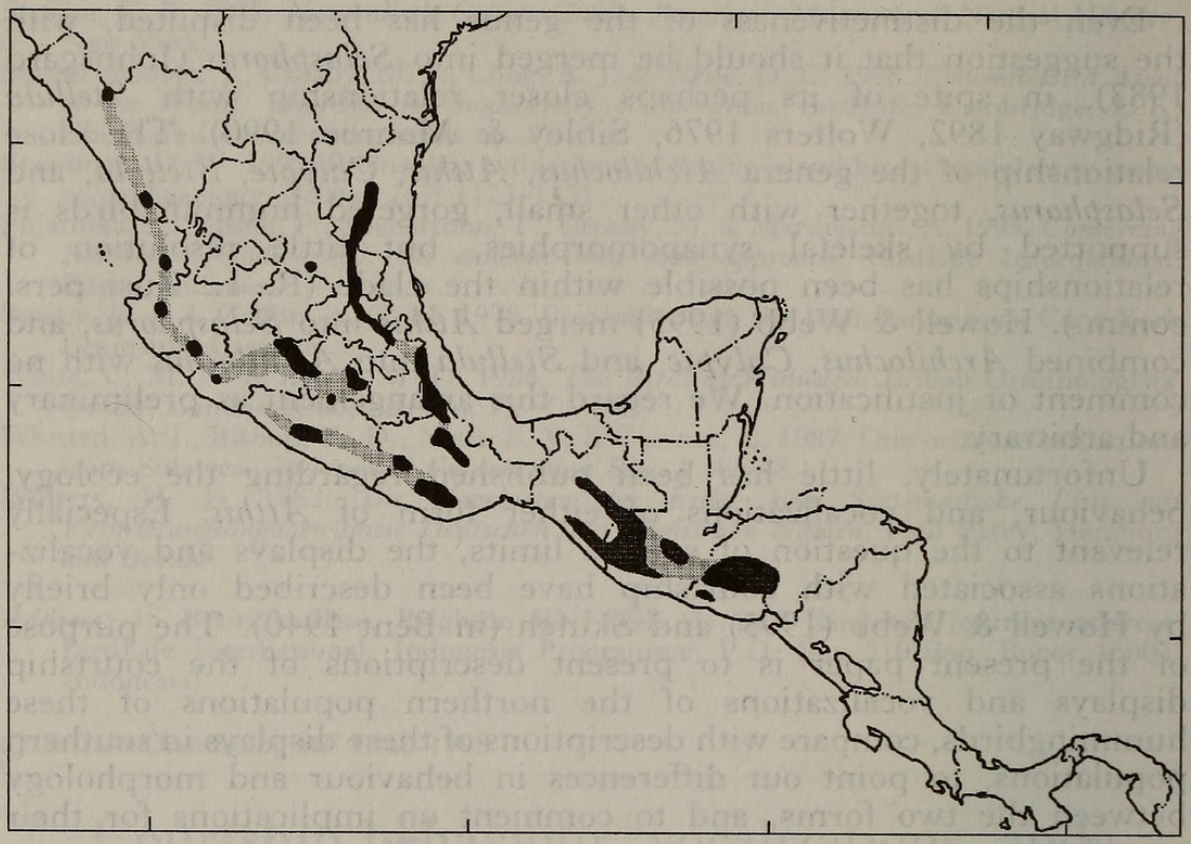

Figure 1. Distribution of hummingbirds of the genus *Atthis*. Black areas indicate populations of *A. heloisa*; dark grey indicates populations of *A. ellioti*; and light shading indicates probable continuity of populations in appropriate habitats.

of Kansas Natural History Museum, Field Museum of Natural History, Southwestern College, and the Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México. In all, we inspected 41 males and 13 females of the northern populations, and 7 males and 2 females of the southern populations. Additional specimen information was kindly provided by the Louisiana State University Museum of Natural Science.

Distribution

The distribution of *Atthis* hummingbirds generally follows the major mountain systems of northern Mesoamerica (Fig. 1). Populations assigned to *A. h. heloisa* range from central Tamaulipas south in the Sierra Madre Oriental to the Nudo de Zempoaltépetl of northern Oaxaca, in the interior in the vicinity of the Federal District and on Cerro San Felipe in northern Oaxaca, and through the Sierra Madre del Sur of Guerrero and Oaxaca; but the species was not detected on the peripheral montane forest island of Cerro Piedra Larga in east-central Oaxaca (Peterson *et al.* in prep.). An isolated population apparently occurs in southcentral San Luis Potosí in the vicinity of Alvarez; Salvin & Godman (1879–1904) reported a specimen, perhaps of doubtful veracity, collected by A. Dugés in Guanajuato (not

included on map for lack of a more specific locality). A specimen collected by Mario del Toro Avilés at "Montañas Gineta", Oaxaca, is an example of *A. h. heloisa* outside of that form's range, another example of that collector's notoriously unreliable labelling of specimen material (Binford 1989).

Populations referred to as *A. h. margarethae* are restricted to the coastal slopes in Sinaloa, Nayarit, and Jalisco, and then apparently in the Transvolcanic Belt east to western Estado de México. Their absence from the higher peaks of the main body of the Sierra Madre Occidental is odd, given their occurrence in similar habitats in the Transvolcanic Belt. Our limited reexamination of the characters used by Moore (1937) indicated that the differences appear real, although the distributional gap that he mentioned does not, based on ranges outlined in Friedmann *et al.* (1950) and Howell & Webb (1995). Two female specimens described as *A. morcomi* by Ridgway (1898) from southeastern Arizona appear to represent either stragglers or mislabelled specimens; Bangs (1929) pointed out that both fall completely within the range of variation of *A. h. heloisa*. Hummingbirds of this genus have not been found subsequently at the type locality, in spite of its extreme popularity among birdwatchers. Although these extralimital records might suggest seasonal or altitudinal movements, evidence available is insufficient to demonstrate this phenomenon convincingly.

Courtship behaviour

Observations of courtship behaviour of *A. h. heloisa* were as follows. Males were distributed relatively uniformly through the habitat, especially along ridgetops, frequently perching on high, exposed branches of *Podocarpus* sp. in disturbed vegetation along trails. Females were less obvious, often hidden nearby in dense vegetation closer to the ground. Individuals of both sexes were observed to feed low to the ground from red-flowered *Salvia* sp. (Lamiaceae) at Puerto de la Soledad, and from yellow-flowered *Palicourea galeottiana* (Rubiaceae) at San Martín Caballero.

Males sang from perches, and appeared to be consistent in their use of particular branches, being seen in the same positions on as many as 12 consecutive days. Vocalizations included a rather soft, short *tsi*! given by individuals of both sexes. Perched males, however, gave the same *tsi*!, followed by a thin whistling *weeeeeeeeeew* that rose and then fell in pitch, lasting a total of two or three seconds (Fig. 2), the whistled portion being reminiscent of songs of *Calypte costae* (Wells *et al.* 1978, KZ pers. obs.). Some immature-plumaged males at San Martín Caballero were heard to sing two or three repetitions of a briefer version of this song in quick succession, much as described by Wells *et al.* (1978) for *C. costae*.

Perched males oriented themselves towards nearby females, which were often perched or foraging. As frequently as once per minute, a male would fly to within 10 cm of a female and hover horizontally in front of her, spreading his gorget and cocking his spread tail vertically

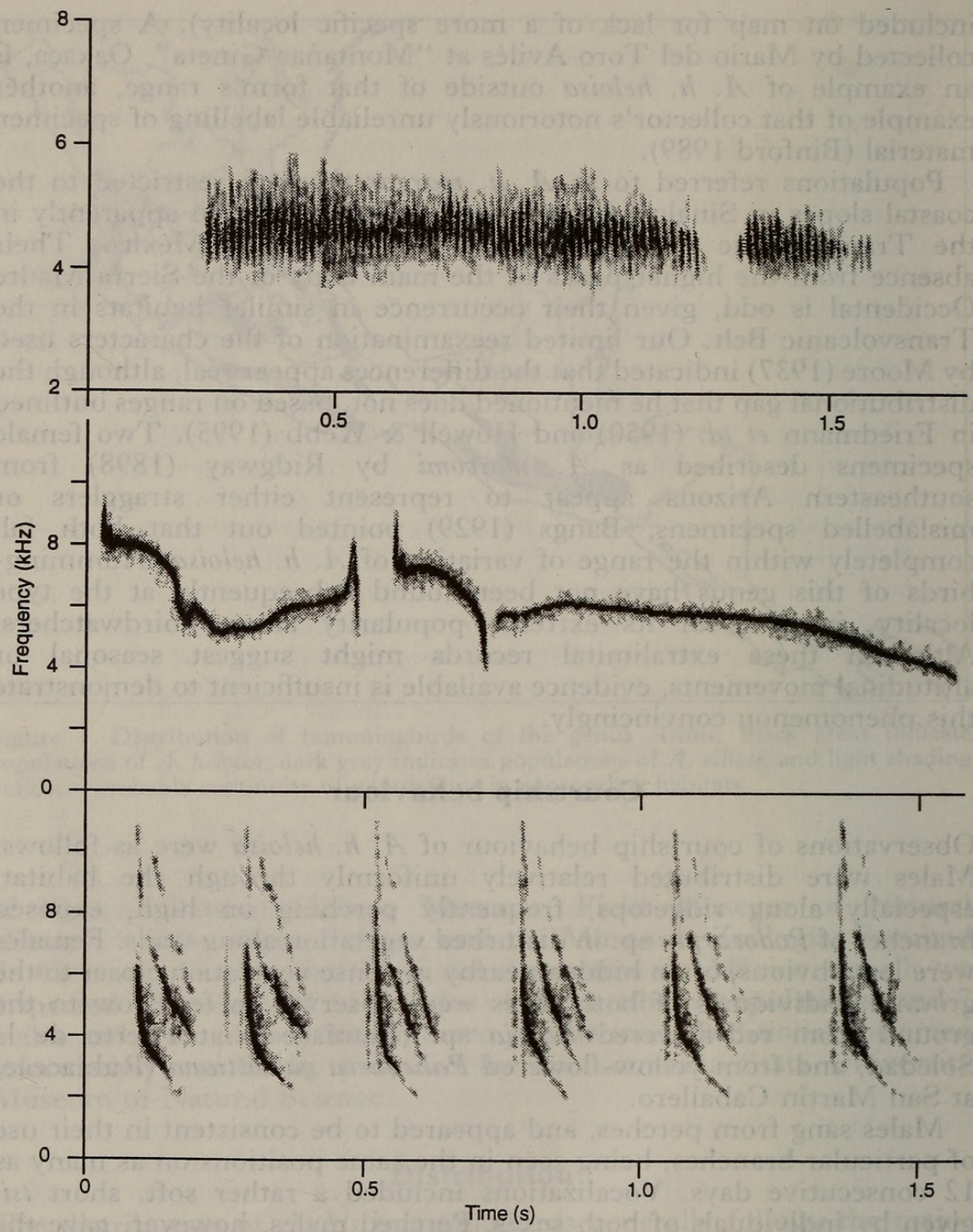

Figure 2. Sounds made by *Atthis* hummingbirds: wing noise (top) and song (middle) of *A. heloisa*, recorded in Jalisco, Mexico; and song of *A. ellioti* (bottom), recorded in El Salvador.

over his back, but was not observed to make any display dive, as do other related genera (Wells *et al.* 1978, Johnsgard 1983). During the hovering, the male's wings produced a wavering thrumming noise (Fig. 2; Robins & Heed 1951), and he often followed the female's movements closely. The noise produced by the wings was similar to that of courting *Selasphorus platycercus*, although somewhat softer (KZ pers.

obs.). Occasionally, while courting females, males flew in horizontal loops as long as 8 m, making the wing noise continuously. The wing noise was also noticeable when males flew in non-courtship behaviours such as foraging, but whether it is always produced during flight is unclear; Howell & Webb (1995) also noted that wing noise is louder during displays, but produced continuously. Immature males were not seen to court females; nor were immature males or females heard to produce wing noise when flying. Observations in January included both singing and courtship, but in May only singing was noted, suggesting that nesting was already well underway or completed.

These observations contrast in some respects with those of Skutch (Bent 1940) of *A. ellioti* in Guatemala and of Thurber *et al.* (1987) from El Salvador. They described assemblies of males spaced 25–30 m apart, with no other such assemblies detected within 2 km. Similar to our observations, the males sang from exposed perches, but their song was described as rising and falling in pitch, more rich and varied (lacking the whistling quality) than in *A. heloisa*, and lasting 30–40 seconds, much longer than in *A. heloisa*, as was borne out by the recordings we studied (Fig. 2). No pronounced wing noise was noted. Excepting the latter point, these differences are largely in accord with descriptions in Howell & Webb (1995). Displaying males apparently moved their gorgets, and often sang while in looping flights, but were not observed to approach the females closely (but see Howell & Webb 1995).

Hence, several marked differences seem to exist in the vocalizations and courtship behaviours of the two forms of *Atthis* hummingbirds. The northern form (*A. heloisa*) sings a simpler song and only while perched, approaches closely to females while in flight, and produces a loud humming wing noise while flying. Observations (ATP) at close range of *A. ellioti* in El Salvador indicated that its wing noise is much quieter and less throbbing than in *A. heloisa*; this observation contradicts a brief mention of display behaviours in Howell & Webb (1995). Finally, and perhaps most interesting, is the possibility that the southern birds display in groups (leks?), whereas the northern birds show no obvious tendency towards clumping; S. N. G. Howell, however, reports observations of clumped and nonclumped displaying males in each form (pers. comm.).

Morphology

Our examinations of study skins revealed several differences between males of the northern and southern forms of *Atthis*. The inner web of the outermost primary of all adult males of *A. heloisa* examined was notched for an average of 6.5 mm from the feather tip (Fig. 3). No females or immature males showed this modification, nor did any individual examined of *A. ellioti*. This structural modification, noted by Ridgway (1892), probably accounts for the humming noise produced by adult male *A. heloisa* (Monroe 1968). An interesting sidelight of this observation, if the pulses in the noise represent wingbeats (Fig. 2), is that the wingbeat frequency for *A. heloisa* can be calculated at 61.3 beats per second.

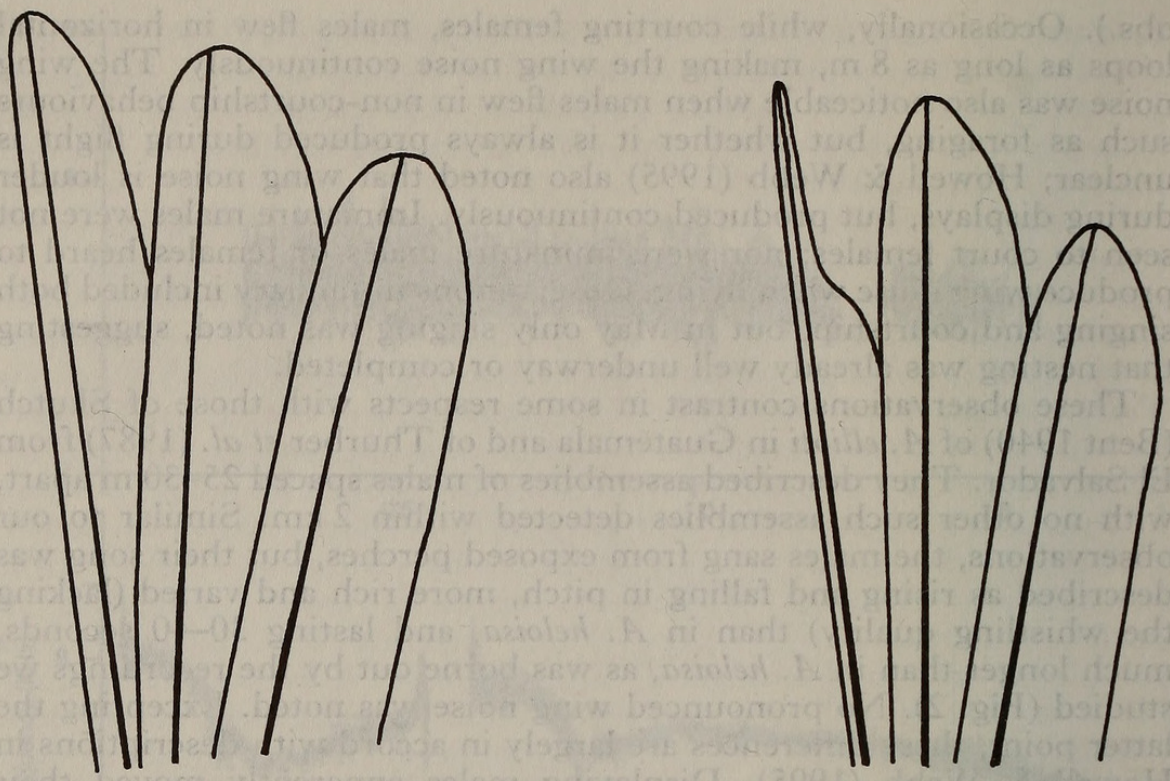

Figure 3. Shape of outer primaries of left wings in *Atthis ellioti* (left, FMNH 42768) and *A. heloisa* (right, KU 46137), both adult males.

This notch of the inner web of the outer primary in *A. heloisa* is the most extreme within the five closely related genera *Selasphorus*, *Atthis*, *Archilochus*, *Calypte*, and *Stellula*. The latter three genera and *Selasphorus flammula* show no notch of the outer primary, whereas *S. platycercus* shows a notch of the distal portion of the feather only. Other *Selasphorus* (*S. rufus*, *S. sasin*, and *S. scintilla*; *S. ardens* not determined) have a pointed outer primary, but no notch.

The colour of the two *Atthis* forms' gorgets differs, in that gorgets of *A. heloisa* are of a rich magenta purple or bluish purple, but those of *A. ellioti* lack blue almost completely and are decidedly more reddish, especially in Honduran *A. e. selasphoroides* (Monroe 1968), even when specimens of similar time since collection are compared. Additionally, the length of the gorgets of adult males may differ, although this feature is difficult to evaluate quantitatively; gorgets of *A. ellioti* seem to be about 3–5 mm longer than those of *A. heloisa*. Our measurements of body dimensions were based on too few individuals to permit statistical testing, but seem generally to support the notion that *A. ellioti* is somewhat smaller than *A. heloisa* in bill and tail length, but slightly larger in wing length, as documented by Ridgway (1892, 1911).

Species limits

The sum of the information presented above is that the northern and southern forms of *Atthis* differ in several regards. The two forms differ in courtship behaviour, song structure, wing morphology, and

coloration. Character distributions are nonoverlapping in several cases, and their status as valid phylogenetic species is unquestionable.

The unresolved question, however, is whether they should be considered as representing two biological species. Because of their allopatric distributions, no test of sympatry is available to aid in this decision. Comparisons with sympatric species pairs in related genera are not illuminating because sympatry among congeners (e.g. *Calypte* spp.) is relatively rare; however, species pairs in more distantly related hummingbird clades (e.g. *Amazilia* spp.) are maintained in sympatry even though they are more similar in courtship behaviours than the *Atthis* species treated herein. The marked differences in courtship behaviour and associated morphological modifications strongly suggest that they would not interbreed were populations to come into contact. Hence, we recommend that these two forms be recognized as full biological species.

Acknowledgements

This contribution is dedicated to the memory of Ted Parker, for his many insights, observations, and records that have enriched so much of our work with Neotropical birds, and for his contributions of the recordings used in this paper. We would like to thank our field companions, especially Griselda Escalona-Segura, Blanca E. Hernández-Baños, and Laura Gonzáles-Guzmán, for their assistance and support. We also thank the curators and staff of the American Museum of Natural History; Natural History Museum, Tring; Canadian Museums of Nature; Carnegie Museum of Natural History; Delaware Museum of Natural History; Field Museum of Natural History; Louisiana State University Museum of Natural Science; Moore Laboratory of Zoology; Musée d'Histoire Naturelle de Paris; Museo de Zoologia, Facultad de Ciencias, U.N.A.M.; Museum of Comparative Zoology, Harvard; Museum of Vertebrate Zoology, Berkeley; Royal Ontario Museum; San Diego Natural History Museum; Southwestern College; Texas Cooperative Wildlife Collections; Universidad Michoacana San Nicolás de Hidalgo; University of Arizona; Western Foundation for Vertebrate Zoology; and Yale Peabody Museum for access to specimens and data under their care; Gary R. Graves, Steve N. G. Howell, Adolfo G. Navarro-Sigüenza, James V. Remsen, and Mark B. Robbins for critique of the manuscript; and Greg F. Budney of the Library of Natural Sounds, Cornell University, for providing the sound recordings.

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A new taxon of the Barred Honeybuzzard *Pernis celebensis* from the Philippines

by Anita Gamauf & Monika Preleuthner

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The Barred Honeybuzzard *Pernis celebensis* is restricted to Sulawesi and the Philippines. Two subspecies have been distinguished: The very colourful and uncrested nominate subspecies *Pernis celebensis celebensis* Wallace, 1868, is found on Sulawesi, including Muna and Peleng Islands; the paler banded and crested *Pernis celebensis steerei* Sclater, 1919, has been reported from all over the Philippines, except Palawan (Delacour & Mayr 1946, Brown & Amadon 1969, del Hoyo *et al.* 1994). Dickinson *et al.* (1991) compiled a list of 17 islands where the occurrence of this subspecies has been documented.

In the course of an ecomorphological study of Philippine birds of prey (Gamauf *et al.* 1998) we carried out morphological measurements on 21 raptor species in various museum collections. Sixty external measurements were taken from each specimen. While comparing the specimens from different Philippine islands, we were struck by clearcut differences in colour and plumage pattern among birds from northern and southern provenances. To investigate these geographic differences in greater detail, we looked for representatives of this species in 30

different museum collections. Finally, from nine museums (for abbreviations of museum names, see Acknowledgements), a total of 37 specimens was available, from 10 different islands. In addition, 75 observations in the field were available, carried out over a period of more than 9.5 months.

Plumage variation

The most striking difference between the two population groups is the uniformly brown colour of the adults in the northern population which does not display the rich contrast and coloration of specimens from the southern islands. This may be the reason for some confusion in the past concerning age classes, since plumage characteristics were often used to determine age (Stresemann 1940, Brown & Amadon 1969). The holotype of *steerei* (Sclater 1919), now in the Natural History Museum, Tring—BM 1896.4.15.40, is an adult male of the south Philippine subspecies which was collected by Steere on 17 February 1888, in San Antonio (Negros). We agree with Sclater's statement that ". . . other examples from Samar, Mindanao, and Basilan closely resemble the type . . .", since we were able to confirm the occurrence of representatives of the southern population on those islands.

Morphological variation

Table 1 gives a comparison of 14 external morphological measurements of individuals from northern and southern provenances. From the total of 37 specimens we could include 29 sexed and fully feathered birds in a discriminant function analysis (12 from the north and 17 from the south). With a combination of 6 variables (Fig. 1) we were able to discriminate unambiguously between populations as well as between age classes. In the northern population the separation according to sex and age class was clearcut without any overlap: females are larger than males, immatures are smaller than older birds (adults and subadults) in some measurements. In the slightly smaller southern form no clear discrimination was found between the sexes. This may be partly due to incorrect sexing of the museum specimens, as has been proven for other species with much more pronounced sexual dimorphism. Nevertheless, the age class could be determined correctly. Discriminant function (DF) 1 concerns characters related to the mode of handling the prey as well as the flight apparatus. It segregates the subspecies largely by the length of the bill and middle toe. A negative correlation exists with the number of notches and Kipp's distance. Along DF 2 the honeybuzzards fall into two distinct groups largely according to the length of the tail as a character for flight (lift and ability for manoeuvring) and the tarsus length (presumably connected with feeding habits).

Thus, based on the characters discussed above, the northern population is distinct in both plumage pattern and morphology. Every specimen can be clearly diagnosed. We therefore consider this population to represent a third taxon, for which we propose the name

TABLE 1

Morphological measurements (mm) of the two Philippine populations of the Barred Honeybuzzard *Pernis celebensis* according to age and sex. Numbers of study skins are given in parentheses. F=female, M=male

	Northern population (*winkleri*)										
		Adult and subadult M (5)[1]			Adult and subadult F (5)			Immature M (3)			
Age and sex	Holotype Adult M (1)	$\bar{x}$	s.d.	Range	$\bar{x}$	s.d.	Range	$\bar{x}$	s.d.	Range	Immature F (1)
Body length	530.0	543.0	8.3	530.0–553.0	556.4	24.8	520.0–590.0	561.0	27.9	525.0–593.0	535.0
Wing length	375.0	371.6	3.6	367.0–376.0	395.6	12.0	375.0–408.0	366.7	13.4	348.0–379.0	363.0
Kipp's distance	113.0	111.0	4.2	103.0–115.0	116.8	3.8	112.0–123.0	115.0	4.3	111.0–121.0	125.0
Number of notches	7.0	7.0	0.0	7.0–7.0	7.0	0.0	7.0–7.0	6.3	0.5	6.0–7.0	7.0
Length of central tail feather	245.0	240.8	7.5	226.0–260.0	241.4	9.8	222.0–267.0	235.0	6.2	227.0–247.0	230.0
Length of outermost tail feather	251.0	246.8	10.8	227.0–260.0	254.4	6.7	247.0–267.0	239.3	9.5	226.0–247.0	227.0
Length of hindtoe	21.4	22.7	1.4	21.4–25.2	22.5	2.2	20.0–25.8	24.1	3.0	20.0–27.1	27.7
Length of middle toe	42.2	44.2	1.5	42.2–46.0	41.8	2.1	39.0–44.2	45.5	0.5	45.0–46.0	45.5
Length of hindclaw	—	21.5	0.6	21.0–22.5	21.5	0.6	20.5–22.3	21.8	0.9	20.9–23.0	20.4
Length of middle claw	—	21.3	1.0	20.0–22.7	22.5	0.9	21.5–24.0	22.1	0.7	21.6–23.1	20.0
Tarsus length	40.2	42.3	2.3	40.0–46.0	41.7	2.7	40.0–47.0	41.3	2.4	38.0–43.0	44.0
Bill length with cere	37.9	38.2	0.4	37.8–38.8	37.2	1.9	35.0–40.6	37.2	1.5	35.6–38.7	36.8
Bill width with distal edge of cere	21.7	23.0	1.1	21.7–24.1	24.3	0.8	23.5–25.6	22.9	0.1	22.8–23.1	24.0
Bill depth	17.9	18.4	0.5	17.9–19.0	18.5	0.7	17.5–19.5	19.2	0.0	19.2–19.2	—

[1]Holotype included

TABLE 1 (*Continued*)

	Southern population (*steerei*)							
	Adult and subadult M (12)			Adult and subadult F (4)			Immature M (1)	Immature F (1)
Age and sex	x̄	s.d.	Range	x̄	s.d.	Range		
Body length	529.0	9.9	525.0–542.0	554.8	15.2	533.0–575.0	582.0	553.0
Wing length	371.6	10.7	355.0–395.0	381.0	4.9	375.0–388.0	361.0	381.0
Kipp's distance	110.5	6.1	102.0–125.0	115.3	3.1	112.0–120.0	117.0	110.0
Number of notches	7.3	0.7	6.0–9.0	7.3	0.4	7.0–8.0	7.0	7.0
Length of central tail feather	229.5	10.5	212.0–251.0	241.0	6.4	231.0–245.0	249.0	242.0
Length of outermost tail feather	236.6	9.0	223.0–251.0	242.8	3.3	237.0–245.0	252.0	265.0
Length of hindtoe	22.9	1.0	21.3–24.3	22.8	0.6	22.0–23.4	22.4	26.7
Length of middle toe	40.9	1.8	38.5–43.9	43.0	1.6	41.0–45.4	40.5	38.6
Length of hindclaw	20.4	1.1	19.0–22.4	20.8	0.9	19.6–22.2	19.3	24.0
Length of middle claw	21.1	0.9	19.5–22.5	21.8	1.2	20.2–23.0	19.8	22.4
Tarsus length	40.2	2.1	38.0–46.0	39.1	2.2	37.0–42.0	38.0	39.8
Bill length with cere	35.6	0.7	34.0–37.0	35.1	0.7	33.9–35.7	35.5	35.0
Bill width of distal edge of cere	23.2	1.6	20.5–25.8	22.6	1.6	20.5–25.0	23.7	21.5
Bill depth	17.5	1.2	15.4–19.3	16.8	0.5	16.2–17.3	—	18.2

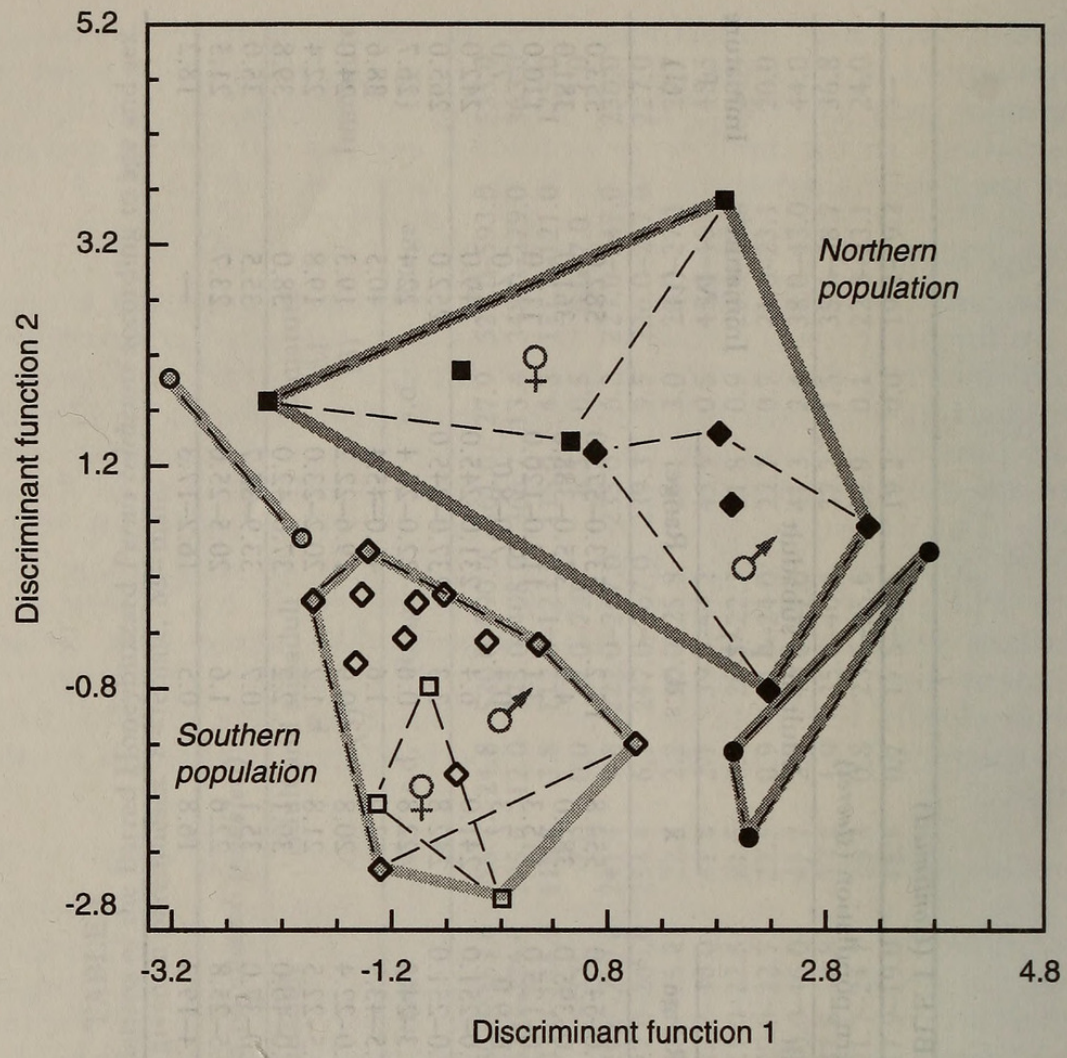

Figure 1. Separation of the two Philippine populations of the Barred Honeybuzzard *Pernis celebensis* (12 study skins from the north, filled symbols; 17 study skins from the south, open symbols) according to discriminant function analysis of 6 morphological variables (bill length, length of the middle toe, number of notches, Kipp's distance, length of the tail, tarsus length). Immatures are marked by round symbols.

Pernis celebensis winkleri subsp. nov.

Holotype. Adult male, from Bataan, Luzon, collected by O. Koch, 17 August 1881, Zoologisches Museum der Humboldt Universität Berlin, Germany, cat. no. ZMB 25.464 (Fig. 2). This is the specimen listed as "immature?" by Stresemann (1940, pp. 192/193).

Diagnosis. The subspecies can be distinguished unequivocally in subadult and adult specimens. In contrast to *winkleri*, individuals of *steerei* are much more contrasting in plumage. The ground colour of crown and neck is paler with dark stripes, the long pointed crest (up to 73 mm) is black. The throat is white with black mesial and lateral stripes. The breast is whitish to buffy with bold black streaks. The lower breast is white with narrow rufous-brown bars. Lower belly, undertail coverts, leg feathers and underwing coverts are barred medium to dark brown and white. All illustrations in publications to date show *steerei* (duPont 1971, Brown & Amadon 1969, Weick 1980,

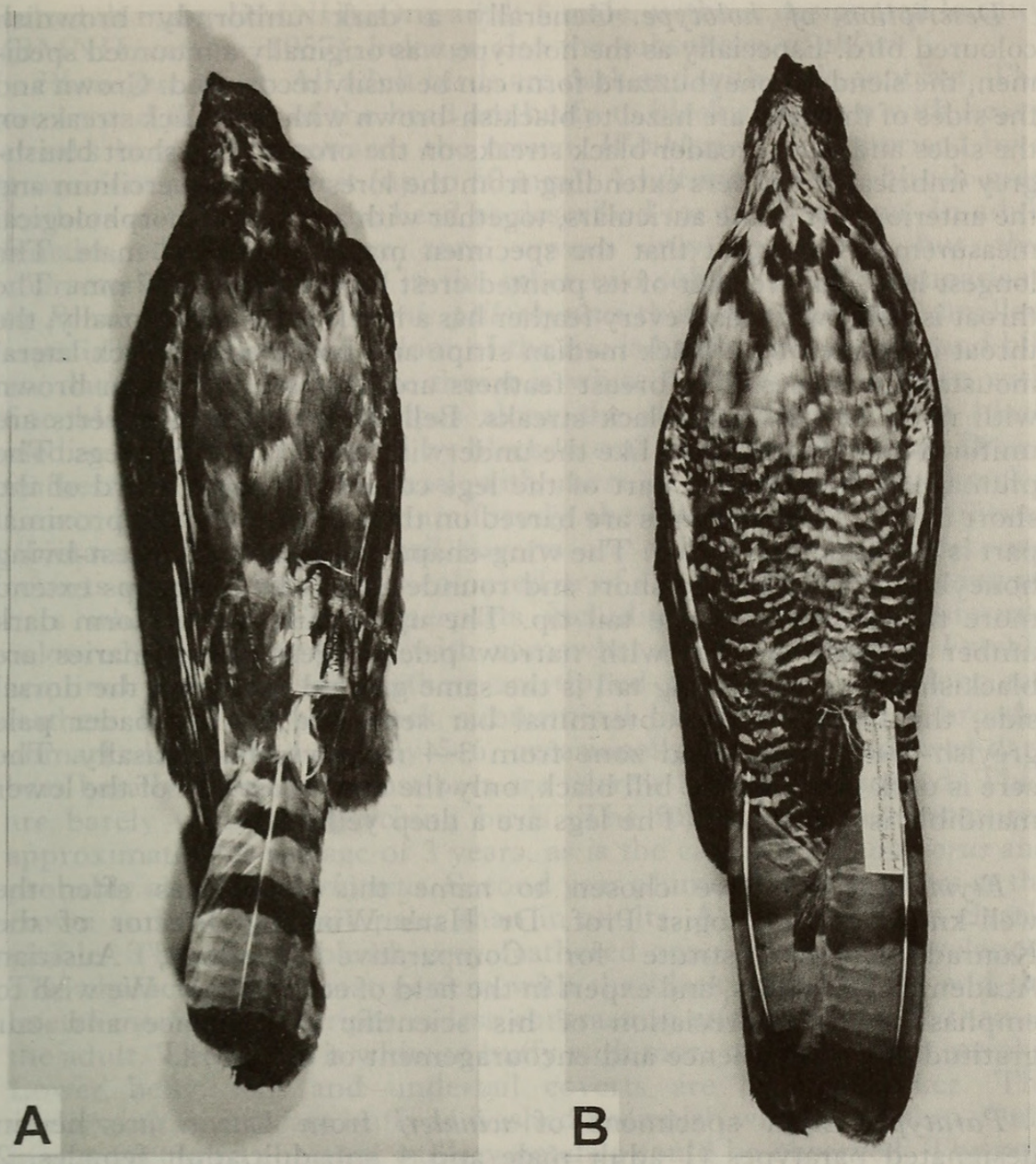

Figure 2. A. Holotype of *Pernis celebensis winkleri* subsp. nov. (Zoologisches Museum der Humboldt Universität Berlin, Germany, cat. no. ZMB 25.464). B. Typical adult representative of *Pernis celebensis steerei*, Universitets Zoologiske Museum, København, Denmark, cat. no. 940).

del Hoyo *et al.* 1994). In the course of our investigations we discovered several misidentified specimens among study skins, as was also noted by Dickinson *et al.* (1989). These obvious errors are due to close similarities between corresponding subspecies of the Philippine Hawk-Eagle *Spizaetus philippensis* (Preleuthner & Gamauf 1998) and of the Barred Honeybuzzard *Pernis celebensis*. The respective northern subspecies from both species resemble each other, as also is the case with the southern subspecies. Whether this could be caused by mimicry will be discussed elsewhere.