

GEOGRAPHIC VARIATION IN SIZE AND REVERSE SIZE DIMORPHISM OF THE GREAT HORNED OWL IN NORTH AMERICA¹

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Abstract. Geographic variation in body size and reverse size dimorphism (RSD) of the Great Horned Owl (*Bubo virginianus*) was assessed from a suite of 18 variables measured on 418 specimens. Great Horned Owls varied considerably in size across both geographic and subspecific boundaries. In a comparison of regional means, the largest owls were from Ontario, the smallest from Texas and California, but strong support for Bergmann's Rule was absent. There was also no obvious relationship between geographic variation in body size of Great Horned Owls and the size of typical prey species. Reverse size dimorphism (RSD) was virtually constant across all regions. This lack of variation implies that RSD is a species-specific character which does not covary in a systematic way with body size. There was more geographic variation in the size of body core variables than there was for skull, leg, and wing characters. Great Horned Owls from southern localities had relatively small body cores providing weak support for Allen's Rule.

Average body sizes and levels of RSD were calculated for seven subspecies (*virginianus*, *occidentalis*, *wapacuthu* [subarcticus], *pallescens*, *pacificus*, *saturatus*, and *lagophonus*). The largest subspecies is *occidentalis*, which is widely distributed in the mid-western and western U.S. The smallest is *pacificus*, which is restricted to California. Significant size differences were found between subspecies even where their ranges overlapped. This suggests either that gene flow across subspecific boundaries is restricted or that strong selection maintains the size differences. An evaluation of the genetic differences among subspecies is needed to assess the significance of racial variation in this species.

Key words: Great Horned Owl; *Bubo virginianus*; morphometrics; reverse size dimorphism.

INTRODUCTION

Variation among raptors in the degree of reverse size dimorphism (RSD) has prompted numerous hypotheses accounting for large females and small males in hawks and owls (e.g., Earhart and Johnson 1970, Mueller and Meyer 1984, Mueller 1986, McGillivray 1987). I have argued that many samples used in multi-species comparisons are not large enough to define species-specific levels of RSD (McGillivray 1987). Other workers (Earhart and Johnson 1970) have demonstrated subspecific variation in RSD for external characters of Great Horned (*Bubo virginianus*) and Screech (*Otus asio*) owls. If intraspecific variation in RSD is widespread in raptors and large enough to mask interspecific differences then the conclusions from multi-species comparisons may need reassessment.

The numerical analysis of RSD has depended on quantifying behavioral and ecological traits

of species and examining the correlation of these traits with the degree of RSD (Mueller and Meyer 1984, Mueller 1986). The advantage of an *intra*-specific comparison, particularly for behavioral traits, is that the list of factors possibly contributing to RSD variation within a species should be smaller than one needed to account for RSD differences in distantly related taxa. Therefore, in a study of intraspecific variation of RSD it may be possible to assess the relationship of ecological variation to size.

To date, there have been no quantitative studies of geographic variation in the Great Horned Owl in North America, and skeletal data have been used in few studies of geographic variation, all on passerines (Zink and Remsen 1986). This paper presents the first examination of variation in size, shape, and RSD of Great Horned Owls in North America, north of Mexico and adds to the short list of species for which this has been assessed using skeletal data.

Despite extensive polytypy in the Great Horned Owl (AOU 1957), my first approach was to assume that morphometric variation in the species

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was primarily geographic in origin. This was suggested in part by the ecogeographic trends in body size variation found for several North American passerines (Power 1969, James 1970, Johnston and Selander 1971, Murphy 1985) and the weak overall support shown for Bergmann's Rule in other studies of geographic variation in birds (Zink and Remsen 1986). As well, in an earlier analysis of Great Horned Owls in Alberta (McGillivray 1985) I found numerous intermediates between the two or three subspecies presumed to occur in the province (AOU 1957, Godfrey 1986). My assumption was that racial differences among Great Horned Owls were by-products of geographic variation, and where subspecies overlapped, these differences would disappear. Therefore, the initial analyses excluded racial differences as a factor contributing to morphological variation. In several museum collections throughout North America, however, many skeletons of Great Horned Owls have been classified into subspecies. Accepting these identifications as sound, I used these specimens in a quantitative examination of subspecific variation in size and RSD.

METHODS

DATA COLLECTION

A suite of 18 measurements was taken on skeletons of 418 Great Horned Owls from museum collections across North America. A description of the measurements is given in McGillivray (1985). All measurements were taken with digital calipers, and except for widths of the skull, sternum, synsacrum, and tarsometatarsus describe lengths of bones or bone complexes. Because some skeletons had been prepared with the rhamphotheca removed and others with it attached, composite measures for skull length and mandible length were used (see McGillivray 1985, McGillivray and Johnston 1987). Great Horned Owls are nonmigratory but do wander (Houston 1978). The majority of skeletal specimens of this species in North American museums was acquired outside of the breeding season. Some of the birds I measured undoubtedly were not resident in the region from which they were collected. From a statistical standpoint, this should increase variances about regional means making differences among regions harder to detect. Overall this indicates that the assessment of geographic variation presented here is likely to be conservative.

DATA CORRECTION

Studies of birds based on skeleton collections in museums are often limited by the quantity and quality of specimens. Two common problems that reduce sample sizes are: (a) specimens with missing or broken elements; and (b) specimens which are either unsexed or wrongly sexed. For missing elements, estimated measures were substituted if a multiple regression using two characters could predict known values for the variable with an R^2 higher than 0.80. When sample sizes are small, one observation which is missexed (i.e., an outlier) can change the assessment of size for that sex or the estimate of sexual size dimorphism for the sample. All options for dealing with outliers have the potential to contribute error to the study. Arbitrarily changing the sex, or deleting the observation, cleanup the data set but may result in the loss of a significant specimen from the analysis. By contrast, retaining an observation that appears to contradict relationships found elsewhere can incorrectly modify conclusions.

In this study, Discriminant Function Analyses (SAS Institute 1985) were used to optimally separate males from females. Potentially missexed specimens were evaluated on the discriminant axes. If the probability of a misclassification exceeded 95%, the sex of the specimen was changed. Similarly, unsexed specimens were sexed if the probability of correctly classifying them to either male or female exceeded 95%.

DATA ANALYSIS

As specimens were obtained from museums and not actively collected, samples do not represent specific localities. Therefore, to examine geographic variation, it was necessary to group specimens somewhat arbitrarily. Initially, specimens were grouped regionally with consideration given to ensuring an adequate sample size for each region. Groups generated this way were: (1) Alberta; (2) Ontario + Quebec + New York + Ohio + Pennsylvania; (3) Michigan + Wisconsin + Minnesota; (4) Kansas; (5) Florida; (6) Texas + Oklahoma + Arizona; and (7) California + Oregon + Washington + British Columbia. For specimens identified to the subspecific level, a second analysis was conducted using subspecies as groups.

The estimate of overall size used was the sum of all skeletal measures. A detailed rationale for this approach is in McGillivray and Johnston

TABLE 1. Size ($\bar{x} \pm SE$) of male and female Great Horned Owls grouped by region. Size is defined as the sum of all variables. Sample sizes are in parentheses below each mean. The *t*-statistic indicates the difference between male and female mean size. Scheffé's *a posteriori* means test was used to compare regional means within each sex. Means not significantly different are connected by solid vertical lines.

Region	Male	Female	<i>t</i>	<i>P</i>
Ontario ¹	1,087.17 ± 4.80 (15)	1,125.88 ± 5.12 (29)	4.82	0.0001
Michigan ²	1,071.41 ± 5.40 (16)	1,123.29 ± 6.57 (23)	5.71	0.0001
Kansas	1,070.21 ± 3.21 (35)	1,123.98 ± 3.23 (39)	11.75	0.0001
Florida	1,069.36 ± 9.20 (6)	1,117.30 ± 8.76 (10)	3.57	0.0030
Alberta	1,054.78 ± 2.48 (53)	1,106.20 ± 2.15 (79)	15.46	0.0001
Texas ³	1,017.74 ± 9.22 (15)	1,069.44 ± 10.10 (16)	3.77	0.0008
California ⁴	1,020.78 ± 6.56 (21)	1,072.05 ± 6.97 (23)	5.32	0.0001

¹ Specimens from Ontario, Quebec, New York, Ohio, and Pennsylvania.

² Specimens from Michigan, Wisconsin, and Minnesota.

³ Specimens from Texas, Oklahoma, and Arizona.

⁴ Specimens from California, Oregon, Washington, and British Columbia.

(1987) and the relationship of this estimate to ones obtained through principal components analysis are explored in McGillivray (1985). Sexual size dimorphism is defined as the difference between male and female scores on this axis. All multivariate analyses were run using the SAS statistical programs (SAS Institute 1985).

RESULTS

The largest Great Horned Owls in this study were from the Ontario region. They were followed closely by those from the Michigan region, Kansas, and Florida (Table 1). The smallest owls were from the Texas and California regions. There was no obvious relationship between locality and size that was consistent with Bergmann's ecogeographic rule (see James 1970). Florida Great Horned Owls were not significantly different in size from those in Kansas or Ontario (Table 1). Male Great Horned Owls in Ontario averaged 6.8% larger than those from Texas whereas females were only 5.3% larger. These percentages were slightly greater than the average difference in size between males and females (RSD) (Table 2), which varied little among regions except for a reduction in Ontario. The mean level of RSD in each region was not correlated with the average size of owls in that region ($r = -0.51$, $n = 7$, ns).

Variation in size of different skeletal compo-

nents was not uniform. There was more geographic variation in the size of body core variables than there was for skull, leg, and wing characters (Figs. 1A, 1B). In four of the six two-way comparisons for males and females, the coefficient of variation computed from regional means for body core characters was significantly larger than those for skull, leg, and wing characters ($F > 4.30$, $df = 6, 6$ —using McKay's [1932] approximation to an *F*-distribution given in Miller and Kahn [1962, 124]). A smaller body core as an indication of small overall size might be expected in warmer areas (Gould and Johnston 1972); but if climate modifies body size in Great Horned Owls then Florida owls should not be as large as those from Alberta (Table 1).

The geographic variation in body core size

TABLE 2. Absolute reverse size dimorphism (RSD) and RSD as a percentage of male size in Great Horned Owls grouped by region.

Region	RSD—absolute	RSD—% of male size
Ontario	38.71	3.6
Michigan	51.88	4.8
Kansas	53.77	5.0
Florida	47.94	4.5
Alberta	51.42	4.9
Texas	52.03	5.1
California	51.27	5.0

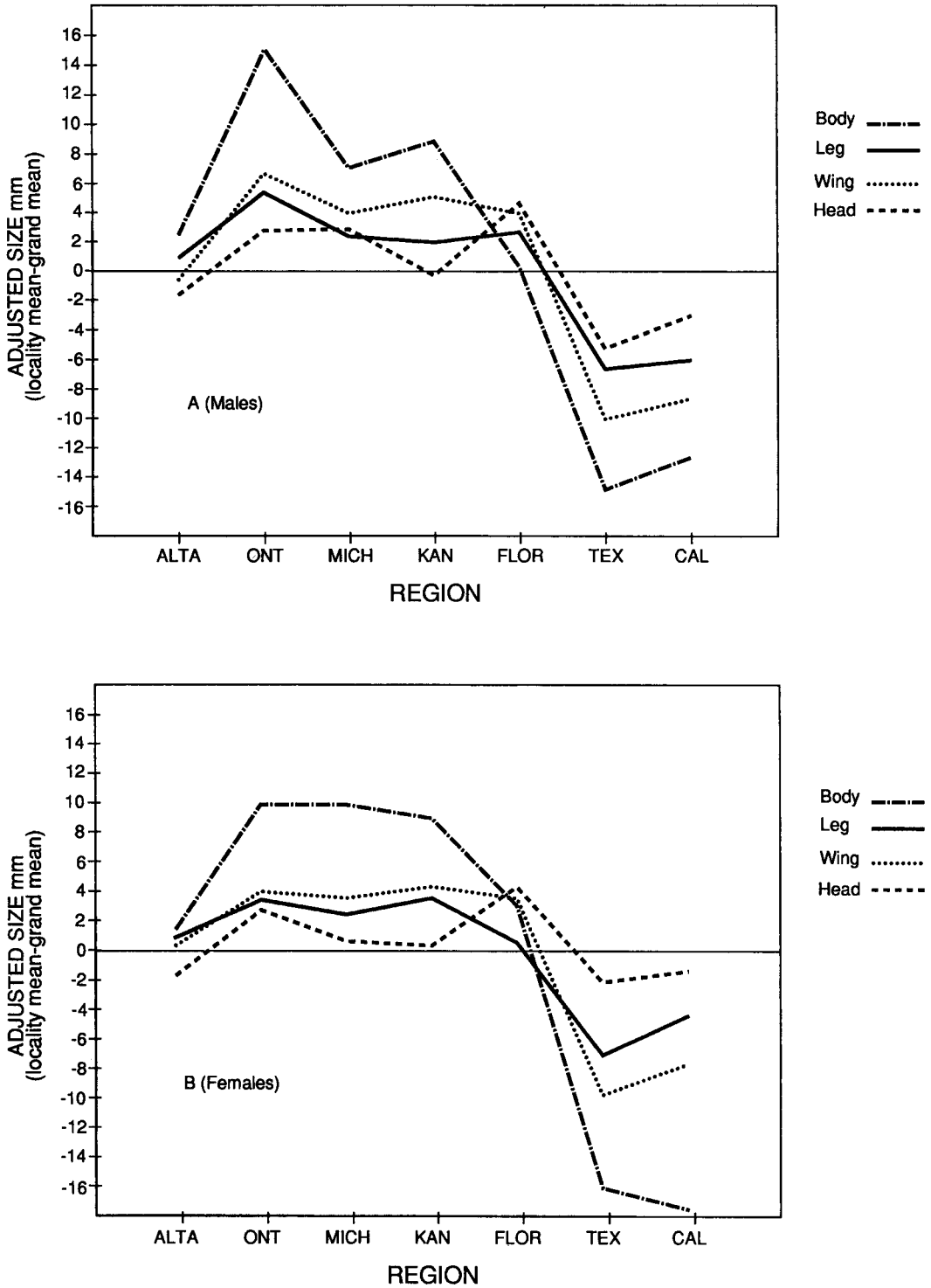


FIGURE 1. Geographic variation in sizes of skeletal complexes for (A) male and (B) female Great Horned Owls. Data are presented as deviation scores—mean locality values minus grand means to facilitate comparisons among curves on the same scale.

prompted a look at relative dimensions in body parts. If Allen's Rule applies, small body cores relative to overall size would be expected in owls living in warm climates, large body cores relative to overall size would be expected in owls from northern localities. Table 3 indicates that owls from northern regions show relatively large body cores. Because of its continental climate, particularly in the west, I consider Kansas to be a northern locality. The lack of statistical differences between Florida owls and those from the north, particularly for the sample of males, reflect in part, the small sample size from Florida.

Rough distributions of the subspecies of Great Horned Owls in North America (for which good samples of skeletons exist) show some correspondence with the geographic regions used earlier (Fig. 2). Where two subspecies occur in the same region, size variation between subspecies is evident (e.g., *pacifus* and *saturatus* in the California region and *virginianus* and *occidentalis* in Kansas, Table 4). Surprisingly, the largest subspecies is *occidentalis*, which is found in the mid-western U.S. The owls identified as *wapacuthu/subarcticus* are all birds from Alberta. When acquired, these birds were not identified to subspecies but are likely to be *wapacuthu* (AOU 1957) which Godfrey (1986) considers equivalent to *subarcticus*. The subspecies *occidentalis* is not in Alberta according to Godfrey (1986) in contrast to the distribution given in the 1957 AOU checklist.

The size differences between *occidentalis* and *virginianus* in Kansas are examined in Table 5. All of the *occidentalis* specimens were collected in Meade County in southwestern Kansas. While the majority (64%) of the *virginianus* were collected in Douglas and Jefferson counties in the northeastern part of the state, 20 (36%) were taken from Meade County.

The degree of RSD varies among subspecies (Table 6) but shows no relationship with size. Consistently, the average level of RSD is near 5%.

DISCUSSION

GEOGRAPHIC VARIATION

There is a suggestion in the data presented here (Table 1), that in eastern North America, larger Great Horned Owls are associated with higher latitudes. In general, however, there is no support for Bergmann's Rule in these data. Great Horned Owls in Kansas are larger than those in Alberta.

TABLE 3. An ANOVA and Scheffé's a posteriori means test on the differences among regions in relative size of body core variations. Relative size is assessed as the natural log of the sum of body core variables divided by the sum of all variables (size). Owls from Kansas, Ontario, Michigan, and Alberta show larger body cores relative to body size than birds from California and Texas. Florida owls are intermediate.

	Region	ln(body core/size)
Males		
ANOVA $F = 19.67$ $P < 0.0001$	Kansas	-1.265
	Ontario	-1.265
	Michigan	-1.273
	Alberta	-1.273
	Florida	-1.293
	California	-1.300
	Texas	-1.301
Females		
ANOVA $F = 20.89$ $P < 0.0001$	Michigan	-1.248
	Kansas	-1.251
	Ontario	-1.253
	Alberta	-1.260
	Florida	-1.265
	Texas	-1.281
	California	-1.291

There is little difference in the average size of the birds found from Minnesota south to Florida. It has long been known that Great Horned Owls in western Texas and coastal California are small (Ridgway 1914, Earhart and Johnson 1970). I assumed initially that the small size of Great Horned Owls in these areas might reflect a thermoregulatory adaptation promoting more effective cooling. Given the large size of *virginianus* in Florida, however, this assumption is difficult to support. Studies of variation in Great Horned Owls in Central America and Mexico (Webster and Orr 1958) and South America (Traylor 1958) do not indicate a clinal relationship of wing length (as an index of size) with latitude. The average wing length (WL) of *B. v. nacurutu* which is found in the tropical lowlands of northern South America is as large as that of *B. v. virginianus* from eastern North America (*nacurutu*: males, WL = 341.4 mm, $n = 15$; females, WL = 363.1 mm, $n = 21$, Traylor [1958]; *virginianus*: males, WL = 339.0 mm, $n = 12$; females, WL = 362.3 mm, $n = 15$, Earhart and Johnson [1970]).

Geist (1987) recently asserted that Bergmann's Rule has no basis in fact. He showed that the relationship of body size of ungulates and wolves with latitude in North America is not linear but

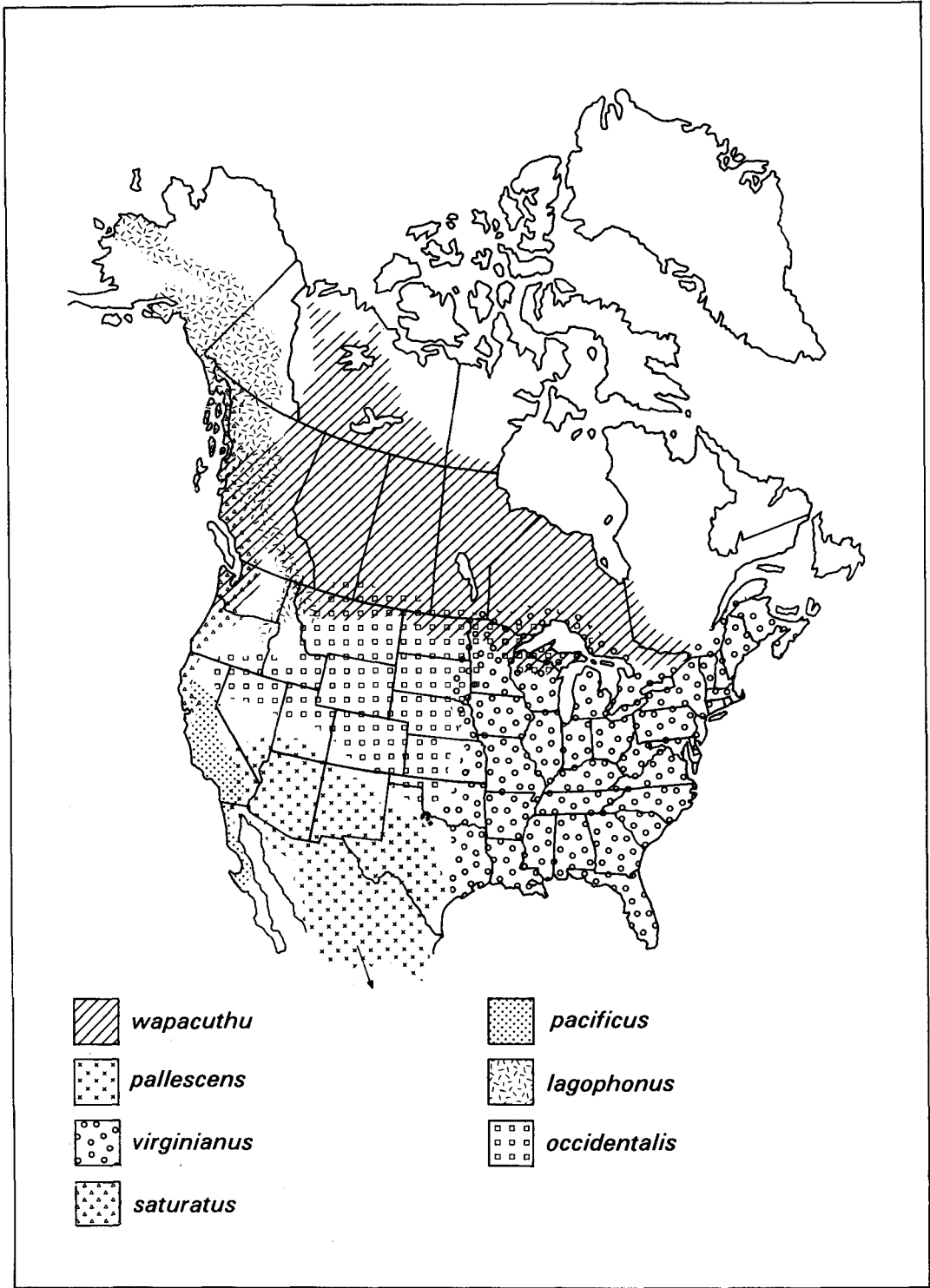


FIGURE 2. Distribution of seven subspecies of Great Horned Owl in North America. These seven subspecies are those with good skeletal representation in North American museums. Data for this map were obtained from Peters (1940), AOU (1957) check-list, Karalus and Eckert (1974), and Oberholser (1974).

TABLE 4. Size ($\bar{x} \pm SE$) of male and female Great Horned Owls grouped by subspecies. Sample sizes are in parentheses below each mean. The *t*-statistic indicates the difference between male and female mean size.

Subspecies	Male	Female	<i>t</i>	<i>P</i>
<i>occidentalis</i>	1,086.33 \pm 4.61 (8)	1,136.99 \pm 8.39 (6)	5.29	0.0008
<i>virginianus</i>	1,071.57 \pm 2.86 (47)	1,122.71 \pm 3.00 (62)	12.32	0.0001
<i>wapacuthu/subarcticus</i>	1,054.78 \pm 2.48 (53)	1,106.20 \pm 2.15 (79)	15.63	0.0001
<i>lagophonus</i>	—	1,092.00 \pm 4.61 (5)	—	—
<i>saturatus</i>	1,041.01 \pm 8.42 (8)	1,082.85 \pm 9.45 (10)	3.30	0.004
<i>pallescens</i>	1,022.15 \pm 8.65 (17)	1,077.29 \pm 10.30 (18)	4.09	0.0003
<i>pacificus</i>	1,007.52 \pm 8.12 (12)	1,056.99 \pm 10.43 (11)	3.74	0.001

follows a curve with the largest individuals found at intermediate latitudes. Above 60°N latitude, average body size of these large mammals decreases. Studies of geographic variation in birds rarely include specimens from localities north of 60° latitude (Zink and Remsen 1986), hence the apparent support for Bergmann's Rule indicated by avian studies needs rethinking. The data presented here are all from specimens acquired south of 60°N latitude but no general relationship between overall body size and latitude is apparent.

There is an indication from analysis of relative dimensions that body core measurements are larger in northern owls (Table 3). In morphometric studies of House Sparrows (*Passer domesticus*) and Red-winged Blackbirds (*Agelaius phoeniceus*) summarized in Gould and Johnston (1972), large body cores relative to extremities are typical of birds breeding at high latitudes. Because of their large size and extensive insulation, Great Horned Owls probably suffer heat stress more frequently than cold stress (Wijnandts 1984). Especially in Texas and Florida, small body cores relative to extremities may be important to allow more efficient cooling.

TABLE 5. Size variation between *virginianus* and *occidentalis* subspecies of Great Horned Owls in Kansas.

	<i>virginianus</i>	<i>occidentalis</i>	<i>t</i>	<i>P</i>
Males	1,066.26 (25)	1,086.33 (8)	2.84	0.01
Females	1,121.86 (30)	1,136.99 (6)	1.76	0.10

DIET

If broad patterns of geographic variation in Great Horned Owls cannot be linked to climate then other factors such as diet or subspecific variation need to be considered. A relationship between raptor size and average prey size has been proposed in a number of studies of RSD (Storer 1966, Reynolds 1972). From analyses of pellet contents across North America, a significant fraction of the Great Horned Owl diet is composed of rabbits (*Sylvilagus* spp.) or hares (*Lepus* spp.; e.g., Errington et al. 1940, Fitch 1947, Korschgen and Stuart 1972, Marti 1974, Adamcik et al. 1978). There are four cottontail species that are widely distributed in North America—*floridanus* in the east, *nuttallii* in the northwest, *audubonii* in the southwest, and *bachmani* in California. In size, the species are ordered *floridanus* > *audubonii* > *nuttallii* > *bachmani* (Hall 1981). If Great Horned Owl size was related to

TABLE 6. Absolute reversed size dimorphism (RSD) and RSD as a percentage of male size for Great Horned Owls grouped by subspecies. The specimens listed as *wapacuthu/subarcticus* represent birds from Alberta.

Subspecies	RSD—absolute	RSD—% of male size
<i>occidentalis</i>	50.7	4.7
<i>virginianus</i>	51.1	4.8
<i>saturatus</i>	41.8	4.0
<i>pallescens</i>	55.1	5.4
<i>pacificus</i>	49.5	4.9
<i>lagophonus</i>	—	—
<i>wapacuthu/subarcticus</i>	51.4	4.8

Sylvilagus size then eastern owls would be the largest, California the smallest, and those in the plains would be intermediate. While this is basically true, the diet relationship breaks down under scrutiny. In central Alberta, snowshoe hares (*L. americanus*, with an average weight 30% greater than *S. floridanus*, Hall 1981) constituted up to 81% of the diet of Great Horned Owls, which on average are smaller than owls in the east (Adamcik et al. 1978). In southern Alberta, the large white-tailed jackrabbit (*L. townsendii*) and the relatively small *S. nuttallii* contribute equally to Great Horned Owl diets (H. Smith, unpubl. data).

Breeding studies show that productivity of Great Horned Owls in Alberta and Saskatchewan is directly linked to snowshoe hare abundance (Houston 1975, Adamcik et al. 1978). While a relationship between hare size and owl size might be expected in Alberta and Saskatchewan, it may also be true that selection for optimal size is strongest in years when hares are absent and the owls survive on much smaller prey. Fitch (1947) showed that the relatively large *S. audubonii* not *S. bachmani* represented 61% of the diet of the small *B. v. pacificus* in California. In Wyoming (Marti 1974), species of *Peromyscus*, *Microtus*, and *Thomomys* contributed 64% to owl diets with *Sylvilagus* providing only 10–15%. Long-term studies by Korschgen and Stuart (1972) for Missouri and Adamcik et al. (1978) for Alberta show great interyear variation in Great Horned Owl diet. With this variability, a clear link between food and body size would be difficult to demonstrate.

SUBSPECIFIC VARIATION

The data presented in Tables 4 and 5 indicate that subspecific differences in size persist even though subspecies are not necessarily separated geographically. In an analysis of RSD in Great Horned Owls based on weight and wing length, Earhart and Johnson (1970) found a positive relationship between subspecies size and RSD. No such relationship was noted here. The subspecies with the highest RSD has one of the smallest body sizes (*pallescens*) and variation among the other subspecies is slight.

Based on skeletal measures, the ordering of subspecies from largest to smallest is *occidentalis* > *virginianus* > *wapacuthu/subarcticus* > *lagophonus* > *saturatus* > *pallescens* > *pacificus*. This ordering is not consistent with two others

based on wing length and weight—that given by Ridgway (1914) *wapacuthu/subarcticus* = *lagophonus* > *occidentalis* > *saturatus* > *virginianus* > *pallescens* > *pacificus* and one derived from Karalus and Eckert (1973) *saturatus* > *lagophonus* > *occidentalis* > *virginianus* = *pallescens* > *pacificus*; (*wapacuthu* and *subarcticus* were not included). McGillivray (1985) found that weight and feather measurements of Great Horned Owls were highly variable and not good measures of size. The skeletal data presented here, though limited by small samples of some subspecies, probably provides a truer reflection of relative size of the subspecies than external measures.

Barrowclough and Coats (1985) derived estimates for the root-mean-square dispersal distance (σ , the standard deviation of juvenile dispersal distances about their nest site) and the effective population number per neighborhood (N_e , the estimated size of the population within a circle of radius 2σ) for six species of owls. Using the band recovery data from Houston (1978) they estimated σ to be 216.35 km and N_e to be 66,396.75 individuals for Great Horned Owls. These values are an order of magnitude larger than those for the other five owl species and if typical of other Great Horned Owl populations, would preclude the maintenance of consistent subspecific or geographic differences. Barrowclough and Coats (1985) assumed that all recoveries made of birds greater than 1 year old represented potential breeders, but the age of first breeding is not well established (C. S. Houston, pers. comm.). If most 1-year-old owls are not breeders and if some long-distance recoveries reflect seasonal rather than dispersal movements (Houston 1978), then the values of both σ and N_e will be much smaller than estimated by Barrowclough and Coats (1985).

CONCLUSIONS

Great Horned Owls show considerable variation in size across both geographic and subspecific boundaries. Latitude and presumably climate do not correlate consistently with body size except to select for relatively smaller body cores in warm climates. Despite this regional size variation, RSD in the Great Horned Owl based on overall size shows little variation across North America. This suggests that RSD is a species-specific character rather than a variable modified by environmental or ecological factors. If so, then studies aimed at resolving the origin of RSD in raptors should

focus on behavioral interactions between members of a pair which may be species-specific rather than exploring a multitude of ecological factors for their effects.

Based on examination of Great Horned Owl skins in Alberta, my initial impression was to reject subspecific variation in Great Horned Owls as being meaningful. Even Ridgway (1914, p. 737) admitted that the naming of so many subspecies of Great Horned Owl was just for convenience. The differences in size among subspecies which appears to be maintained despite geographic overlap suggests otherwise; and indicates either intraspecific segregation of gene pools or strong selection maintaining the differences. I am not aware of any protein electrophoretic or mitochondrial DNA analyses using raptors. The taxonomic question suggested by the morphological differences among subspecies will not be resolved entirely by examination of plumage but should be addressed with biochemical techniques. The extensive distribution and apparent differentiation in populations of the Great Horned Owl make it ideal for an examination of the genetic structure of a bird species.

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