (excluding weight) three principal components explained approximately 83% of morphological variation. They were classified as an overall size component (PC1, 59% of variation), a flight shape component (PC2, 13% of variation) and a tarsus length component (PC3, 11% of variation). There were significant differences between eastern and western Red-tailed Hawks for all three principal components (Fig. 20). The relative weighting and sign of eigenvector loadings were interpreted for information on the importance of each character in either the size or shape variables (Manly 1986). Cape May migrants were highly positive for PC1, indicating generally large size, and significantly different from western migrants. Red-tailed Hawks from Cape May were also significantly positive for PC2, the flight component, and generally have a large size but relatively short wings and tail. Goshute and Manzano migrants were positive for PC3 and significantly different from Cape May migrants. This component is a measure mainly of absolute tarsus length. Cape May migrants have a short absolute tarsus as opposed to western migrants that have long tarsi. Plots of PC2 and PC3 (Figs. 21 and 22) against culmen and tarsus length divided by tail length, respectively, indicated non-random relationships between these variables and confirmed the interpretation of these principal components as flight shape and leg shape. Cape May Red-tailed Hawks are most divergent from western Red-tailed Hawks for PC1 and PC2 (Fig. 23).
Table 8. Red-tailed Hawk morphological measurements by flyway. Significant differences indicated by different letters (p < 0.01). Weight measurements are in grams and lengths in millimeters. Coefficient of variation (CV) is given in [].

**Flyway**

<table>
<thead>
<tr>
<th>Character</th>
<th>Goshutes</th>
<th>Manzanos</th>
<th>Cape May</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weight</td>
<td>932.6(150.4)(^a)</td>
<td>950.2(124.3)(^a)</td>
<td>1134.4(143.6)(^b)</td>
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<tr>
<td></td>
<td>[16.1]</td>
<td>[13.1]</td>
<td>[12.7]</td>
</tr>
<tr>
<td>Tail</td>
<td>233.7(11.3)(^a)</td>
<td>235.8(11.0)(^a)</td>
<td>222.1(9.5)(^b)</td>
</tr>
<tr>
<td></td>
<td>[4.3]</td>
<td>[4.3]</td>
<td>[3.8]</td>
</tr>
<tr>
<td>Wing</td>
<td>397.4(17.2)(^a)</td>
<td>403.6(17.2)(^b)</td>
<td>387.3(14.8)(^c)</td>
</tr>
<tr>
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<td>[4.3]</td>
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<td>87.7(4.2)(^ab)</td>
<td>88.5(4.2)(^a)</td>
<td>85.8(9.0)(^b)</td>
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<tr>
<td></td>
<td>[4.8]</td>
<td>[4.8]</td>
<td>[10.5]</td>
</tr>
<tr>
<td>Tarsus width</td>
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<td>12.8(0.7)(^b)</td>
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<tr>
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</tr>
<tr>
<td>Hallux</td>
<td>28.8(2.0)(^a)</td>
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<td>32.6(2.2)(^b)</td>
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<tr>
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<td>[6.9]</td>
<td>[5.4]</td>
<td>[6.8]</td>
</tr>
<tr>
<td>Culmen</td>
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<td>25.1(1.4)(^a)</td>
<td>28.1(1.4)(^b)</td>
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<td>[5.6]</td>
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Table 9. Correlation analysis of principal component scores, morphological characters and 'shape' ratios for Red-tailed Hawks. Correlations were performed on log-transformed measurements. PC2 = second principal component, PC3 = third principal component, Wt = weight, T = tail, W = wing, Tl = tarsus length, Tw = tarsus width, Hx = hallux, Cn = culmen. Principal component scores were derived from all morphological characters excluding weight.

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<tr>
<th></th>
<th>PC2</th>
<th>PC3</th>
<th>Wt</th>
<th>T</th>
<th>W</th>
<th>Tl</th>
<th>Tw</th>
<th>Hx</th>
<th>Cn</th>
<th>Cn/T</th>
<th>Tl/T</th>
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<td>PC1</td>
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<td>0.003</td>
<td>0.824</td>
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<td>0.459</td>
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<td>Tw</td>
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<td>Hx</td>
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<td>0.418</td>
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Figure 20. Principal component weightings for six morphological variables (T = tail length, W = wing length, Tl = tarsus length, Tw = tarsus width, Hx = hallux length, and Cn = culmen length) for Red-tailed Hawks are presented as bar graphs in the upper panels. Principal component scores were assigned to individuals and significant differences between flyways were determined by ANOVA. Significantly different means (p < 0.05) for flyways (GS = Goshutes, MZ = Manzanos, and CM = Cape May) are indicated by unique letters in the bottom panel.
Figure 21. Scatterplot of PC2 against a shape ratio, culmen divided by tail length, for Red-tailed Hawks. Flyways are represented by different symbols. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 22. Scatterplot of PC3 against a shape ratio, tarsus length divided by tail length, for Red-tailed Hawks. Flyways are represented by different symbols. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 23. Plot of PC1 against PC2 for Red-tailed Hawks. Individual principal component scores are represented by open symbols, flyway means are solid symbols with standard deviation bars. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
American Kestrel

Univariate Results

Hatching-year American Kestrels are generally larger in the east since both sexes were significantly heavier in Cape May than in the west (Table 10). However wings were shorter in the east than in the west. Tails were significantly shorter in males from Cape May. Male American Kestrels were significantly different between all three flyways and Manzano migrants had the longest wings. Females had significantly narrower tarsi in the Goshutes than in the Manzanos while males had significantly wider tarsi in the west. There were no significant differences for tarsus length, hallux and culmen.

Weight was most highly correlated with culmen in male American Kestrels and with tarsus length in females (Tables 11 and 12). Tail and wing length were highly correlated with each other. Neither tarsus length nor tarsus width was highly correlated with any other character. Hallux and culmen were most highly correlated with each other in the males, no high correlations were observed for these characters in the females.

Wing-loading, determined as described, was significantly different between Cape May and western migrants for the males and between all three flyways for females. Male American Kestrels migrating through the Goshutes had a wing-loading of 0.53 (± 0.003), Manzanos 0.54 (± 0.009) and Cape May 0.61 (± 0.16). Females from the Goshutes had a wing-loading of 0.55 (± 0.003), Manzanos 0.58 (± 0.11) and Cape May 0.64 (± 0.013).
Table 10. Multiple analysis of variance results for morphological differences between flyways for male and female American Kestrels. Standard deviations are in parentheses. Significant differences are indicated by unique letters, coefficient of variation []. Weight was measured in grams, linear measurements are in millimeters.

<table>
<thead>
<tr>
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<th>Manzanos</th>
<th>Cape May</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(209)</td>
<td>(25)</td>
<td>(14)</td>
</tr>
<tr>
<td>Weight</td>
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<td>102.5(7.4)^a</td>
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</tr>
<tr>
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<td>[7.8]</td>
<td>[7.2]</td>
<td>[9.3]</td>
</tr>
<tr>
<td>Tail</td>
<td>121.9(4.9)^a</td>
<td>121.1(6.0)^a</td>
<td>116.4(4.5)^b</td>
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<tr>
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<td>[5.0]</td>
<td>[3.9]</td>
</tr>
<tr>
<td>Wing</td>
<td>188.6(5.5)^a</td>
<td>191.6(5.2)^b</td>
<td>180.1(5.5)^c</td>
</tr>
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<td>[3.1]</td>
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<td>[4.6]</td>
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</tr>
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<td>Tarsus Width</td>
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<td>4.1(0.4)^a</td>
<td>3.8(0.2)^b</td>
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<tr>
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<td>[8.0]</td>
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<td>[6.0]</td>
</tr>
<tr>
<td>Hallux</td>
<td>9.4(0.5)^a</td>
<td>9.4(0.6)^a</td>
<td>9.5(0.5)^a</td>
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<tr>
<td></td>
<td>[5.3]</td>
<td>[6.3]</td>
<td>[5.0]</td>
</tr>
<tr>
<td>Culmen</td>
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<tr>
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</table>

**Female American Kestrels**

<table>
<thead>
<tr>
<th></th>
<th>(170)</th>
<th>(16)</th>
<th>(13)</th>
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</thead>
<tbody>
<tr>
<td>Weight</td>
<td>107.4(9.0)^a</td>
<td>114.4(9.5)^b</td>
<td>121.7(7.5)^c</td>
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<tr>
<td></td>
<td>[8.4]</td>
<td>[8.3]</td>
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<tr>
<td>Tail</td>
<td>126.6(5.2)^a</td>
<td>124.3(6.5)^ab</td>
<td>121.9(3.3)^b</td>
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<tr>
<td></td>
<td>[4.1]</td>
<td>[5.3]</td>
<td>[2.7]</td>
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<tr>
<td>Wing</td>
<td>196.9(6.0)^a</td>
<td>196.7(7.9)^a</td>
<td>191.2(5.7)^b</td>
</tr>
<tr>
<td></td>
<td>[3.1]</td>
<td>[4.0]</td>
<td>[3.0]</td>
</tr>
<tr>
<td>Tarsus Length</td>
<td>36.3(1.9)^a</td>
<td>36.0(2.6)^a</td>
<td>35.4(1.7)^a</td>
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<tr>
<td></td>
<td>[5.4]</td>
<td>[7.1]</td>
<td>[4.8]</td>
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<tr>
<td>Tarsus Width</td>
<td>4.2(0.4)^a</td>
<td>4.4(0.4)^b</td>
<td>4.3(0.35)^ab</td>
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<td>[8.6]</td>
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<tr>
<td>Hallux</td>
<td>9.8(0.7)^a</td>
<td>9.8(0.5)^a</td>
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<tr>
<td></td>
<td>[7.0]</td>
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<tr>
<td>Culmen</td>
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<td>[5.4]</td>
<td>[4.8]</td>
<td>[4.4]</td>
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Table 11. Correlation analysis of principal component scores, morphological characters and 'shape' ratios for male American Kestrels. Correlations were performed on log-transformed measurements. PCI = first principal component, PC2 = second principal component, PC3 = third principal component, Wt = weight, T = tail, W = wing, TI = tarsus length, Tw = tarsus width, Hx = hallux, Cn = culmen. Principal component scores were derived from all morphological characters excluding weight.

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>Wt</th>
<th>T</th>
<th>W</th>
<th>TI</th>
<th>Tw</th>
<th>Hx</th>
<th>Cn</th>
<th>Cn/T</th>
<th>Cn/TI</th>
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<tbody>
<tr>
<td>PC1</td>
<td>0.019</td>
<td>0.001</td>
<td>0.263</td>
<td>0.813</td>
<td>0.143</td>
<td>0.420</td>
<td>0.369</td>
<td>0.429</td>
<td>0.102</td>
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<tr>
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<td>-0.004</td>
<td>0.181</td>
<td>-0.299</td>
<td>-0.296</td>
<td>-0.245</td>
<td>0.084</td>
<td>0.674</td>
<td>0.664</td>
<td>0.771</td>
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<tr>
<td>PC3</td>
<td>0.120</td>
<td>-0.224</td>
<td>-0.128</td>
<td>0.863</td>
<td>0.318</td>
<td>0.316</td>
<td>-0.207</td>
<td>-0.115</td>
<td>-0.656</td>
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<tr>
<td>Wt</td>
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<td>0.125</td>
<td>0.164</td>
<td>0.161</td>
<td>0.079</td>
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<td>T</td>
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<td>0.669</td>
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<td>W</td>
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<td>0.078</td>
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<td>-0.089</td>
<td>-0.634</td>
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<tr>
<td>Tw</td>
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<td>0.111</td>
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<td>0.035</td>
<td>0.027</td>
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<tr>
<td>Hx</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Cn/TI</td>
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</tbody>
</table>
Table 12. Correlation analysis of principal component scores, morphological characters and 'shape' ratios for female American Kestrels. Correlations were performed on log-transformed measurements. PCI = first principal component, PC2 = second principal component, PC3 = third principal component, Wt = weight, T = tail, W = wing, Tl = tarsus length, Tw = tarsus width, Hx = hallux, Cn = culmen. Principal component scores were derived from all morphological characters excluding weight.

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>Wt</th>
<th>T</th>
<th>W</th>
<th>Tl</th>
<th>Tw</th>
<th>Hx</th>
<th>Cn</th>
<th>Tw/Hx</th>
<th>Cn/T</th>
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<tbody>
<tr>
<td>PCI</td>
<td>-0.001</td>
<td>0.001</td>
<td>0.222</td>
<td>0.866</td>
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<td>-0.011</td>
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<tr>
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<td>0.106</td>
<td>-0.059</td>
<td>0.008</td>
<td>0.500</td>
<td>0.676</td>
<td>-0.617</td>
<td>-0.109</td>
<td>0.887</td>
<td>-0.079</td>
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<tr>
<td>PC3</td>
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<td>-0.227</td>
<td>-0.176</td>
<td>0.266</td>
<td>0.050</td>
<td>0.124</td>
<td>0.911</td>
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<tr>
<td>Wt</td>
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<td>0.246</td>
<td>0.168</td>
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<td>0.211</td>
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<td>T</td>
<td>-0.051</td>
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<td>0.058</td>
<td>-0.107</td>
<td>-0.331</td>
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<td>Tl</td>
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<td>Tw</td>
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<tr>
<td>Tw/Hx</td>
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</tbody>
</table>
Multivariate Results

In a principal components analysis of the six morphological characters (excluding weight) three principal components explained approximately 60% of morphological variation. They were classified as a flight component (PC1, 27% of variation in males and 29% of variation in females), a predatory shape component (PC2, 18% of variation for both sexes) and a tarsus length component in males (PC3, 15% of variation) and culmen length component in females (15% of variation).

Male Cape May migrants differed from western migrants for the first component and females from Cape May were significantly different from Goshutes migrants for this same component (Figs. 24 and 25). Principal component one was comprised mostly of high weightings for tail and wing length which also had the highest correlation with PC1. A significantly negative average for PC1 in Cape May migrants of both sexes indicated short wings and tail. In male American Kestrels, PC2 consisted mostly of absolute hallux and culmen length. Cape May migrants had a significantly positive average for this component and have large culmen and hallux, perhaps indicative of large size. However, some indication of shape for PC2 is apparent for males in a plot of PC2 vs culmen divided by tail length; there is a non-random relationship (Fig. 26). Female American Kestrels seemed to exhibit a predatory shape component for PC2 since tarsus length and width loaded opposite hallux length. A plot of PC2 and the shape ratio tarsus width divided by hallux indicates the non-random relationship between this component and this measure of shape in females (Fig. 27). There were no significant differences between flyways for this component for females.
The third principal component in male American Kestrels seemed to reflect mainly absolute tarsus length. There were no significant differences between flyways for this component. In female American Kestrels PC3 was heavily weighted for culmen and seemed to be an indication of absolute culmen length. Cape May American Kestrels were positive and significantly different for this component from Goshutes migrants. Morphological shape variation for both PC2 and PC3 in both sexes of American Kestrel was not consistent with predictions from predatory habits. Variation in morphological characters indicative of predatory habits may not be adaptive or there may be no selection for these characters. Male American Kestrels from Cape May were most different from western individuals for PC1 and PC2, female American Kestrels from all three flyways clustered together for PC1 and PC2 (Figs. 28 and 29).

**Molecular Results**

**Sharp-shinned Hawks**

Thirty-four individuals were tested of which 28 (82%) from all three flyways shared the same haplotype (Table 13). Seventeen restriction enzymes were used of which four, *HaeIII, HincII, HinfI* and *Hpai*, yielded different fragment lengths in a total of 6 individuals. The ND2/CO1 region of the mtDNA was estimated to be about 2200 bp or approximately 7.5% of the 16,500 bp genome. A total of 35 sites were scored in all individuals giving information on about 1% of the mtDNA genome. Rare
Figure 24. Principal component weightings for six morphological variables (T = tail length, W = wing length, Tl = tarsus length, Tw = tarsus width, Hx = hallux length, and Cn = culmen length) for male American Kestrels are presented as bar graphs in the upper panels. Principal component scores were assigned to individuals and significant differences between flyways were determined by ANOVA. Significantly different means (p < 0.05) for flyways (GS = Goshutes, MZ = Manzanos, and CM = Cape May) are indicated by unique letters in the bottom panel.
Figure 25. Principal component weightings for six morphological variables (T = tail length, W = wing length, Tl = tarsus length, Tw = tarsus width, Hx = hallux length and Cn = culmen length) for female American Kestrels are presented as bar graphs in the upper panels. Principal component scores were assigned to individuals and significant differences between flyways were determined by ANOVA. Significantly different means (p < 0.05) for flyways (GS = Goshutes, MZ = Manzanos, and CM = Cape May) are indicated by unique letters in the bottom panel.
Figure 26. Scatterplot of PC2 and a shape ratio, culmen divided by tail length, for male American Kestrels. Flyways are represented by different symbols. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 27. Scatterplot of PC2 and a shape ratio, tarsus width divided by hallux, for female American Kestrels. Flyways are represented by different symbols. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 28. Plot of PC1 against PC2 for male American Kestrels. Individual PC scores are represented by open symbols, flyway means are solid symbols with standard deviation bars. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
Figure 29. Plot of PC1 and PC2 for female American Kestrels. Individual values are plotted as open symbols, flyway means are solid symbols with standard deviation bars. GS = Goshutes, MZ = Manzanos, and CM = Cape May.
haplotypes were found in one Cape May migrant and one Goshute migrant. Two individuals from Cape May and two from the Goshutes exhibited a third unique haplotype. All haplotypes differed by only one restriction site except for one Cape May migrant that differed by two. Although there was geographic range structure of rare haplotypes, the haplotype differences are small and haplotype diversities are low.

Cooper's Hawks

Forty-four individuals were examined of which 36 (82%) shared the same haplotype (Table 13). The same sixteen enzymes were used as in the Sharp-shinned Hawks. There was only one alternative haplotype that differed by a single restriction site. Two Manzanos birds and 4 Cape May birds exhibited this haplotype. Frequency of haplotypes was proportionately different between flyways but these differences are slight.

Comparison of Sharp-shinned Hawks and Cooper's Hawks

The two species differed from each other by an estimated 12 restriction sites (Fig. 30). Given the divergence detected between species, for the restriction enzymes used, the low within species diversity is not due to lack of ability of my analysis to detect variation. Relative to the scale of divergence between species the divergence within species must be very recent.
Table 13. Numbers of 4-, 5- and 6-base enzyme haplotypes scored for Sharp-shinned Hawks and Cooper's Hawks from each flyway. Common haplotype in Sharp-shinned Hawks is indicated by the letter A. The common haplotype in Cooper's Hawks is designated by unique letters for restriction site differences compared with Sharp-shinned Hawks. Enzymes used were AcII, AluI, AvaII, BfaI, Bsp1286I, BstNI, BsrUI, DdeI, HaeIII, HhaI, HinclI, HinfI, Hpa I, Mbol, NlaIII, RsaI and TaqI.

**Sharp-shinned Hawks**

<table>
<thead>
<tr>
<th>Haplotype</th>
<th>Goshutes (11)</th>
<th>Manzanos (11)</th>
<th>Cape May (12)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>8</td>
<td>11</td>
<td>9</td>
</tr>
<tr>
<td>2</td>
<td>0</td>
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<td>4</td>
<td>2</td>
<td>0</td>
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</table>

<table>
<thead>
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<th>Haplotype</th>
<th>Goshutes (15)</th>
<th>Manzanos (15)</th>
<th>Cape May (14)</th>
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</thead>
<tbody>
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<td>10</td>
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<tr>
<td>2</td>
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<td>4</td>
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**Cooper's Hawks**

<table>
<thead>
<tr>
<th>Haplotype</th>
<th>Goshutes (15)</th>
<th>Manzanos (15)</th>
<th>Cape May (14)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>B B A B A B A B C A A B B B B</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>B C A B A B A B C A A B B B B</td>
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</tbody>
</table>
Figure 30. Haplotype differences between populations of Sharp-shinned Hawks and Cooper's Hawks and between the two species. n = number of individuals of each haplotype, circles represent each haplotype and hatch marks indicate the number of restriction site differences.
Red-tailed Hawks

Twenty-six individuals were tested and three haplotypes were found, one of which was unique to all individuals migrating through Cape May (Table 14). Sixteen four- and six-base restriction enzymes were used of which two, AluI and Rsal, yielded different fragment lengths. A total of 35 sites were scored in all individuals giving information on about 1% of the mtDNA genome. There were three haplotypes found in Red-tailed Hawks, one of which was specific for the Cape May migrants and differed from one of the western haplotypes by one restriction site. In the western migrants, there were two mtDNA haplotypes, both of which showed a variation in frequencies between Goshutes and Manzano migrants. This geographic structure, although slight, indicates a consistent separation of eastern and western migratory cohorts. Individuals

Table 14. Numbers of 4-, 5- and 6-base enzyme haplotypes scored for Red-tailed Hawks from each flyway. The common haplotype is designated by the letter A. Enzymes used were Acil, AluI, AvaII, BfaI, Bsp1286I, BstNI, BstUI, DdeI, HaeIII, Hhal, HincII, Hinfl, MboI, NlaIII, RsaI and TaqI.

<table>
<thead>
<tr>
<th>Haplotype</th>
<th>Goshutes (8)</th>
<th>Manzanos (8)</th>
<th>Cape May (10)</th>
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</thead>
<tbody>
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<td>5</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Haplotype 2</td>
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</tr>
<tr>
<td>Haplotype 3</td>
<td>0</td>
<td>0</td>
<td>10</td>
</tr>
</tbody>
</table>

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American Kestrels

For the genetic analysis sixteen restriction enzymes were used that recognized approximately 30 restriction sites. This represents a little less than 1% of the mtDNA genome. Birds from all flyways had a single, common haplotype (Table 15) with the exception of one individual from Cape May that differed from the rest by one restriction site.

Table 15. Numbers of 4-, 5- and 6-base enzyme haplotypes scored for American Kestrels from each flyway. Enzymes used were AcI, AluI, AvaII, BfaI, Bsp1286I, BstNI, BstUI, DdeI, HaeIII, HhaI, HinfI, HpaII, MboI, NlaIII, Rsal and TaqI.

| Haplotype 1 | A A A A A A A A A A A A A A A A A A |
| Haplotype 2 | A A A A A A A A A A B A A A A A A |

<table>
<thead>
<tr>
<th>Goshutes (17)</th>
<th>Manzanos (9)</th>
<th>Cape May (12)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Haplotype 1</td>
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<td>9</td>
</tr>
<tr>
<td>Haplotype 2</td>
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<td>0</td>
</tr>
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</table>
CHAPTER 3

DISCUSSION AND CONCLUSIONS

Morphological Variation and Climate

Variation in body weight between the three flyways was not consistent with adaptive predictions of morphological variation in response to climate. The largest mean body weight was not found in the west as predicted from consideration of temperature and aridity. A study of American Robins during the breeding season from across North America indicated that the largest individuals are in the Rocky Mountains, the northern Great Plains and the northern deserts (Aldrich and James 1991). Other studies of geographic variation correlated with climate provided support for Bergmann’s rule, though not for the same geographic areas as this study (James 1970, Aldrich 1984, and Murphy 1985). A comprehensive study of avian morphology revealed that only 42% of studies provided unambiguous evidence of correlation between body size and climate (Zink and Remsen 1986). Additionally, predictions from Bergmann’s rule were not supported for migratory species (Zink and Remsen 1986). The variation in body size revealed by this study is consistent with results of Zink and Remsen’s analysis. Bergmann’s rule may, however, hold true for body size comparisons made with respect to wintering habitat (Johnston and Fleischer 1981,

**Morphological Variation and Migration Distance**

All species exhibited variation in body weight and wing and tail length consistent with predictions based on migration flight except the Cooper's Hawk. I predicted that migratory raptors using western flyways would have longer wings and tail than those using eastern, coastal flyways. Although wing area was not measured, wing length was taken as an approximate indication of relative wing area within a species. Wing and tail length together were expected to influence flight surface area. Longer wings and tail impart a greater flight surface for soaring and adjustments for different flight styles such as gliding could be made by expanding or folding the tail and wings. Longer wings and tail impart a greater surface area which is an advantage to individuals that use soaring flight during migration (Mueller et al. 1981, Kerlinger 1989). In spite of small body weight in the west, wings and tail were longer in western Sharp-shinned Hawks, Red-tailed Hawks and American Kestrels. Increased flight surface in these western individuals would lead towards increased flight efficiency for longer migratory flights or migration through high altitude, arid environments. This pattern was expressed in three unrelated species despite extreme differences in body size, wing length and wing shape. A parallel pattern such as this may reflect consistent, strong natural selection for a particular environmental parameter (James 1991).

Parallel variation between the three species from three flyways points to strong natural
selection relative to migration efficiency. The Cooper's Hawk may not experience
natural selection for flight efficiency during migration.

**Morphological Variation and Habitat Flight**

In male Sharp-shinned Hawks, Cooper's Hawks and Red-tailed Hawks, average
wing and/or tail length was longest in the Manzanos compared with other flyways.
This is consistent with predictions from the hypothesis that openness of habitat on the
breeding grounds of Manzano individuals relative to the other breeding habitats
resulted in natural selection of flight efficiency. Lack of morphological variation
consistent with this prediction resulted in rejection of this adaptive hypothesis for the
American Kestrel and female Sharp-shinned Hawk.

**Morphological Variation and Predatory Habits**

For accipiters, leg structure associated with a predominantly mammalian diet
has been described as short, thick tarsus, short toes and a long bill. Conversely,
avivores have a long, thin tarsus, long toes and a short bill (Wattel 1973, Burton and
Alford 1994). The average Goshutes accipiter possesses a long, thin tarsus
characteristic of avivores. Manzanos accipiters have, on average, a short, thick tarsus.
Accipiters from Cape May were divided as to whether they were grouped with
Manzanos or Goshutes individuals. Although some of these morphological differences
match the predictions based on differences in flyway habitats, there was no overall
correspondence with the adaptive predatory hypotheses. These observations cause a
rejection of the adaptive hypothesis based on ground-dwelling prey. American Kestrels
and Red-tailed Hawks did not exhibit morphological differences consistent with adaptive predictions.

Although specific predictions could not be made about prey species available on breeding grounds for each flyway, it appears that there is variation between flyways for predatory characters. In general, Goshutes Sharp-shinned Hawks and Cooper's Hawks have a long, thin tarsi and long hallux. Manzanos migrants have short, thick tarsi and short hallux. There is a division between the two species and sexes for prey-related characters in Cape May. Male Sharp-shinned Hawks from Cape May are more similar to those from the Manzanos as are female Cooper's Hawks. In contrast, female Sharp-shinned Hawks and male Cooper's Hawks from Cape May are more similar to those from the Goshutes. The match of morphology with adaptive prediction for predatory habits was weak since there was support in only one sex of each of the two species.

**Molecular Genetic Population Structure**

Lack of detectable population structure in Sharp-shinned Hawks, Cooper's Hawks and American Kestrels may be due to recent range expansion, frequent dispersal events between populations, low lifetime reproductive success in most females or a bottleneck in the recent past (Gill et al. 1993). A number of avian studies have failed to find underlying phylogeographic structure to match patterns of morphological differentiation, for example in the Dusky Seaside Sparrow (Avise and Nelson 1989), chickadees (Gill et al. 1993), flickers (Moore et al. 1991), and redpolls (Seutin et al. 1995). These studies have generally looked at subspecies designations based primarily
on plumage characters. In spite of the differences in morphology of weight, wing, tail, leg, foot and beak found in this study, taxonomists have not historically recognized the populations from the three species in this study as unique. The failure to uncover phylogeographic structure in these three species was thus not surprising. Haplotype divergence between the two species of *Accipiter* was much larger than within species. This indicates that variation was detectable at a higher level and not within the populations studied. It is possible that non-migratory populations of these species will exhibit more population-specific haplotype structure.

Variation within the Red-tailed Hawk was consistent with traditional classification of eastern (*borealis*) and western (*calurus*) forms. Individuals from Cape May were of a different haplotype than individuals from either of the western flyways. However, further work needs to be done to establish whether there is a clear distinction between population-specific haplotypes or whether there is a clinal pattern of variation between east and west in haplotype frequency. The pattern observed may result from sampling ends of a continuum in haplotype frequency resulting from gene flow and the morphological patterns could be a result of phenotypic plasticity.

Lack of geographically structured variation in neutral molecular characters seems to indicate that northern populations of Sharp-shinned Hawks, Cooper's Hawks and American Kestrels are of recent origin or are experiencing regular gene flow. If this is true, there has probably not been time or opportunity for genetically-based morphological differences to arise within these species. However, it also appears to be true that natural selection of wing and tail length is strong in response to flight habits.
and that there is a predictable morphological response. Adaptation to local habitat through phenotypic plasticity appears to be a likely explanation for the consistent, predictable variation found in three species of raptors from different geographic areas in northern North America and of different migratory habits.

Conclusions

Two potential responses of migratory raptors to environmental heterogeneity were studied, morphological variation and mitochondrial DNA variation. Throughout the range of each species it was theorized that large scale habitat variation is consistent and that predictions for morphological variation in response to this heterogeneity could be made and compared with realized body size and shape. Additionally, comparisons were made of mitochondrial DNA haplotype structure across the northern portion of the continental distribution of these four species.

Variation in body size relative to climate, specifically with regards to Bergmann's rule, has been documented in some species of birds (see citations in Introduction). However, Zink and Remsen (1986) found unambiguous support for this rule in only 42 species of birds and no support in migratory species. This study supports the conclusions of Zink and Remsen (1986) for the four species studied, the largest individuals found were not from the high, arid regions of the west but from the east. However, if body size is compared for individuals from wintering habitat, variation is consistent with Bergmann's rule as eastern individuals remain further north than do western migrants. This is consistent with stronger natural selection of size on
wintering than on breeding grounds such as that found by Johnston and Fleischer for the house sparrow (1981).

Flight is clearly one of the most energy intensive activities in the daily and yearly energy budget of any bird (Kerlinger 1989). Strategies for different flight styles that vary with habitat and atmospheric parameters entail different morphologies. If movement, either migratory or between perches for hunting, includes a disproportionate amount of soaring or gliding, large wing areas are preferred (Kerlinger 1989). Wing length varied in all four species in a manner consistent with predictions of increased flight surface with flight habits. Longer distance migrants, western individuals, had significantly longer wings and tail in three species. Raptors from open habitat (also in the west) had significantly longer wings and tail in two species. Although the differences are only correlative with respect to environment and flight habits, parallel patterns between several species provides evidence for the importance of flight.

Predictions were made for variation in leg, foot and bill morphology in response to relative areas of open and forested habitat and potential prey from these niches. The nature of the data did not allow for specific matching of individuals with habitat types. It is generally acknowledged, however, that western habitat potentially contains more open areas than comparable eastern habitat (Carter and Mather 1966, Aldrich 1984, and Walter 1985). It was also assumed that open areas would support more ground-dwelling prey than would areas of closed forest. Thus, the prediction was that western individuals, specifically those from the Manzanos, would possess leg, foot and beak
morphology typical of predators that capture animals on the ground. While Manzano
accipters averaged shorter, thicker tarsi than accipiters from the other flyways, male
Sharp-shinned Hawks and female Cooper's Hawks from Cape May were most like
their conspecifics from the Manzanos whereas female Sharp-shinned and male
Cooper's Hawks from Cape May were most like their conspecifics from the Goshutes.
Whether this represents a partitioning of prey types between the sexes in Cape May
individuals or whether the pattern seen is merely random is unclear. Predictions for
predatory morphology relative to habitat were only supported for female Sharp-shinned
Hawks and male Cooper's Hawks. There were no clear differences in toe length and
bill length consistent with predictions for predatory habits.

Of the four species studied, only the Red-tailed Hawk exhibited molecular
phylogeographic structure between the three migratory populations. Results were
generally consistent with traditional taxonomic descriptions of subspecies. The Red-
tailed Hawk is the only species of those investigated in this study that has been
described as having an eastern and a western form. It is important to continue genetic
studies of this species because I only sampled eastern and western ends of a potential
continuum and no attempt was made at classification of subspecies from morphological
characters. Further work is needed to clarify phylogeographic structure and how that
relates to described 'morphs' and subspecies. The other three species were essentially
undistinguishable between flyways. It may be that gene flow is high in these migratory
populations, colonization the northern part of the continent may be recent and/or
resulting from a bottleneck or founder event that may have caused loss of genetic
variation.

If gene flow is high between populations of the Sharp-shinned Hawk, Cooper's Hawk and American Kestrel, morphological variation appears to be a response to strong natural selection for flight characters in a heterogeneous environment. Two potential species/population scenarios are possible. 1) populations may indeed be distinct yet undistinguishable by the methods used in this study. If distinct, these populations may be responding to strong natural selection on the breeding grounds for specific genetically influenced traits that differ between populations. Genetic differentiation of traits may be occurring at a faster rate than mitochondrial DNA is capable of tracking. 2) alternatively, there may be consistent gene flow across North America for these species and the phenotypic responses seen are environmentally induced. Phenotypic plasticity, in which a norm of response is seen, may be a common response to a variable environment such as these raptors are experiencing for flight and potentially for hunting.

Detailed analyses of wing and tail length and shape variation between populations of migratory raptors may elucidate the role of flight surface in response to migration and habitat flight. Also further comparison of coastal- vs ridge-migrating populations may describe differences in wing and tail shape for these migration strategies. It is also important to investigate variation among adult migratory raptors. Hatching-year migrants are known to appear in high numbers along coastal routes whereas the proportion of adults at inland migratory routes tends to be high (Clark 1985).
Any studies of flight surface morphology in different breeding habitats may provide information on flight habits in forested and open habitat. Further studies of population genetic structure of these species is important, especially of non-migratory populations. Southern populations may be older and, because of their non-migratory nature, may be subdivided into distinct genetic units. Additional study of the different subspecies of the Red-tailed Hawk are especially important. Analysis of different gene regions on both mtDNA and nuclear DNA may lend support to the phylogeographic pattern found in this study. There are additional color variants and described subspecies in the northeastern coastal forests, great plains and regions of Canada. There is much yet to be done in order to understand variation in morphology and population genetics in North American raptors.
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