FEEDING HABITS AND BILL POLYMORPHISM IN HOOK-BILLED KITES

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ABSTRACT.—The Hook-billed Kite (*Chondrohierax uncinatus*), a neotropical, snail-eating raptor, exhibits extraordinary intraspecific variation in bill size, which is unrelated to sex and age and is largely independent of geographic origin. Bill size varies much more than overall body size and is bimodally distributed in many parts of the kite's range. Plumage is also highly variable; sex and age differences, individual variation, and a distinct melanistic phase exist. Variations in bill size and plumage are unrelated. Variation in bill size is best interpreted as a polymorphism evolved and maintained by disruptive selection, although the possibility that there might be two species of Hook-billed Kites cannot be completely ruled out. Kites of different bill size feed differentially on snails of different sizes by using a unique snail-extraction procedure not previously described. The distribution of bill sizes within regional populations of kites is correlated strongly with the sizes of terrestrial snails found in the region. Except for cases of sexual dimorphism, there are few, if any, other examples of a morphometric trait being polymorphic in birds. The ecological, evolutionary, and taxonomic implications of bill polymorphism are discussed. *Received 19 February 1981, accepted 31 August 1981.*

THE Hook-billed Kite (*Chondrohierax uncinatus*), a neotropical, snail-eating raptor, shows extreme individual variation in bill size and plumage. Brown and Amadon (1968) have pointed out that this intraspecific variability is greater than in any other bird of prey. Beginning with the early work of Des Murs (1855), the variation in bill size has generated considerable controversy, especially among taxonomists. It was generally agreed that the extreme variation in bill size of Hook-billed Kites (Fig. 1) was unique among raptors, but there was disagreement over whether the distribution of bill sizes was continuous. The plumage variation of the Hook-billed Kite is also more variable than that of any other raptor and includes melanistic phases and sexual dichromatism, as well as considerable individual variation. For the nominate race, Friedmann (1934) described three different color varieties for males and two for females.

The objectives of this paper are: (1) to show the relationships in Hook-billed Kites between bill size and sex, age, plumage and mensural traits, and geographical region; (2) to describe the feeding habits of Hook-billed Kites, especially how bill size relates to the size of snail eaten; and (3) to propose possible explanations for the occurrence of the extraordinary variations in bill size and plumage.

METHODS

EXAMINATION OF MUSEUM SPECIMENS

We examined bill and plumage variation in 358 museum specimens of Hook-billed Kites. For each specimen 27 mensural and scored characters were recorded. To facilitate statistical comparisons, the specimens were classified by age, sex, and geographical region.

Age determination.—Adults were differentiated from juveniles on the basis of the number of bands on the tail (in the typical phase adults have three, juveniles have four; in the melanistic phase adults have one, juveniles have two). We double-checked this age difference by looking for the presence of "fault bars" (Hamerstrom 1967) at the same point on adjacent tail feathers.

Sex determination.—Because adult kites are sexually dichromatic, sex was easily determined in most cases. Juvenile and melanistic birds, however, could be sexed only if the collector had noted sex and recorded gonadal weights or size or if some adult feathers were present in the juvenile plumage.

Regions.—On the basis of major geographical barriers and Haffer's (1974) zoogeographical regions, we defined nine geographic subdivisions of the Hook-billed Kite's range (Fig. 2). The subdivisions allowed us to compare inter- and intraregional variation in mensural and plumage characters. The nine regions are: (1) Cuba, (2) Grenada, (3) eastern Mexico, (4) western Mexico, (5) Central America, (6) western South America (west of Andes), (7) northern South America, (8) central South America, and (9) southern South America.

The Auk 99: 197–207. April 1982

Fig. 1. Profiles of large- and small-billed kites collected in the same region of eastern Peru. Bills are drawn to the same scale from photographs.

Plumage characters.—We classified plumage patterns using three characters: (1) presence or absence of a nuchal collar; (2) pattern of breast (solid dark, dark bars wider than light bars, light bars equal to dark bars, light bars wider than dark bars, and solid light), and (3) number of light and dark tail bands. Breast and dorsum coloration was scored on a linear scale using the color standards of Ridgway (1912).

Size characters.—We took the following linear measurements in accordance with the methods described by Baldwin et al. (1931): (1) length of closed wing; (2) tarsus length; (3) tail length; (4) toe length; (5) claw length; and (6) length of exposed culmen without cere. In addition, bill size was determined by photographing the bill from the side and measuring the silhouette area of the upper mandible. We mounted the camera on a tripod above the specimen and attached a plumb bob to the camera to assure that the camera lens was perpendicular to the sagittal plane of the upper mandible. A ruler was placed in the sagittal plane of the upper mandible for scale. We took a photograph, placed the resulting negative in a photographic enlarger, and enlarged the image to scale. The profile or silhouette area of the upper mandible was then measured using either a planimeter or a dot grid.

Statistical analyses were done using the computing facilities at the University of Wisconsin–Madison. Unless otherwise stated, a significant difference was taken to mean a 5% level of probability or less ($P < 0.05$).

Field Studies

We studied Hook-billed Kites in the field in Mexico during June and July 1979 and January, February, and May 1980. Research took place in the State of Tamaulipas in northeastern Mexico and along the Pacific coast of Mexico in the States of Sinaloa, Nayarit, Jalisco, Colima, Guerrero, Oaxaca, and Chiapas. Field work was also conducted in south Texas during May 1979, in western Peru during January 1980, and on the island of Grenada in July 1980.

The feeding ecology of Hook-billed Kites was studied in several ways. During the breeding season, we constructed blinds near active kite nests and observed the feeding behavior of the adult birds and the types and sizes of snails they brought to the nests. During the nonbreeding season, we observed foraging kites by following individual birds in areas where they fed frequently. When a foraging kite was observed, we recorded its bill size and the type and size of snail upon which it fed. Determining the size of a kite's bill in the field was relatively easy in most instances; the birds usually allowed us to observe them closely, and large-billed birds have bills that are frequently over twice the size of those of small-billed birds. We determined the sizes of snails available to kites by collecting both live snails and empty shells in regions where kites occurred. We also collected remains of extracted snails from beneath nests or perches where kites had fed.

Results

Sources of Variation in Bill Size

Sex and age.—Within each of the nine geographic regions, we used *t*-tests to compare the bill size of kites of different sex and age. We found no significant differences between adult males and adult females, between all adults and all juveniles, or between birds of known sex and age and birds of unknown sex and age. We conclude there is no relationship between bill size and the sex or age of the kite. Furthermore, large-billed kites were found in all sex and age classes.

Geographical region.—Average bill size differed significantly between the nine geographic regions, but within each region, except Grenada and Cuba, the range of variation was extreme (Table 1). In the seven continental regions, coefficients of variation for bill area

Fig. 2. Distribution of Hook-billed Kite specimens within the nine geographic regions.

were between 15 and 42%. Furthermore, in the four regions where coefficients of variation for bill size were highest (western Mexico, central, western, and southern South America), bill sizes were not normally distributed (Fig. 3) and appeared bimodal. The birds with the largest bills of any specimens in our sample came from these four regions. Some large-billed specimens from Peru had bills three times the size of birds collected in the same region (Fig. 1 and 3); similarly, large-billed specimens from western Mexico had bills over twice the size of small-billed specimens collected from the same region.

There was no geographic segregation of large-billed birds in any of the regions. Rather, we found that both large- and small-billed kites had been collected during the same year (in some instances during the same day) from the same locality.

Body size.—Of eight highly intercorrelated measurements, we used wing length to index body size. Wing length was significantly correlated with bill area in every region except Cuba and southern South America. Wing length remained significantly correlated with bill area in five of the nine regions even after large-billed birds were removed from the sample. Like bill size, mean wing length was significantly different between regions, but the intraregional variation in wing length was not as extreme (Table 2). The greatest regional coefficient of variation for wing length was 5%, several times less than that of bill size. We could discern no pattern of wing-length variation within the range of the kite.

Plumage characters.—From t-tests and pairwise correlations, we found no significant relationship between bill size and plumage color or pattern.

TABLE 1. Variation in bill size of Hook-billed Kites within geographic regions.

Geographic region	Number of specimens	Mean bill area ± SD (cm²)[a]	Coefficient of variation (%)
Cuba	23	3.19 ± 0.33	10
Grenada	10	2.07 ± 0.20	10
Eastern Mexico	32	1.98 ± 0.37	19
Western Mexico	48	3.03 ± 0.91	30
Central America	54	2.07 ± 0.32	15
Western South America	71	2.41 ± 1.06	42
Northern South America	29	2.19 ± 0.40	20
Central South America	46	2.41 ± 0.91	38
Southern South America	34	2.04 ± 0.59	30

[a] Analysis of variance showed a significant difference in bill size between regions ($F = 10.58$; df = 8,338; $P < 0.001$).

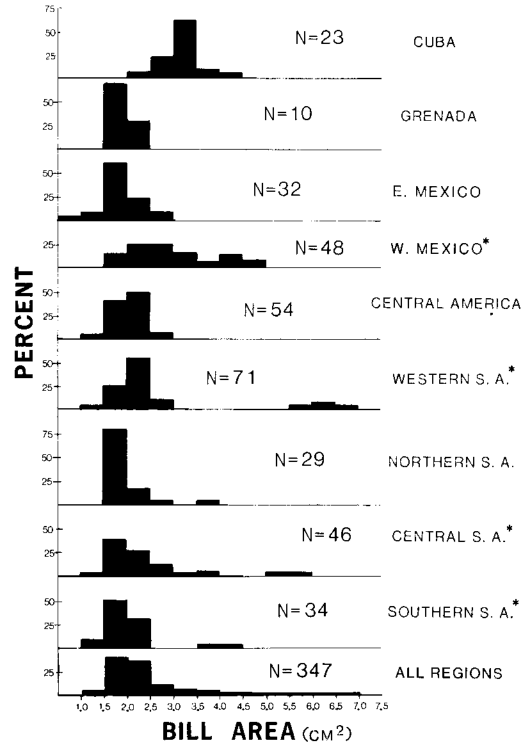

Fig. 3. Frequency distributions of bill sizes of Hook-billed Kites from each geographical region. Regions marked with asterisks have distributions that are significantly different from normal ($P < 0.05$) on the basis of Chi-square goodness-of-fit tests.

Island populations.—Bill size varied little in both island populations of Hook-billed Kites and was normally distributed (Table 1). Coefficients of variation were 10% on both Cuba and Grenada, a third less than the values for the least variable continental region. The coefficients of variation for wing length in both island populations were similar to those from continental regions (Table 2).

SOURCES OF VARIATION IN PLUMAGE PATTERN AND COLOR

Sexual variation.—Sexual dichromatism is marked in Hook-billed Kites. In general, females tend to have brown-barred breasts, most being russet, and brown dorsums, most being fuscous. Males tend to have gray-barred breasts, usually deep neutral gray, and gray dorsums, usually dark neutral gray, but the shades of brown and gray vary within each sex.

Age variation.—In general, juveniles of both sexes have the same plumage color as adult females. Juveniles have 4–5 bands in the tail, whereas adults have 2 or 3. Juveniles also tend to have darker heads, and the breast is often incompletely barred.

Geographical variation.—Using Chi-square tests, we found no significant differences in plumage color or pattern among continental regions within the different sex and age groups except Central America, where there was a high proportion of adult females that had unusually dark-colored dorsums. Melanistic kites were found in all regions except the islands. Mexican kites, which Friedmann (1934, 1950) described as a distinct race, *C. u. aquilonis*, on the basis of adult male coloration, showed no significant differences in plumage characters from kites in other continental regions.

Island populations.—Chi-square tests of plumage characters showed the two island populations to be significantly different from continental kites in plumage color and pattern. These differences have been described previously by Friedmann (1934) and Amadon (1960).

FOOD HABITS AND FEEDING BEHAVIOR

Our observations of Hook-billed Kites support previous suggestions (Haverschmidt 1962, Fleetwood and Hamilton 1967, Delnicki 1978) that kites feed almost exclusively on tree snails, although other types of prey may be taken rarely (Brown and Amadon 1968). It has been assumed that the unusual bill of the Hook-billed Kite is in some way adapted for extract-

TABLE 2. Variations in wing length of Hook-billed Kites within geographic regions.

Geographic region	Number of specimens	Mean wing length ± SD (cm)[a]	Coefficient of variation (%)
Cuba	20	25.3 ± 0.8	3
Grenada	12	25.5 ± 1.2	5
Eastern Mexico	33	27.9 ± 1.2	4
Western Mexico	48	29.6 ± 1.2	4
Central America	54	28.4 ± 1.5	5
Western South America	67	28.5 ± 1.2	4
Northern South America	31	27.9 ± 1.1	4
Central South America	53	28.4 ± 1.3	5
Southern South America	34	28.3 ± 1.3	5

[a] Analysis of variance showed a significant difference in wing length between regions ($F = 27.59$; df = 8,343; $P < 0.001$).

ing snails from their shells (Wetmore 1965, Brown and Amadon 1968, Paulson 1973), but no one has described how the bill functions.

Our observations of both large-billed and small-billed kites feeding in Colima and our observations of small-billed birds feeding in Tamaulipas indicate that all kites, irrespective of bill size, extract snails from their shells in the same fashion. Typically, after a kite removes a tree snail from the vegetation with its bill, it flies to a branch and transfers the snail to the left foot. Bracing the shell against the perch with the left foot (or both feet if the snail is large) with the aperture of the shell facing the bill (Fig. 4), the kite pierces and removes the epiphragm (a dried membrane covering the aperture), wiping its bill several times on the perch to remove any adherent pieces of the shell or epiphragm. Usually, the shell is then chipped away to enlarge the diameter of the aperture. The kite then inserts its bill into the aperture of the shell and, using the wall of the outer body whorl as a fulcrum and upper mandible as a lever, breaks the inner whorls of the shell by driving the tip of the bill toward the apex of the spire of the shell. By breaking each consecutive inner whorl with the tip of the bill, the kite frees the body of the snail from the shell, leaving very characteristic damage to the shell (Figs. 4 and 5). The extracted snail is then swallowed whole.

In observations of over 60 extractions, we found only slight individual variation in this method. For example, one female, rather than bracing the shell against the perch, held the snail off the perch, almost parrot-like, in her left foot and moved the snail back and forth with her foot while inserting her bill into the aperture. The method used by Hook-billed Kites to extract snails from their shells is very different from the methods used by a variety of other snail-eating birds described by Snyder and Snyder (1969).

BILL SIZE AND SNAIL SIZE

We found that kite bill size was closely related to the sizes of common tree snails found in a given region. For example, in Tamaulipas, Mexico, where only small-billed kites have been collected and observed, Hook-billed Kites fed solely on the small tree snail *Rabdotus alternatus,* the only snail available to kites in this region (Smith in press). Similarly, on Grenada, where kite bill size is relatively small and uniform, we observed kites feeding on the tree snail *Bulimulus wiebesi* and found evidence (i.e. kite-extracted shells) that they may occasionally feed on *Endolichotus grenadensis;* both snails are of essentially the same small size (Smith and Temple in press).

On the other hand, in Colima, Mexico, where both large- and small-billed kites occur in sympatry, we found that kites fed on two distinctly different size classes of snails: a larger tree snail, *Orthalicus ponderosus,* and a smaller tree snail, *Dryameus colimaensis* (Fig. 5). While individuals of *D. colimaensis* are very uniform in size, snails of the genus *Orthalicus* occur in different size classes, which apparently correspond to different ages (Comfort 1957). Age-related size classes occur in the genus *Orthalicus* because these snails live for more than 1 yr but grow and reproduce only during the short rainy season (July–September). On the other hand, *D. colimaensis* and *R. alternatus* generally live less than 1 yr and reach full size very rapidly, thus producing only one uniform size class.

In areas where both large- and small-billed birds occur sympatrically, we were unable to locate breeding pairs. Kites were very scarce, and only in two instances in western Mexico were we able to determine the bill size of the kite and simultaneously collect and measure the size of snails on which it fed. These observations were of a large-billed kite feeding

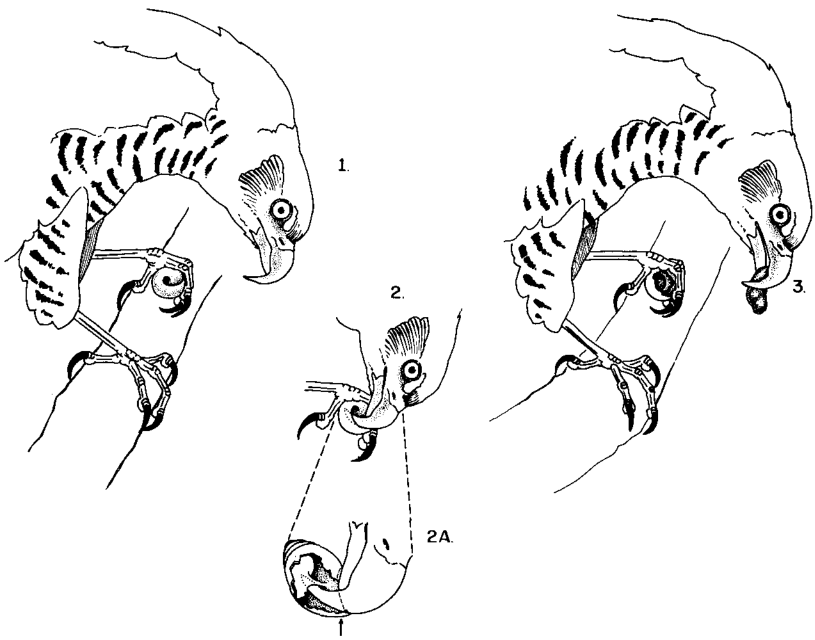

Fig. 4. Hook-billed Kite extracting snail. (1) Kite holds snail in left foot. (2) Kite places bill into the aperture and, using the outer wall of the whorls as a fulcrm and the bill as a lever, breaks the inner whorls of the shell by forcing the tip of the bill towards the apex of the spire. (2A) Cut-away of tip breaking inner whorls of shell; arrow shows fulcrum. (3) Kite holding extracted snail.

on the large size-class of *O. ponderosus* and of a small-billed kite feeding on the small size-class of the same species.

DISCUSSION

VARIATION IN BILL SIZE

The extreme variation in bill size in Hook-billed Kites appears to be unique among birds. For comparison, we calculated coefficients of variation in length of exposed culmen in two common raptors that have wide geographic distributions: the Red-tailed Hawk (*Buteo jamaicensis*) and the American Kestrel (*Falco sparverius*). The culmen length in Hook-billed Kites is twice as variable as that in either of these two raptors (Table 3).

Interspecific differences in bill size are often interpreted as being a mechanism that allows two species to coexist because they exploit prey of different sizes (Lack 1944). Discontinuous variation in bill size, however, may also be present within the same species. Selander (1966) examined sexual dimorphism in birds and described several examples of extreme sexual differences in bill morphology that tended to reduce intraspecific competition. Similarly, Schoener (1968) found morphological differences between sex and age classes to be important in reducing intraspecific competition. Whether morphological differences occur between species or within species, by age-class or sex, the results are similar: a reduction of competition through expanding and partitioning available resources.

In Hook-billed Kites, however, if large-billed and small-billed birds were considered to be conspecific, the variation would have to be explained outside the context of sexual dimorphism or differences in age classes. We found that sex and age were unrelated to bill size. There are at least three alternative explanations, however, for the unusual variation in bill size in Hook-billed Kites: (1) Hook-billed Kites consist of two distinct, sympatric species, a large-billed species and a small-billed species; (2) there are distinct races, a large-billed race and a small-billed race; or (3) Hook-billed Kites are polymorphic in bill size, and

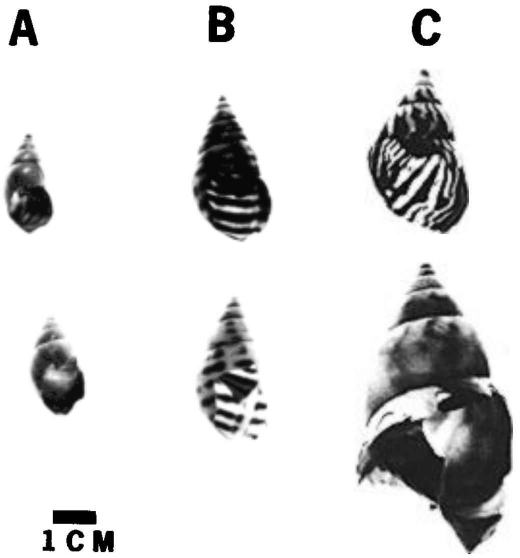

Fig. 5. Typical kite-damaged shells collected from eastern and western Mexico, showing the species of terrestrial snails on which kites feed in these regions. (A) *Rabdotus alternatus* from Tamaulipas; (B) *Drymaeus colimaensis* from Colima; (C) *Orthalicus ponderosus* from Colima, both size classes. Snail specimens were deposited in the University of Wisconsin Zoological Museum (Accession No. 81-1).

there are large-billed and small-billed morphs. The three explanations are discussed below.

Are there two distinct species of Hook-billed Kites?—Bill sizes in western, central, and southern South America and western Mexico appear bimodally distributed, and in each region there is an unusually high coefficient of variation, suggesting the possibility that the sample may contain more than one species. But variation in bill size in other regions is also high, even though not bimodal (Table 1).

Variation in bill size of the magnitude seen in Hook-billed Kites is great, even for congeneric, sympatric species. Schoener (1965), comparing several hundred congeneric, sympatric species of birds from 46 different families, found the Merlin (*Falco columbarius*) and Peregrine Falcon (*F. peregrinus*) to show one of the highest ratios of mean culmen lengths. For these two sympatric, congeneric falcons the ratio of culmen lengths was 1:1.57. By comparison, the ratio of the means for small- and large-billed kites from western South America, calculated in a similar way, was 1:1.6. One

TABLE 3. Variation in culmen lengths of three raptors (irrespective of age, sex, and geographical region).

Species	Number of specimens	Mean culmen length ± SD (mm)	Coefficient of variation (%)
Hook-billed Kite	347	31.7 ± 4.3	14
Red-tailed Hawk	99	25.3 ± 1.8	7
American Kestrel	385	11.9 ± 0.9	7

generally finds body size in sympatric species of raptors differing as much or more than bill size (Schoener 1965). Schoener (1965) found the mean ratio of wing lengths of the Merlin and Peregrine Falcon to be 1:1.66, which is similar to the ratio of culmen lengths of these two species. In contrast, the coefficient of variation for wing length in Hook-billed Kites was much less than for bill size (Tables 1 and 2). The ratio of the mean wing lengths of small- and large-billed kites was 1:1.1, considerably less than the 1:1.6 ratio of culmen length. This suggests that if large- and small-billed birds are separate species, they are atypical in bill size and wing-length variation when compared to the several hundred conspecific, sympatric species described by Schoener (1965). In addition, large- and small-billed kites cannot be differentiated from one another by plumage pattern or color, which is unusual, though not unique, for congeneric, sympatric species. Furthermore, during our field work in Mexico, we found the habitat, feeding behavior, and vocalizations of large- and small-billed kites to be indistinguishable.

If two species existed, there should be assortive mating on the basis of bill size. It was impossible to test strictly whether or not large- and small-billed kites mated assortively, because we were unable to find breeding pairs in regions where birds of both types occurred sympatrically. In western Mexico we did, however, observe a possible family group, a small-billed kite in immature plumage foraging in close company with an adult pair of which the female had a large bill. Lacking data on assortive mating, we believe that the available evidence fails to support the hypothesis of two distinct species of Hook-billed Kites.

Are there distinct races characterized by bill *size?*—If large- and small-billed races, rather than separate species, occurred, we could account for the morphological and plumage similarities shown by kites of different bill types. By most definitions (e.g. Mayr 1963), however, subspecies must occupy geographically distinct subdivisions of a species' range. This clearly is not the case in Hook-billed Kites; large-billed and small-billed birds occur in sympatry over wide geographic areas, and neither bill type is restricted to a unique geographic region.

Is bill size polymorphic in portions of the kite's range?—Although the unusual distributions of bill size cannot be explained by sex or age differences, an alternative explanation is that Hook-billed Kites are polymorphic in regions where bill size appears bimodally distributed. Polymorphisms in plumage color and pattern are well documented in birds (Huxley 1955, Selander 1971), but, excluding cases of sexual dimorphism and one possible case of polymorphic bill sizes in Darwin's finches (Grant and Grant 1979), there are no known examples of a morphometric character being polymorphic in birds.

In most instances of polymorphism in birds, the selective advantage of the different morphs is poorly understood (Selander 1971). Color phases have been correlated with humidity and temperature (Selander 1959); these correlations with climatic conditions are believed to represent weakly adaptive traits, however, which are associated with more subtle physiologial traits (Selander 1971). In one of the few instances in which a physiologial trait has been related to color phase, Mosher and Henny (1976) found that color phase in Screech Owls (*Otus asio*) was related to metabolic differences that allowed one phase to dominate the other in the colder portions of the species' range.

A polymorphism in a morphometric trait, such as bill size, offers a unique opportunity for examining the adaptive significance of polymorphism. The adaptive significance of a polymorphism in bill size in Hook-billed Kites should be related to their feeding ecology and the advantage of separate feeding subniches. We have shown that bill size in Hook-billed Kites is directly related to the sizes of snails that are present in a region. We therefore conclude that it is most likely that Hook-billed Kites exhibit polymorphism in bill size in portions of their range. At present, this is the only explanation that is compatible with all of the observed characteristics of bill size, body size, plumage traits, geographic distributions, and field observations.

RELATIONSHIP BETWEEN BILL SIZE AND SNAIL SIZE

This bill polymorphism in Hook-billed Kites appears to be the result of disruptive selection in which large- and small-billed morphs are maintained in certain geographical regions through the selective advantage of feeding on distinct size classes of tree snails. Disruptive selection has been proposed as one mechanism that produces and maintains polymorphisms (Mather 1955, Mayr 1963, Dobzhansky 1970, Pianka 1978).

Although we have only a few pertinent observations, they all lead us to believe kites of different bill size feed on different size classes of snails. In addition to our field observations, which verify this, we believe it is very improbable that a small-billed kite could extract a large snail from its shell. A typical small bill is not large enough to fit snugly into the aperture of a large shell; this poor fit makes it difficult or impossible for small-billed kites to generate the leverage required to crush the inner whorls of a heavy shell with the tip of the bill. Small-billed kites, therefore, can feed only on small snails.

Birds usually feed on the largest food item that they can handle efficiently, and there is usually a strong positive correlation between bill size and the size of food items eaten (e.g. Lack 1947, Morris 1955, Hespenheide 1966, Myton and Ficken 1967, Newton 1967, Willson 1971). We believe large-billed kites should preferentially feed on large snails, because they are capable of extracting them from their shells and can obtain more energy per unit of feeding time. Furthermore, it seems likely that a large bill would be awkward to use in extracting small snails.

We believe the bill polymorphism is maintained in Colima, Mexico, because the small-billed morph feeds on the small tree snail *D. colimaensis* and the small age-classes of *O. ponderosus,* whereas the large-billed morph feeds on the larger age-class of *O. ponderosus.* In other regions of western Mexico where both morphs are found but where *D. colimaensis* does not occur, we believe the polymorphism is maintained by kites feeding solely on the discontinuous size classes of snails in the genus *Orthalicus* (mainly *O. sphinx*).

Another region where kites are polymorphic for bill size is in western South America, but, in contrast to western Mexico, where kites of intermediate bill size occur, in western South America bill size is discontinuously distributed (Fig. 3). In addition, large-billed kites from western South America have bills much larger than those found in western Mexico. Although our data regarding size classes of snails in all parts of western South America are incomplete, shells we collected at a locality in eastern Peru where large-billed birds had been collected suggest that kites do feed on species of tree snails that typically grow much larger than any species in Mexico.

Voous (1969) provides the only information on the species of snails taken by kites in central South America. He reported that a female (which we determined from his photograph to be a small-billed kite) collected in Surinam had its stomach filled with *Strophocheilus oblongus*, a very large species of tree snail. In fact, *S. oblongus* is one of the largest land snails in the western hemisphere (Webb 1948). Voous did not indicate the size class of *S. oblongus* that the kite had eaten, but, because this kite had a small bill, we suspect it had fed on a young age-class.

In Costa Rica, where only small-billed kites have been collected (Fig. 3), T. Moermond (pers. comm.) observed small-billed kites near Puerto Viejo feeding on a uniformly small-sized species of tree snail.

Variation in Bill Size on Islands

Bill size in the two island populations shows little variability. The coefficients of variation in bill size in both island forms are 10%, a third less than the least variable continental population. This is unusual for a species in which there are both continental and insular populations. Typically, island populations are freed from much of the interspecific competition associated with continental avifaunas, and they exploit a broader niche, a condition referred to as ecological release (Selander 1966). Allowed to occupy a wider niche, insular bird populations will often show greater morphological variability than their continental counterparts (Van Valen 1965). Selander (1966) compared insular and continental species of *Centurus* woodpeckers and found increased sexual dimorphism in bill size on islands. He attributed this difference to the scarcity of competitors.

On the other hand, island populations are often subject to the founder effect (Mayr 1963), and this could partly explain the relatively uniform bill size of island kites. We found, however, that the reduced variation in bill size of Hook-billed Kites on islands is also related to the sizes of snails available there. On the island of Grenada a very narrow size range of snails was available to the kites. This suggests that the kite's highly specialized feeding method may make ecological release difficult.

Evolution of Bill Polymorphism

We speculate that Hook-billed Kites were originally derived from an ancestral kite with a uniformly small-sized bill. Once the kite developed its specialized method of extracting snails from their shells, however, it became advantageous for intraspecific variation in bill size to increase, thus allowing the kites to exploit a broader size range of snails. We know of no interspecific competitors that would have prevented the resultant expansion of the kite's feeding niche.

Disruptive selection could have produced a polymorphism in bill size if a region had distinctly different sizes of snails with no intermediate size for kites to exploit. Directional selection may then have caused a further separation of the bill morphs to take advantage of larger or smaller snails in a particular region. In the case of dispersal to the Caribbean Islands, where a narrow size range of snails occurred, an appropriate uniform bill size was selected for, and individual variation was reduced in these populations.

Variability in Plumage

It is interesting that a species that shows such extreme variation in bill size also exhibits great individual variation in plumage, and yet the two variable characters are unrelated. Payne (1967) and Paulson (1973) have suggested that polymorphisms in the plumage of birds of prey may arise through apostatic selection, in which contrasting color phases are maintained by frequency-dependent selection. Prey, by learning to recognize the most common color phase of the predator, give the least common phase a selective advantage. As Paulson (1973) points out, apostatic selection clearly cannot operate in the Hook-billed Kite, because kites feed exclusively on terrestrial snails, which are incapable of recognizing and avoiding a particular color phase. The selective advantage of individual color variation and melanism in this species is not clearly understood and requires further work.

NOMENCLATURE AND SUBSPECIES

Friedmann (1934) was the first to describe both bill and plumage variation of the Hook-billed Kite thoroughly. Prior to his work, large-billed individuals were considered to be a separate species, *Chondrohierax megarhynchus* (Peters 1931). Friedmann, however, believed that *C. megarhynchus* was merely a large-billed variety. He did recommend, however, that extremely large-billed birds from western South America be given the subspecific designation, *C. u. immanis.* Hellmayr and Conover (1949) later pointed out that birds fitting the description of *C. u. immanis* also occurred in Mexico and indicated that kites of intermediate bill sizes occurred in both regions. Amadon (1964) later supported Friedmann's assessment that large-billed kites were somewhat geographically segregated, but he also concurred with Hellmayr and Conover that, because intermediates occurred in the same areas, all forms should be considered conspecific until fieldwork could prove otherwise.

Peters (1979) recognizes four subspecies of Hook-billed Kites. The nominate race, *C. u. uncinatus,* occurs in Central and South America; *C. u. aquilonis* occurs in central Mexico, and two island races are found on Cuba (*C. u. wilsonii*) and Grenada (*C. u. mirus*). Based on the results of our analyses of morphology and plumage pattern and color, we concur with the present subspecific designations for the two island populations. However, we find no basis for the subspecific designation *C. u. aquilonis,* first proposed by Friedmann (1934). We believe only the nominate race, *C. u. uncinatus,* occurs throughout the continental portions of the kite's range. Variations within *C. u. uncinatus* are attributable to individual differences and polymorphisms.

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