

## PHILIPPINE BIRDS OF PREY: INTERRELATIONS AMONG HABITAT, MORPHOLOGY, AND BEHAVIOR

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**ABSTRACT.**—We sought to clarify relationships among morphometrics, behavior, and ecological variables for 21 species of raptors in the Philippines. Morphological space was defined by 42 external characters analyzed as shape variables with respect to body length (without tail). Seventeen variables were used to characterize habitat and five to characterize foraging behavior. Three PCA components accounted for 68% of the total variance in the habitat data and separated species living in dense forests from those using degraded habitats or coastal areas. Two PCA components explained 81% of the variance in hunting mode, with transitions from sit-and-wait to flap-gliding, and with contrasts between soaring and flap-gliding. Three PCA components accounted for 70.5% of the variance in morphological shape. The first component separated species with narrow wings and less-pronounced notches from species with broad, deeply notched wings. The second and third components were associated with the contrast between pointed and rounded wings and prey-capture apparatus (feet, bill). Five morphological characters were highly correlated ( $R = 0.934$ ) with the first principal component of the habitat data, indicating that species inhabiting forested habitats have square tails, rounded wings, and strong claws. Hunting mode and habitat also were closely related ( $R = 0.900$ ). Soaring correlated well with the number of notched primaries, tail shape, and measures of the trophic apparatus, but poorly with wing loading and aspect ratio. Behavior, ecology, and morphology of this subset of raptors were closely interrelated. Among the Philippine raptors, species that inhabit rain forests are the most endangered, and we suggest that morphological constraints limit their use of secondary habitats. *Received 21 January 1997, accepted 2 February 1998.*

DIFFERENCES IN EXTERNAL MORPHOLOGY among species can reliably predict differences in habitat use and foraging behavior. That this is true is the premise of ecomorphological analyses of bird communities (Karr and James 1975, Leisler 1980, Miles and Ricklefs 1984, Niemi 1985, Miles et al. 1987, Wiens 1989). Yet, this assumption is rarely tested with data on behavior and habitat acquired simultaneously in the field, and comparatively few studies have attempted to clarify relationships among morphometry and the behavior or environment of the species in question (but see Leisler et al. 1989, Price 1991, Landmann and Winding 1993, Stiles 1995). Such work is needed to corroborate premises of ecomorphology and to provide the necessary link between resource use, performance, and morphology demanded for a deeper understanding of the relationship between

the design of birds and their environment (Lederer 1984, Winkler 1989, Wainwright 1991). Common difficulties in ecomorphological analyses of this kind are character sets that contain only few or irrelevant characters, or both (Leisler and Winkler 1997). Analyses of closely related species are usually most successful in showing ecomorphological relationships (Lederer 1984, Leisler and Winkler 1985), whereas hypotheses of wider phylogenetic scope face increasing difficulties because of oversimplification (Lederer 1984) and because phylogeny may confound analyses at the community level (Miles et al. 1987).

To strike a balance between the difficulties noted above, we studied the diurnal birds of prey of the Philippines. This group is ecologically and phylogenetically well defined but is heterogeneous enough to mediate between studies confined to closely related species and those of guilds and communities. So far, no integrative investigations are available for birds of prey, although some studies on size differences (Schoener 1984) and morphology (Rochon-Duvigneaud 1952, Voous 1969, Nieboer

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1973, Brown 1976, Bierregaard 1978, Jaksić 1985, Kemp and Crowe 1994, Hertel 1995, Jenkins 1995) exist in which morphological patterns were related to some aspects of ecology. However, studies on raptors that combine data on hunting modes and habitat use have not been attempted. The Philippines is an excellent area for this kind of investigation because a large variety of raptor species can be observed in an area of less than 300,000 km<sup>2</sup>. Moreover, habitats in the Philippines span distinctive ecological gradients from tropical primary rain forest to deforested regions and coastlines. Originally, the Philippines were almost completely covered by tropical rain forest. Because the proportion of forested area was reduced from 58 to 17% between 1932 and 1991, several species of raptors currently are threatened by extinction (Collins et al. 1991, Dickinson et al. 1991, ICBP 1992, Collar et al. 1994).

Our objectives were to: (1) examine the strength, consistency, and functional basis of the relationships among foraging mode, habitat use, and morphology in this assemblage of raptors; and (2) integrate these findings with respect to the question of morphological constraints on behavior and habitat use. We also discuss the consequences of our findings for the future of these species in the face of continued habitat loss.

#### METHODS

*Species and study areas.*—Members of three of the five falconiform families (del Hoyo et al. 1994) occur in the Philippines (Dickinson et al. 1991). We were able to observe 21 species of 14 genera (Appendix), including three endemic species and nine endemic subspecies.

Habitat analyses and behavioral observations were made during a field study over a period of 9.5 months (January to April 1993, November to February 1994, and March to July 1994). Investigations were carried out in 19 study areas at elevations ranging from sea level to 2,500 m on the islands of Luzon (Sierra Madre, Quirino and Isabela; Mt. Makiling, Laguna), Mindanao (Mt. Kitanglad, Bukidnon; Carmen-Cantilan, Surigao del Sur; Mt. Apo, Davao City and North Cotabato; Initao, Misamis Oriental), and Palawan (El Nido and Bacuit Archipel, northern Palawan). Observations in each particular area lasted from a few days to three weeks.

*Morphometry.*—Study skins were measured using 384 specimens from various museum collections: British Museum (Tring), National Museum of Scotland (Edinburgh), Rijks Museum van Natuurlijke

Historie (Leiden, The Netherlands), Universitets Zoologiske Museum (Kobenhavn, Denmark), Zoologisches Museum der Humboldt Universität (Berlin), Staatliches Naturhistorisches Museum Braunschweig (Brunswick, Germany), Naturhistorisches Museum Wien (Vienna), American Museum of Natural History (New York), Smithsonian Institution (Washington, D.C.), Field Museum of Natural History (Chicago), Museum of Natural History (Cincinnati, USA), Delaware Museum of Natural History (Wilmington, USA), National Museum of the Philippines (Manila), Wildlife Biology Laboratory at the University of the Philippines (Los Baños), and the Zoological Garden (Manila).

Up to 39 study skins of adult specimens were analyzed for common species, whereas for rare species and subspecies, the number of individuals was much smaller. Sex ratios within samples of species varied between 0.45 and 0.55. External morphological features were measured mostly as defined in Leisler and Winkler (1985, 1991). The flight apparatus was represented with 23 variables. These included length of all primaries; length of alula; lengths of the first, central, and innermost secondaries; lengths of outer and central rectrices; and wing length. Also used were the primary projection, or Kipp's distance, measured as the distance from the wing tip to the first secondary; and tail gradation, the difference in length between the innermost and outermost rectrices (Leisler and Winkler 1985, 1991). The mean correlation (absolute values) within this data set was 0.525 (range 0.007 to 0.991). Thirteen characters represented morphology of the hind limb. They comprised all toe lengths, talon chords, and diameters of talons at the base, and length of the tarsus. The mean correlation among these variables was 0.395 (range 0.005 to 0.977). The length, width, and depth of the bill were measured: (1) including the cere at the base of the bill, and (2) on the bill proper at the distal edge of the cere. The mean correlation among these six characters was 0.532 (range 0.006 to 0.935).

Two additional characters, aspect ratio (wing span squared divided by wing area) and wing loading (body mass divided by wing area), were calculated from photographs of soaring birds. Data for the Philippine Falconet (*Microhierax erythrogenus*) were taken from a freshly killed specimen. No suitable photographs were available for the Philippine subspecies of Jerdon's Baza (*Aviceda jerdoni magnirostris*), so we used photographs of its closest equivalent, the Pacific Baza (*A. subcristata*) from the Australian region (Marchant and Higgins 1993). We also had no photographs of the Eastern Marsh Harrier (*Circus spilonotus*). Photographs were scanned using the computer program Imagein 3.0, and contrast of the silhouettes was enhanced with program Coral Photopaint 3.0 to optimize image analysis with program Lucia 2.11. All measurements of soaring birds refer to fully outstretched wings. Because the tail can be fanned to

TABLE 1. Characteristics of the flight apparatus of 16 Philippine raptors and one ecological equivalent from Australia (in brackets).

Species	Body mass (g)		Body length (cm)		Aspect ratio		Wing loading w/o tail (N m <sup>-2</sup> )		Wing loading w/tail (N m <sup>-2</sup> )		Linearized wing loading
	M	F	M	F	M	F	M	F	M	F	F
[ <i>Aviceda subcristata</i> ]	307	347		40.0	5.64	5.95	20.6	25.0	17.6	20.1	0.209
<i>Pernis ptilorhynchus</i>	1,000		58.0	65.0	5.68	5.61	34.4	30.8	30.0	23.4	0.179
<i>Pernis celebensis</i>	679	738	53.5	55.4	5.32	5.41	26.0	26.0	22.4	22.4	0.175
<i>Haliaastur indus</i>	450	581	47.1	48.9	6.26	6.45	17.2	21.3	15.6	19.6	0.171
<i>Haliaeetus leucogaster</i>	2,570	3,150	70.0	77.0	7.67	7.25	44.4	46.3	43.0	42.6	0.209
<i>Spilornis cheela</i>	688	853	52.4	54.5	5.26	5.29	25.5	28.9	22.5	25.6	0.185
<i>Accipiter virgatus</i>	95	154	25.7	28.1	4.72	4.34	21.1	28.4	16.5	22.2	0.247
<i>Accipiter trivirgatus</i>	199	353	33.2	37.5	5.75	5.77	25.4	35.9	19.7	27.7	0.241
<i>Accipiter soloensis</i>	156	204	27.8	29.0	5.68	6.14	27.3	33.1	22.1	26.9	0.256
<i>Butastur indicus</i>	375	433	42.6	42.9	6.34	6.44	27.2	30.7	22.0	25.8	0.216
<i>Pithecophaga jefferyi</i>	4,464	6,000	95.2	105.2	3.89	3.83	48.7	51.0	42.2	44.3	0.178
<i>Hieraetus kienerii</i>	733	800	46.8	52.6	5.61	5.68	33.2	31.6	27.1	26.1	0.200
<i>Spizaetus cirrhatus</i>	1,360	1,600	58.4	64.9	5.48	5.35	44.9	41.9	37.2	33.5	0.214
<i>Spizaetus philippensis</i>	—	1,225	56.6	58.2	4.98	4.55	—	46.5	—	38.5	0.203
<i>Microhierax erythrogenys</i>	46	52	15.9	17.2	5.74	5.66	25.4	26.4	21.9	22.9	0.217
<i>Falco tinnunculus</i>	186	217	33.8	36.2	7.07	6.92	24.1	24.5	18.0	18.4	0.268
<i>Falco peregrinus</i>	650	1,000	48.9	52.8	5.61	6.13	47.5	57.2	39.1	46.8	0.266

various degrees, we used 60° as the standard tail-fanning angle for measurements of all species, and the silhouettes were modified accordingly. This value is the approximate average angle shown by soaring birds. Relevant values were calculated as described in Pennycuik (1975), Kerlinger (1989), and Norberg (1990). Wing loading (N m<sup>-2</sup>) was calculated according to Norberg (1990), either with the tail excluded or included. The two measures of wing loading differ widely in long-tailed species (Table 1). We also calculated linearized wing loading (Jaksić and Carothers 1985), except that we used the sum of wing and body area instead of wing area alone. Body-mass data were taken from Bennet (1986), Goodman and Gonzales (1989), Dunning (1993), Marchant and Higgins (1993), and del Hoyo et al. (1994), and from labels attached to museum specimens.

All measurements were taken as indices relative to body length (total body length minus tail length) because we intended to analyze aspects of shape rather than size (Mosimann 1970), and all measurements were log-transformed. Even in raptors with pronounced sexual size dimorphism, morphological variation between the sexes is low compared with that among species (see Leisler and Winkler 1991). Therefore, we used species' means for all analyses.

*Field data.*—Point observations (>2 h per observation) were carried out at exposed sites, e.g. cliffs, clearings, and prominent trees. Through recurrent visits to each point at different times of the day, the observations covered the full daylight period (0600 to 1800). Observations made along line transects

were carried out primarily for the study of birds within the forest interior. To maximize the number of different individuals, large areas (30 to 50 km<sup>2</sup>) were investigated using both methods. These two methods have been used successfully in other studies of tropical forest raptors (Thiollay 1989, Whitacre et al. 1992). Sample sizes ranged from 2 to 219 observations per species. Only species with more than five observations were included in subsequent analyses.

Behavioral and habitat variables were noted simultaneously for each undisturbed hunting raptor at the first sighting. To assure as much statistical independence as possible (see Hejl et al. 1990), the behavior of raptors on the wing was recorded again only after five minutes had elapsed and, for perched individuals, additional data were taken only after the birds had changed their perches. These secondary observations comprise only 1.1% of the total of 896 observations.

Five behavioral traits associated with hunting were chosen: perching, powered flight (continuous flapping), flap-gliding, gliding, and soaring (Kerlinger 1989). Perching denotes a search mode during which the bird scans its surroundings from a perch. When gliding, the wings are held stretched out from the body in a fixed position without flapping, and the flight path is more or less straight. Soaring is a circular gliding mode used to gain altitude in thermals or slope updrafts. Powered flight comprises two forms, continuous flapping and flap-gliding (powerglide), a flight mode during which flapping is

interspersed with gliding. The data were analyzed as arcsine square-root transformed percentages expressing the proportion of these behavioral modes in the observations.

To characterize habitat use by raptors, we estimated forest canopy cover and the proportion (in 5% increments) of 16 habitat types (primary rain forest, secondary rain forest, degraded secondary forest, tree plantations, clearings, fallow land, grassland, pasture, banana, rice, other cultivation, road, settlement, water, coconuts, cliffs) within a 250-m radius of the location of every bird that we observed. Data were averaged for each species and then arcsine square-root transformed for analyses.

**Data analysis.**—The data were evaluated using principal components analysis (PCA) and stepwise multivariate regression analysis. Principal components were based on correlation matrices. Particularly when many characters are used, there may be many relevant components judged by eigenvalues  $>1$ . In order to avoid over-interpretation of the data, however, we adopted the following criterion: a component was deemed to be relevant if its corresponding eigenvalue was greater than 1 in 95% of 10,000 bootstrap samples and explained more than 10% of the total variance. By applying this rule, we avoided discussing "significant" but biologically irrelevant components. PCA was used solely to describe relationships within our data set, which was not intended to represent a sample of a large, unknown statistical population. The results of the bootstrap analysis were also helpful in the interpretation of component loadings. Stepwise methods have been widely criticized (see James and McCulloch 1990), mainly because they do not guarantee a selection of the most influential variables or even the best correlations. Consequently, we used stepwise multiple regression analysis mainly to show that a particular set of data can be used to predict the criterion variable; we have also tried to point out the biological relevance of the variables selected in each individual case. Although we cannot rule out the possibility that other variable combinations may produce better predictions, we are confident that our results provide good estimates for the strength of the association among ecological attributes, behavior, and morphology.

Similarities due to phylogenetic inertia may cause statistical bias in correlational analyses (Felsenstein 1985, Harvey and Pagel 1991). Available phylogenetic analyses of raptors are widely divergent and do not include all of the taxa treated by us. Therefore, we constructed our own phylogenetic tree (Fig. 1) based on studies by De Boer and Sinoo (1984), Boyce and White (1987), Olsen et al. (1989), Marchant and Higgins (1993), Seibold et al. (1993), Helbig et al. (1994), Holdaway (1994), Griffiths (1994), Wink and Seibold (1995), and Wink et al. (in press).

Independent contrasts were computed for the statistical evaluation of stepwise multiple regression

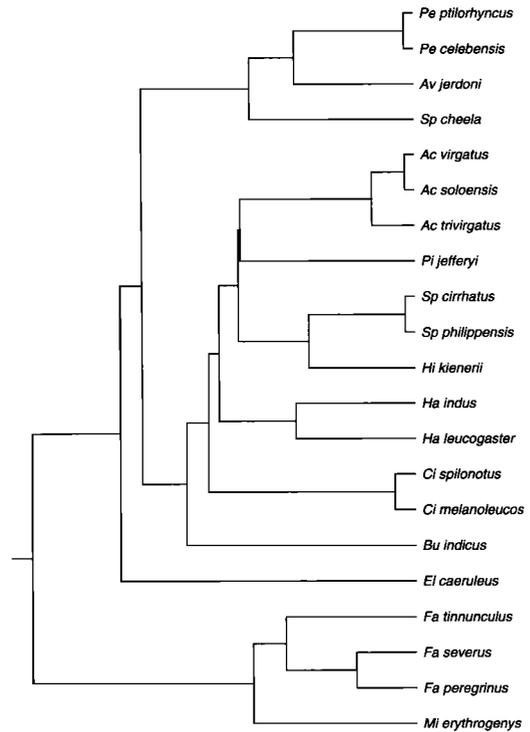


FIG. 1. Classification of Philippine raptors used to compute independent contrasts.

analysis results. The variables were analyzed with multiple linear regression through the origin (Felsenstein 1985). The independent contrasts were rather sensitive to the branch lengths. Therefore, in some cases we also present results with corrections that assume constant branch lengths between nodes. We used independent contrasts only as a means of reducing bias, and not as estimates for correlated evolutionary changes; that is, we did not necessarily assume that characters evolved homogeneously throughout the phylogeny of the group. All results of the regression analyses are presented as plots of the observed values of the criterion variable based on predictions from the multiple regression equations. To conserve the functional relationship, and to display the positions of individual species in the scatter, we present the relations of the original variables and not those of the contrasts. All calculations were carried out with programs written by us.

## RESULTS

**Habitat.**—Among the 21 raptors studied, 13 species occurred in habitats with more than 50% forest cover and therefore were defined as forest dwellers; the other 8 species occupied

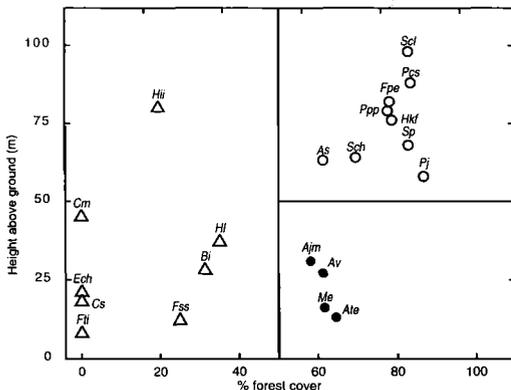


FIG. 2. The relationship between height above ground at which a species forages and forest cover in Philippine raptors. Open circles denote species that hunt above the canopy, filled circles denote species that inhabit forest interior, and open triangles denote species that use open habitats. See Appendix for the abbreviations used to designate species.

open habitats (Fig. 2). All forest dwellers except the Chinese Goshawk (*Accipiter soloensis*) are residents. Four species of the open and semi-open habitats are winter visitors only. The forest dwellers fall into two distinct groups (Fig. 2): (1) four species that hunt inside the forest below the canopy (below 40 to 50 m), and (2) nine species that hunt within and above the canopy zone.

Three principal components accounted for 68% of the total variation in habitat ( $n = 18$  species). The first component (PC1) explained 34% of the variation (eigenvalue = 5.83) and described the contrast between densely forested habitats and open and extremely "disturbed" habitats consisting of grasslands and rice fields. PC2 explained 21% of the variation (eigenvalue = 3.60) and was related to an increasing proportion of water (effectively, the sea), coconut palms, and rocky areas in the habitat versus degraded and secondary forest stands and banana cultivations. PC3 explained 13% of the variation (eigenvalue = 2.18) and described variation within cultivated areas, from settlements and neighboring farming areas to abandoned fields. Much of the variation in habitat use concerned the open country birds, as defined above. Forest species formed a tight cluster, and those of the interior scored lower on the first principal component ( $t = 3.06, P = 0.011$ ) but were not separated from those hunting

mainly above the canopy in the second component ( $t = 1.68, P = 0.121$ ).

**Behavior.**—Two principal components explained 81% of the overall variation in hunting mode ( $n = 18$  species). PC1 explained 48% of the variation (eigenvalue = 2.57) and was associated with the transition from sit-and-wait to flap-gliding hunting modes. PC2 explained 33% of the variation (eigenvalue = 1.26) and represented the contrast between soaring and the other flight modes. This suggests that in these birds, the difference between the use of different flight modes was nearly as important as the transition from active-search to sit-and-wait hunting.

**Morphology.**—Three principal components accounted for 70.5% of the variation associated with flight and feeding apparatus. PC1 explained 36% of the variation (eigenvalue = 15.25) and arranged the 21 species along a continuum from species with narrow wings and less-pronounced notches to those with broad, deeply notched wings. The width of the wings was reflected in a positive correlation with length of the inner primaries (P1 to P6), the secondaries, and the scapulars. PC2 combined characters of the flight apparatus with claw measurements and explained 20% of the total variance (eigenvalue = 8.51). With respect to the wing, this axis denotes a decrease in wing length that was mainly due to a reduced distal section of the wing and thus reduced pointedness of the wing (Kipp's distance), and to an increase in the number of wing slots. The claw measurements referred to increasingly large (length, diameter) inner and hind claws. Species scoring high on this axis are well equipped for killing comparatively large prey with their feet. PC3 explained 14% of the total variance (eigenvalue = 6.01) and was related to the feet and the bill; this component represented the major variation in the feeding apparatus together with the "killing-grip variables." PC3 denoted an overall increase in the length of the toes together with lengthened outer and middle claws. Bill size increased along this axis with a relatively smaller increase of the distal section and an almost parallel increase of bill width and height. This axis thus represents an increase in the relative size of the capture apparatus (feet) and bill that together are well suited for killing avian or insect prey.

The sixth primary (P6) can be considered as

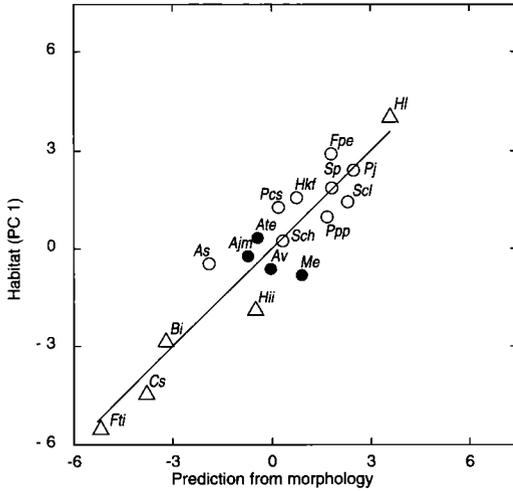


FIG. 3. Morphological correlates of habitat use in Philippine raptors. Results are from a multiple regression of morphological variables as predictors of habitat data based on PC1 scores. Values predicted from the regression equation are plotted on the X-axis, and observed scores are plotted on the Y-axis. Of the five morphological variables extracted, Kipp's distance and length of central rectrices negatively correlated with predicted habitat use, and diameter of hind claw, length of inner toe, and length of innermost secondary positively correlated with predicted habitat use (see text).

a key structure for the form of the wing. If P6 is long, the outer primaries (P7 to P10) are short, giving the wing a rounded appearance. If P6 is short, the outer primaries become longer, and the wing is more slender and pointed. The length of P6 correlates well with PC1 ( $r = 0.89$ ), and the lengths of P7 to P10 correlate negatively with PC2 ( $r = -0.47$  to  $-0.79$ ).

*Integration.*—To identify morphological correlates of habitat use, we conducted a stepwise multiple regression analysis using PC1 of the habitat data against 42 morphological variables. The five morphological variables extracted explained 87% of the total variance ( $R = 0.934$ ; Fig. 3). Two characters (Kipp's distance, length of central rectrices) were negatively correlated with predicted habitat use, whereas length of the inner toe, diameter of the hind claw, and length of the innermost secondary were positively correlated with predicted habitat use. The multiple  $R$  for the corresponding independent contrasts was 0.811 ( $P < 0.05$ ). Thus, species that occurred in habitats with a higher percentage of forest cover tend to pos-

sess square-cut tails and round, broad wings. They also possess hind limbs that are typical of raptors that prey on vertebrates.

Stepwise multiple regression analysis of habitat using PC2 (forest interior vs. coastal) yielded a high multiple correlation ( $R = 0.900$ ,  $P < 0.0001$ ) with three morphological predictors. Wing length and tail gradation were positively correlated, and length of outer rectrices was negatively correlated, with the tail becoming more wedge-shaped with increasing use of coastal habitats. When the clearly outlying White-bellied Sea-Eagle (*Haliaeetus leucogaster*) was excluded from analysis, the multiple correlation between the same variables and PC2 was still substantial ( $R = 0.785$ ,  $P < 0.005$ ), and the regression coefficients were similar. The difference between the observed PC2 score of the sea-eagle and that calculated from the regression equation is well within acceptable error limits (deviation  $< 90\%$  of overall standard deviation of observations around the regression). The  $R$ -value was 0.596 ( $P > 0.05$ ) when computed from standardized independent contrasts and 0.845 ( $P < 0.001$ ) when computed with branch lengths set to equal.

The most important structural habitat variable was canopy cover (cf. Thiollay 1996). Stepwise multiple regression analysis with canopy cover as the criterion variable produced a multiple correlation of  $R = 0.906$  ( $P < 0.0001$ ), with Kipp's distance and length of central rectrices correlating negatively, and inner toe length and bill height correlating positively, with the prediction (Fig. 4). The corresponding  $R$ -value was 0.644 ( $P > 0.05$ ;  $P < 0.05$  using Kipp's distance and tail length alone) for the standardized independent contrasts and 0.901 ( $P < 0.0005$ ) for the independent contrasts calculated with branches set to equal length. As in the preceding analysis, these results indicate that raptors living in forested areas tend to possess rounded wings.

Species of the forest interior differed from those hunting within or above the canopy by being smaller ( $t = 3.30$ ,  $P = 0.007$ ; log-values of female body mass). No significant size differences were found between the forest species and the open country species.

We expected that the most important structural habitat variable, canopy cover, would show the strongest association with flight mode. Stepwise multiple regression analysis

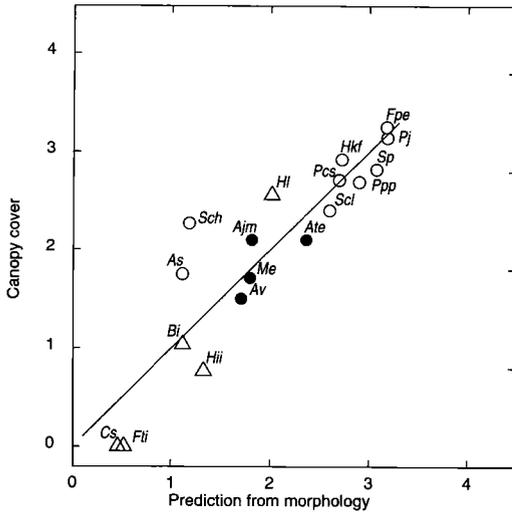


FIG. 4. Morphological correlates of use of canopy cover by Philippine raptors. Results are from a multiple regression of morphological variables as predictors of habitat canopy cover. Values predicted from the regression equation are plotted on the X-axis, and observed scores are plotted on the Y-axis. Of the four morphological variables extracted, Kipp's distance, and length of inner remiges were negatively correlated with predicted canopy cover, and inner toe length and bill depth (without cere) were positively correlated with predicted canopy cover (see text).

(backward variable selection) showed that the search mode used in foraging predicted habitat use with respect to canopy cover very well. Perching, gliding, and soaring accounted for 81% of the variance in canopy cover ( $R = 0.900$ ,  $P < 0.0001$ ;  $R = 0.765$ ,  $P < 0.01$  for the standardized independent contrasts). All coefficients were positive; perching, however, was negatively correlated with the regression score. Basically, the results mean that soaring and gliding occurred mainly in connection with closed habitats. The plot of predicted versus observed values (Fig. 5A) shows that the species observed in totally open habitats, Eurasian Kestrel (*Falco tinnunculus*) and Eastern Marsh Harrier, may have determined the results. Thus, we repeated the analysis excluding these species in order to corroborate the results. The same variables were selected in the stepwise multiple regression analysis; the signs and magnitudes of the coefficients, as well as the correlations with the regression scores, were similar to the foregoing analysis. In particular,

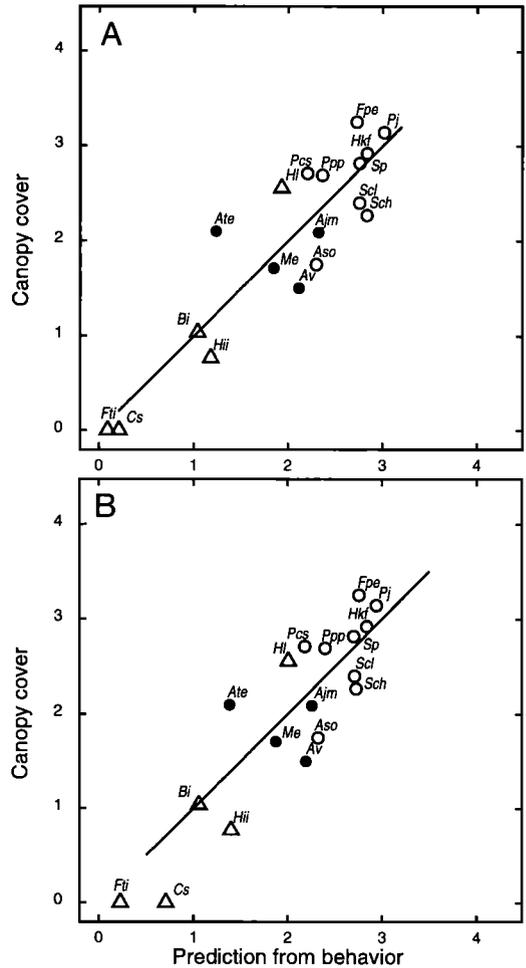


FIG. 5. Behavioral correlates of use of canopy cover by Philippine raptors. Results are from a multiple regression of behavioral variables as predictors of habitat canopy cover. Values predicted from the regression equation are plotted on the X-axis, and observed scores are plotted on the Y-axis. Three behavioral variables were extracted: perching, gliding, and soaring (see text). (A) Analysis based on all species. (B) Analysis based on all species except Eurasian Kestrel and Eastern Marsh Harrier.

we obtained  $R = 0.783$  ( $P < 0.01$ ;  $R = 0.760$ ,  $P < 0.025$  for the independent contrasts), and the predicted scores for the two omitted species were very close to the observations (Fig. 5B).

Stepwise multiple regression analysis was applied to test the correlation between modes of locomotion and morphological characters, including aspect ratio and wing loading (Table 1). First, we analyzed the relationship between

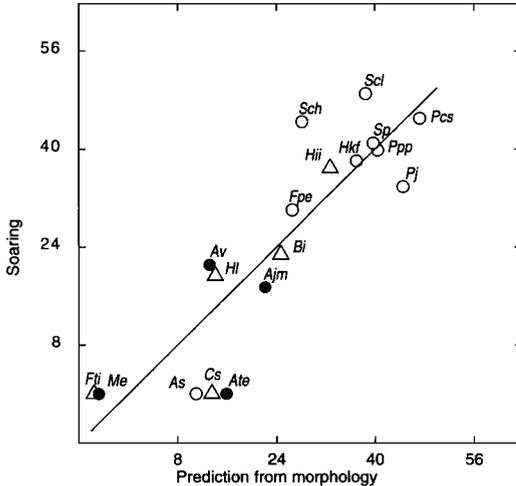


FIG. 6. Morphological correlates of soaring behavior in Philippine raptors. Results are from a multiple regression of morphological variables as predictors of proportion of time soaring. Values predicted from the regression equation are plotted on the X-axis, and observed scores are plotted on the Y-axis. All three of the morphological variables extracted (bill width without cere, tail graduation, and tarsus length) were negatively correlated with proportion of time soaring (see text).

morphology and soaring. A strong correlation ( $R = 0.878$ ,  $P < 0.0001$ ;  $R = 0.849$ ,  $P < 0.001$  for the independent contrasts) was found with three characters (all of them entered with a negative sign): (1) width of bill (without cere), (2) tail gradation, and (3) length of tarsus (Fig. 6). Raptors that soar frequently have a short tarsus, narrow bill, and a square-cut tail. With respect to the flight apparatus alone, the number of primary notches was positively correlated with soaring ( $r = 0.599$ ,  $P < 0.01$ ;  $r = 0.570$ ,  $P < 0.05$  for the corresponding independent contrasts). Wing loading and aspect ratio together explained only 21% ( $P > 0.05$ ) of the variance in soaring frequency.

We also examined the claim by Jaksić and Carothers (1985) that linearized wing loading is related to the sit-and-wait versus active-flight continuum of hunting mode. We used ordinary multiple regression, with the first two principal components derived from the behavioral data as predictors (Fig. 7). The correlation ( $R = 0.801$ ,  $P < 0.001$ ;  $R = 0.536$ ,  $P > 0.05$  for standardized contrasts;  $R = 0.744$ ,  $P < 0.01$  for contrasts with equal branch lengths) indicated that wing loading is low in large species in which

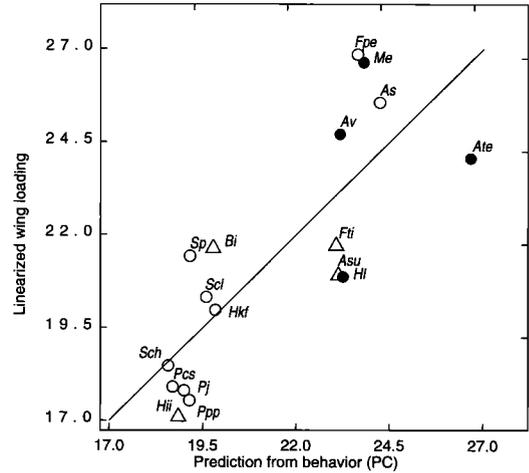


FIG. 7. Behavioral correlates of wing loading in Philippine raptors. Results are from a multiple regression of behavioral variables as predictors of linearized wing loading. Values predicted from the regression equation are plotted on the X-axis, and observed scores are plotted on the Y-axis. The two variables extracted were scores of PC1 and PC2 of the behavioral data. The Pacific Baza (Asu) was used as a surrogate for Jerdon's Baza in this analysis (see text).

foraging behavior is dominated by soaring in combination with a moderate proportion of sit-and-wait hunting.

#### DISCUSSION

Our analyses revealed consistent components of morphological covariation with foraging habitat and behavior. We also showed that the relationships among foraging behavior, habitat, and morphology to a large extent are independent of phylogenetic relationships. The shape variables that were the most important components of morphological variation pertain to characters that usually are not measured at all—wing shape and the feet. Features of the bill figured only marginally in this variation. One of the most popular characters in ecomorphological studies, tarsus length, did not contribute substantially to the three major components of morphological variation, and even wing length was not very important as a shape variable. The correlation analyses yielded similar results, although tarsus length was relevant for predicting the frequency of soaring (see below). Our findings stress how important

it is to work with sufficiently large morphological character sets (Leisler and Winkler 1985, 1997), and they should be considered when discussing results obtained in studies based on character sets restricted in number or on the functional complexes to which they belong (e.g. Schoener 1984, Hertel 1995).

Several studies have discussed the flight style of raptors with respect to wing loading and aspect ratio (Pennycuick 1975, Rayner 1988, Jaksic and Carothers 1985, Janes 1985, Kerlinger 1989, Norberg 1981, 1990). These characters were not the best predictors of the frequency of certain flight modes in our study. Soaring, for instance, was best predicted by the number of notched primaries, and its close relationship with features of the feeding apparatus hints at the complex web of factors that may influence the evolution of behavioral and morphological traits. Wing loading and aspect ratio were not correlated significantly with soaring frequency. Although Rayner (1988) found it surprising that soaring hawks have low aspect ratios, subsequent discussions of the subject stressed that long wings may be disadvantageous for taking off from perches and that thermal soaring requires a small turning radius (see Norberg 1990). Our findings confirm the notion that for raptors that are limited in wing span (and hence have low aspect ratio and rounded wings), notched primaries are the appropriate alternative to reduce induced drag (Pennycuick 1972, Withers 1981, Kerlinger 1989, Norberg 1990). This, and the fact that low wing loading also is related to other aspects of flight performance (i.e. slow flight; Norberg 1990), may be responsible for the poor predictions derived from aspect ratio and wing loading alone. The hypothesis that raptors with high wing loading typically use sit-and-wait hunting modes, whereas species with low wing loading are active-search foragers (Jaksic and Carothers 1985), was supported by our data. However, light wing loading also was characteristic of most species for which sit-and-wait hunting was an important component of foraging.

Our correlative results concur with ideas developed by Rochon-Duvigneaud (1952) and Voous (1969) on the functional and ecological importance of talon length, and they also stress that associated features, such as talon diameter and toe length, are relevant. Habitat, diet, and

foraging mode may be considered independent niche dimensions (Price 1991), or they may be seen as completely congruent with each other. Although Rosenzweig (1985) adheres to the latter view, Price (1991) showed that within *Phylloscopus* warblers, foraging behavior and habitat use largely are independent. Janes (1985) found no strong or consistent relationships between habitat structure and the foraging behavior of hawks. In our study, hunting behavior correlated well with habitat use, and the morphological predictors for habitat use and locomotion obtained with stepwise multiple regression revealed the complex interactions among these functions. We conclude that habitat use and foraging are neither completely equivalent nor uncorrelated with one another. This is due, at least in part, to morphological constraints posed by conflicting demands of hunting, migration, and habitat use (Winkler and Leisler 1985, 1992).

Forest-dwelling raptors are small, and they have short, rounded wings as a general adaptation to flight in dense vegetation. This results in a low aspect ratio and moderately high wing loading, and therefore a rather energetically expensive flight mode (Jaksic and Carothers 1985, Kerlinger 1989, Norberg 1990). High-speed powered flight can be attained only by flying at a speed that is a large multiple of minimum-power speed (Pennycuick et al. 1994). Thus, a sit-and-wait strategy combined with short pursuits is the most economical hunting mode for raptors in the forest interior but is not possible in open areas that lack suitable perches, even if prey are abundant (Preston 1990, Widén 1994). The accipiters are typical representatives of this group; only the migratory Chinese Goshawk, with the longest wing tip of the genus (Wattel 1973), hunts most frequently above the forest.

Larger species are not able to hunt within densely vegetated areas. Therefore, they rely on the soaring mode of hunting, and they often perch in tree tops from which they launch their attacks. Their flight apparatus can be considered a compromise among various constraints. The wings are not too long, because these raptors need to dive into the canopy (see also Brown 1976). Among the species that inhabit open and semiopen habitats, the four winter visitors are completely independent of forest habitats. Species of open habitats, particularly

migrants, are characterized by high aspect ratios and long, pointed wings. These morphological specializations support, among other things, efficient long-distance flight (Winkler and Leisler 1992, Yong and Moore 1994, Mönckönen 1995) and prevent these species from overlapping with species of the forest interior in morphology, behavior, and habitat requirements (Thiollay 1985).

In the Philippines, 13 species occur primarily in tropical rain forest, including the most endangered species observed during our field work, the Philippine Eagle (*Pithecopaga jefferyi*; Kennedy 1977). Eight of these species are obligate inhabitants of mature rain forest. Their main prey, relatively large mammals and birds, also are restricted to these forest habitats. Some of these species also use secondary rain forests to some extent. These areas, however, are rather small and short-lived, and because of extensive exploitation, these forest remnants usually are converted within a few years into grasslands. Owing to the deterioration of the environment through human activities (e.g. Salvador 1994, Thiollay 1994, 1996), all forest species are nearing extinction. Those residents needing only a minimum of forest have similar morphological characteristics developed as adaptations for hunting over open surfaces, e.g. lakes, shores, or the air space high above the forest canopy. After deforestation, these species were able, to some extent, to exploit new habitat types such as grasslands or rice fields. Not actually threatened are the winter visitors. Members of these species find sufficient habitat in which they appear to thrive. That species of primary forests are the most threatened has been stated for Sumatra, involving in part the same or closely related species, and for other nearby tropical countries (Thiollay 1996). Our study sheds some light on the ecological relationships underlying the conservation of these raptor species and how they were shaped by ecomorphological constraints.

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APPENDIX. Species treated in this paper and their diets. Our observations augmented by data from Brown and Amadon (1969), Wattel (1973), Kennedy (1977), Cade and Digby (1982), H. Miranda (pers. comm.), Marchant and Higgins (1993), and del Hoyo et al. (1994). Diet: (?) = possibly, (o) = occasionally, (+) = regularly, (++) = frequently, (+++) = very frequently.

Code	Species	Diet	
<b>Hunting above the forest</b>			
Ppp	<i>Pernis ptilorhyncus philippensis</i>	Oriental Honey-Buzzard	Wasp larvae (+++), frogs (+), lizards (+), small nestlings (+)
Pcs	<i>Pernis celebensis steerei</i> <i>Pernis celebensis winkleri</i>	Barred Honey-Buzzard	Wasp larvae (+++), frogs (?), lizards (+), small nestlings (+)
Sch	<i>Spilornis cheela holospilus</i>	Crested Serpent Eagle	Reptiles (+++), small birds (+), small mammals (++)
As	<i>Accipiter soloensis</i>	Chinese Goshawk	Insects (+), frogs (++), lizards (+), small birds (+), small mammals (+)
Pj	<i>Pithecophaga jefferyi</i>	Philippine Eagle	Reptiles (+), medium and large birds (++), medium and large mammals (+++)
Hkf	<i>Hieraaetus kienerii formosus</i>	Rufous-bellied Eagle	Small and medium birds (++)
Scl	<i>Spizaetus cirrhatus limnaetus</i>	Changeable Hawk-Eagle	Reptiles (+), medium and large birds (++), small to large mammals (+)
Sp	<i>Spizaetus p. philippensis</i> <i>Spizaetus p. pinskeri</i>	Philippine Hawk-Eagle	Reptiles (o), small birds (+), medium birds (+++), small mammals (+)
Fpe	<i>Falco peregrinus ernesti</i>	Peregrine Falcon	Small birds (++), medium birds (+++)
<b>Hunting in the forest interior</b>			
Ajn	<i>Aviceda jerdoni magnirostris</i>	Jerdon's Baza	Insects (+++), frogs (+), lizards (+)
Av	<i>Accipiter virgatus confusus</i> <i>Accipiter virgatus quagga</i>	Besra	Small birds (+++), small mammals (+)
Ate	<i>Accipiter trivirgatus extimus</i>	Crested Goshawk	Lizards (+), small birds (++), medium birds (++), small mammals (+)
Me	<i>Microhierax e. erythrogegnys</i> <i>Microhierax e. meridionalis</i>	Philippine Falconet	Insects (+++), especially dragonflies, butterflies and cicadas; small birds (o)
<b>Hunting outside the forest</b>			
Ech	<i>Elanus caeruleus hypoleucus</i>	Black-shouldered Kite	Insects (+++), lizards (+), small mammals (+++)
Hii	<i>Haliastur indus intermedius</i>	Brahminy Kite	Carrion (++) , grasshoppers (+), fish (+), frogs (+), reptiles (+), small birds and mammals (+)
HI	<i>Haliaeetus leucogaster</i>	White-bellied Sea-Eagle	Carrion (o), fish (+++), reptiles (+), medium and large mammals (o)
Cs	<i>Circus spilonotus</i>	Eastern Marsh Harrier	Carrion (o), insects (+), fish (o), frogs (++) , lizards (+), small birds (+), small mammals (++)
Cm	<i>Circus melanoleucos</i>	Pied Harrier	Insects (++) , frogs (+), lizards (+), small birds (+), small mammals (+++)
Bi	<i>Butastur indicus</i>	Grey-faced Buzzard	Fish (o), frogs (++) , reptiles (++) , small mammals (++)
Fti	<i>Falco tinnunculus interstinctus</i>	Eurasian Kestrel	Insects (++) , reptiles (+), small birds (o), small mammals (++)
Fss	<i>Falco severus severus</i>	Oriental Hobby	Insects (+++), small birds (++) , bats (++)