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ECOGEOGRAPHIC VARIATION IN MORPHOLOGY OF RED-TAILED HAWKS IN WESTERN NORTH AMERICA

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ABSTRACT.—Geographic variation in external morphology of one subspecies of Red-tailed Hawk (*Buteo jamaicensis calurus*) in western North America was analyzed by comparing measurements of 249 museum specimens from seven ecoregions. Male and female Red-tailed Hawks showed substantial regional variation within the geographic range of this single subspecies. We used exploratory and confirmatory data analysis to investigate relationships between morphological and environmental variables. Canonical correlation indicated associations between morphology and continuous environmental variables. Five of six morphological measurements varied concordantly and were taken, collectively, to indicate size. In general, largest hawks occurred in the arid southwestern deserts and California grasslands, and smallest in the cool, humid Pacific Northwest. Tarsus length showed a pattern of variation opposite from other measurements, with longest tarsi in the Pacific Northwest. The traditional ecogeographic rules of Bergmann and Allen were not supported, nor did size appear to be related to availability of food. Our results were found to be consistent with some other ecomorphological hypotheses, such as James' "Neo-Bergmannian" hypothesis and those involving niche breadth, prey size and water conservation. Studies of the development, quantitative genetics and functional significance of size and shape are needed to understand the causes of ecogeographic variation.

KEY WORDS: *Red-tailed Hawk;* Buteo jamaicensis; *canonical correlation; geographic variation; morphometrics; biogeography; evolutionary ecology.*

Variación ecogeográficas en la morfología de *Buteo jamaicensis* en el oeste de Norteamérica

RESUMEN.—La variación geográfica en la morfología externa de una de las subespecies de gavilan cola roja (*Buteo jamaicensis calurus*) en el oeste de Norteamérica fué analizada al comparar las medidas de 249 especímenes de museo de siete ecoregiones. Machos y hembras mostraron una variación regional substancial dentro del rango geográfico de esta subespecie. Utilizamos el análisis de datos exploratorios para investigar las relaciones entre las variables morfológicas y ambientales. La correlación canóniga indicó asociaciones entre la morfología y las variables ambientales continuas. Cinco o seis medidas morfológicas variaron en concordancia y fueron tomadas colectivamente para indicar tamaño. En general los gavilanes de mayor tamaño ocurrieron en los desiertos del suroeste y en los pastizales de California. Los más pequeños en la región húmeda y fría del noroeste pacífico. La longitud del tarso mostró un patrón de variación opuesto al de otras medidas con los tarsos mas largos en el noroeste Pacífico. Las reglas tradicionales de ecorregiones de Bergmann y Allen no fueron sustentadas como tampoco el tamaño estuvo relacionado con la disponibilidad de comida. Nuestros resultados fueron consistentes con otras hipótesis ecomorfológicas como la de James' "Neo-Bergmannian" y aquellas que involucran el tamaño del nicho, el tamaño de la presa y la conservación de las aguas. Los estudios relacionados con el desarrollo, la genética cuantitativa y el significado funcional del tamaño y la forma son necesarios para entender las causas de la variación ecogeográfica.

[Traducción de César Márquez]

Patterns of intraspecific variation are often viewed as key factors in understanding processes of adaptation and speciation (e.g., Darwin 1859, Wallace 1859, Power 1969, Johnston and Selander 1971, Gould and Johnston 1972, Zink and Remsen 1986). Geographic variation in quantitative phenotypic traits may arise through a number of processes including adaptation to the physical environment (McNab 1971, Geist 1987, Aldrich and James 1991, James 1991), coevolution in local communities (Brown and Wilson 1956), historical barriers to gene flow (Cracraft 1982, Patton et al. 1994), isolation by distance (Wright 1943, Aldrich and James 1991) and developmental plasticity and environmental induction (James 1983). Many processes are likely to influence species evolution, and nonheritable variation is likely to introduce uncertainty to adaptive interpretations of patterns.

Red-tailed Hawks (*Buteo jamaicensis*) are wide-ranging and show significant geographic variation in morphology (Schmidt 1994), plumage (Lish and Voelker 1986) and behavior (Knight et al. 1989). Preston and Beane (1993) listed 14 and recognized 13 North American subspecies (it is doubtful that *B. j. krideri* is a valid subspecies). These subspecies intergrade readily, but differences in plumage and morphometrics are apparent (Mindel 1983, Lish and Voelker 1986, Preston and Beane 1993). Such differences may be due to isolation in glacial refugia during the Pleistocene and, in the case of *B. j. harlani,* possible gene flow with *B. buteo* across Beringia (Mindel 1983). While we recognize that subspecific designations are imperfect, real phylogenetic entities can exist within species (McGillivray 1989, Avise 1994, Zink 1996). Such phylogenetic structure within species may need to be accounted for in evolutionary studies (Edwards and Kot 1995, Martins 1996). We focused on western North America, within the range of a single recognized subspecies, *B. jamaicensis calurus* (Fig. 1). Our analysis of geographic variation in Red-tailed Hawks was descriptive and exploratory. We examined the relationship between the physical environment and geographic variation within a large geographic area. We entertained several propositions in our discussion, but did not test any causal hypotheses.

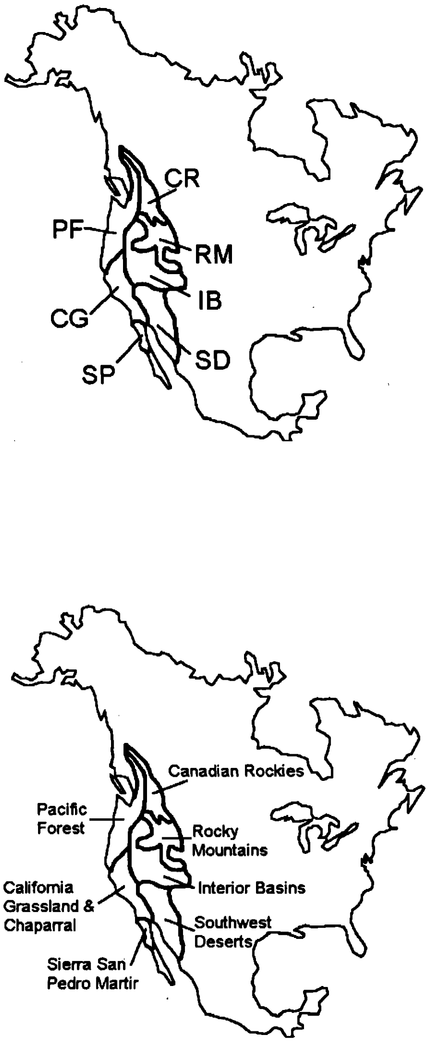

Figure 1. Regions: CG = California grasslands and chaparral, CR = Canadian Rockies, IB = Interior basins, PF = Pacific forests, RM = Rocky Mountains, SD = southwest deserts, SP = Sierra San Pedro Martir (Bailey 1976, Bailey et al. 1994).

METHODS

Specimens and Data. Museum skin specimens of *B. j. calurus* were designated "summer" or "winter" based on date of collection; specimens collected during the periods of peak migration given by Preston and Beane (1993) were excluded. Specimens were grouped into regions based on the second-order ecoregions of Bailey (Bailey 1976, Bailey et al. 1994, Ecological Stratification Working Group 1995) (Fig. 1). Specimens from the Sierra San Pedro Martir (SP) were treated as different from California Grasslands (CG) based on Dickerman (1994). Males and females were analyzed separately. Sex, location of collection, date of collection and subspecies, if designated, were recorded from the museum tag of each specimen. Each collection location was matched up to the nearest weather station in the Meteorological Office (1980). Sample sizes are given in Table 1 and Fig. 2.

Six external measurements (in mm) were taken on each specimen. Measurements are described in the Golden Gate Raptor Observatory Bander's Training and Reference Manual (GGRO 1992), and were as follows: (1) wing chord (WC) = top of the wrist to the tip of the longest primary, (2) tail length (TA) = length of the longest middle retrix, (3) culmen (CU) = chord measurement of the exposed culmen, (4) tarsus depth (TD) = diameter of the narrowest section of the tarsometatarsus

Table 1. Likelihood ratio tests of independence and dimensionality of association between the set of morphological variables and the set of environmental variables. These were sequential tests of joint nullity of the smallest i through 4 canonical correlation coefficients, r_k^2 ($k = i, \ldots, 4$). Bartlett's approximate χ^2 criterion was used according to Gittins (1985). $\chi^2 = -\{(N - 1) - \frac{1}{2}(p + q + 1)\}\ln\Lambda_i$. Wilks' $\Lambda = \Pi_{j=i}^{4} (1 - r_j^2)$.

i	ROOTS, r_k^2	r_i^2	df	WILKS' Λ	χ^2	P
Summer males N = 41						
1	$r_1^2, r_2^2, r_3^2, r_4^2$	0.461	24	0.26	45.9	0.005
2	r_2^2, r_3^2, r_4^2	0.421	15	0.49	24.5	0.057
3	r_3^2, r_4^2	0.096	8	0.85	5.7	0.686
4	r_4^2	0.061	3	0.94	2.2	0.537
Winter males N = 55						
1	$r_1^2, r_2^2, r_3^2, r_4^2$	0.455	24	0.43	40.6	0.018
2	r_2^2, r_3^2, r_4^2	0.121	15	0.79	11.2	0.737
3	r_3^2, r_4^2	0.074	8	0.90	5.0	0.761
4	r_4^2	0.025	3	0.97	1.2	0.743
Summer females N = 43						
1	$r_1^2, r_2^2, r_3^2, r_4^2$	0.388	24	0.43	30.7	0.162
2	r_2^2, r_3^2, r_4^2	0.218	15	0.70	12.8	0.618
3	r_3^2, r_4^2	0.070	8	0.90	3.8	0.871
4	r_4^2	0.032	3	0.97	1.2	0.756
Winter females N = 49						
1	$r_1^2, r_2^2, r_3^2, r_4^2$	0.531	24	0.28	53.7	0.001
2	r_2^2, r_3^2, r_4^2	0.275	15	0.60	21.5	0.121
3	r_3^2, r_4^2	0.122	8	0.83	7.9	0.444
4	r_4^2	0.055	3	0.95	2.4	0.502

measured anteroposteriorly, (5) tarsus length (TL) = diagonal measurement from the medial bony protuberance of the ventral part of the proximal end of the tarsometatarsus to the joint of the middle digit and (6) hallux claw (HA) = chord measurement of the exposed hallux talon. The importance and reliability of tail length measurements are questionable due to feather wear.

Environmental variables obtained from the Meteorological Office (1980) were: Altitude (ALT), July maximum average daily temperature (JLMX), July minimum average daily temperature (JLMN), January maximum average daily temperature (JNMX), January minimum average daily temperature (JNMN) and annual precipitation (PPT).

Relative, rather than absolute, morphological measurements would have been desirable for certain comparisons. However, ratios present controversial statistical problems, especially in multivariate analysis (e.g., Albrecht 1978, Atchley and Anderson 1978, Pimintel 1979, but see James and McCulloch 1990). Further, without an independent measure of body size to work with, defining relative measures is problematic. WC has been used as an index of body size (e.g., Power 1969, James 1991). Exploratory analysis of relative measures defined as ratios of our other measurements over WC or as residuals from simple linear regression on WC produced qualitatively similar results to those we present here (B. Fitzpatrick, unpubl. data).

Analysis of Regional Differences. Due to small sample sizes and potentially nonnormal data, we described differences among regions using box plots (McGill et al 1978, Benjamini 1988). A box plot displays a rectangle oriented on a coordinate system where the vertical axis has the scale of the data. The rectangle represents the middle half of the data, that is, its top and bottom are drawn at the upper and lower quartiles, respectively. The "whiskers" are drawn to the furthest value within 1.5 inter-quartile distances from the box. Data points outside of the whiskers are represented by thin horizontal lines and the median is represented by a thick horizontal line With the data partitioned into regions, individual sample sizes were too small and uneven to make effective use of more formal statistical analyses (Fig. 2).

Analysis of Relationships Between Morphology and Climate. Multivariate relationships between morphology and physical environmental variables were investigated using canonical correlation (Gittins 1985, James and McCulloch 1990). Following Moran (1986), linear regression was used as a critical technique to assess confidence in patterns suggested by canonical correlation. This is an example of overlapping exploratory and critical data analysis (OCDA, Tukey 1982). Overlapping data analysis is a legitimate form of analysis, but it lacks the definitiveness of confirmatory analysis of carefully sampled independent data. In order to make more effective use of the linear techniques, ALT and PPT were log transformed as $x' = \log_{10}(x + 1)$ to adjust for skews to the right, and JNMN was transformed as $x' = (x + 21)^2$ to make all values positive and then adjust for a skew to the left (Zar 1984). Other variables showed approximately gaussian (normal) distributions. Analyses were performed using S-Plus 4.0 for Windows (MathSoft 1997).

Canonical correlation analysis. James and McCulloch (1990) reviewed statistical techniques in ecology and evolutionary biology. They argued that multiple regression analysis, a commonly used technique in this kind of study, has been overused and abused. They suggested that canonical correlation, although not free of limitations, may be more appropriate for descriptive ecomorphological studies. They stressed the descriptive role of multivariate analysis, and suggested deemphasizing formal statistical inference.

Our notation was that of Gittins (1985). Most simply, canonical analysis can be characterized as a generalization of multiple regression where there are multiple y variables in addition to multiple x variables. This analysis is appropriate when the attributes of a data set can be divided naturally into two sets (e.g., morphological and environmental measurements). If there are N observations, p x-variables, and q y-variables, canonical analysis generates two sample spaces, $\mathbf{Z}^{(x)}$ ($N \times p$) and $\mathbf{Z}^{(y)}$ ($N \times q$). Then, linear transformations of each set of variables, $u_i = \mathbf{a}_i^t\mathbf{z}^{(x)}$ and $v_i = \mathbf{b}_i^t\mathbf{z}^{(y)}$, are found simultaneously such that the simple correlation r_i between the canonical variates u_i and v_i is maximized. In all, s pairs of canonical variates are produced, $i = 1, \ldots, s$ where s is the smaller

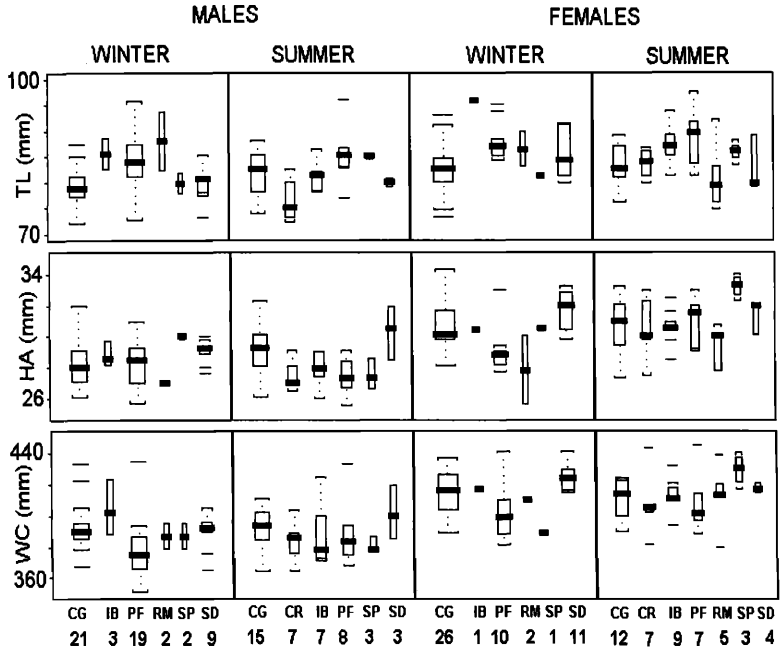

Figure 2. Box plots comparing some morphometric measurements of Red-tailed Hawks from different regions Regions are identified in Fig. 1. Only those comparisons with marked differences are shown. The width of each box is proportional to sample size. Sample sizes are given along the bottom.

of *p* and *q*. Successive pairs of variates are required to be orthogonal to preceding pairs. Although multiple regression can be thought of as a special case where $q = 1$, it is important to note that in canonical analysis the two sets of variables are treated symmetrically. That is, it makes no difference which set is assigned to *x* and which is assigned to *y*; both sets can be thought of as simultaneously predicting each other (Gittins 1985). Canonical correlation analysis is primarily a descriptive technique for exploring holistic relationships among variables of different kinds (Gittins 1985, Moran 1986, James and McCulloch 1990). Pimintel (1979), Gittins (1985), and Rencher (1995) are good references for canonical analysis.

RESULTS

Regional Differences. Only those box plots indicating differences among regions are shown in Fig. 2. Substantial variation among regions in TL, HA and WC was indicated for all groups, with summer females showing the weakest patterns and winter data sets the strongest (Fig. 2). WC and HA tended to be large in arid regions, while TL was generally greatest in the Pacific Northwest (PF).

Morphology and Environment. Squared canonical correlation coefficients, r_i^2 ($i = 1, 2, 3, 4$), are reported in Table 1. These coefficients express the proportion of the variance of the *i*th morphological canonical variate that is accounted for by its conjugate environmental canonical variate (Gittins 1985). Values of r_1^2 ranged from 0.388–0.531 (Table 1), suggesting weak to moderate overall relationships between morphology and environment.

Independence. Likelihood ratio tests of the null hypothesis that the vector of morphological variables and vector of environmental variables were linearly independent are presented in the first line of each subtable of Table 1. Bartlett's χ^2 approximation lead to the rejection of linear independence for winter females and summer males ($P = 0.0005$ and 0.0046, respectively). Evidence against independence for winter males was strong ($P = 0.0184$). The null hypothesis of independence for summer females should not be rejected by this analysis ($P = 0.1622$). These results suggested that Red-tailed Hawk morphology in western North America varies systematically with the physical environment.

Dimensionality. No significant relationship between morphology and environment remained after the first canonical correlation coefficients were eliminated (Table 1). Accordingly, we only exam-

Table 2. Correlations between original measurements and the first canonical variates. JNMN* = (JNMN + 21)^2. PPT** = $\log_{10}$(PPT + 1).

MEASUREMENT	1ST CLIMATE	1ST MORPH
Summer males		
TL	0.19	0.28
TD	0.60	0.89
WC	0.24	0.35
TA	0.19	0.27
HA	0.49	0.73
CU	0.49	0.72
ALT	−0.23	−0.16
JLMX	−0.02	−0.01
JLMN	0.98	0.66
PPT**	−0.36	−0.25
Winter males		
TL	−0.51	−0.75
TD	0.11	0.16
WC	0.35	0.52
TA	0.27	0.40
HA	0.38	0.56
CU	−0.09	−0.14
ALT	0.16	0.11
JNMX	0.82	0.55
JNMN*	0.69	0.47
PPT**	−0.75	−0.51
Winter females		
TL	−0.46	−0.63
TD	0.42	0.58
WC	0.42	0.58
TA	0.20	0.28
HA	0.44	0.61
CU	0.41	0.56
ALT	−0.20	−0.15
JNMX	0.92	0.67
JNMN*	0.94	0.69
PPT**	−0.35	−0.25

ined the possible implications of the canonical variates corresponding to the largest root, r_1^2 (Gittins 1985). Summer females were not subjected to further analysis due to the independence of their morphological measurements to environmental variables in this small data set.

Canonical variates. We used the correlations between the original measurements and the first canonical variates to interpret the data (Table 2). Intraset correlations indicated that the first environmental variate primarily reflected temperature, although precipitation figured strongly in the winter males data set and only July *minimum* temperature had a strong correlation in the summer males data set. The first morphological variate was moderately correlated with all variables except TA for winter females, strongly correlated with TL for winter males, and fairly strongly correlated with TD, HA and CU for summer males. Intra- and interset correlations were concordant (Table 2).

Linear regression. For winter males and females, the single temperature measure with the highest correlation with the first canonical variate was chosen for further analysis. The independent variables used for simple linear regression analyses were JNMN for winter females, JLMN for summer males, and JNMX and PPT for winter males. Regression analyses confirmed a negative relationship of TL with winter temperature (P = 0.0005 and P = 0.0018 for females and males, respectively), and positive associations with temperature for WC, TD, HA and CU (Table 3). A positive correlation between TL and PPT for winter males agreed with the observation of relatively long tarsi in the Pacific Forest region (Fig. 2). Results for males and females were concordant.

DISCUSSION

Wing chord, tarsus depth, tail length, hallux claw and culmen varied concordantly and were interpreted collectively to represent body size. Tail length clearly varied independently, its correlations with temperature and precipitation generally being opposite those of other measurements.

Bergmann's rule, which predicts that larger individuals are favored in colder environments because low surface area to volume ratios are advantageous in conserving heat, while smaller individuals dissipate heat more effectively in hot climates (Pianka 1988), is not supported by our results. In fact, size tended to be positively correlated with temperature. In large, well-insulated birds like Red-tailed Hawks, heat dissipation is probably accomplished mostly through the tarsi and feet (Mitgard 1980, Butler 1982, Gill 1990). Further, in cold areas, insulating feathers are likely to be more important than surface area in controlling heat loss, while the cost of heating a large body may be limiting (McNab 1971). Another thermoregulatory prediction, Allen's rule, states that individuals in hot climates should have longer appendages relative to body core size in order to dissipate heat more efficiently (Pianka 1988). It was also not supported by our data.

Positive correlation of winter male tail length with annual precipitation and positive correlations

Table 3. Simple linear regression analyses of morphological and environmental variables selected using canonical correlation. TL = tarsus length, TD = tarsus depth, WC = wing chord, HA = hallux length, CU = culmen length. JNMN = January minimum temperature, JNMX = January maximum temperature, JLMN = July minimum temperature, PPT = annual precipitation. JNMN* = $(\text{JNMN} + 21)^2$, PPT** = $\log_{10}(\text{PPT} + 1)$.

GROUP	DEPENDENT VARIABLE	INDEPENDENT VARIABLE	CORRELATION COEFFICIENT (r)	P-VALUE
Summer males	TD	JLMN	0.56	0.0001
	HA	JLMN	0.51	0.0006
	CU	JLMN	0.43	0.0048
Winter males	TL	JNMX	−0.41	0.0018
	TL	PPT**	0.38	0.0042
Winter females	TL	JNMN*	−0.48	0.0005
	TD	JNMN*	0.43	0.0019
	CU	JNMN*	0.38	0.0079
	WC	JNMN*	0.35	0.0136
	HA	JNMN*	0.35	0.0151

of the other variables, notably tarsus diameter with temperature, suggested that water stress rather than temperature could explain the clinal variation. Short, thick tarsi (smaller surface area to volume ratio) might reduce evaporative water loss. Despite the thermal disadvantage of large body size suggested by Bergmann's rule, larger individuals may be favored in arid regions by their ability to conserve water.

Climate may indirectly influence the development and adaptation of hawk morphology through variation in food types and availability. Overall size of animals may reflect food availability (Geist 1987, Zeveloff and Boyce 1988), while sizes of food capturing structures such as beaks and claws are likely to be adapted to the mode of foraging and the type of prey taken (Pianka 1988, Gill 1990). Prey type and availability both vary geographically. However, the large size of Red-tailed Hawks in southwest deserts and interior basins was inconsistent with a large effect of productivity on size. Rather, large size may be an adaptation to prey scarcity by increasing niche breadth (Reig 1992, Cohen et al. 1993).

Red-tailed Hawks vary in a systematic way within the range of *B. j. calurus.* They are largest in deserts and smallest in the wet Pacific Northwest, even in winter. This is generally the same as the pattern described for Northern Goshawks (*Accipiter gentilis*) (Squires and Reynolds 1997) and for 20 of 22 passerine species (James 1991). Further, tarsus lengths are relatively long in the Pacific Northwest in both Red-tailed Hawks and American Robins (*Turdus migratorius,* Aldrich and James 1991). Morphometrics of widespread birds of disparate sizes and life histories exhibit concordant geographic variation, suggesting the need for a general explanation. James (1970, 1991) has proposed a "neo-Bergmannian" hypothesis, which emphasizes the interaction between moisture and temperature in their effects on thermoregulation; largest individuals are expected in cold and dry environments. Our results indicate that the role of temperature is less important for Red-tailed Hawks, and we suggest that water stress may modify and contribute to the neo-Bergmannian pattern.

Great Horned Owls (*Bubo virginianus*) are smallest in California, Baja California and the southwest, showing geographic size variation opposite to what we have described for Red-tailed Hawks (McGillivray 1989, Houston et al. 1998). Turkey Vultures (*Cathartes aura*) also appear to be smallest in California and the southwest, based on differences between subspecies described in Kirk and Mossman (1998). These conflicting trends testify to the complexity of causes of geographic variation. Even when the same selective pressures act on different populations, differences in their relative importance can cause different adaptive responses (McPeek 1996). Although sympatric species probably experience similar physiological challenges, different components of the physical environment (e.g., heat vs. water) may vary in importance among species. Further, selective pressures owing to diet, mating system, predation and competition are likely to interact in complex ways with the physical environment in creating the overall selective regime experienced by a population.

Although natural selection provides elegant hypotheses for the causes of morphological variation, this study was entirely descriptive; causal explanations await explicit tests. Statistically significant variations in body size and proportions may not be biologically significant in the functional morphology of Red-tailed Hawks (but see references in James 1991). The geographic variation described for Red-tailed Hawks is not necessarily adaptive or heritable. Morphometric differences that result from external factors during development may continue to vary regardless of gene flow and selection (James 1983). Further, environmental induction could explain concordant patterns among species as easily as selection. Analyses of the development, functional significance and quantitative genetics of morphometric variation are necessary to elucidate the implications of geographic patterns and environmental correlations.

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