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REGIONAL SIZE DIFFERENCES AMONG FALL-MIGRANT ACCIPITERS IN NORTH AMERICA

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Abstract.—Measurements of fall-migrant accipiters from four regions in the United States were compared. Cooper's Hawks (*Accipiter cooperii*) from Goshute Mountains, Nevada and Marin Headlands, California were significantly smaller and had longer wings and tails in proportion to their weight than those from Cedar Grove, Wisconsin and Cape May Point, New Jersey. Northern Goshawks (*A. gentilis*) from the Goshutes weighed significantly less, but had longer wings and tails than those from Cedar Grove. The same was true for Goshute Sharp-shinned Hawks (*A. striatus*) in comparison with those from Cedar Grove and Marin Headlands, but differences were less pronounced. These data demonstrate the need for regional identification criteria. Among the four samples, Goshute migrants averaged the lowest flight-surface loading (i.e., proportionately low weight and long wings and tail) and inland migrants averaged lower flight-surface loading than coastal migrants. Low flight-surface loading may be adaptive for inland migrants, which average longer migrations and occupy habitats with more open vegetation, and particularly for Goshute migrants which may depend more on exploiting thermal updrafts.

DIFERENCIAS REGIONALES EN EL TAMAÑO DE MIGRATORIOS OTOÑALES (ACCIPITRINAE) EN NORTE AMERICA

Sinopsis.—Se compararon los tamaños de partes de la anatomía de individuos migratorios otoñales de Accipiteres de cuatro regiones de los Estados Unidos. Individuos de *Accipiter cooperii* de las montañas Goshute, Nevada y Marin Headlands, California resultaron significativamente más pequeños y con alas y rabos más largos en proporción a su peso, que individuos de Cedar Grove, Wisconsin y Cape May Point, New Jersey. Por su parte individuos de *A. gentilis* originados de Goshute mostraron tener alas y rabos más largos, pero con peso significativamente menor que aves de Cedar Grove. Lo mismo aplica a individuos de *A. striatus* de Goshute en comparasión con otros de Cedar Grove y Marin Headlands, aunque la diferencia fue menos marcada. Los datos de este trabajo demuestran la necesidad de criterios para la identificación de estas aves a nivel regional. Entre las muestras, los migrantes de Goshute promediaron la menor carga superficie-vuelo (Ej. menos peso proporcional a alas y rabos largos). Los migrantes de tierra adentro promediaron una menor carga superficie-vuelo que los migrantes costaneros. Cargas pequeñas de superficie-vuelo podrían ser una adaptación para migrantes de tierra adentro, los cuales promedian vuelos migratorios más largos y ocupan habitats con vegetación más abierta. Esto aplica

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particularmente a los migrantes de Goshute que muy bien pudieran depender de explotar adecuadamente corrientes termales de aire.

To illustrate morphological differences among Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks (*A. cooperii*), and Northern Goshawks (*A. gentilis*) we compared measurements of fall migrants trapped at four sites in the United States: Marin Headlands, California (37°38′N, 122°49′W); Goshute Mountains, Nevada (40°53′N, 114°28′W); Cedar Grove, Wisconsin (43°34′N, 87°49′W); and Cape May Point, New Jersey (39°09′N, 74°46′W). The comparisons demonstrated the need for regional species identification and sexing criteria for Cooper's Hawks and Northern Goshawks; disclosed interspecific differences in the patterns of size variation among North American accipiters; and revealed morphological differences between eastern and western, and between coastal and inland migrants. In this paper we discuss the possible adaptive significance of these trends and the implications for in-flight identification of species. Regional species identification and sexing criteria are discussed in Hoffman et al. (1990).

METHODS

Hoffman et al. (1990) summarized measurements from the Goshute Mountains and Mueller et al. (1976, 1979a, 1981a) provided data from Cedar Grove. Data from Marin Headlands and Cape May Point were obtained in raw form for analysis. Many individuals collected the Marin Headlands measurements from August through December 1986 and 1987. William S. Clark and his associates collected the Cape May Point measurements during October from 1970–1980. In all cases hawks were aged by plumage criteria described in Mueller et al. (1976, 1979a, 1981a). Adult or AHY (after-hatching-year) included hawks in their second year or older, except that we used means for the Adult II category (hawks in at least their third year) of Mueller et al. (1976) to represent adult goshawks from Cedar Grove. Immature or HY (hatching-year) included hawks less than one year old.

We sexed Goshute migrants by the criteria presented in Hoffman et al. (1990). Cooper's Hawks from Cape May Point were sexed using criteria now represented in the Canadian Wildlife Service and United States Fish and Wildlife Service raptor age-sex key (CWS and USFWS 1980) and in Mueller et al. (1976, 1979a, 1981a). Marin Headlands migrants also were sexed using the CWS and USFWS age-sex key; however, according to the criteria we developed from measurements of Goshute migrants, nine of the Marin Headlands Cooper's Hawks had been incorrectly sexed as males. Golden Gate Raptor Observatory personnel discussed this problem in their biannual newsletter The Pacific Raptor Report (Winter 1986–1987). For this analysis, we sexed the Marin Headlands migrants by the Goshute criteria.

We obtained only wing chord and weight measurements for immature Cooper's Hawks from Cape May Point. Fewer than 10 adult sharpshins, of each sex, and 10 adult male Cooper's Hawks were captured and

TABLE 1. Regional comparisons of means with sample sizes (in parentheses) for measurements from fall-migrant Sharp-shinned Hawks.[a]

Measure	Age-sex	Marin Headlands[b]	Goshute Mountains	Cedar Grove[c]
Weight (g)	HY-M	102 (17) NS	96 (714)	98 (489)
	AHY-M	—	102 (175)*	103 (435)
	HY-F	167 (72)	160 (427)	166 (522)
	AHY-F	—	171 (298)	174 (487)
Wing chord (mm)	HY-M	170 (17) NS	171 (901)	169 (493)
	AHY-M	—	174 (264)	171 (437)
	HY-F	201 (74)	204 (860)	200 (544)
	AHY-F	—	206 (524)	203 (489)
Standard tail length (mm)	HY-M	135 (17) NS	136 (475)	134 (494)
	AHY-M	—	134 (94)	132 (440)
	HY-F	159 (74)	161 (537)	158 (548)
	AHY-F	—	160 (204)	156 (492)

[a] All pairwise comparisons of means, within a sex and age, are significant (t-test, $P <$ 0.001) unless indicated by * (significant, $P < 0.05$) or NS (not significant, $P > 0.05$); there are no significant differences between means for Marin and Cedar Grove.
[b] Data provided by Golden Gate Raptor Observatory, California.
[c] Data from Mueller et al. 1979a.

measured in the Marin Headlands; we excluded these data from comparison. Data for goshawks were unavailable from the coastal sites. Standard measurements of weight, unflattened wing chord, tail length, exposed culmen length, and tarsus width were compared when possible. The t-test was used to identify significantly different means ($P < 0.05$).

RESULTS

Regional size differences were least pronounced in Sharp-shinned Hawks. Goshute migrants weighed less and had longer wings and tails than those from the Marin Headlands and Cedar Grove (Table 1), but sharpshins from the latter two sites did not differ significantly. Cooper's Hawks consistently exhibited the greatest percent variation in size, and also generally varied more in terms of absolute measurements (Table 2). Western Cooper's Hawks were significantly smaller than eastern migrants; however, in proportion to their weight, western migrants had longer wings and tails (Table 3). Goshawks showed an intermediate level of variation; Goshute migrants usually weighed less and had consistently longer wings and tails than those from Cedar Grove (Table 4).

Among Sharp-shinned and Cooper's hawks, with one exception, mean weight increased from inland sites to the nearest coastal site, whereas mean wing chord and tail length decreased (Tables 1–2). Marin Headlands migrants also had longer beaks and thicker tarsi than Goshute migrants (Table 5), which further suggested that the coastal migrants were larger overall, despite having shorter wings and tails.

Measurements revealed smaller differences in size between western Sharp-shinned and Cooper's hawks, and between eastern Cooper's Hawks

TABLE 2. Regional comparisons of means with sample sizes (in parentheses) for measurements from fall-migrant Cooper's Hawks.[a]

Measure	Age-sex	Marin Headlands[b]	Goshute Mountains	Cedar Grove[c]	Cape May Point[d]
Weight (g)	HY-M	288 (50)	269 (183)	335 (53)	347 (119)
	AHY-M	—	281 (177)	349 (51)	—
	HY-F	417 (117)	399 (310)	499 (58)	518 (44)
	AHY-F	443 (18)	439 (416)	529 (57)	—
Wing chord (mm)	HY-M	219 (61)	224 (317)	234 (52)	232 (121)
	AHY-M	—	225 (287)	238 (48)	—
	HY-F	249 (130)	254 (444)	266 (59)	263 (46)
	AHY-F	253 (18)*	256 (545)	270 (56)	—
Standard tail length (mm)	HY-M	187 (60)	190 (194)	196 (53)	—
	AHY-M	—	181 (128)	191 (51)	—
	HY-F	212 (124)	214 (286)	221 (58)	—
	AHY-F	212 (15) NS	209 (285)	217 (58)	—

[a] All pairwise comparisons of means, within a sex and age, are significant (*t*-test, $P < 0.006$) unless indicated by * (significant, $P < 0.05$) or NS (not significant, $P > 0.05$).
[b] Data provided by Golden Gate Raptor Observatory, California.
[c] Data from Mueller et al. 1981a.
[d] Data provided by Brian Millsap.

and goshawks. Wing chords and tail lengths of western Sharp-shinned and Cooper's hawks overlapped significantly (Hoffman et al. 1990), unlike in the East (Mueller et al. 1979a, 1981a). Furthermore, differences between mean weights of female Sharp-shinned and male Cooper's hawks (within age groups) were consistently less for Goshute migrants than for Cedar Grove migrants (Tables 1–2). In contrast, weight differences between female Cooper's Hawks and male goshawks were consistently less for Cedar Grove migrants (Tables 2–3). Similar results emerged when we compared maximum and minimum values for observed ranges (Hoffman et al. 1990; Mueller et al. 1976, 1979a, 1981a).

TABLE 3. Regional comparisons of wing chord/weight and tail length/weight ratios for fall-migrant Cooper's Hawks.

Measure	Age-sex	Marin Headlands[a]	Goshute Mountains	Cedar Grove[b]	Cape May Point[c]
Wing chord/weight	HY-M	0.76	0.83	0.70	0.67
	AHY-M	—	0.80	0.68	—
	HY-F	0.60	0.64	0.53	0.51
	AHY-F	0.57	0.58	0.51	—
Tail length/weight	HY-M	0.65	0.71	0.59	—
	AHY-M	—	0.64	0.55	—
	HY-F	0.51	0.54	0.44	—
	AHY-F	0.48	0.48	0.41	—

[a] Data provided by Golden Gate Raptor Observatory, California.
[b] Data from Mueller et al. 1981a.
[c] Data provided by Brian Millsap.

TABLE 4. Regional comparisons of means with sample size (in parentheses) for measurements from fall-migrant Northern Goshawks.[a]

Measure	Age-sex	Goshute Mountains	Cedar Grove[b]
Weight (g)	HY-M	748 (26)	808 (105)
	AHY-M	797 (8) NS	925 (38)
	HY-F	942 (48)	1005 (52)
	AHY-F	967 (20)	1152 (59)
Wing chord (mm)	HY-M	325 (37)	319 (109)
	AHY-M	327 (15) **	323 (41)
	HY-F	358 (57)	346 (52)
	AHY-F	357 (31) **	353 (60)
Standard tail length (mm)	HY-M	243 (20)	239 (106)
	AHY-M	227 (7) NS	230 (41)
	HY-F	281 (40)	272 (53)
	AHY-F	269 (12) NS	266 (60)

[a] All pairwise comparisons of means are significant (*t*-test, $P < 0.005$) unless indicated by ** (significant, $P < 0.01$) or NS (not significant, $P > 0.05$).
[b] Data from Mueller et al. 1976; AHY is equated to Adult II.

DISCUSSION

Proportionately low weight and high wing- and tail-surface area indicate low "flight-surface loading" (sensu Amadon 1980, Mueller et al. 1981b; different from "wing-loading" in that it includes lift generated by both wing and tail surfaces). Surface area is directly proportional to the square of linear dimensions (Greenewalt 1962). A proportional decrease in wing width could offset an increase in length and cause surface area to remain constant; however, the result would be a higher aspect-ratio wing which also would reduce wing-loading (Saville 1957). Since the "width" of the tail depends on differential spreading of the rectrices

TABLE 5. Regional comparisons of mean culmen length and tarsus width with sample size (in parentheses) for fall-migrant Sharp-shinned and Cooper's hawks.[a]

Measure	Species	Age-sex	Marin Headlands[b]	Goshute Mountains
Culmen length (mm)	SS	HY-M	10.0 (16)	9.8 (478)
	SS	HY-F	12.0 (70)	11.9 (505)
	CH	HY-M	15.3 (60)	14.8 (246)
	CH	HY-F	17.8 (124)	17.4 (374)
	CH	AHY-F	18.6 (18)	18.3 (447)
Tarsus width (mm)	SS	HY-M	3.8 (12)	3.5 (185)
	SS	HY-F	4.7 (65)	4.4 (152)
	CH	HY-M	5.8 (35)	5.5 (90)
	CH	HY-F	7.1 (76)	6.7 (73)
	CH	AHY-F	7.1 (7)	6.8 (73)

[a] All pairwise comparisons of means differ significantly (*t*-test, $P < 0.001$).
[b] Data provided by Golden Gate Raptor Observatory, California.

(Mueller et al. 1981b), a longer tail will always provide more available surface area and lower tail-surface loading. Thus, despite the lack of actual surface area measurements, we feel confident that low weight and long wings and tail are valid indicators of low flight-surface loading. Temple (1972) provides additional support for this assumption: a wing-loading index calculated for Merlins (*Falco columbarius*) by dividing the cube root of body weight by wing chord "showed a high correlation with the actual wing loading value computed as body weight in grams per total wing area in cm^2."

Accordingly, we suggest that fall-migrant accipiters from the Goshute Mountains average lower flight-surface loading than those from Cedar Grove; that western Cooper's Hawks, in general, average lower flight-surface loading than eastern migrants; and that coastal migrants average higher flight-surface loading than inland migrants. Two aberrant results—Marin versus Goshute tail length in AHY female Cooper's Hawks (Table 2) and tail length in AHY male goshawks (Table 3)—were likely due to small sample sizes. Small samples also may have prevented the demonstration of significant differences in some cases. Proportionately long wings and low flight-surface loading have been considered adaptive for long distance migration (Averill 1920, Hamilton 1961, Salomonsen 1955, Zink and Remsen 1986) and for exploiting open country where strong, sustained flying is required (Behle 1942, Hamilton 1961, Linsdale 1938, Pitelka 1951, Temple 1972, Wattel 1973, Zink and Remsen 1986). Low flight-surface loading may also help Goshute accipiters exploit strong thermal updrafts.

Band returns indicate that Cape May Point sharpshins rarely originate north of southern Ontario or winter farther south than Florida (Clark 1985). In contrast, Cedar Grove migrants originate as far north as central Alberta and generally winter in the south-central United States (Mueller and Berger 1967a). Similarly, Goshute migrants routinely travel to central and southern Mexico to winter and many originate as far north as central British Columbia and Alberta (Stephen W. Hoffman, unpubl. data). The few band returns from Marin Headlands suggest that most west-coast migrants winter in California, with some in northwestern Mexico (Allen Fish, pers. comm.). There are no breeding season recoveries from Marin Headlands accipiters yet; however, a morphological study of accipiter museum specimens revealed that Marin Headlands migrants were most similar to breeders from the Pacific Coast south of British Columbia (Smith 1988a). Together these data suggest that inland migrants may have lower flight-surface loading to facilitate longer migrations.

Proportionately long wings and tail, and small overall size are characteristic of breeding accipiters from inland and open habitats (Smith 1988a). Similarly, the prairie-parkland (open habitat) subspecies of Merlin, *F. c. richardsonii,* has the longest wings and tail and lowest wing-loading of the North American subspecies (Temple 1972). Inland migrants generally breed in and travel through habitats that are more open than the mesic, coastal forests. Thus, low flight-surface loading in inland accipiters may be an adaptation to both open habitats and long migrations. Furthermore, the xeric, central and southern intermountain west supports sparser vegetation than the more mesic forests of the Midwest. This may favor lower flight-surface loading among Goshute migrants compared to Cedar Grove migrants.

The Goshute migrants occupy a region where strong thermal updrafts are prevalent. Thermal production is greatest where the air is clear, dry, and hot, where vegetation and soil organic matter are lacking, and where exposed slopes are inclined toward the sun. Such conditions are characteristic of the Great Basin and southern Rocky Mountain regions. Furthermore, long, leading-line ridges, which migrating raptors tend to follow because they produce strong obstruction-current updrafts (Mueller and Berger 1967b), are more erratically distributed in the West (Hoffman 1985). Consequently, migrating raptors must cross valleys and plains between discontinuous ridges. By riding the strong thermals generated at the bases of and in between ridges, the hawks can sail across long expanses of flat, often barren land. Low flight-surface loading would maximize a hawk's ability to exploit such updrafts.

Some authors argue that accipiters do not soar (Eckert 1987) and might therefore discount the importance of thermal updrafts to these species. However, along the Goshute flyway it is common to find all three species of accipiter soaring with the buteos and eagles. Calm, hot days produce tremendous thermals in the Great Basin. Often the only place migrants, including accipiters, can be spotted is silhouetted against a single cloud high in the sky. Low flight-surface loading would certainly facilitate such activity.

Thermal production also may be greater in the Midwest than on the east coast. However, the Great Lakes, like the ocean, probably dampen most thermal production. The lower flight-surface loading of Cooper's Hawks from Cedar Grove relative to those from Cape May is therefore more likely an adaptation to facilitate longer migrations and exploitation of open habitats. In contrast, all three factors—open habitat, long migrations, and strong thermal production—may favor the even lower flight-surface loading of Goshute migrants.

We are less able to explain why regional variation should be more pronounced in Cooper's Hawks. Additional research may clarify the causes of this trend.

The observed patterns of regional size variation also have implications for field identification. Flight-style is an important characteristic to consider when identifying accipiters. Differences in flight-style relate directly to differences in body size and weight (Mueller et al. 1979b, Smith 1988b). Cooper's Hawks are closer in size to goshawks in the East, but closer in size to sharpshins in the West. Therefore, female Sharp-shinned and male Cooper's hawks in flight are more likely to be confused in the West, whereas female Cooper's Hawks and male goshawks are more likely to be misidentified in the East.

Finally, this analysis demonstrated that accipiter weight and wing chord do not follow the same pattern of variation across the United States. Wing chord is generally considered a good indicator of overall body size (James 1970, Lanyon 1960, Selander and Johnston 1967), but if we had only analyzed wing chord, we would have concluded that migrant sharpshins and goshawks from the Goshute Mountains were larger than those from Cedar Grove. Instead, because we also compared weight data, we discovered that the Goshute migrants were not larger overall, just long winged and tailed, a combination that reduces flight-surface loading.

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