GEOGRAPHICAL DIFFERENTIATION IN THE GENUS *ACCIPITER*

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I

INTRODUCTION

Scope of the Study

The present study forms part of a larger series on the taxonomy, zoogeography, and ecology of predatory birds. Some of these have already been published (Voous, 1964; Voous and Wijsman, 1964; Voous, 1969) and others are in progress. Two basic themes lie behind this contribution. The first is the question of whether Gause's principle, viz., that two species with closely similar ecology cannot survive in the same habitat, holds true for birds. The application of this principle means that two closely related sympatric species must differ in ecology if they are to co-exist. The second underlying theme is that study of any group of avian predators, such as the genus *Accipiter,* will provide information on the principles governing the distribution of terrestrial animals in general. Furthermore, it may be presumed that the vicissitudes of the environment in the recent geological past are reflected in the distribution of the species of *Accipiter.*

Accipiter has been the subject of a great number of taxonomic studies, notably by Hartert (e.g., 1910; 1912-1921; 1929), Stresemann (e.g., 1922; 1923a; 1924a; 1925; 1926; 1929), and Mayr (1940; 1945a; 1949; 1957). The genus was treated at length by Brown and Amadon (1968) but they considered its taxonomy as still insufficiently known. The present study is an attempt, therefore, to fill this deficiency. Because the taxonomy of *Accipiter* has been based to a large extent on the structure of the bill and foot, i.e., those organs employed in securing prey, it seemed appropriate here to focus attention on the relations between structure and ecology, providing at the same time a view of ecological differentiation within the genus and of the value of structural characteristics in taxonomic arrangement. Long discussions of plumage, clinal variation, behavior, and reproduction have deliberately been avoided. A wealth of information on these subjects will be found in the book by Brown and Amadon (1968).

Forty-three species of *Accipiter* are recognized here. A taxonomic arrangement is given in the checklist (p. 214), but in the main text the species are grouped geographically. Chapter III treats the species of Eurasia, IV those of Africa, V those of North and South America, and VI those of Australia and the southwest Pacific islands. The peculiar endemic *Accipiter* fauna of Celebes is dealt with separately (Chapter VII). Each chapter concludes with a survey of ecological differentiation in the *Accipiter* fauna of the area under consideration, comparing it with other regions.

INTRODUCTION

For every species the breeding distribution is concisely characterized and mapped. In migratory species the winter range is roughly delimited. The data on distribution, habitat, hunting behavior, and food were derived from the literature and from specimen labels. The various plumages are described from museum specimens. These descriptions try to convey a general picture of the species rather than giving a feather-by-feather description. Trends of geographical variation are presented in a separate section where appropriate. Consideration of the significance of the variation is not given under this heading, but instead is included with a discussion of the taxonomic affinities in the concluding paragraph of the species account. In preparing the lists of currently recognized subspecies I usually followed a recent checklist or revision of the species. It was not my purpose to study critically all slightly different forms which might have been named.

Where I had to make a choice between conflicting opinions this choice was based on considerations discussed in the species accounts.

DELIMITATION OF THE GENUS *Accipiter*

Believing that changes in generic limits should be made only after a careful study of all genera in a particular family, I felt no justification in departing from the limits of the genus *Accipiter* as conceived by Peters (1931). I have included all forms placed by him under *Accipiter* and added only those taxa that were discovered or rediscovered after 1931. As far as species boundaries are concerned, I sometimes have had to deviate from Peters or from other authors, but I have tried to give the reasons for most shifts within the discussion of the species in question.

The species of *Accipiter* share a number of common features. In all but a few the difference in plumage between juvenile and adult birds is considerable. Ventrally the adult plumage if often barred transversally while the juvenile plumage is spotted or streaked longitudinally. In all species the female is significantly larger than the male; the smallest female of a given species is often larger than the largest male. Structurally the Accipiters are characterized by long legs, a long tail, and short, rounded wings. Ecologically they are birds of wooded country and are absent from open regions. The nests are always in trees. In hunting they rely on surprise rather than on long-sustained pursuit. Often an Accipiter sits quietly and inconspicuously at a vantage point, launching a sudden attack when its prey happens to come near. This behavior is called still-hunting.

Formal diagnoses of *Accipiter* are to be found in Hartert (1912-1921) and Friedmann (1950).

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Discussions with C. J. O. Harrison and E. Nieboer have substantially helped in shaping my thoughts. H. Brüll and his son Ulrich kindly offered an opportunity for studying *A. gentilis* in the field. Methods for statistical analysis were developed by the staff of the Mathematical Centre, Amsterdam, particulary by W. N. van Nooten, who also ran the computer program. I owe a great debt to R. A. Paynter, Jr., Museum of Comparative Zoology, who first criticized parts of an earlier draft of this paper and subsequently took great pains to make the English of the manuscript straightforward and understandable. I wish to thank Mrs. A. C. J. E. Knipping-Schuurmans and Mrs. N. M. Wink-Carton for typing and retyping the manuscript and D. Sminia for drawing the figures.

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The revised manuscript was accepted by the Nuttall Ornithological Club on 29 June 1972.

II

MATERIAL AND METHODS

Material

Nearly 1,800 specimens of all species of *Accipiter,* except *A. princeps,* were studied. In about half of these specimens the following measurements were taken: wing, tail, tarsus, middle toe, hind claw (chord from base to tip), bill (chord from distal rim of cere to tip) (Fig. 1), wing tip (distance from tip of first primary to tip of longest one) and distance from tip of sixth primary to tip of longest one (referred to as wt–6), the primaries being numbered ascendantly, i.e., from the outermost inward. Of the remaining specimens at least the wing length was taken. The wing was measured by flattening it against a ruler and stretching the primaries. The tail was measured by means of dividers; all other measurements were taken with vernier calipers. Values were rounded to full millimeters, but taken to tenths of millimeters for the chords of the bill and hind claw.

Data on wing length are presented in a table for each species giving the mean, standard deviation, standard error of the mean, observed range, and size of the sample. In order to facilitate comparison of the structure of different sized birds (e.g., male and female of a species or birds of different species) the actual measurements of the tail, tarsus, etc. have been converted to percentages of wing length (relative measurements). If the sample was sufficiently large the statistical significance of the observed differences in relative measurements between the sexes, and in polytypic species between the subspecies, was tested. The results of these tests are presented for each species in a table in which estimates of mean relative measurements are also given. For several of the rarer species the number of specimens available for study was too small to permit statistical analysis. In such cases only mean relative measurements and sample sizes are presented.

Statistical Analysis

The statistical analysis of my data was performed at the Mathematical Centre of Amsterdam. An analysis of variance was applied to all sufficiently large samples of relative measurements. For the purpose of this analysis the data for a given species were grouped into a number of so-called cells. The data pertaining to a single sex, a single age-class, and, if applicable, a single subspecies are considered to fill a single cell. As an example the cells for *A. gentilis* are shown in Table 1. For the analysis of variance the average of the data in a given cell, m_{ijk}, is as-

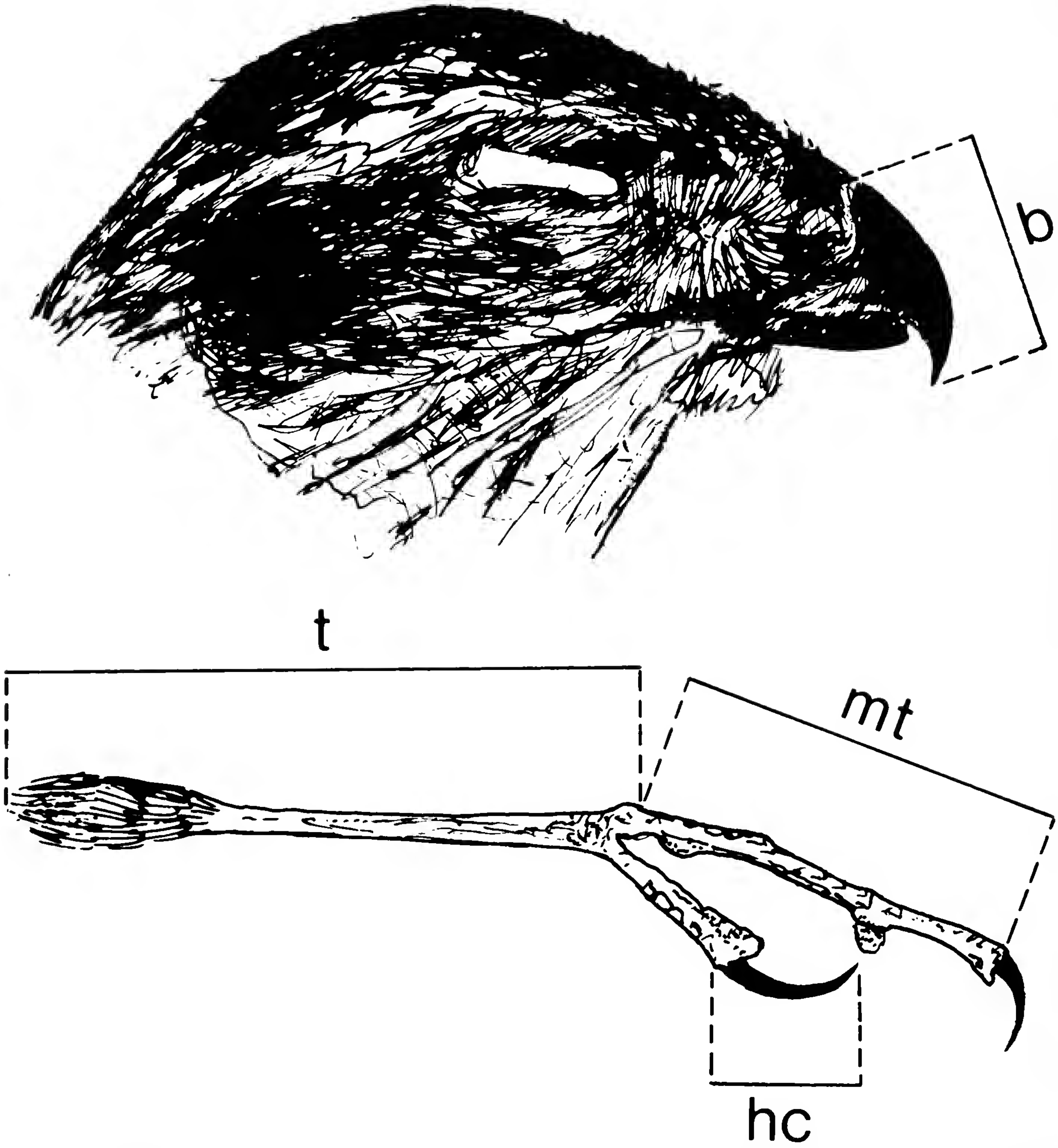


FIG. 1. Measurements taken to study the structure of the foot and bill: b = bill; mt = middle toe; t = tarsus; hc = hindclaw.

sumed to be composed of a number of contributions, the model constants:

$$m_{ijk} = m + a_i + b_j + c_k$$

In this equation m denotes the general average of all data of the given

TABLE 1
CELLS IN THE STATISTICAL ANALYSIS OF *A. gentilis*. IN EACH CELL THE NUMBER OF OBSERVATIONS FOR RELATIVE LENGTH OF TAIL IS GIVEN.

	gentilis		'gallinarum'		atricapillus	
	♂	♀	♂	♀	♂	♀
Adult	1	3	4	8	5	3
Juvenile	3	1	6	7	3	1

kind pertaining to the species in question, a_i being the contribution of the subspecies to the cell average, b_j the contribution of sex, and c_k the contribution of age. The contributions of subspecies, sex, and age are called the main effects. In the given model it is assumed that only the main effects are of importance and that the interactions between these main effects are negligible. It may be noted that the sum of the possible model constants of each main effect is always zero:

$$a_{gentilis} + a_{gallinarum} + a_{atricapillus} = 0$$

In the case of sex and age, where there are only two possibilities, the model constants are equal in absolute value, differing only in sign.

This method of estimating the cell average has an advantage in that with few data in a particular cell the estimate of the cell average is improved by information about the main effects derived from other cells. Provision must be made so that the given model is indeed applicable to the series of data under discussion. Therefore, the first test carried out was on the applicability of the statistical model. The value P_{model} in the tables of relative measurements denotes the probability that the assumed model would produce the obtained results if applied to a given set of data. The null hypothesis that the model is adequate is rejected at a value of P_{model} of less than 0.05. In that case the significance of the difference between either the subspecies of the sexes could not be tested and the estimate of the cell average was likely to be biased.

When the statistical model is adequate ($P_{model} > 0.05$), the values P_{ssp} and P_{sex} indicate whether the estimated differences are statistically significant. The limit for significance was fixed at $P \leq 0.05$.

In the tables of relative measurements sample size is denoted by n, and the number of degrees of freedom by df. Of the main effects the sex and age effect are presented by giving the appropriate model constants and the subspecies effect by adding the model constants to the general average, obtaining a subspecies average disregarding probable sex and age differences:

$$m_{subspecies} = m + a_i$$

DIAGRAMS

The estimates of the general average and subspecies averages were used in comparing the structure of the various species. To facilitate these comparisons diagrams were drawn in which not the relative measurements but rather especially calculated diagram values were plotted. The relative measurements were converted to diagram values by expressing them as percentages of the average of the mean relative measurements of all studied forms:

$$M = \frac{\Sigma m}{N}$$

$$d = \frac{m}{M} \times 100$$

In these equations M denotes the average of the means, m the individual mean, viz., the species mean for monotypic species or the means of the separate forms for polytypic species, N the total number of forms, and d the diagram value corresponding to a given mean m. By this procedure the values for all measurements were made to center around 100.

The following example will elucidate the principle. The separate absolute measurements, relative measurements, and diagram values for a single adult male of *A. nisus* and *A. gentilis* are listed in Table 2. For the tarsus M = 27.10, for the middle toe M = 16.00, for the hind claw M = 8.20, for the bill M = 7.43, and for the tail M = 76.16. In Figure 2 the data of Table 2 are plotted diagrammatically. From the first diagram it may only be deduced that *A. gentilis* is larger than *A. nisus,* the second one gives indications of the main structural differences, which are brought out much clearer in the third one, however. In the same way structure diagrams were drawn for all studied forms. Wing tip and wt–6 were not converted to diagram values, but are shown in the form of a simple sketch of the tip of the wing (Fig. 3).

In forms in which the wing tip is long, the relative measurements tend to be small. To indicate bias of this kind the average diagram value is indicated by a broken line in the structure diagram. In forms with a short wing this line lies high, in forms with a long wing it is low. This can be seen by comparing the diagrams of *A. virgatus virgatus* and *A. virgatus gularis* in Figure 7.

TYPES OF STRUCTURE

The structure diagrams are divided into two parts, the upper half showing tarsus, middle toe, hind claw, and bill, the lower half showing

TABLE 2

DIFFERENT WAYS OF COMPARING THE STRUCTURE OF TWO Accipiters.

	TARSUS	M. TOE	H. CLAW	BILL	TAIL
absolute measurements in mm:					
A. nisus, ♂, RMNH Cat 56	52	32	13.1	11.4	149
A. gentilis, ♂, RMNH 26696	74	42	26.6	21.7	213
relative measurements:					
A. nisus	26.0	16.0	6.5	5.7	74
A. gentilis	24.2	13.7	8.7	7.1	70
basic value of diagram values	27.10	16.00	8.20	7.43	76.16
diagram values:					
A. nisus	96	100	79	77	97
A. gentilis	89	86	106	96	92

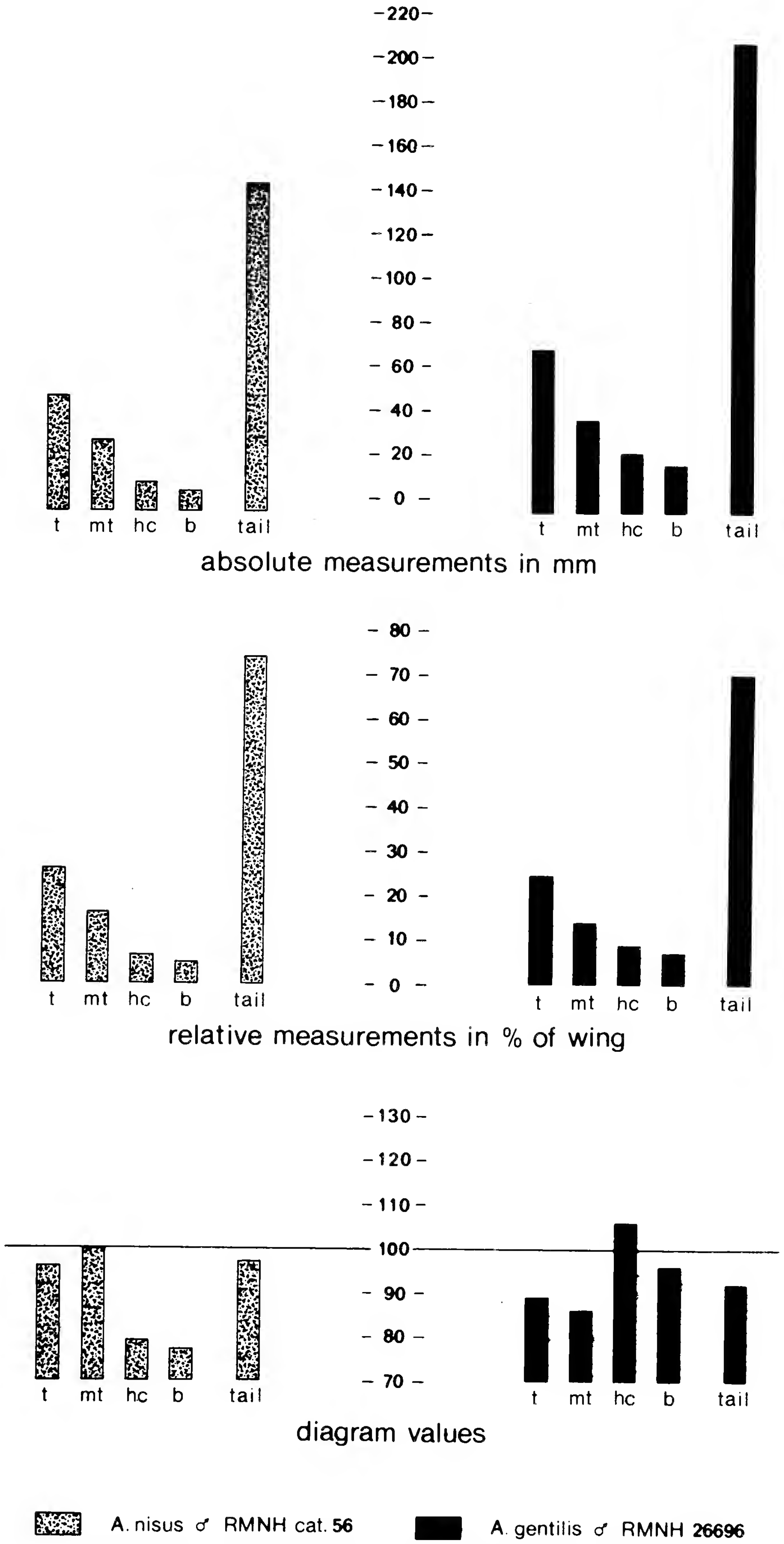


FIG. 2. Different ways of comparing the structure of two Accipiters.

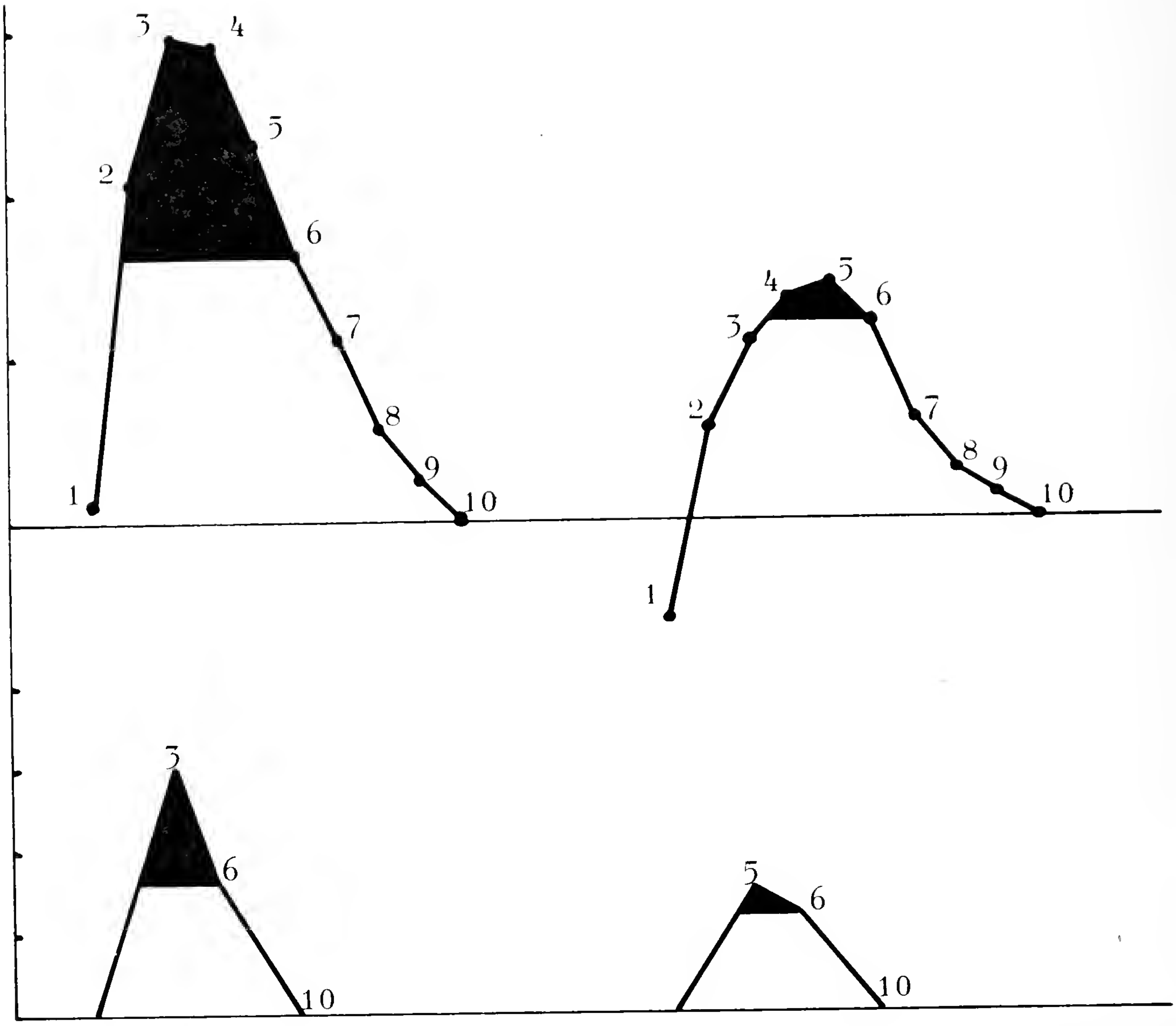


Fig. 3. Method of showing size and shape of wing tip. Top row: all primaries figured. Bottom row: only distinctive primaries figured. Left: *Accipiter soloensis*. Right: *Accipiter castanilius*.

tail and wing tip. Both parts of each diagram were compared independently with the other diagrams. In this way seven more or less clearly defined types of structural modifications could be recognized. For the foot and bill these types are the following:

nisus-type: tarsus and middle toe long, hind claw and bill small (Figure 8)
gentilis-type: tarsus and middle toe short, hind claw very large, bill medium to large (Figure 10)
bicolor-type: tarsus and middle toe long, hind claw large, bill rather large (Figure 14)
brevipes-type: tarsus and middle toe short, hind claw and bill small (Figure 6)
trinotatus-type: tarsus long, middle toe short, hind claw small, bill large (Figure 4)
tachiro-type: tarsus long, middle toe short, hind claw and bill large (Figure 11)
albogularis-type: tarsus short, middle toe short to medium, hind claw medium to large, bill large (Figure 18).

For the tail and wing tip the following types were recognized:

Wing rounded:

nisus-type: wing tip long, tail medium to long (Figure 8)
novaehollandiae-type: wing tip medium, tail medium (Figure 17)
bicolor-type: wing tip medium, tail long (Figure 14)
tachiro-type: wing tip short, tail long (Figure 11)

Wing pointed:

minullus-type: wing tip short to medium, tail medium to long (Figure 12)
brevipes-type: wing tip long, tail short (Figure 6).

The borderlines between the various structural types are not absolutely sharp. Several species are intermediate. In addition a few species show an altogether aberrant structure.

III

EUROPE AND ASIA

INTRODUCTION

The species of *Accipiter* occurring in Europe and Asia are listed in Table 3. Generally speaking, southeastern Asia, i.e., the Oriental Region, has a fauna which is strongly differentiated from that of the remaining parts of Asia and of Europe, i.e., the Palearctic Region. With *Accipiter,* however, it appears impracticable to consider these two regions separately because the distribution of the Palearctic forms *A. brevipes, A. soloensis,* and *A. virgatus gularis* would be incomprehensible without study of their Oriental counterparts.

Of the listed species, *A. badius, A. nisus,* and *A. gentilis* are not confined to Europe and Asia. *A. badius* and *nisus* have African races and *gentilis* has American races, but all are treated in the present chapter.

ACCIPITER TRIVIRGATUS (TEMMINCK)

DISTRIBUTION

Oriental region from Ceylon to Java and Taiwan (Map 1).

SUBSPECIES

cf. Mayr (1949). *A. t. javanicus* Mayr, Java; *A. t. trivirgatus* (Temminck), Sumatra; *A. t. niasensis* Mayr, Nias Island, west of Sumatra; *A. t. microstictus* Mayr, Borneo; *A. t. palawanus* Mayr, Palawan, Calamianes, and possibly Natuna Islands; *A. t. extimus* Mayr, Mindanao, Negros, Leyte, and Samar; *A. t. formosae* Mayr, Taiwan; *A. t. indicus* (Hodgson), southern slopes of Himalayas and southern China south to Godavari River of India, Malaya, and Hainan; *A. t. peninsulae* Koelz, southwestern India (Ripley, 1961); *A. t. layardi* (Whistler), Ceylon.

PLUMAGE

Adult male.—Crown dark gray with a conspicuous crest. Back brown. Underparts white, throat with a conspicuous dark mesial line, breast with heavy rufous brown spots forming a breast shield in most subspecies, abdomen and flanks barred dark brown or rufous brown. Thighs narrowly barred blackish. Sides of head gray. Tail with distinct dark crossbars.

Adult female.—Darker and more brown on head, paler on back than male. Underparts more heavily marked, browner. Breast shield dissolved into a number of dark brown spots.

Juvenile.—Crown blackish brown streaked buff, crest smaller than

TABLE 3

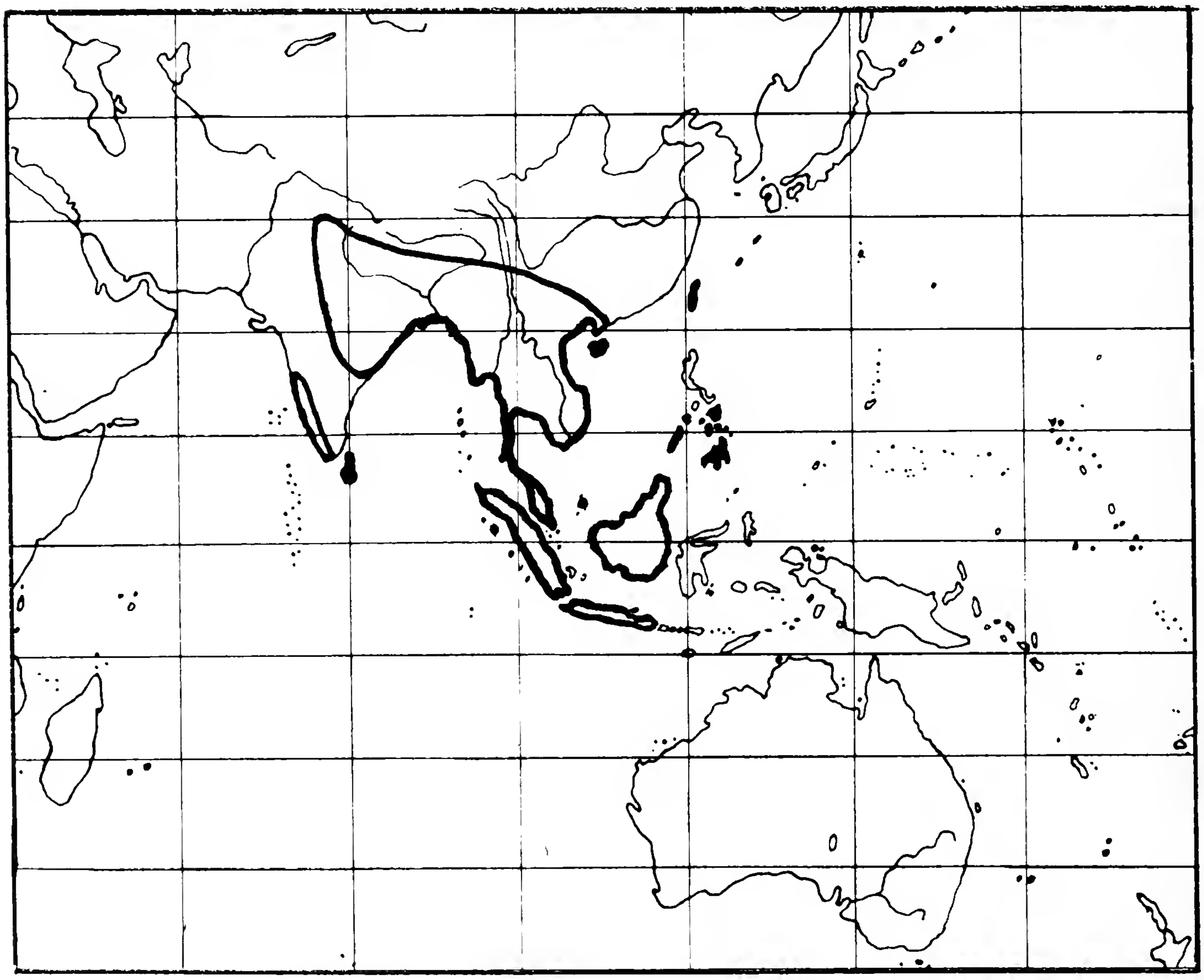
Species of *Accipiter* in Europe and Asia.

SPECIES	DISTRIBUTION
Accipiter trivirgatus	South-East Asia
Accipiter badius	South Asia and Africa
Accipiter brevipes	South-East Europe
Accipiter soloensis	China
Accipiter butleri	Nicobar Islands
Accipiter virgatus	South-East Asia and East Palearctic
Accipiter nisus	Palearctic and Africa
Accipiter gentilis	Holarctic

in adult. Back mottled, light gray brown with broad blackish brown subterminal bands and narrow white apical lines to the feathers. Underparts white, washed rufous with a pattern of dark spots or streaks, varying geographically in shape and extent.

Geographical Variation

A. trivirgatus varies markedly in size (Table 4). The smallest subspecies (*layardi, niasensis, extimus*) inhabit outlying islands (Ceylon,



Map 1. Distribution of *Accipiter trivirgatus*.

TABLE 4
WING LENGTH IN *Accipiter trivirgatus.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
trivirgatus	198.5	-	-	197 - 200	2
javanicus	195.3	4.65	1.20	189 - 203	15
extimus	189	-	-	186 - 192	2
layardi	191	-	-	-	1
indicus	227	-	-	-	1
formosae	232.5	-	-	231 - 234	2
			♀		
trivirgatus	220.2	3.59	1.80	217 - 225	4
niasensis	218	-	-	-	1
javanicus	215.8	5.71	1.53	210 - 228	14
extimus	206	-	-	-	1
indicus	247	-	-	-	2
formosae	259.5	-	-	259 - 260	2
				Total	47

Nias, Philippines) while the biggest (*indicus, formosae*) occur in the northern parts of the species' range. In addition there is a somewhat irregular variation in the tinge of the colors and the extent of the markings on the underside. This variation has been described in detail by Mayr (1949).

SIZE AND STRUCTURE

Size medium to large. Tarsus and toes short and sturdy. Claws and bill heavy. Wing short and rounded. Tail medium. Figure 4; Table 5.

On account of the scarcity of data the variation among the subspecies could not be analyzed. The statistical model was unsatisfactory for the bill. The difference between the sexes is significant for the tail (longer in male).

TABLE 5
RELATIVE MEASUREMENTS IN PERCENT OF WING LENGTH IN *Accipiter trivirgatus.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	27.77	15.32	9.93	8.41	78.45	22.65	4.63
♂	-0.07	-0.27	-0.22	+0.06	+1.85	+0.33	+0.30
♀	+0.07	+0.27	+0.22	-0.06	-1.85	-0.33	-0.30
Adult	-0.13	-0.37	-0.23	+0.10	+0.08	-0.91	-0.44
Juvenile	+0.13	+0.37	+0.23	-0.10	-0.08	+0.91	+0.44
P model	0.592	0.053	0.116	0.014	0.797	0.806	0.321
P sex	0.808	0.103	0.115	-	0.024	0.749	0.332
n	15	12	17	17	17	14	17
df	11	8	13	13	13	10	13

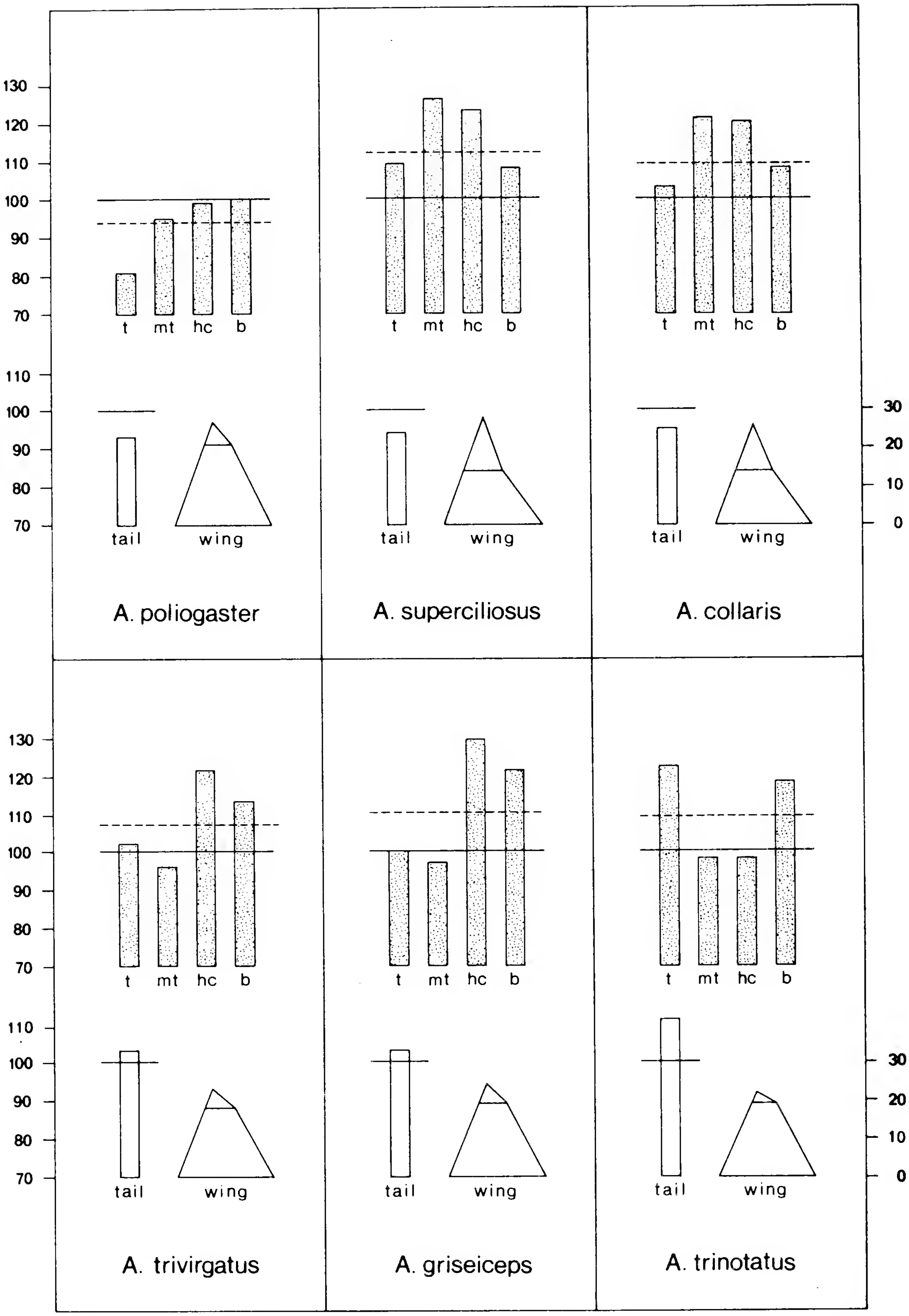


Fig. 4. Structure of *Accipiter poliogaster, A. superciliosus, A. collaris, A. trivirgatus, A. griseiceps,* and *A. trinotatus.*

Bill and foot.—These are of the *gentilis*-type, but aberrant in having the tarsus longer and the bill heavier. Owing to the short wing the relative measurements appear large.

Wing and tail.—Intermediate between the *bicolor*-type and the *tachiro*-type. The tail is relatively shorter than in *A. bicolor*. The wing and tail are similar to those in *A. griseiceps* and several Australasian forms.

HABITAT

Primary and secondary evergreen and deciduous forest in tropical lowlands as well as in subtropical mountain zones. Preferably broken country, where patches of jungle alternate with open spaces (Betts, 1947; Junge and Kooiman, 1957). In Java, among other habitats, overgrown botanic garden (Hoogerwerf, 1953) and teak forest (Sody, 1953). Up to 1,050 m in peninsular India, to 1,500 m in northern Burma and on Mount Victoria, to 2,000 m on the southern flanks of the Himalayas (Ludlow, 1944) and even to 2,400 m in Mindanao (Ripley and Rabor, 1961). Nest usually is in a tall tree, densely foliaged or overhung with creepers, often in the vicinity of a pond or river.

HUNTING BEHAVIOR

The hunting style is imperfectly known. *A. trivirgatus* practises still-hunting. It may be seen soaring (Hoogerwerf, 1953), though it prefers to remain in the cover of the forest (Harrison, 1963). *A. t. indicus* was seen chasing middle-sized birds (Betts, 1947).

FOOD

The diet is various animals from the forest floor and perhaps from the thicker branches of trees, viz., lizards, frogs, large insects, birds, and mammals (Baker, 1928). *A. t. indicus* takes fairly large birds, such as green pigeons, wood partridge, jungle fowl, and pheasants. Betts (1947) believes that it preys heavily on jungle fowl chicks. According to Baker the northern Indian race takes larger birds than do the forms of southwestern India and Ceylon, although Ali (1953) mentions spurfowl and jungle fowl taken by *A. t. peninsulae* of southern India. Henry (1955) denies that *A. t. layardi* of Ceylon takes fowl; it preys on lizards and small birds. Sody (1953) records rats and shrews among the prey of *A. t. javanicus* in teak forests. Apparently *A. trivirgatus* catches prey of different sizes, more or less in proportion to the size of the hawk itself.

DISCUSSION

Although *A. trivirgatus* is rather similar to *A. gentilis* in the structure of its bill and feet and in its choice of prey, the species certainly are not closely related. *A. trivirgatus,* with its crest and peculiar color pattern, stands rather isolated in the genus. Mayr (1949) considers it an old element of the Oriental rainforest fauna. Its only direct relative is *A. griseiceps* on Celebes, which is commonly regarded as an old colonist from the stock of *trivirgatus* (see p. 191).

The range of *A. trivirgatus* encompasses a large continuous continental area, inhabited by a single subspecies (*indicus*) which shows, however, much individual and some clinal variation (Mayr, 1949), and also consists of a number of isolated fragments, each with its own race. All the races inhabit islands, excepting *peninsulae* of southwestern India, but during the height of the Pleistocene glaciations nearly all the islands were connected with the Asian mainland. As *A. trivirgatus* lives mainly in tropical lowland jungle, its range in the Pleistocene may have been uninterrupted, occupying the extensive lowlands of the Sunda shelf. Simultaneously Ceylon was united with southern India, and during a humid interglacial period the forests of southern India were connected with those of Assam and Burma (Ali, 1949). The only parts of the present range of *trivirgatus* which must have been colonized across the sea are Nias and the southeastern Philippines. According to Mayr (1949) the species reached the southeastern Philippines from Borneo and not from Palawan, while Nias was obviously colonized from Sumatra. From the absence of the species in the northern Philippines it may be deduced that oceanic colonizations of *A. trivirgatus* rarely have been successful. The population on Taiwan is apparently very isolated because on the mainland *A. trivirgatus* has never been recorded east of Yaoshan, Kwangsi (Yen, 1930). However, it may once have been distributed in southeastern China but because it is restricted to dense forest habitats, may have been extirpated as a consequence of habitat destruction by man.

Superficially the pattern of the distribution of *A. trivirgatus* is parallel to that of the Oriental races of *A. virgatus*. In the last we also find a wide-ranging continental subspecies and a number of isolated insular forms. In both species the population of Taiwan is most similar to the Himalayan race. In contrast to *A. trivirgatus*, however, *A. virgatus* probably never had a continuous distribution across the Sunda shelf, because at present it is restricted to hill and mountain country. Therefore, its dispersal must have taken place earlier or was achieved by long-distance colonization. The occurrence of *A. virgatus* on the Andamans and on Flores prove that such long-distance colonizations have occurred in that species, whereas in *A. trivirgatus* this type of dispersal is virtually absent. Thus the similarity in distribution of these two species is not a reflection of a similar distributional history, but rather of the geographical features of Southeast Asia.

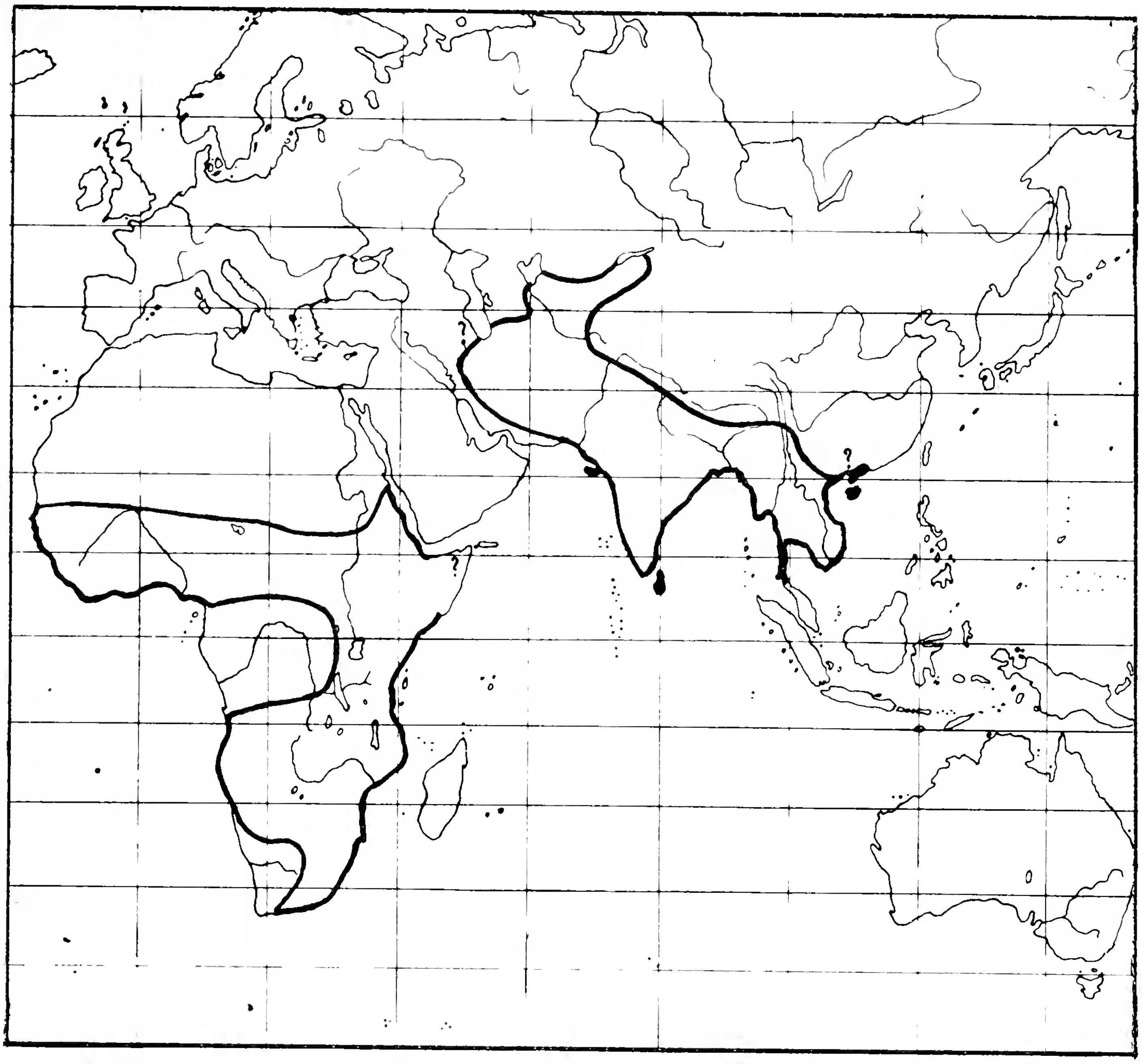
ACCIPITER BADIUS (GMELIN)

DISTRIBUTION

Southern Asia and Africa. Absent from tropical rainforest and from treeless desert (Map 2).

SUBSPECIES

cf. Ripley (1961) and White (1965). *A. b. badius* (Gmelin), Ceylon and southern India; *A. b. dussumieri* (Temminck), India and Pakistan,



MAP 2. Distribution of *Accipiter badius*.

intergrading with *badius* in south and with *cenchroides* in northwest; *A. b. cenchroides* (Severtzov), north-central Iran, Transcaspia, and southern Kazakhstan south to Baluchistan and North West Frontier Province, Pakistan; *A. b. poliopsis* (Hume), foothills of eastern Himalayas east to southern China and south to Isthmus of Kra; *A. b. sphenurus* Rüppell, Africa north of equatorial forest belt (in East Africa south to northern Tanzania) and, formerly, in southwestern Arabia (Meinertzhagen, 1954); *A. b. polyzonoides* A. Smith, Africa south of the equator.

MIGRATION

Many populations are migratory. The northern Asian populations leave the breeding grounds in winter while the African populations move about with the succession of dry and rainy seasons.

The northernmost populations of *A. b. cenchroides* are absent from their breeding quarters from September-October to April-May (Korelov, 1962), wintering in Pakistan as far south as Sind (Ripley, 1961). They pass in numbers through Afghanistan (Meinertzhagen,

1959) and northern Baluchistan (Meinertzhagen, 1920; Christison, 1941), probably taking a route from southern Transcaspia through the relatively low desert country along the Iran-Afghanistan border. *A. b. poliopsis* migrates to southern Indochina and has also been collected in Sumatra.

The migrations in Africa are not easily described in general terms because they are dependent mainly on the local rainfall. *A. b. sphenurus* breeds in southern Nigeria in the dry season and moves north during the rainy season (Marchant, 1953; Elgood, 1959). In the northeastern Congo and southern Sudan it also breeds during the dry period and goes north during the rainy season (northern summer), appearing at Khartoum at lat. 17°N; it does not normally breed beyond lat. 12°N (Cave and Macdonald, 1955). Chapin (1932) records an appreciable increase in numbers in the savanna of northeastern Uelle district during the dry season (Nov.-Feb.).

A. b. polyzonoides is a migrant in northern South West Africa, being most numerous during the rainy season, although a few seem to remain all year (Andersson, 1872). Collected specimens were found to be in breeding condition at the start of the rains in October (Hoesch and Niethammer, 1940), which is also the breeding season in Zambia. It appears, therefore, that in regions with a relatively high annual rainfall, as in southern Nigeria, *A. badius* breeds in the dry season, but in arid regions breeding takes place during the rains.

Plumage

Adult male.—Upperparts gray, or brownish gray in some forms with a rufous nuchal collar. Underparts white with narrow rufous to gray-brown bars, which vary in tinge geographically and individually. Throat white, vaguely mottled gray, with a feeble dark mesial line. Sides of head gray, lighter than back. Upperside of central rectrices unmarked or with dark spots adjacent to the shaft; the lateral feathers, except the outermost, show pronounced dark bars.

Adult female.—Browner than male on upperparts; browner tinge to the bars of the underside.

Juvenile.—Upperparts brown with the feathers edged with rufous. Underparts white, upper breast marked with brown spots or streaks, lower breast and abdomen with streaks or bars (varying geographically) and flanks with bars. Dorsum of tail with six dark bars which may be obsolete on central and outermost pairs of feathers.

Geographical Variation

Geographical variation occurs mainly in size (Table 6) and in color of the underparts.

A. b. badius is narrowly barred cinnamon-rufous underneath in adult plumage and streaked dark brown in the juvenile. A rufous nuchal collar is slightly evident in most adults, being conspicuous in some specimens.

TABLE 6
WING LENGTH IN *Accipiter badius.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
badius	176.4	2.96	1.33	173 - 181	5
dussumieri	187.0	7.87	3.94	178 - 197	4
cenchroides	189.4	2.51	1.12	185 - 191	5
poliopsis	196.7	7.63	3.81	190 - 206	4
sphenurus	177.3	6.20	1.42	167 - 187	19
polyzonoides	173.9	3.40	0.60	167 - 182	32
			♀		
badius	198.7	4.51	2.25	195 - 205	4
cenchroides	212	-	-	210 - 214	2
poliopsis	216.9	7.42	2.80	209 - 227	7
sphenurus	196.2	4.02	0.97	189 - 203	17
polyzonoides	188.8	4.31	0.58	178 - 198	54
				Total	156

A. b. dussumieri and *cenchroides* are clinally larger and are paler in adult plumage. *A. b. poliopsis* is still larger and the bars on the underparts are darker rufous and broader than in the other subspecies, almost forming a dark breast shield in some specimens. The female is still darker than the male. The upperparts are pure pale gray, lacking a rufous collar.

The African subspecies *sphenurus* is similar in color to nominate *badius* and of about the same size, but it never has a rufous collar. The juvenile is more transversally marked on the lower breast and abdomen. The central tail feathers protrude beyond the rest of the tail. *A. b. polyzonoides* differs markedly from *sphenurus* in adult plumage by having the bars on the underside narrower and gray-brown, not cinnamon-rufous. Gray pigments are much more in evidence than rufous ones. In addition, *polyzonoides* is decidedly smaller and lacks the elongated central rectrices. The differences in plumage between juveniles of the two races are negligible, however.

SIZE AND STRUCTURE

Size small to medium. Tarsus and toes short. Claws and bill small. Wing medium to long and pointed. Tail medium. Figure 5, Table 7.

For the purpose of statistical analysis, the few available specimens of *A. b. dussumieri* were grouped with *A. b. badius.* The difference between the subspecies is significant for all series of data. The difference between the sexes is significant for the tarsus (longer in male) and hind claw (smaller in male).

Bill and foot.—Of the *brevipes*-type. In the Asian races, *badius* and *cenchroides,* the bill and feet, and particularly the hind claw, are relatively larger than in *A. b. brevipes.* In *A. b. polyzonoides* the tarsus is longer.

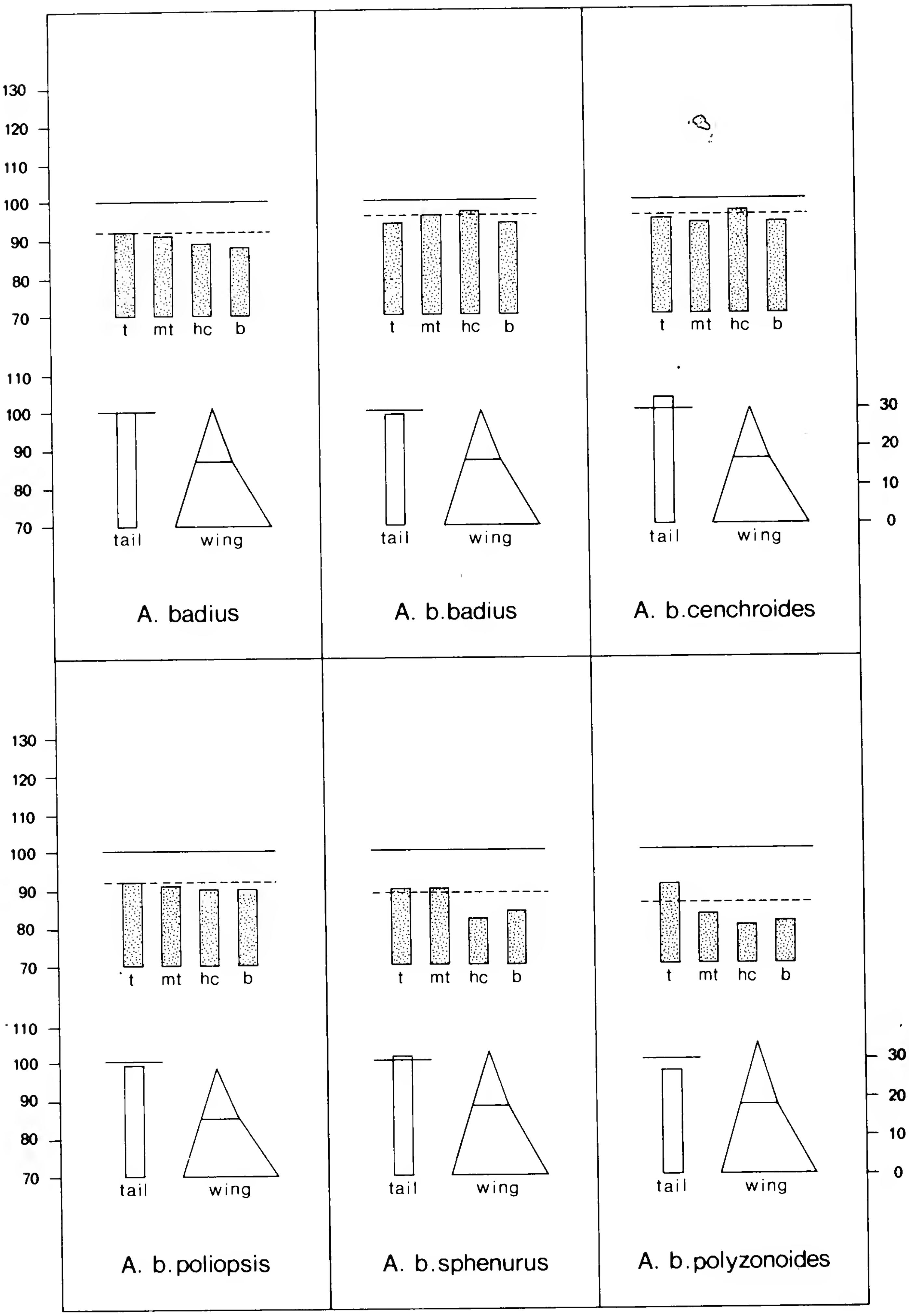


FIG. 5. Structure of *Accipiter badius.*

Wing and tail.—Intermediate between the *minullus*-type and *brevipes*-type. *A. b. poliopsis* is most similar to *minullus* and *A. b. polyzonoides* to *brevipes.* The tail is rather long in the races *cenchroides* and *sphenurus.*

TABLE 7

Relative measurements in percent of wing length in *Accipiter badius.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	25.01	14.56	7.31	6.54	76.18	30.69	13.68
'badius'	25.40	15.43	7.95	7.00	75.28	29.92	13.40
cenchroides	25.69	15.10	7.98	6.73	78.74	29.93	12.61
poliopsis	25.00	14.55	7.34	6.70	75.65	27.88	12.40
sphenurus	24.29	14.38	6.76	6.21	77.02	31.51	13.76
polyzonoides	24.66	13.34	6.52	6.04	74.22	34.22	16.23
♂	+0.42	-0.07	-0.16	-0.10	-0.48	+0.16	+0.44
♀	-0.42	+0.07	+0.16	+0.10	+0.48	-0.16	-0.44
Adult	-0.26	-0.10	+0.04	-0.01	-0.15	+0.40	-0.32
Juvenile	+0.26	+0.10	-0.04	+0.01	+0.15	-0.40	+0.32
P model	0.237	0.681	0.538	0.621	0.551	0.297	0.880
P ssp	0.001	0	0	0	0	0	0
P sex	0	0.664	0.049	0.348	0.131	0.333	0.520
n	101	95	44	47	117	53	43
df	85	79	28	31	101	37	27

HABITAT

Inhabits open woodland and trees in cultivated country and residential areas; not dense forests or treeless deserts. *A. badius* is one of the most numerous birds of prey in many parts of its range.

In southern Asia the Shikra, as this species is known, is common in open woodland and park-like country, in groves of dense trees amid cultivated ground, in towns and villages, country gardens and orchards. In Kazakhstan and Transcaspia it is mainly found in forests and plantations along rivers and irrigation canals (Korelov, 1962), in stands of *Tamarix* near brackish lagoons (Radde and Walter, 1889) and also in villages and settlements. In India and Pakistan its habitat comprises scrub jungle, tropical dry deciduous forest, tropical thorn forest, and tea plantations with shade trees. It ranges from sea level up to 1,500 m in the foothills of the Himalayas and to 1,400 m on Mount Victoria (Stresemann and Heinrich, 1940). *A. b. cenchroides* is thought to breed up to 1,500 m (Schüz, 1957) and even to 2,000 m in Astarabad, Iran (Heinrich, *in* Stresemann, 1928). The nest is placed in a thickly leafed tree.

The African populations occur in various types of savanna country, viz., *Brachystegia* woodland (*A. b. polyzonoides* only, because this type of country is unknown north of the rainforest belt), acacia woodland, thorny scrub, fairly open savanna with isolated baobab trees, and in trees and brush fringing water. Larger clearings, patches of native cultivation and secondary growth are inhabited in the forest belt of Ghana and Nigeria. In Zambian and Rhodesian townships, e.g., Livingstone, Mazabuka, and Mongu (Winterbottom, 1960; Voous, pers.

comm.), the species is common. Its altitudinal range extends from sea level up to about 1,500 m, which is the lower boundary of montane conditions in tropical Africa.

According to Vincent (1945) *A. b. polyzonoides* prefers to nest in the fringe of *Brachystegia* and *Isoberlinia* woodland, making its nest at a height of 6-15 m in the fork of a branch well removed from the trunk. McLachlan and Liversidge (1961) mention nesting in thorny trees.

Hunting Behavior

Typical still-hunter. Many records refer to its habit of sitting motionless, concealed by foliage or on a dead branch in the open, and attacking any small animal that appears in the neighborhood of its perch. The attack may end in a short pursuit in which the Shikra shows itself a very adroit flyer, although it would seem to be less speedy than *A. nisus. A. badius* may also stealthily approach potential prey in an attempt to strike by surprise.

Food

The diet is mostly lizards and large insects, particularly grasshoppers. Also a wide variety of other small animals, viz., small birds, mice, bats, other small mammals, and frogs.

Of the Asian forms *A. b. cenchroides* is reported to take birds but other types of prey predominate. Korelov (1962) lists the prey in Kazakhstan as small rodents, lizards, frogs, insects, and sparrows. *A. b. dussumieri* has an equally wide food spectrum, although it apparently has difficulty in handling middle-sized birds such as a roller and a parakeet (MacDonald, 1960). In this respect it is interesting that falconers have trained it for hunting quail and even small herons. Stomachs of specimens collected in Gujarat contained skinks, large insects, and small birds (Ali, 1954). The main prey species of nominate *badius* are frogs and lizards. Mice, rats, squirrels, large insects, and small birds are also taken (Baker, 1928; Ali, 1953). Stomachs of *A. b. poliopsis* from northern Thailand held mostly insects, frogs, and lizards and only a few birds and rodents (Deignan, 1945). In Indochina frogs and lizards are also the most important prey (Delacour and Jabouille, 1931).

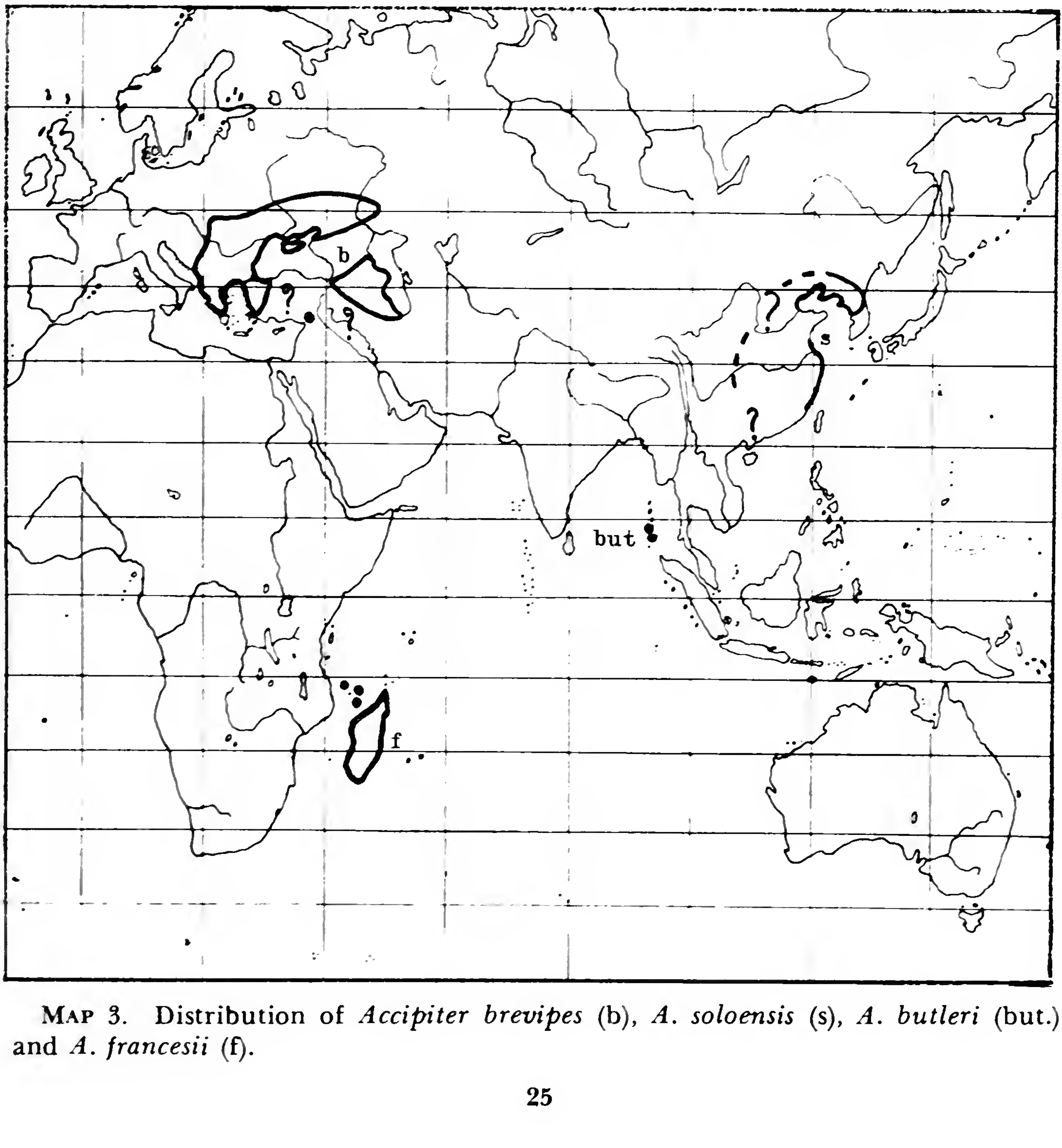
Analysis of stomachs of 20 specimens from various parts of Africa yielded the following (data from literature and specimen labels): insects (10 times), lizards (8 times), small birds (4 times), small mammals (twice, plus one bat in claws), and frog (once).

In Zambia nestlings were fed on grasshoppers and large soft larvae (White, 1943) and in Nigeria the pellets from young birds contained mostly insect remains (Serle, 1950). Swarming termites may be caught in numbers.

Although the same prey is taken in Asia and Africa it seems as if in Africa the balance is shifted toward insects. In Africa the Shikra lives side by side with other species of *Accipiter*, while in many regions of Asia it is the only species of the genus. Interspecific competition may therefore compel the races *sphenurus* and *polyzonoides* to turn their attention more to insects than do Asiatic populations.

DISCUSSION

A. badius belongs to a group of allopatric species, which are similar in several respects and which may be considered as a geographical species complex. The other forms of this complex are *A. butleri* (p. 32), *A. brevipes* (p. 26), *A. soloensis,* and *A. francesii* (p. 77). The details of the relationship of each to *A. badius* are discussed under the respective species. The *badius* complex has a clear Indian-African distribution (Maps 2 and 3). In several places it has penetrated the Palearctic. The colonizations that have given rise to *A. brevipes* and *A. soloensis,* respectively, date far back, but at a more recent stage, presumably only after the close of the last glaciation, *A. badius* again invaded the Palearctic (race *cenchroides*), extending its range to Turkestan. Here it can be regarded as the ecological counterpart of *A. nisus* in sparsely wooded, dry country (Voous, 1960), although it captures relatively fewer birds and more mammals, reptiles, and insects.



MAP 3. Distribution of *Accipiter brevipes* (b), *A. soloensis* (s), *A. butleri* (but.), and *A. francesii* (f).

With regard to geographical variation, it is remarkable that the closely similar races *badius* and *sphenurus* are separated by a wide gap in southwestern Asia, while the ranges of *sphenurus* and the more conspicuously different South African race *polyzonoides* border each other. This may indicate that the western Asian and the northeastern African populations have been separated only rather recently. It has been shown by Moreau (1966) that Africa has quite a number of savanna inhabiting species in common with the Oriental region. In his opinion their ranges may have been continuous across Arabia in the very recent past. During the Pleistocene glaciations, and also during the Neolithic humid period no more than 6,000 years ago, the vegetation of southern Arabia could sustain a savanna fauna, which may well have included *A. badius.*

The morphological differentiation between *sphenurus* and *polyzonoides* may indicate that in a more distant past a geographical barrier separated the populations of northern and southern Africa. Apart from treeless desert, two other types of country are unfit for *badius* and may have acted as barriers, viz., tropical lowland forest and montane vegetation. At present the upper limit in Africa is at 1,500 m. No more than 25,000 to 18,000 years ago the lower boundary for montane conditions was situated below 1,000 m, considerably restricting the area suitable for *badius* (Moreau, 1966). At present the boundary between *sphenurus* and *polyzonoides* lies somewhere in the region of southern Kenya and northern Tanzania. Nests are so seldom found in this region that it is not certain whether these races come in direct contact during the breeding season. In this area the coastal strip below 1,000 m is very narrow. Probably this lowland strip was clad in forest during cold periods in the Pleistocene. Together with the montane area more inland this coastal forest may have formed a complete barrier between two groups of populations of *A. badius.*

ACCIPITER BREVIPES (SEVERTZOV)

DISTRIBUTION

Southeastern Europe, Asia Minor, and western Iran (Map 3, p. 25).

MIGRATION

Present on the breeding grounds from April to late August. Winter quarters virtually unknown but there are scattered records from various Near East and northeastern African countries, from southwestern Iran west to Tunisia and south to northern Tanganyika (Wattel, 1966).

On migration fairly large numbers of *A. brevipes* have been seen at the Bosphorus (Porter and Willis, 1968) and in Lebanon in the autumn (Cameron, Cornwallis, Percival, and Sinclair, 1967) and at the head of the Gulf of Aqaba (Phillips, 1915; Safriel, 1968) and in northwestern Syria in the spring (Hollom, 1959). Farther south records are extremely scarce.

EUROPE AND ASIA

PLUMAGE

Adult male.—Upperparts dark gray, underparts white, broadly and regularly barred with cinnamon. Sides of face gray. Central tail feathers gray with a faint indication of dark crossbars, which are much more conspicuous on the lateral rectrices.

Adult female.—Upperparts more brownish than in male; bars on the underparts darker, varying from deep rufous to tawny brown.

Juvenile.—Dorsum dark brown with tawny feather edges. Underparts white with brown drops or streaks on the breast and arrowheads or imperfect bars on the abdomen and the flanks.

SIZE AND STRUCTURE

Size medium. Tarsus and toes short, but not heavy. Claws and bill small. Wing very long and pointed, the third primary being longest, not the fourth or fifth as in almost all other Accipiters. Tail medium. Figure 6, Tables 8 and 9.

Through lack of data no statistical analysis of the tarsus and middle toe could be carried out. Between the sexes no significant differences exist for the other sets of data.

HABITAT

Open woodland interspersed with fields, meadows, and gardens, edge of forest and steppe, sunny and stony hillsides with scattered trees or brush, vineyards, olive yards, and orchards, open country with large isolated trees, and stands of young trees with a few older ones rising

TABLE 8
WING LENGTH IN *Accipiter brevipes.*

SEX	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
♂	221.6	2.63	0.99	218 - 226	7
♀	234.9	4.90	1.63	229 - 242	9
				Total	16

TABLE 9
RELATIVE MEASUREMENTS IN PERCENT OF WING LENGTH IN *Accipiter brevipes.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	21.65	12.89	6.22	5.82	70.78	35.79	15.63
♂	-	-	+0.03	-0.09	+0.16	-0.26	-0.52
♀	-	-	-0.03	+0.09	-0.16	+0.26	+0.52
Adult	-	-	-0.10	0	-0.52	+0.05	-0.20
Juvenile	-	-	+0.10	0	+0.52	-0.05	+0.20
P model	no analysis		0.126	0.749	0.658	0.986	0.465
P sex	-	-	0.251	0.402	0.808	0.444	0.447
n	15	13	16	16	16	16	13
df	-	-	12	12	12	12	9

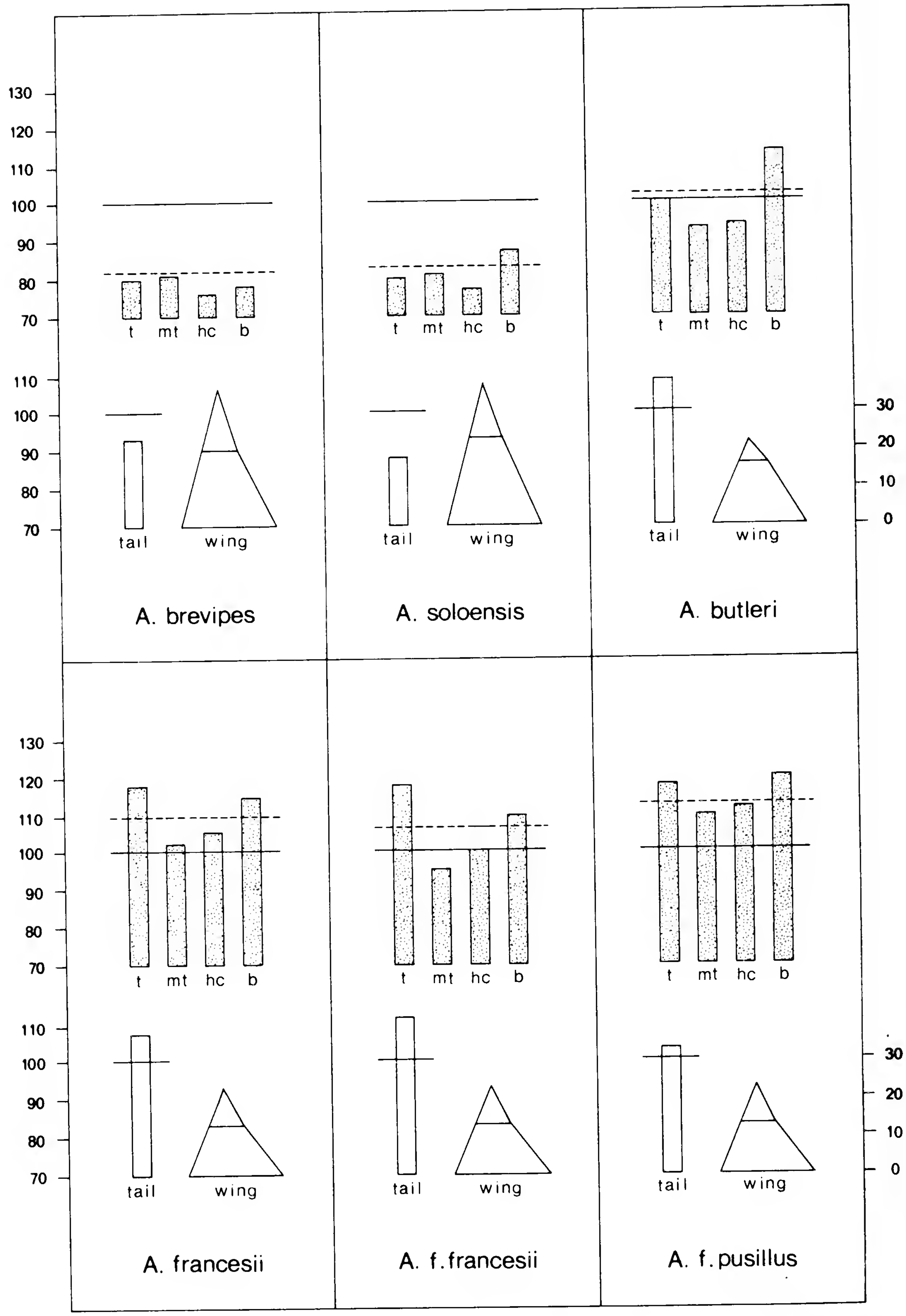


FIG. 6. Structure of *Accipiter brevipes, A. soloensis, A. butleri,* and *A. francesii.*

high above the others. *A. brevipes* is often found in the vicinity of running water. It does not occur in coniferous forests. Occasionally found close to human habitation or even in town gardens.

Its altitudinal range is from the lowlands up to 500 m, rarely to

950 m (Peus, 1954). Occurs in dryer, more open country and in lower mountain zones than *A. nisus* (Matvejev, 1950).

Hunting Behavior

Quite different from *A. nisus.* Less active in the pursuit of flying birds. *A. brevipes* was observed searching a plot of ground in an elegant gliding flight then suddenly swooping swiftly and deftly into the vegetation and rising immediately into the air again (Stegmann, 1933). Hovers frequently (Reiser and von Führer, 1896). Tries to stalk small birds by flitting from one tree to another (Aradi, 1964).

Food

Birds, mammals, lizards, snakes (Bodenstein, 1943), and large insects are eaten. It is doubtful that birds are as important a food as the literature seems to indicate. Birds are conspicuous when being hunted and their remains are easily recognizable, so the casual observer may be biased in his conclusions. The behavior described by Stegmann (1933) is suggestive of lizard hunting. Dombrowski (1912) found mainly lizards and large insects in the gizzard and stomach of collected specimens; birds and mammals were scarce. Captive young *A. brevipes* were fond of grasshoppers and took birds only reluctantly (Reiser and von Führer, 1896).

Discussion

A. brevipes is similar to *A. badius* in many respects and it belongs in the *badius* complex. It probably penetrated southeastern Europe during an interglacial period in the Pleistocene. Subsequently it was isolated from the main body of the group when during a glacial period colder conditions prevailed in eastern Turkey and northwestern Iran. The occurrence in the eastern Mediterranean area of relicts of several other warm region species suggests that *A. brevipes* may have survived there also. From the pattern of the present distribution it is clear that *brevipes* never crossed the Caucasus range, but spread into the southwestern U.S.S.R. through Rumania. This may also be deduced from the pattern of its migration, which is characterized by a southwesterly flight in southern Russia (Stegmann, 1933), and by the species' absence on the eastern shore of the Black Sea (Safriel, 1968). The species is probably still expanding its range eastward; breeding east of the Volga was not established before 1951 (Korelov, 1962).

In the older literature a difference of opinion existed as to whether or not *A. brevipes* is conspecific with *A. badius.* Stresemann (1923a) drew attention to the fact that not only *A. brevipes* but also *A. soloensis* closely resemble *A. badius.* He considered the three groups as conspecific. With regard to *brevipes* he was followed by many authors (e.g., Hartert and Steinbacher, 1932-38; Dementiev, 1951; and Voous, 1960).

Recently Schüz (1959, citing a letter from Stresemann) and Vaurie (1961) have again separated *badius* and *brevipes.* Vaurie based his conclusion (a) on the possibility of overlap in ranges; (b) on the fact that hybrids are unknown; and (c) on morphological differences. *A. brevipes* differs from *cenchroides,* the adjacent form, not only in wing formula but also in being larger and in the pattern of the barring on the underparts. The extent of overlap in range has not been accurately established. Birds belonging to both forms have been collected in May and June at Lenkoran on the southwestern corner of the Caspian sea (Dementiev, 1938), but Schüz (1959) did not find the taxa together at any locality in northwestern Iran. Recently *cenchroides* has been collected at a nest at Gulega, only 70 km southeast of Gale Lissar, where Schüz (1959) found *brevipes* in breeding condition (Genenger and Genenger, 1968).

It is not entirely clear whether *brevipes* and *badius* behave as separate species in the southwestern Caspian region. Also, an alleged hybrid is in the Zoological Museum of Moscow (Dementiev, 1951). However, in my opinion the indications that they have already passed the species limit are strong enough to follow Vaurie (1961) and to consider *A. brevipes* as an independent species. It was probably isolated from *A. badius* long before the Indian and African populations of that species were separated by the desiccation of southern Arabia (p. 26).

ACCIPITER SOLOENSIS (HORSFIELD)

DISTRIBUTION

Eastern China and Korea (Map 3, p. 25). Breeding range imperfectly known and records of breeding very scarce. Said to be resident in Taiwan (Hachisuka and Udagawa, 1951) but, as in the case of *A. virgatus gularis,* spring records may pertain to late migrants rather than to breeding birds; nesting has never been recorded.

Winters in southeastern Asia. Particularly numerous in northern Celebes and not uncommon in eastern Java. Recorded from the Andamans in the west to western New Guinea in the east.

PLUMAGE

Adult male.—Upperparts blue-gray to slate black. Venter variable, cinnamon to vinaceous and in some specimens strongly washed dove gray. A pale variant was named *Astur cuculoides* Temminck (Sharpe, 1874), but there is no evidence that the variation is of a geographical nature. Sides of face gray; dorsum of tail gray without bars.

Adult female.—More brown on the upperparts than in the male and more heavily pigmented below. Breast deep vinaceous or tawny with vestigial light bars.

Juvenile.—Above dark brown with inconspicuous rufous edges to the feathers. Underparts creamy white with rufous brown streaks on the breast, arrowheads and more or less regular bars on the abdomen and the flanks. Upperside of tail grayish with five dark brown bars.

EUROPE AND ASIA

Size and Structure

Size small. Tarsus and toes short, but not heavy. Claws small. Bill comparatively heavy. Wing very long and pointed, the third primary being longest. Tail very short. Figure 6, p. 28; Tables 10 and 11.

No significant differences between the sexes.

The bill and feet and the wings and tail are of the *brevipes*-type. Differs from *A. brevipes* by the heavier bill and the shorter tail.

Habitat

Its habitat is little known. In central Korea *A. soloensis* breeds in small woodlots in low hilly country, always close to rice fields or marshy ground, and does not occur high in the mountains (Wolfe, 1950). On the other hand, in China Shaw (1936) and von Jordans and Niethammer (1940) assume that it nests in mountainous country. Also in Taiwan it is believed to inhabit the mountains. It was found nesting in a grove of pines near Canton (Swinhoe, 1861). Nests were found in chestnut, oak, and pine (Wolfe, 1950) and in unspecified kinds of large (David and Oustalet, 1877) and small (Courtois, 1912-18) trees.

In its winter quarters in Java *A. soloensis* frequents habitats similar to those occupied during the breeding season, viz., open forest, rice fields, gardens, and plantations from sea level to 1,500 m (Hoogerwerf, 1948). In North Celebes Coomans de Ruiter (1954) found it mainly in the densely populated lowlands and rarely on small coastal islands and in the foothills of the mountains.

TABLE 10
Wing length in *Accipiter soloensis*.

SEX	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
♂	186.8	4.68	1.30	179 - 195	13
♀	195.5	4.37	1.31	186 - 203	11
				Total	24

TABLE 11
Relative measurements in percent of wing length in *Accipiter soloensis*.

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	21.66	12.96	6.36	6.46	66.61	36.51	18.15
♂	+0.09	-0.18	-0.09	-0.12	+0.24	-0.13	-0.17
♀	-0.09	+0.18	+0.09	+0.12	-0.24	+0.13	+0.17
Adult	-0.04	-0.20	+0.02	0	-0.01	+0.01	-0.28
Juvenile	+0.04	+0.20	-0.02	0	+0.01	-0.01	+0.28
P model	0.647	0.590	0.598	0.911	0.283	0.416	0.636
P sex	0.798	0.312	0.092	0.243	0.467	0.662	0.802
n	22	19	24	22	24	24	22
df	18	15	20	18	20	20	18

HUNTING BEHAVIOR

A. soloensis practices still-hunting. It is known to hover occasionally (Swinhoe, 1861). The method of capturing frogs (see below) has not been described but it may necessitate a type of low searching flight as recorded for *A. brevipes*.

FOOD

It feeds on large insects, such as grasshoppers, dragonflies, and large beetles, lizards, frogs, and occasionally small birds. In central Korea a population of *A. soloensis* subsisted exclusively upon frogs (Wolfe, 1950). The stomachs of seven other Korean specimens contained frogs (4 times), insects (3 times) and a mammal (once) (Fennell, 1965). Coomans de Ruiter (1954) analysed 14 stomachs of birds collected in Minahassa, Celebes and found grasshoppers (5 times), other insects (3 times), lizards (3 times), small birds (twice), a small fish (once), a small crawfish (once), grubs (once), unidentified remains (once), and one empty stomach (data from specimen labels).

DISCUSSION

A. soloensis is very imperfectly known, but from the information available it may be concluded that it occupies a place in the eastern Palearctic similar to that of *A. brevipes* in the western Palearctic. In structure *A. soloensis* is closer to *A. brevipes* than to *A. badius*, but a direct relationship between *soloensis* and *brevipes* is out of the question; the similarity is due to parallel evolution. It may be surmised that *A. soloensis* is a colonist from the *badius*-group of the Chinese region that became isolated as a result of the climatic vicissitudes in the late Pleistocene.

It is unknown whether there is any range overlap between *A. badius* and *A. soloensis*. *A. soloensis* occurs as a breeding bird near Canton (Swinhoe, 1861), meaning that overlap with *A. badius* may occur in southeastern China. The morphological difference between *A. soloensis* and *A. b. poliopsis* is larger than the difference between *A. brevipes* and *A. b. cenchroides*. Even without geographical corroboration I would recommend treating *A. soloensis* and *A. badius* as separate species, which is similar to my treatment of the parallel situation between *A. brevipes* and *A. badius*.

ACCIPITER BUTLERI (GURNEY)

DISTRIBUTION

Nicobar Islands, Indian Ocean (Map 3, p. 25).

SUBSPECIES

A. b. butleri (Gurney), Car Nicobar; *A. b. obsoletus* (Richmond), Katchall, probably also on Camorta.

PLUMAGE

Adult.—Upperparts pure bluish gray. Underparts white, with delicate barring on upper breast and flanks. Upperside of tail unbarred.

Juvenile.—Above rufous-chestnut with dark centers to the feathers. Breast and abdomen light rufous with vaguely delimitated dark spots. The feathers on the flanks have rufous centers and creamy white edges.

GEOGRAPHICAL VARIATION

The Katchall population, *obsoletus,* is described as differing from the Car Nicobar population, *butleri,* by being paler on the nape and the sides of the head in adult plumage. In addition the bars on the breast and flanks are light rufous in *butleri,* pale fawn in *obsoletus.* The iris is crimson in *obsoletus,* yellow or orange in *butleri* (Richmond, 1903).

SIZE AND STRUCTURE

Size small. Tarsus medium. Toes and claws small. Bill heavy. Wing very short and intermediate in shape. Tail medium. Figure 6, p. 28; Tables 12 and 13.

No statistical analysis.

Bill and foot.—Of the *trinotatus*-type, but the difference between the relatively large tarsus and bill and the relatively small middle toe and hind claw not so extreme as in *trinotatus.*

Wing and tail.—These are of the *minullus*-type and resemble *A. virgatus affinis* in having a short, but nevertheless rather pointed, wing and a relatively long tail.

HABITAT AND FOOD

A. butleri is rather common in the forest on Car Nicobar and in the dense jungle on Katchall; it is not found in the open or in scrub jungle (Richmond, 1903). A nest was placed at the end of a horizontal branch of a huge *Ficus* about 12 m from the ground (Butler, 1899).

Apparently the main prey consists of lizards; of five stomachs four

TABLE 12
WING LENGTH IN *Accipiter butleri.*

SEX	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
♂	168.5	-	-	167 - 170	2
♀	181	-	-	-	1
				Total	3

TABLE 13
RELATIVE MEASUREMENTS IN PERCENT OF WING LENGTH IN *Accipiter butleri.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	27.20	14.90	7.70	8.40	82.00	22.30	6.50
n	3	3	1	1	3	3	1

contained lizards and one insects (Butler, 1899; Abbott, *in* Richmond, 1903).

DISCUSSION

A. butleri shows a definite resemblance to the *badius* complex, though it differs in several respects including a much lighter color in the adult, the chestnut-rufous juvenile plumage, and a somewhat different general build. The different build may be interpreted as a reflection of the different ecology. A very short wing tip is found also in other Accipiters of dense forest, and feet and legs of the *trinotatus*-type occur in several other tropical forest species preying mainly on lizards. *A. butleri* shares the comparatively short sixth primary with the other species of the *badius* complex. It can be regarded as a colonist to the Nicobars from one of the continental populations of *A. badius* around the Bay of Bengal.

A. butleri is considered as conspecific with *A. badius* by many ornithologists including Voous (1960) and Ripley (1961). In view of the considerable morphological difference between *A. badius* and *A. butleri* I prefer to regard *butleri* as a separate species, as did Peters (1931), although neither opinion can be substantiated because of the lack of contact between the two forms.

In the case of *A. badius* and *A. brevipes* distributional arguments can be brought forward for treating the taxa as separate species (p. 00). Because *A. brevipes* is more similar to *A. badius* than is *A. butleri*, support is lent to the hypothesis that *badius* and *butleri* are better considered specifically separate.

ACCIPITER VIRGATUS (TEMMINCK)

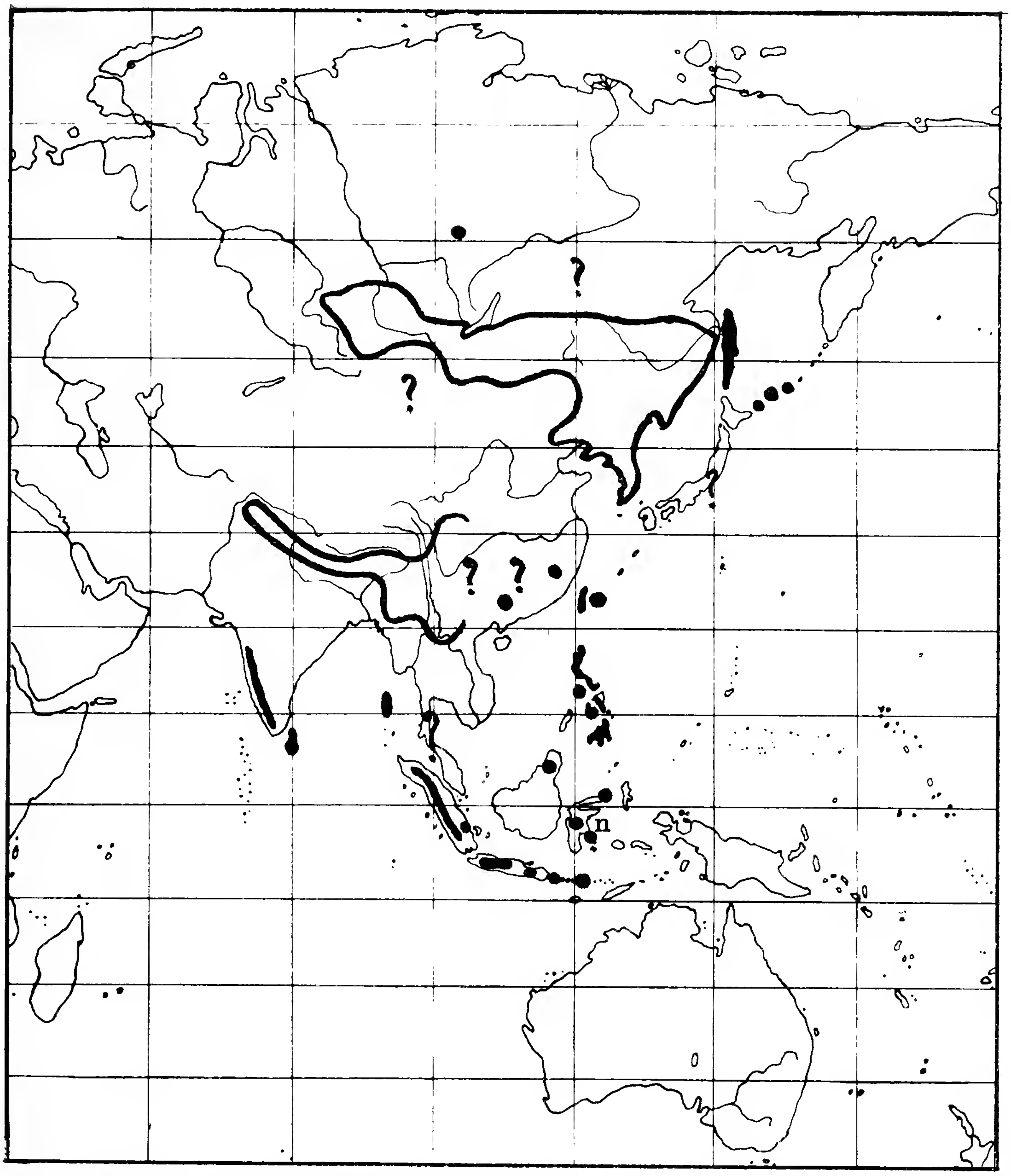
DISTRIBUTION

Southeastern Palearctic, Himalayas, Taiwan, Philippines, Malay Archipelago, and southern India (Map 4).

SUBSPECIES

The gularis *group* (*Palearctic*).—*A. v. gularis* Temminck and Schlegel, southeastern Siberia, northern Mongolia, northeastern China, Korea, Sakhalin, southern Kuriles (Bergman, 1935), and possibly breeding in mountains of central Honshu but not proved, migratory; *A. v. iwasakii* Mishima, islands of Iromoto and Ishigaki, southern Riu Kius, resident.

The affinis *group* (*Himalayas to Taiwan*).—*A. v. affinis* Hodgson, southern slopes of Himalayas from Kashmir east to western Yunnan and Szechwan, Upper Burma south to Mount Victoria, and on mountains of Taiwan. Recorded in the breeding season from mountainous areas in southeastern China (Yaoshan, Kwangsi, by Yen, 1930; Kuatun, Fohkien, by von Jordans and Niethammer, 1940), probably sparsely distributed throughout the mountains of southern China.



MAP 4. Distribution of *Accipiter virgatus* and *A. nanus* (Celebes, n).

The virgatus *group* (*Oriental*).—*A. v. virgatus* (Temminck), mountains on Java and Bali, a specimen from Flores may represent an undescribed subspecies (Voous, 1950); *A. v. vanbemmeli* Voous, mountains on Sumatra; *A. v. rufotibialis* Sharpe, mountains on northeastern Borneo, *A. v. confusus* Hartert, Luzon, Mindoro, Guimaras, Negros, Leyte, and Mindanao, Philippine Islands; *A. v. nisoides* Blyth, range very imperfectly known, the name has been applied to birds supposed to breed in Malacca, Tenasserim, and the Andaman Islands; *A. v. besra* Jerdon, mountains of Ceylon and southern India.

MIGRATION

A. v. gularis is strongly migratory, visiting the breeding grounds for only four months in the summer (mid-May to mid-September). The main winter quarters are in the western parts of the Malay Archipelago (Malaya, Sumatra, Borneo, and Java), although outside the breeding season this form has been recorded from places as far apart as East Pakistan and Guam (Marianas). Rarely it is found as far north as Japan in winter.

On migration it has been recorded in Japan, Taiwan, and the Philippines and also in eastern China. At Shaweishan Island (Kiangsu) it passes through in the autumn from early October to mid-November and in the spring throughout May and the first half of June (La Touche, 1931-34). Farther south at Nanking, Kolthoff (1932) witnessed passage in October and May. Heavy migration is also recorded from Malaya (Medway and Wells, 1964) and Singapore (Hurrell, 1961). In addition there are several records of specimens captured aboard ships in the South China Sea.

A. v. affinis shifts to lower levels and to the plains of India, Indochina, and southern China in winter. It appears in fair numbers on Hainan (Hartert, 1910). The population on Taiwan also descends from the mountains in the winter.

Plumage

Adult male.—Upperparts blackish slate, darker than in *A. nisus.* Underparts variously patterned with rufous, flanks mostly uniform rufous. Sides of face gray or brownish gray, not rufous as in *nisus.* Narrow dark mesial line on throat.

Adult female.—Dorsum browner than in male of corresponding subspecies; underparts less rufous, lacking the rufous flanks in some races.

Juvenile.—Above brown with narrow rufous feather edges. Underparts creamy white, breast with rufous or brown streaks tending to bars on the flanks. Throat with a dark mesial line.

Geographical Variation

The three groups of races differ both in plumage and in structure. The *gularis* group and the *affinis* group are rather uniform, while the *virgatus* group shows some geographical variation. The *gularis* group is characterized by its long wing tip and its pronounced sexual dimorphism in plumage. In the other groups male and female are rather similar in plumage, but tend to differ more in size (Voous, 1950; cf. Table 14). The *affinis* group is much larger than the *virgatus* group, the *gularis* group being intermediate in size.

The gularis *group.*—Adult male: underparts pale grayish buff to light ferruginous tawny with inconspicuous white crossbars on center of breast and abdomen. Flanks plain buff, tawny, or ferruginous. The palest males have been named as a separate subspecies (*A. v. stevensoni* Gurney) but there is no reason to suppose that they are geographically isolated from the more intensely pigmented ones. It was thought that the dark birds were breeding in Japan and the pale ones in continental eastern Asia, but Austin and Kuroda (1953) doubt if the species breeds

TABLE 14

Wing length in *Accipiter virgatus.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
gularis	165.9	3.80	0.67	158 - 174	32
virgatus	147.4	2.88	0.74	142 - 153	15
vanbemmeli	150.5	6.85	3.42	146 - 160	4
confusus	150.3	3.41	1.29	145 - 154	7
nisoides(Andamans)	146	-	-	-	1
besra	151.5	-	-	151 - 152	2
affinis	165.6	5.27	1.67	155 - 170	10
affinis(Taiwan)	174.3	2.77	0.93	169 - 178	9
			♀		
gularis	189.1	4.38	0.95	180 - 197	21
virgatus	173.3	4.87	1.54	164 - 180	10
vanbemmeli	180.0	-	-	179 - 181	2
confusus	175.7	3.58	1.26	170 - 181	8
nisoides(Andamans)	185.0	2.64	1.53	182 - 187	3
besra	181.5	-	-	180 - 183	2
affinis	204.0	3.39	0.93	199 - 211	13
affinis(Taiwan)	210.0	4.12	1.56	202 - 215	7
				Total	146

in Japan at all. If so, their numbers are certainly far too small to explain the preponderance of the *gularis* type in the winter quarters.

Adult female: underparts white, distinctly and regularly barred light brown. No trace of rufous on the flanks and gular stripe wider than in male.

Juvenile: underparts light cream with rufous brown streaks on the breast, spots on the abdomen, and wide bars on the flanks.

A. v. iwasakii differs from *gularis* by being smaller and having a more rounded wing (Mishima, 1962). Hartert (1912-22) already suspected that the population on Ishigaki was subspecifically distinct from *gularis.*

The affinis *group.*—Adult male: upperparts darker than in *gularis.* Breast with a cinnamon-buff breast shield, interrupted in the center by a white patch which is heavily streaked dark brown. Abdomen barred cinnamon-buff and white. Flanks cinnamon-buff. Thighs barred pale rufous, gray, and white. Some specimens have a deeper rufous pigmentation and no interruption of the breast shield.

Adult female: similar to the male, but the dark streaks on the center of the breast are more pronounced, almost black, forming a continuation of the gular stripe. Back and mantle browner. Back contrastingly lighter than crown.

Juvenile: resembles juvenile *gularis.* Underparts with dark brown, sharply delimitated streaks and spots.

Birds from Taiwan are darker, more earthen brown, and larger than those from the Himalayas. They have been named *A. v. fuscipectus* by Mees (1970).

The virgatus *group.*—Adult male: similar to *affinis* in pattern, but deeper rufous in tinge. Center of breast more or less mottled dark brown, rufous brown, and white. Abdomen broadly barred rufous brown and white. Gular stripe very pronounced.

Adult female: differs from the male by the more distinct longitudinal spots on the center of the breast.

Juvenile: similar to juvenile *gularis* and *affinis* but markings on underside more suffused and the ground color darker cream.

The geographical variation in the Malay archipelago is discussed by Voous (1950). In *A. v. vanbemmeli* the underparts are more extensively rufous than in nominate *virgatus* and the breast shield is not interrupted. In the Bornean population, *rufotibialis,* the rufous of the underparts has a more vinaceous tinge than in birds from Java and Sumatra. The thighs are entirely deep rufous. Vinaceous tinges of a slightly different hue are found in the Philippine subspecies *confusus.* In males the breast is plain vinaceous lacking brown and white mottling on the center and the abdomen is barred. Females are barred all over, the bars being more pronounced in specimens from the northern Philippines, fainter in those from the southern islands. Thighs barred gray and white or plain pearl gray. The peninsular Indian and Ceylonese form, *besra,* resembles nominate *virgatus* in pattern, but is somewhat paler, particularly on the upperparts. In addition it averages larger.

Birds from the Andaman islands, here tentatively referred to *nisoides* (Peters, 1931) are more brightly rufous in adult and juvenile plumage than any other population. An adult female in the British Museum is barred rufous and white underneath, resembling females from Luzon. Juvenile specimens have wide, bright rufous feather edges on the upperside and rufous streaks on the underparts, being similar to juvenile *besra,* but markedly more rufous. The brighter rufous of Andaman birds was also noted by Hume (1876). Abdulali (1964) mentions three specimens from South and Middle Andaman as *gularis,* but seems to describe an adult male as immature.

Voous (1950) is very skeptical about a breeding population of *A. virgatus* in Malaya. The nest purportedly found near Selama, Perak (Cairns, 1963) has made the existence of such a population more plausible, but no specimens were collected and the record requires confirmation. Baker (1928, 1935) reports equally unverified nests from Tavoy, Tenasserim. Until more is known about these populations it remains doubtful whether the name *nisoides* can be used in the sense as has been done here, following Peters (1931).

SIZE AND STRUCTURE

Size very small to rather small. Tarsus and toes long and slender. Claws and bill delicate. Wing in *A. v. gularis* long and pointed, in

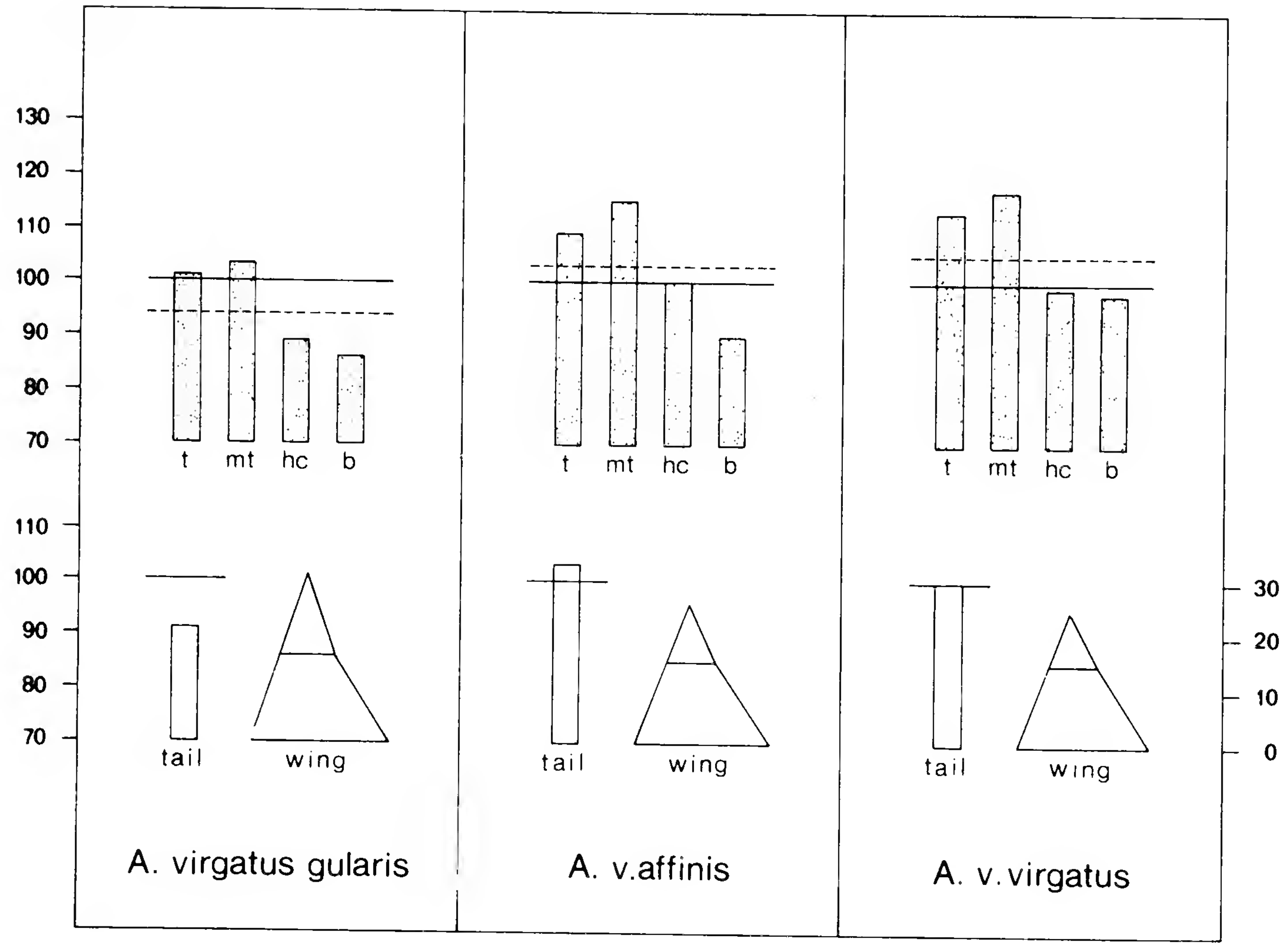


FIG. 7. Structure of *Accipiter virgatus*.

A. v. affinis and *"virgatus"* (for taxa included see below) short and pointed. Tail short, but medium in *affinis*. Figure 7; Table 14, p. 37 and Table 15.

For the purpose of statistical analysis all tropical Asian races were grouped under the name of *"virgatus."* The difference between the

TABLE 15

RELATIVE MEASUREMENTS IN PERCENT OF WING LENGTH IN *Accipiter virgatus*.

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	29.14	17.85	7.88	6.81	74.87	27.30	12.23
gularis	27.31	16.42	7.30	6.42	69.47	31.49	15.93
'virgatus'	30.56	18.80	8.13	7.29	75.82	24.78	10.02
affinis	29.55	18.83	8.21	6.72	78.32	25.62	10.74
♂	+0.89	-0.01	-0.20	-0.14	-0.17	-0.16	+0.39
♀	-0.89	+0.01	+0.20	+0.14	+0.17	+0.16	-0.39
Adult	-0.14	-0.06	+0.03	+0.08	-0.73	-0.13	-0.78
Juvenile	+0.14	+0.06	-0.03	-0.08	+0.73	+0.13	+0.78
P model	0.498	0.060	0.825	0.086	0.074	0.241	0.117
P ssp	0	0	0	0	0	0	0
P sex	0	0.896	0.001	0	0.091	0.256	0.040
n	79	63	77	78	84	81	77
df	67	51	65	66	72	69	65

groups is significant for all series of data. The difference between the sexes is significant for tarsus (longer in male), hind claw (smaller in male), bill (smaller in male), and wt–6 (longer in male).

Bill and foot.—Of the *nisus*-type. Due to the short wing, the relative measurements of the bill and feet appear larger in *affinis* and *"virgatus"* than in *gularis,* but the structure is essentially similar. In *affinis* the hind claw is comparatively heavy.

Wing and tail.—In *"virgatus"* and *affinis* these structures are of the *minullus*-type. In *affinis* the tail is relatively longer than in *minullus.* In this respect *affinis* resembles *A. badius butleri* and *A. francesii pusillus.* In *gularis* the wing and tail are of the *brevipes*-type, but the wing tip shorter.

HABITAT

The habitat is broken forest. Migratory populations occur in more open country after the breeding season.

The gularis *group.*—Occurs in mixed and deciduous forest in the southern parts of the taiga and in lower mountain zones. Pine-fir woods with scattered aspen and birch (Johansen, 1957), luxuriant oak woods with many gaps in the canopy along watercourses, mixed taiga with elm, maple, and birch along rivers. Where the species occurs in large stretches of taiga, it is always found in mixed stands near water (Vorobiev, 1954). Stegmann (1936) believes that *A. virgatus* is essentially an element of the fauna of broad-leaved forests, which in southern Siberia can be regarded as a relict from a slightly warmer period.

On migration and in its winter quarters *gularis* is often found in relatively open country, such as rice fields alternating with patches of jungle, plantations, and wooded villages.

The affinis *and* virgatus *groups.*—Occur in evergreen and deciduous mountain forest often interspersed by gullies and narrow valleys, in the neighborhood of cultivation, or in well-wooded gardens (La Touche, 1931-34). The species is found in moist deciduous forests and plantations in the mountains of southern India and Ceylon, in secondary pine forest and dense secondary growth in Sumatra (Chasen and Hoogerwerf, 1941), and in teak forest in Java (Sody, 1953). Nests have been found in various trees, often close to a road or a rivulet, sometimes in a high tree in dense forest or in an isolated tree in a clearing. The altitudinal range extends from 300 to 3,050 m; in the equatorial belt it ranges mostly between 1,000 and 2,200 m (Voous, 1950). Only in the Andaman Islands was this hawk reported to breed in mangroves at sea level (Osmaston, 1906).

A. virgatus shows a preference for dense patches of forest alternating with open spaces; this is apparent also in *A. nisus* and *A. gentilis.* It occupies a somewhat different habitat in Siberia, inhabiting forests of a more southern type. In the Himalayas and the mountains of western China it occurs in subtropical forests at altitudes of 600 to 2,100 m (Baker, 1935). In these same areas *A. nisus* and *A. gentilis* are typically birds of the temperate forests at the higher levels, ranging from 1,200-4,500 m.

Hunting Behavior

The hunting style is little known, but it resembles the behavior of *A. nisus. A virgatus* is a very active and speedy flyer and is able to take its prey by complete surprise (Meinertzhagen, 1959). It can also turn to still-hunting, and is often seen sitting on tall dead trees on the margin of evergreen jungle (Ali and Ripley, 1968).

Food

The gularis *group.*—Mostly small birds are taken, but also insects and more rarely mammals. Warblers, nuthatches, buntings, titmice, and sparrows were found in stomachs of specimens collected in Ussuriland (Vorobiev, 1954). Small mammals are only taken when they are extremely abundant. Stomach analyses of Japanese birds yielded 76% birds, 28% insects, and 4% mammals; in another series of specimens it was 46% birds, 41% insects, 9% mammals, and 1% other material (Ishizawa and Chiba, 1967). From the winter quarters of *gularis* birds are also most frequently reported as prey.

The affinis *group.*—This group also feeds on small birds, such as barbets, bulbuls, thrushes, sparrows, tits, and warblers (Ali and Ripley, 1968); large insects and mammals, e.g., small flying squirrels, mice and bats (Baker, 1928). Biswas (1960) found birds in several stomachs from Nepal.

The virgatus *group.*—Little is known of the feeding habits. For *besra* lizards are important as prey, but insects, birds, and mammals are taken as well (Baker, 1928). Three stomachs of *vanbemmeli* from Acheen contained birds (Chasen and Hoogerwerf, 1941) and on Korinchi Peak, northern Sumatra, it was assumed to take *Turdus poliocephalus* in the heather zone.

Discussion

The similarity in structure of the bill and feet of *A. virgatus* and *A. nisus* is related to a similar choice of prey, both species taking mainly small animals while in flight. *A. virgatus* differs from *A. nisus* in basic wing and tail shape and in addition varies geographically. The strongly migratory subspecies *gularis* has a much longer wing tip than the slightly migratory or sedentary forms of the *affinis* and *virgatus* groups. This may be correlated with migration (Voous, 1950) and probably also with a difference in habitat. Long-winged *A. v. gularis* passes the better part of the year either on migration or in the winter range, where it is found in more open country than the forms of the *virgatus* group, which are confined to dense mountain forest throughout the year.

The three subspecies groups show considerable differences in plumage and in structure of the wing. In the older literature they are sometimes considered as three separate species (e.g., Hartert, 1910, 1912-22). Stresemann (1923a) advocated combining the groups into a single species and this was followed by Peters (1931), Hartert and Steinbacher (1932-38), and Voous (1950). As the three groups are allopatric, it is impossible either to prove or disprove Stresemann's thesis.

Recently Vaurie (1965) suggested, on morphological grounds, a specific separation of *gularis* on the one hand and *affinis* and *virgatus* on the other. The delimitations of the ranges which are given by him imply a considerable overlap of *gularis* and *affinis*, and that would settle the question of species status unequivocally. However, his inclusion of eastern China in the breeding range of *gularis* is an unwarranted supposition. Certainly *gularis* is recorded there in late spring and early summer, but these birds may well be late migrants, the last wintering individuals not departing from Indonesia until the middle of May and passing Shaweishan Island as late as 13 June. When Hachisuka and Udagawa (1951) stated that *gularis* is a resident of Taiwan they were certainly deceived by the presence of migrants. The common belief of earlier authors that the species was breeding in numbers in Japan may have had a similar origin. The fact that La Touche (1931-34) and Baker (1928), following "various writers on Eastern ornithology," were of the opinion that *gularis* could be separated specifically from *virgatus* and that the form *A. gularis nisoides* occurred sympatrically with *A. virgatus affinis* in South China added to the confusion. Careful comparison of the descriptions which are given of *affinis* and *nisoides* leads to the conclusion that these descriptions at least partly refer to the same birds. In my opinion the present information leads one to believe that the mountainous parts of China south of the Yangtze River are inhabited by only one population of small sparrow hawks. The birds collected in this region resemble most closely *A. virgatus affinis* (von Jordans and Niethammer, 1940). No overlap of the breeding ranges of the *affinis* group and the *gularis* group has been proven. Thus Vaurie's opinion is not corroborated by geographical data.

The *affinis* group and the *virgatus* group are birds from montane and submontane habitats, which are absent in large areas of tropical lowland jungle in Southeast Asia. Consequently their ranges are very disjunct, although *affinis* inhabits a large continuous area along the southern flanks of the Himalayas.

The *virgatus* group differs from *affinis* by more rufous pigments, though single strongly rufous specimens are also known from the range of *affinis*. A similar increase in rufous pigments in tropical mountain forms is found in *A. nisus* and *A. striatus*. In the *virgatus* group four more or less clearly separate groups can be discerned. The races of the Greater Sunda Islands are very close to each other, but *confusus* differs from these races in several respects, viz., the coloration of the thighs, the hue of the rufous, and the absence of dark streaks on the center of the breast. Apparently *confusus* originated independently whereas *vanbemmeli, virgatus,* and *rufotibialis* had a common origin. The Andaman population is again different, being very strongly rufous. Birds from southern India and Ceylon, on the other hand, are closely similar to the Malaysian races, but this similarity is due to convergence rather than to former geographical contact. The above-mentioned populations may all have been derived from *affinis.* Apparently the species is an old inhabitant of the Oriental region. During glacial periods a general fall in temperature may have increased the range of populations of the *virgatus* group by lowering the boundary of submontane conditions, at the same time reducing the gap which at present separates these populations.

Nevertheless, the geographic origin of the Oriental forms of *virgatus* is based upon the assumption that the species is of Himalayan and hence ultimately of Palearctic origin and not an autochthonous Oriental element. The present distribution of *A. virgatus* in the tropical mountains is indicative of a Palearctic element that has invaded the Oriental region. Further back in history *A. virgatus* possibly had a common origin with *A. nisus* and hence may be regarded as a very old Himalayan isolate of the group of Holarctic, long-toed, bird-hunting Accipiters.

The distribution and the habitat of *gularis* point to an Oriental origin. After having become isolated in the Himalayas and adjacent mountains, the ancestors of *A. virgatus* recolonized the eastern parts of the Palearctic and differentiated into the present form *gularis.* This may have happened during one of the earlier Pleistocene interglacials. Several other Oriental birds of prey penetrate the eastern Palearctic in a similar way, e.g., *Butastur indicus* and *Spizaetus nipalensis orientalis. Accipiter soloensis* may be another instance, but it goes less far north (see p. 30).

The occurrence of a population on the southern Riu Kiu Islands which is most closely similar to Palearctic *gularis* can be understood by supposing that a group of migrants of the northern form settled in these islands. The islands probably offered opportunities for survival as they were previously devoid of Accipiters.

ACCIPITER NISUS (LINNAEUS)

DISTRIBUTION

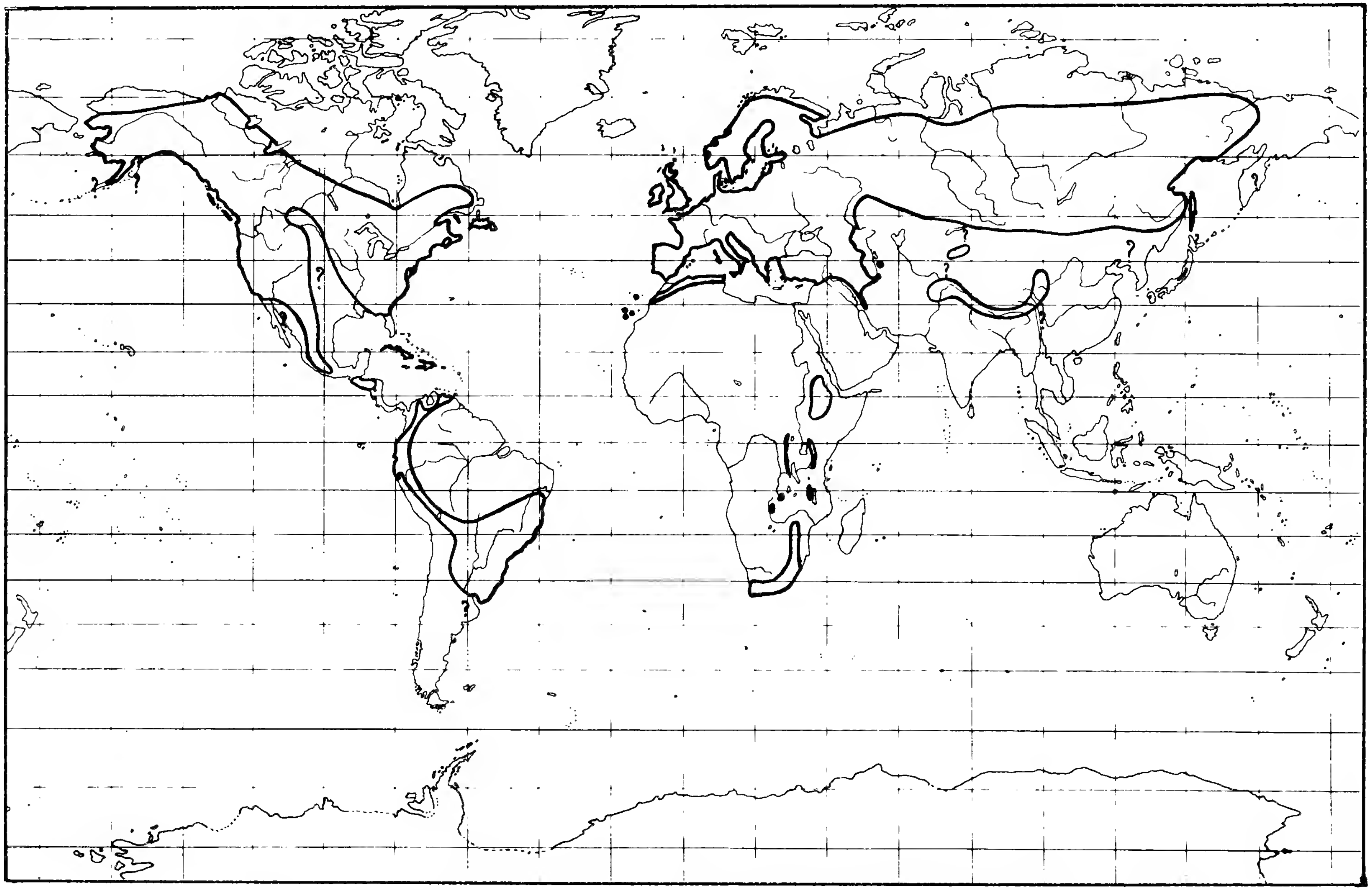
Palearctic, in forested country. Mountains of East Africa, down to sea level in South Africa (Map 5).

Birds of the northern parts of the range are migratory, wintering in the southern Palearctic, East Africa south to Tanzania, India south to Travancore, Burma, and Indochina. Populations living on mountains winter at lower elevations.

SUBSPECIES

cf. Vaurie (1965), Stepanyan (1958), White (1965).

The nisus *group (Palearctic).—A. n. nisus* (Linnaeus), Europe, east



MAP 5. Distribution of *Accipiter nisus* (Old World) and *A. striatus* (New World).

to western Siberia, intergrading with next race; *A. n. nisosimilis* (Tickell), from western Siberia east to the Pacific, south to about lat. 50°N in central Asia, to Hopeh, China, and the mountains of Hondo, Japan; *A. n. dementjevi* Stepanyan, central Tien Shan and adjacent mountain ranges; *A. n. melaschistos* Hume, Himalayas, from Baluchistan east to mountains of western China; *A. n. wolterstorffi* Kleinschmidt, Sardinia and Corsica; *A. n. punicus* Erlanger, northwestern Africa; *A. n. granti* Sharpe, Madeira, Gran Canaria, Teneriffe, and La Palma.

The rufiventris *group (African).*—*A. n. perspicillaris* (Rüppell), highlands of Ethiopia; *A. n. rufiventris* A. Smith, Kenya south to Cape Province.

According to Mees (1967) the name *exilis* (Temminck) should be used instead of *rufiventris.* Though *exilis* may conform better to the rules of nomenclature, in my opinion it is of no value to drop an established name in favor of an obsolete one.

PLUMAGE

Adult.—Upperparts dark slate gray, paler on rump, darker on head, tinged browner in the female than in the male. Underparts variable geographically and individually. Sides of face rufous with dark brown shaft streaks. Throat marked with narrow dark shaft streaks. Tail gray with wide dark crossbars, inconspicuous on the upperside, more pronounced underneath.

Juvenile.—Upperparts dark brown with rufous feather edges. Underparts variable.

GEOGRAPHICAL VARIATION

The *rufiventris* group differs from the *nisus* group in the intensity of rufous pigmentation and in the pattern on the underparts. In the *nisus* group there is pronounced sexual dimorphism in adult plumage, which is absent in the *rufiventris* group.

The nisus *group.*—Adult male: underparts white with rufous-gray bars. Each bar consists of a gray line and a rufous line, the last extending to a drop near the shaft. The width of the bars and the amount of rufous vary enormously from one specimen to another. Occasional birds are entirely washed with rufous and resemble adults of the *rufiventris* group. Most have a few wholly rufous feathers on the flanks. Thighs barred.

Adult female: underparts barred, but bars less rufous, more brown-gray than in male. Some specimens, however, particularly second year birds, are strongly tinged rufous, approaching the situation in the male.

Juvenile: underparts pale buff with a pattern of lighter or darker brown bars, arrowheads, or hearts. Some juvenile females are similar to adults, but the bars on the underside are generally a little warmer brown and the upper tail coverts are tipped cinnamon-rufous, not white as in adult birds.

Individual variation is considerable. It has been described and figured in detail by Kleinschmidt (1923-37).

Geographical variation in the Palearctic populations is slight and partly clinal. A size cline runs from southwest to northeast, *granti* being on the average smaller than *nisus* and *nisosimilis* larger. *A. n. punicus* is a rather pale form. The best defined races are *wolterstorffi* and *melaschistos,* both being darker than *nisus* and *nisosimilis.* In addition *wolterstorffi* is smaller and has a relatively short wing tip, whereas *melaschistos* is large.

Until recently *melaschistos* was thought to be separated by a gap of more than 1,600 km from the nearest populations of *nisosimilis* at Lake Zaysan (Vaurie, 1961). Stepanyan (1958), however, studied four specimens collected in June and July in the region of Issyk-Kul and in Fergana, which he described as being lighter and smaller than *melaschistos* and darker than *nisosimilis.* Fourteen additional specimens collected in the same region in May, August, September, and October are similar. Stepanyan considered these birds to belong to a separate subspecies, which he named *A. n. dementjevi.* In characters *dementjevi* is intermediate between *nisosimilis* and *melaschistos.* It thus appears that *melaschistos* is less isolated geographically than was formerly thought.

The rufiventris *group.*—Adult: below ranging from white, with faint narrow cinnamon bars, to plain deep rufous; most frequently cinnamon-rufous with slightly darker bars. Thighs rufous.

Juvenile: underparts cinnamon or cinnamon-rufous marked with dark brown shaft streaks and faint spots. Flanks cinnamon-rufous with dark bars. Thighs deep cinnamon with hardly any bars.

A. n. perspicillaris is a trifle smaller and more heavily pigmented than *rufiventris.*

SIZE AND STRUCTURE

Size rather small to medium. Tarsus and toes long and slender. Claws and bill delicate. Wing long and rounded, tail medium to long. Figures 8 and 9; Tables 16 and 17.

The statistical model was unsatisfactory for the tail and wing tip. The difference between the subspecies is significant for all series of data that could be analysed. The difference between the sexes is significant for the tarsus (longer in male), hind claw (smaller in male), and bill (smaller in male).

Bill and foot; wing and tail.—These are of the *nisus*-type. The subspecies vary slightly in the relative proportions of the tarsus and middle toe, hind claw and bill. In *A. n. rufiventris* and *A. n. perspicillaris* the bill is slightly larger in relation to the hind claw than in the Palearctic races. This phenomenon is also found in the South American form *A. striatus ventralis* versus Nearctic *A. striatus velox.*

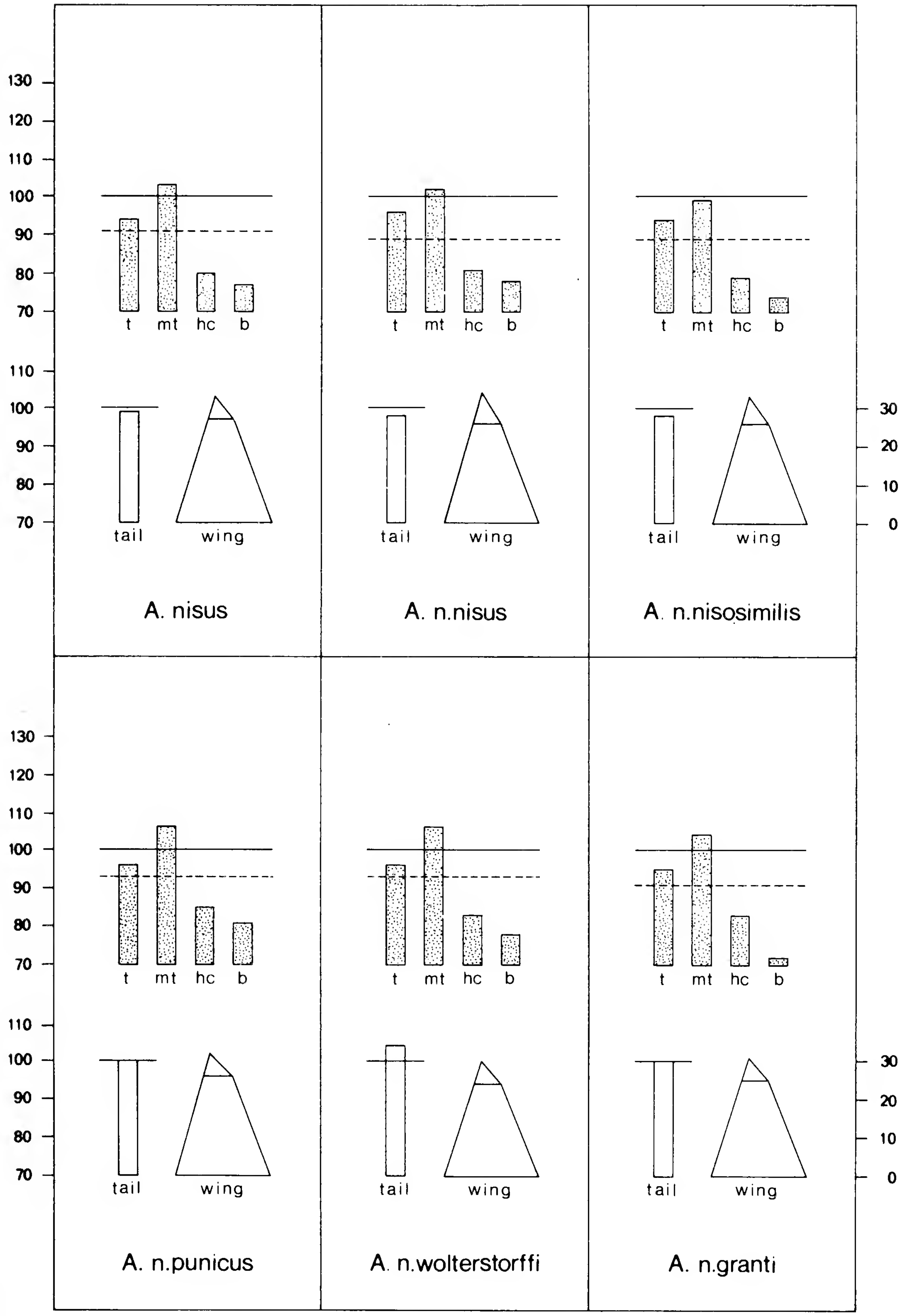


FIG. 8. Structure of *Accipiter nisus.*

The insular race *wolterstorffi* has a shorter wing tip and a relatively longer tail than *nisus* and *nisosimilis*. The races *punicus* and *granti* are intermediate in this respect.

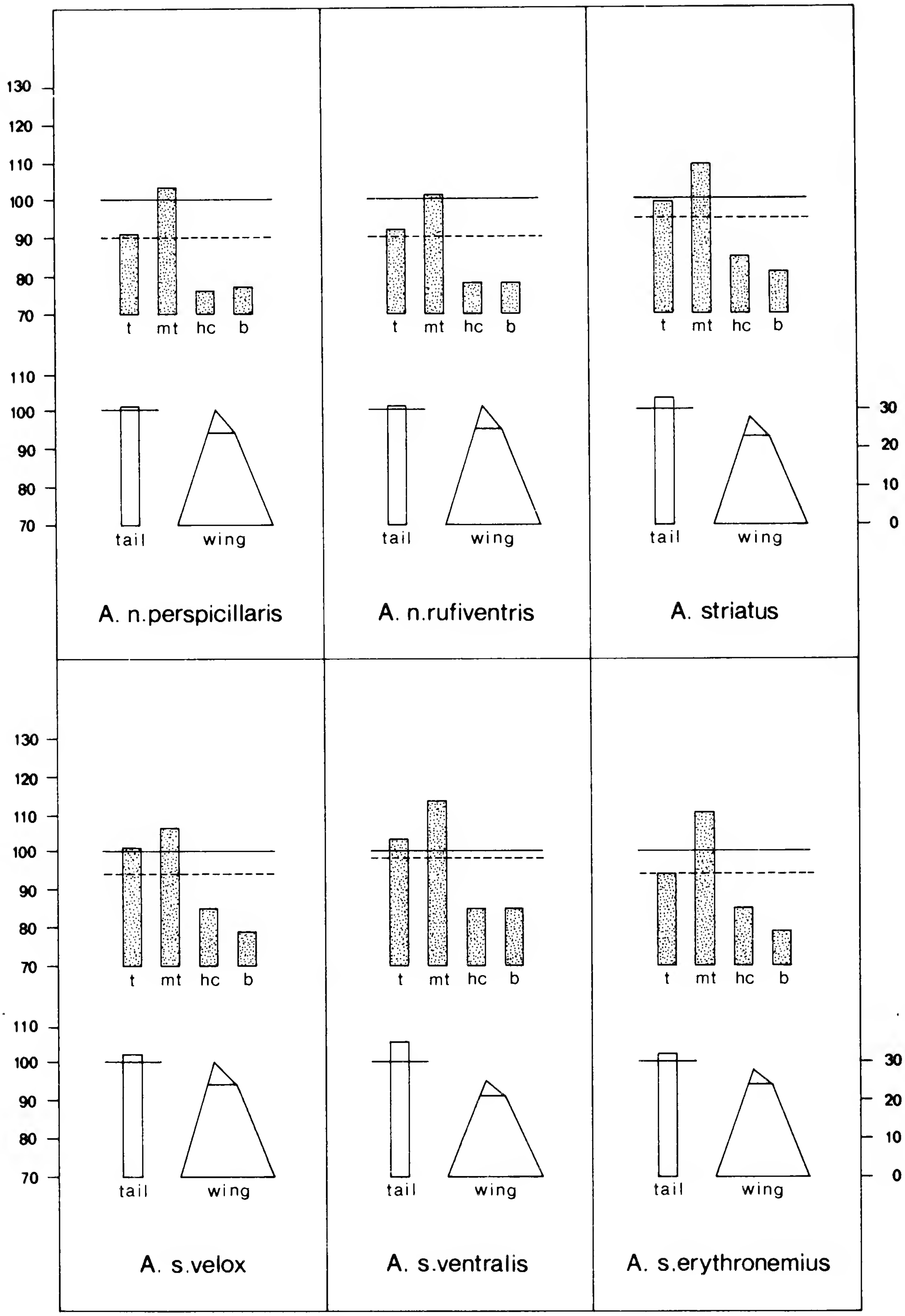


Fig. 9. Structure of *Accipiter nisus* (African subspecies) and *A. striatus*.

Habitat

The sparrow hawk inhabits forests and small dense woods from the arctic timber line south to the edge of treeless steppe country and also subtropical and temperate mountain forests, up to the timber line.

TABLE 16

Wing length in *Accipiter nisus.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
nisus	200.6	3.97	0.39	188 - 209	101
nisosimilis	210.4	6.35	2.40	200 - 216	7
punicus	204	-	-	-	1
wolterstorffi	185.5	-	-	184 - 187	2
granti	193.3	7.02	4.05	186 - 200	3
perspicillaris	196.1	2.46	1.10	194 - 200	5
rufiventris	201.2	4.38	0.89	194 - 208	24
			♀		
nisus	237.8	4.80	0.59	225 - 247	67
nisosimilis	247.7	6.65	3.33	242 - 254	4
punicus	233.5	-	-	233 - 234	2
wolterstorffi	218.0	-	-	217 - 219	2
granti	230.0	1.73	1.00	229 - 232	3
perspicillaris	229.0	3.60	2.08	225 - 232	3
rufiventris	232.6	5.97	1.58	224 - 244	15
				Total	238

It is found in wooded tundra, dark spruce-pine forests with small glades, rich deciduous woodland on fertile soil, intrazonal pine woods in steppe country, and cultivated groves of pine; occasionally in copses

TABLE 17

Relative measurements in percent of wing length in *Accipiter nisus.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	25.54	16.49	6.60	5.70	76.48	31.69	6.56
nisus	25.91	16.36	6.64	5.79	74.68	33.54	7.51
nisosimilis	25.44	15.89	6.46	5.48	74.21	33.55	7.11
punicus	26.09	16.90	6.96	5.99	75.79	31.75	5.58
wolterstorffi	26.07	16.95	6.78	5.77	79.50	30.00	6.45
granti	25.80	16.70	6.77	5.33	76.50	31.32	6.48
perspicillaris	24.59	16.48	6.20	5.72	77.91	30.25	5.97
rufiventris	24.87	16.14	6.39	5.81	76.78	31.41	6.81
♂	+0.51	-0.09	-0.24	-0.15	+0.05	-0.13	+0.03
♀	-0.51	+0.09	+0.24	+0.15	-0.05	+0.13	-0.03
Adult	-0.04	-0.06	+0.03	+0.03	-0.68	+0.13	-0.40
Juvenile	+0.04	+0.06	-0.03	-0.03	+0.68	-0.13	+0.40
P model	0.158	0.142	0.782	0.623	0.001	0.002	0.133
P ssp	0	0.010	0	0	-	-	0.001
P sex	0	0.081	0	0	-	-	0.169
n	185	146	191	205	233	211	207
df	162	123	169	183	210	189	185

and brushwood or even urban parks. Coniferous or mixed woods are preferred to pure deciduous woods, especially in eastern Asia.

In many mountain ranges (e.g., the Alps) *A. nisus* is found breeding from the valley floor up to the tree line and regularly hunts far beyond. In the southernmost parts of its range it is absent from the warmer lower zones during the breeding season. In northwestern Africa it occurs chiefly in mixed forests of cedar and oak between 1,400 and 1,700 m, but it ranges up to 1,900 m (Heim de Balsac and Mayaud, 1962). In northern Iran it occurs at about 1,500 m in tall open woods with much undergrowth (Streseman, 1928). In western Tien Shan it ranges through forests of spruce and silver fir (Korelov, 1962). In the Himalayas it is found in rhododendron forest and typical Palearctic forest where it is a breeding bird up to the tree limit at 4,200 m and has been observed hunting at about 4,600 m (Biswas, 1960; Diesselhorst, 1968). The lower limit of the breeding distribution apparently lies at 1,200 m, but usually the species does not descend lower than 1,800 m in the summer (Baker, 1928; Whistler, 1926). It was also found at high altitudes (2,900-4,500 m) in southeastern Tibet in forest fringing steep-sided river valleys and in brush along rivers on the high plains (Schäfer, 1938; Ludlow, 1944). In Japan it occurs in mountain forest from 600 to 1,400 m, with occasional birds to 2,800 m (Jahn, 1942).

The African subspecies inhabit subtropical evergreen mountain forest including the bamboo belt (Chapin, 1932), short open grassland interspersed with patches of evergreen forest (Benson, 1940), parkland and spacious gardens, *Brachystegia* woodland at high altitude, and groves of cultivated eucalyptus or pine. *A. n. rufiventris* ranges from 1,200-2,850 m in the eastern Congo, from 1,800-2,400 m in Malawi, from 1,300 to 2,150 m in Rhodesia, from 600 to 1,800 m in Natal, and down to sea level in the southern Cape Province. *A. n. perspicillaris* was observed at about 2,400 m in Eritrea (Smith, 1957).

Essential for *A. nisus* is a patch of dense trees in which the birds can hide and nest, and a stretch of more or less open ground from which it can swiftly reach its breeding territory (Uttendörfer, 1939). It avoids the interior of extensive forests and usually keeps to the neighborhood of a watercourse, forest road, clearing, or forest edge. Thus *A. nisus* can be numerous where small woodlots dominate the scenery, alternating with villages and cultivated ground. It may be presumed that in parts of its range the species is or was more numerous than it would have been without man-made diversification of the country. In this respect it can be termed an attendant of cultivation.

The habitat of *A. nisus* resembles that of *A. gentilis.* In central and western Europe in particular the main difference is that *A. gentilis* is partial to woods with old and tall trees (more than 60 years old), whereas *A. nisus* prefers smaller and younger trees (from 20 to 60 years old). *A. nisus* is more often found in small woodlots and is more numerous in intensely cultivated areas than is *A. gentilis* (Uttendörfer, 1939). In high mountains *A. nisus* often reaches the timber line, while

A. gentilis is decidedly rare in the upper reaches of the forest. In the border regions of the arctic tundra, however, *A. gentilis* penetrates farther north beyond the limits of the forest than does *A. nisus* (Pleske, 1886).

In southeastern Siberia *A. nisus* is sympatric with *A. virgatus gularis.* There *A. nisus* is a breeding bird of the spruce forest and *A. v. gularis* of the broad-leaved forest. In the Himalayas *A. nisus* is found at higher altitudes than is *A. virgatus affinis.*

In southeastern Europe and Asia Minor *A. nisus* overlaps with *A. brevipes.* According to Matvejev (1950) *A. nisus* occurs chiefly at medium altitudes, whereas *A. brevipes* is confined to the lowlands. Peus (1954), however, suspected breeding of *A. nisus* in the remnants of primeval forest in the lowlands of northern Greece. This suggests that the habitats of *A. nisus* and *A. brevipes* differ not only in altitude, but also in the character of the vegetation, *A. brevipes* being confined to more open country with scattered trees (p. 27).

HUNTING BEHAVIOR

This species' hunting is characterized by sudden attack at short range. Two types of hunting can be discerned, viz., still-hunting and searching.

This hawk captures song birds by still-hunting from an exposed perch. On the other hand, when actively searching for prey it flies dextrously and secretively through a wood or copse or along a hedgerow or fence taking advantage of the landscape to conceal itself. Catching sight of potential prey it can turn very abruptly and seize a completely surprised bird (Owen, 1932; Tinbergen, 1946; Rudebeck, 1950-51). On other occasions the prey is chased over some distance, often into the branches of dense brush. Sometimes the hawk pursues its quarry with such doggedness that it neglects its own security. Attacks can be directed against sitting as well as flying birds, either solitary or in flocks. A nice sketch of the hunting flight is given by Tinbergen (1946, pp. 96-97).

Owen (1932) describes a harrier-like searching flight over open meadows. During such flights birds or mammals may be picked up from the ground and nestlings of pigeons and song birds are taken from the nest.

The hunting behavior of the African races is like those of the Palearctic (Meinertzhagen, 1959).

FOOD

The food of *A. nisus* is predominantly birds, ranging from the goldcrests and small warblers up to jays, wood pigeons, moorhens, and rooks. The majority of the prey consists of song birds.

In Germany the most frequent prey species are House Sparrows, Song Thrushes, Chaffinches, Skylarks, Yellow-hammers, Whitethroats, Great Tits, and swallows (for details see Uttendörfer, 1939 and 1952).

In Holland also very important are Starlings and Willow Warblers (Tinbergen, 1946). In Finland P. Sulkava (1964) found that Chaffinches and Willow Warblers are most numerous. Generally it can be said that the diet of *A. nisus* reflects the composition of the song bird population within its hunting territory. Some prey species, however, are less frequently represented than would be expected (e.g., 51 Wrens in contrast to 1,723 Robins in Uttendörfer's study). This suggests the probability that some species avoid attack through their choice of habitat and their behavior (Tinbergen, 1946). When this hawk is providing food for his mate and offspring at the nest, he catches a large proportion of newly fledged young birds.

Mammals are poorly represented in the diet; only in years when voles are exceptionally numerous do they form a substantial part of the prey. Sulkava (1964) found in Finland a higher proportion of mammals than was observed in Uttendörfer's study. However, it is probable that the difference is partly due to different methods of investigation. When searching for the remains of prey, mammals may be more easily overlooked than birds. Small numbers of lizards, frogs, and insects, are caught. In years when cock-chafers (*Melolontha*) are numerous this hawk may feed almost exclusively on these beetles during the days when they are swarming.

In Africa small birds are the main prey, but fruit bats (Vincent, et al., 1962), lizards, termites, grasshoppers, and other insects are also recorded.

Discussion

The long slender feet and needle-like claws of *A. nisus* are adapted to catching small birds in flight. The species on the average takes much smaller birds and fewer mammals than does *A. gentilis.* Thus they do not seem to compete for food; it is not surprising that both are often found side by side in the same area, and that any difference in habitat preference is not clear-cut. The similarities in their wings and tails reflect their similar habitats and methods of hunting in flight.

The wing tip and tail are slightly longer in *A. nisus* than in *A. gentilis.* This probably gives *nisus* a little more speed and dexterity, which might be useful in chasing small birds. In addition, migratory forms tend to have a longer wing tip than residents, as may be seen by comparing nominate *nisus* with the race *wolterstorffi.*

The Palearctic *nisus* group and the African *rufiventris* group are very similar in structure. Nevertheless, they are almost universally considered as separate species, presumably on account of the pronounced difference in plumage. Actually this difference is less important than it might seem to be. It can be ascribed to one single factor: increase of rufous pigmentation obscuring the pattern on the underside. In occasional specimens of the *nisus* group with a strong rufous pigmentation (as opposed to birds with gray-brown bars), the pattern on the underparts may be obliterated in such a way that some adult and juvenile males resemble the *rufiventris* group. Similarly, in females an increase in rufous tinges has reduced sexual dimorphism, in contrast to the situation in the *nisus* group. Parallel geographical variation in color is found in American *A. striatus,* in which the South American form *ventralis* may show more saturated rufous pigments than North American *velox.*

The distribution of the *rufiventris* group conforms to the pattern of African mountain taxa of Palearctic origin (e.g., *Gypaetus barbatus meridionalis, Buteo buteo oreophilus;* cf. Voous, 1960). This type of distribution accentuates the close connection between the *nisus* group and the *rufiventris* group. At present the breeding ranges of both groups are separated by a gap of about 2,000 km. During the height of a glaciation when montane conditions prevailed over the greater part of Africa this gap was probably considerably narrowed or perhaps almost entirely absent. Obviously *A. nisus* colonized East Africa during such a cold period. In my opinion the differentiation of the African forms has not gone far enough to justify a specific separation of these forms.

The *nisus* group has a Palearctic distribution which is in general similar to that of *A. gentilis,* though more extended in the extreme southwest (Madeira, Canaries). In the western Palearctic *nisus* inhabits temperate as well as boreal forest; in the eastern Palearctic it is restricted to boreal forest, temperate forest in that region being inhabited by *A. virgatus gularis.*

The geographical variation in *A. nisus* is less than in *A. gentilis.* In the entire region from Ireland to Japan the variation is slight and clinal. Well-differentiated races are found in Sardinia and Corsica, on the one hand, and in the Himalayas on the other. It may be supposed that the population on the Mediterranean islands has been isolated since the last glaciation and probably much longer. Other populations of *A. nisus* must have survived this last glaciation in a number of refuges in the southern Palearctic. The existing great morphological variation among individuals is probably the result of the mixing of the populations of these refuges after the Pleistocene. Nothing definite about the post-glacial distribution of these populations can, therefore, be deduced.

So far the history of *A. nisus* and *A. gentilis* runs closely parallel (cf., p. 61). In the Himalayas, however, the history of *A. nisus* must have been entirely different from that of *A. gentilis. A. gentilis* is a recent invader from the northeast, whereas *A. nisus* is a much older colonist, having developed a well-characterized subspecies and having extended its range through the entire mountain system. Whether *A. nisus melaschistos* has ever been in contact with *A. nisus nisosimilis* in western China is not clear, but comparatively recent contact in central Asia is highly probable. According to Stepanyan (1958), *A. n. dementjevi* is linked to *A. n. melaschistos* by a cline of mountain forms, whereas Dementiev (1938) states that *A. nisus nisosimilis* occurs in the Tarbagatai mountains in summer. *A. n. nisosimilis* and *A. n. melaschistos* are, therefore, connected by an interrupted chain of populations (cf., also, Korelov, 1962), which probably marks the route which *A. nisus* took in colonizing the Himalayas. During a glacial period the boreal forests may have been contiguous in this region and the populations of *A. nisus* were presumably separated in post-glacial times when the forests retreated higher up the mountains. Thus the distribution history of *A. nisus* in the Asian mountains shows a parallel to that in the African mountains, although in Africa the species has penetrated much farther south than in Southeast Asia. The presence of mountain forms of *A. virgatus* in the suitable habitats probably has blocked the spread of *A. nisus* farther southward.

ACCIPITER GENTILIS (LINNAEUS)

DISTRIBUTION

The Palearctic and northern parts of the Nearctic, in forested country, penetrating far south in mountains (Map 6).

Resident, but partly migratory in the northern parts of its range, although even in eastern Siberia individuals winter in the far north (Dementiev, 1951). In years of food shortage large irruptions occur and many birds appear south of their normal range, particularly in America (Mueller and Berger, 1967).

SUBSPECIES

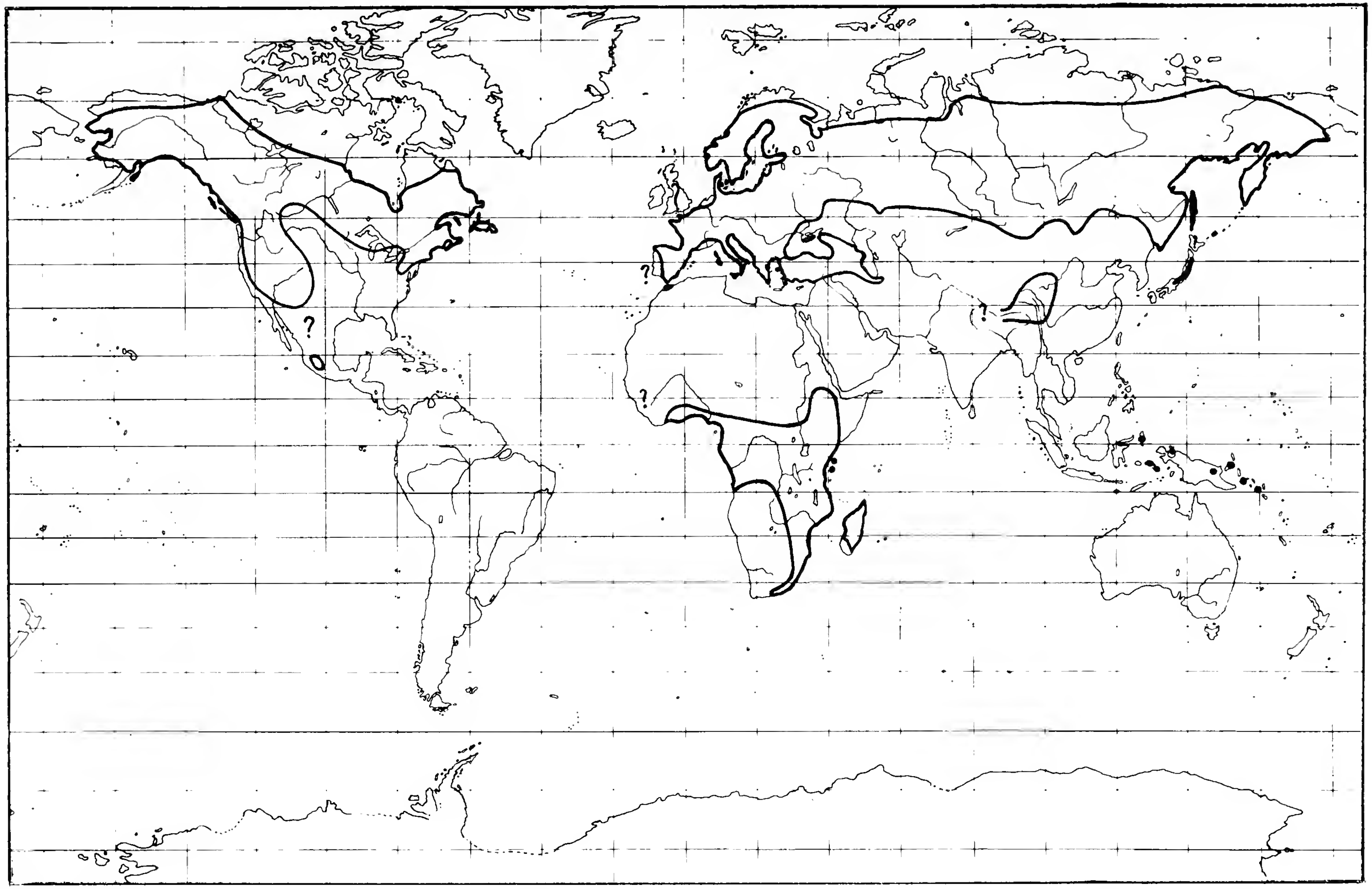
cf. Vaurie (1965) and Hellmayr and Conover (1949).

The gentilis *group* (*Palearctic*).—*A. g. gentilis* (Linnaeus), Europe east to central Russia; *A. g. buteoides* (Menzbier), northern Europe and Asia from northern Sweden east to Lena River and south to about lat. 56°N; *A. g. albidus* (Menzbier), northeastern Siberia from Yana River eastward to Kamchatka; *A. g. arrigonii* (Kleinschmidt), Sardinia and Corsica; *A. g. schvedowi* (Menzbier), southern Siberia from the Urals to Ussuriland, northern Japan, and southwestern Chinese mountains; *A. g. fujiyamae* (Swann and Hartert), Honshu Island.

The atricapillus *group* (*Nearctic*).—*A. g. atricapillus* (Wilson), Alaska, Canada, mountains of western and eastern U.S.A.; *A. g. laingi* (Taverner), islands off the Canadian Pacific coast; *A. g. apache* Van Rossem, mountains of southern Arizona and northern Mexico.

PLUMAGE

Adult.—Upperparts dark brown, washed gray, browner in female than in male, becoming more strongly tinged gray with age. Underparts cream or white with a pattern of dark brown bars and shaft streaks. In some birds the bars are wider than in other ones. It is doubtful that this is always related to age, as believed by Bährmann (1965). Second year birds may show on the upper breast a pattern of wavey bars on a creamy buff background, reminiscent of the juvenile plumage. Super-



Map 6. Distribution of *Accipiter gentilis* (Holarctic), *A. melanoleucus* (Africa), *A. henstii* (Madagascar), and *A. meyerianus* (Papuasia).

ciliary stripe conspicuous, white with a few narrow brown shaft streaks. Sides of face white, streaked brown. Tail gray with wide dark bars.

Juvenile.—Dorsum brown with buff or rufous feather edges. Venter white, cream, buff, or cinnamon-rufous with heavy dark brown streaks or drops. Tail light brown with wide dark bars.

Geographical Variation

The Nearctic *atricapillus* group differs from the Palearctic *gentilis* group mainly in the adult plumage. In the *atricapillus* group the back and wings are delicately blue-gray, the crown is contrastingly dark and the underparts have a pattern of fine gray vermiculations and black shaft streaks instead of the bold bars, that characterize the *gentilis* group. Juveniles of both groups are closely similar, but in the American races the ground color of the underparts is a characteristic rich cream.

In the Palearctic variation is clinal and it is very difficult to draw exact boundaries between the subspecies. The birds are smaller and darker in the southwestern and southeastern parts of the range, larger and lighter in the northern and particularly in the northeastern parts. In northern Siberia a whitish variant occurs which becomes increasingly numerous toward the northeast (in Anadyrland and Kamchatka half the population belongs to this variant). The island races *arrigonii* and *fujiyamae* are dark and heavily barred.

A number of subspecific names have been given to the populations that are hardly separable. The populations from central and western Europe are on the average smaller than those from Scandinavia. Bährmann (1937) has shown that this applies more strongly to the dimensions of the skeleton. On account of this difference several authors retain *A. g. gallinarum* (Brehm) as a separately named form (Commissie voor de Nederlandse Avifauna, 1962). Rather small and dark forms inhabiting Spain and northern Morocco and southeastern Europe are sometimes designated, respectively, as *A. g. kleinschmidti* von Jordans and *A. g. marginatus* (Piller and Mitterspacher). Vaurie (1965) considers all these as synonyms of *A. g. gentilis.*

A discussion of the Palearctic races is found in Hartert and Steinbacher (1932-38) and in Gladkov (1941), among others.

The American marginal subspecies *laingi* and *apache* are only weakly differentiated from *atricapillus, laingi* being darker (Taverner, 1940) and *apache* slightly larger (Blake, 1950).

Size and Structure

Size very large. Tarsus and toes short and sturdy. Claws impressive and bill large. Wing long and rounded. Tail medium. Figure 10. Tables 18 and 19.

For the purpose of statistical analysis single specimens of both *A. g. buteoides* and *A. g. schvedowi* were grouped with *A. g. gentilis,* whereas birds from west and central Europe were separated under the name of

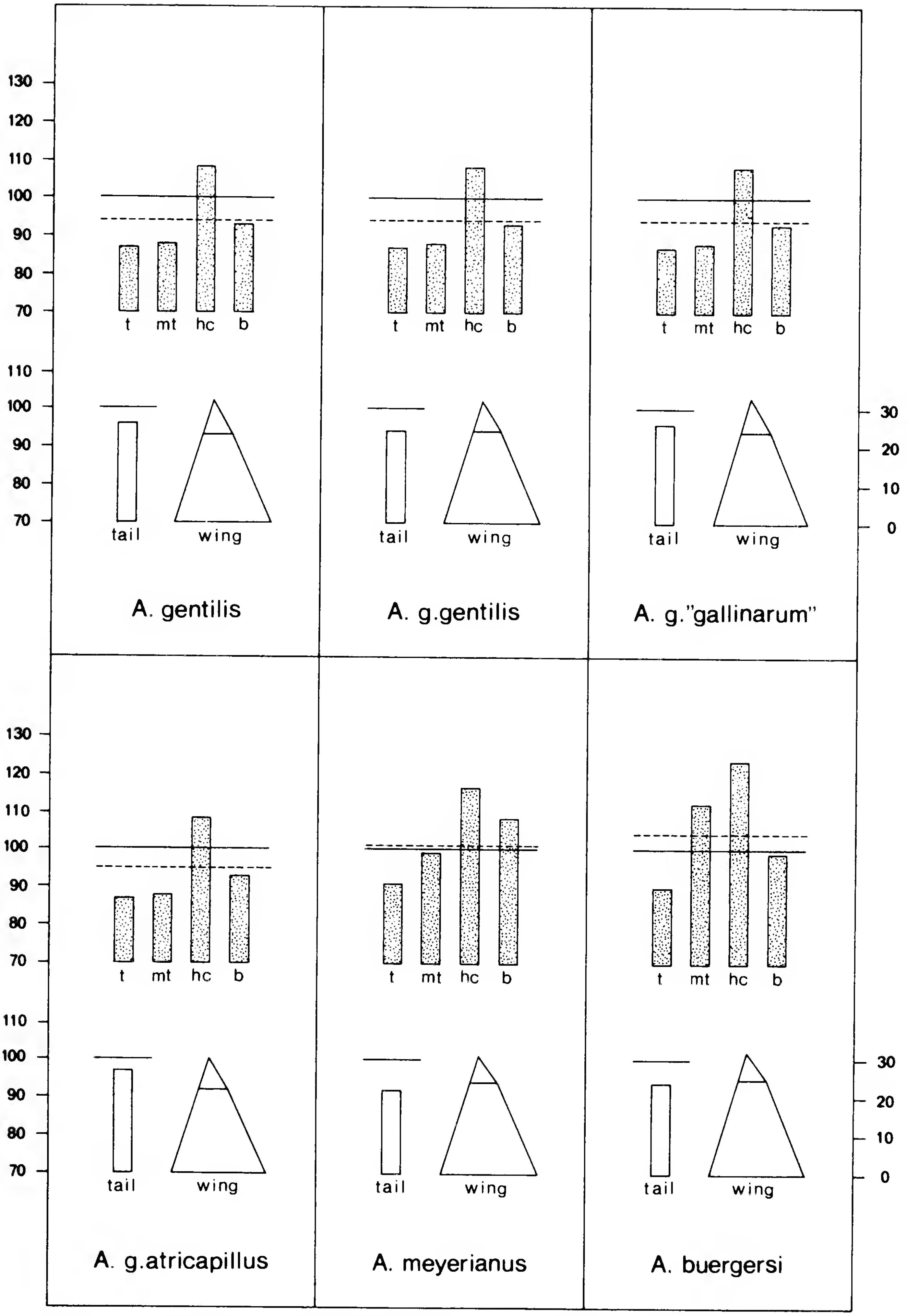


FIG. 10. Structure of *Accipiter gentilis, A. meyerianus,* and *A. buergersi.*

gallinarum. The statistical model was unsatisfactory for the tail. The difference between the subspecies is significant for the wing tip. The difference between the sexes is significant for the hind claw (smaller in male) and the wing tip (longer in male).

TABLE 18

Wing length in *Accipiter gentilis.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
gentilis	323.0	4.45	1.99	316 - 328	5
'gallinarum'	314.0	5.92	1.71	306 - 322	12
atricapillus	324.7	8.68	3.07	308 - 337	8
			♀		
gentilis	362.7	5.03	2.90	358 - 368	3
'gallinarum'	351.3	9.01	2.33	338 - 367	15
buteoides	356	-	-	-	1
schvedowi	355	-	-	-	1
atricapillus	355.5	3.11	1.56	352 - 359	4
				Total	49

Bill and foot.—Of the *gentilis*-type.

Wing and tail.—These are of the *nisus*-type. The wing tip and tail are relatively slightly shorter than in *A. nisus.* The wing and tail are very similar to these structures in *A. meyerianus* and *A. buergersi.*

HABITAT

The preferred habitat is wooded areas from beyond the arctic tree line south to temperate regions and temperate mountain zones, e.g., forest tundra, taiga with scattered glades, tall coniferous, mixed, and deciduous woods, luxuriant river forest, cultivated plantations of conifers, birch-aspen stands in steppe woodland, and isolated pine woods in steppe. In North America the species is absent from the more southerly lowland regions with mixed temperate forests.

TABLE 19

Relative measurements in percent of wing length in *Accipiter gentilis.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	23.60	14.05	8.87	6.92	73.16	31.82	8.39
'gentilis'	23.96	14.23	9.06	6.98	71.81	32.25	9.04
'gallinarum'	23.97	14.19	8.98	7.08	73.33	32.73	8.65
atricapillus	22.87	13.73	8.57	6.70	74.34	30.49	7.48
♂	-0.06	-0.22	-0.23	-0.08	-0.24	+1.02	+0.74
♀	+0.06	+0.22	+0.23	+0.08	+0.24	-1.02	-0.74
Adult	-0.08	-0.12	+0.06	+0.01	-1.04	-0.20	+0.16
Juvenile	+0.08	+0.12	-0.06	-0.01	+1.04	+0.20	-0.16
P model	0.638	0.402	0.756	0.824	0.040	0.122	0.945
P ssp	0.078	0.287	0.174	0.279	-	0.004	0.395
P sex	0.730	0.212	0.038	0.684	-	0.001	0.135
n	34	36	45	42	45	43	37
df	24	25	34	30	33	31	26

In the European mountains, *A. gentilis* inhabits coniferous forest, especially that consisting of spruce and fir, but it also frequents beech and oak woodland. In the Alps it ranges from the valley floor to the subalpine zone, being scarce at high altitudes. In Japan it occurs in montane and subalpine forest and is most numerous at about 1,000 m. The isolated population in the mountains of central Asia is confined to coniferous forests with a typically Palearctic avifauna (Schäfer, 1938). In the North American mountains the species penetrates far southward in the Hudsonian and Canadian life zones, more rarely in the Transition zone. In the southwestern mountain ranges it is generally confined to pine forests and is only sparingly found in the lower pine-oak woodland (Marshall, 1957).

The habitat of *A. gentilis* characteristically has tall trees, in which the nest can be built, and small open tracks within the forest. Only at the border of the arctic, where tall trees are not available, is the nest placed quite low or even on rocks (Pleske, 1886) or on the ground. In temperate regions the species is more numerous in an area with many small woodlots than in extensive forest. It makes its appearance as a conspicuous attendant of cultivation when large forests are partially felled (Schnurre, *in* Niethammer, 1938). It may thrive quite close to large cities. Locally in Europe, however, the bird has been seriously reduced in numbers or even extirpated by persecution (e.g., in Great Britain) and recently by pesticides.

In winter *A. gentilis,* particularly the juvenile, is less confined to stands of tall trees and may be met in more open country. Many birds descend to lower levels in mountain ranges and are found in scrub covered or parklike foothills.

Hunting Behavior

Hunting by this hawk is characterized by rapid attacks at short range. When hunting the Goshawk flies rapidly and secretively through forest or varied countryside and captures its prey by a very quick dash as soon as it is sighted. Its skill in finding its way through dense stands of trees, turning around and pursuing its quarry in dense thickets, is astonishing for a bird of its size. It can also show a remarkable tenacity in trying to dislodge an animal from its shelter (Westcott, 1964). At times the Goshawk resorts to still-hunting.

Food

Its food is medium-sized and large birds and medium-sized mammals. Small birds, even those as small as the Goldcrest, and small mammals, such as voles, are taken incidentally as also are frogs and large insects.

In Uttendörfer's study (1939 and 1952), based on prey remains found near the nest in numerous central European localities, the principal prey items were pigeons, jays, partridges, thrushes, starlings, and crows. Together these accounted for nearly 70% of the total number of prey animals. The squirrel was the most numerous mammal. In his ten-year study of a single goshawk territory Brüll (1964) obtained slightly different results. Squirrels are all but absent from his prey list, but rabbits are much in evidence, comprising about 12% of the total number of animals. By weight the rabbit was certainly the most important single prey in Brüll's area. In Holland rabbits were also a main food of the Goshawk when this species was still common. Partridges figure much higher on Brüll's list than on Uttendörfer's, but Jays are less numerously represented on the former than on the latter. These differences may, of course, reflect differences in the prey populations.

Voles are occasionally fed to small nestlings (Schiermann, 1925). In areas with many lakes a fair number of water birds are caught, e.g., ducks and grebes. In autumn and winter mammals are proportionally more numerous in the diet than during the breeding season (Sladek, 1962).

In Scandinavia grouse and ptarmigan are well represented in the diet with a large proportion of the tetraonid chicks being fed to the nestlings. Squirrels are mainly taken when tetranoids are scarce (Hoglund, 1964; S. Sulkava, 1964). These data suggest that gallinaceous birds are the most important prey of *A. gentilis* in regions where the impact of cultivation on the fauna is relatively small. This is in accordance with Schäfer's (1938) observations of *A. gentilis* hunting *Tetrastes, Ithaginis,* and *Tetraophasis* in southeastern Tibet.

The food of *A. gentilis* in America is similar to that in the Palearctic. *Sylvilagus, Bonasa, Lepus, Tamiasciurus,* and *Phasianus* are most numerous in Goshawks wintering in the U.S.A. (Storer, 1966). A very large proportion of stomach analyses of wintering Goshawks reveal the presence of domestic poultry. Storer considers this to be artificial because the birds are often shot when raiding poultry yards, and he does not include these analyses in his comparisons. Studies of the food of the Goshawk during the breeding season are scarce in America. Meng (1959) found 83 *Corvus brachyrhynchos* and 58 *Tamiasciurus hudsonicus* among 185 prey items brought to 14 nests in New York State and Pennsylvania. When it was still numerous the Passenger Pigeon evidently was an important source of food.

Discussion

The robust feet and bill of *A. gentilis* are adapted to catching a wide variety of comparatively heavy animals by pouncing on them. The rather long wing tip is correlated with the species' style of hunting in dense woods as well as in more open types of country.

The Nearctic *atricapillus* group differs from the Palearctic *gentilis* group in adult plumage, but hardly in juvenile plumage and in physical structure. In North America *A. gentilis* is primarily a bird of the boreal forests, not penetrating far beyond the lower limit of the Canadian life zone. According to Voous (1960) this may be interpreted as evidence for a comparatively recent colonization of the Nearctic, implying that *A. gentilis* is a species of Old World origin. This is confirmed by the presence of related species of considerable antiquity in Africa (*A. melanoleucus*) and Madagascar (*A. henstii*).

The Old World races of the species are not sharply delimitated. Well-characterized forms are to be found on Sardinia and Corsica on the one hand and on Honshu on the other. On these islands *A. gentilis* has apparently had a long uninterrupted history, having passed at least one glaciation in isolation. Undoubtedly there have also been a number of continental refuges during the Pleistocene glaciations, but subsequent developments have thoroughly obscured the location of such refuges. Probably the populations occupying various continental refuges have become mixed in post-glacial times. Large, light colored hawks may have colonized Europe from the east and populated eastern Asia from the northwest. Their penetration has partly blurred the geographical variation that existed between the populations isolated in different southern refuges, and has instead imposed upon these populations the characters of ordinary clinal variation. The wealth of races that have been described from southern Europe (*kleinschmidti, trischittae, marginatus, caucasicus*) but which are very difficult to separate from nominate *gentilis* (including *gallinarum*) and from one another may be taken as an example of this phenomenon. *A. g. gallinarum* may be regarded as a population in which "southern" and "northern" characters are almost equally strongly represented.

Because *A. gentilis* in the central Asian mountains is restricted to a small area on the eastern edge of the great mountain system, it is clear that it reached this area comparatively recently and along an eastern route. Presumably this population has become isolated through the post-Pleistocene retreat of the forests in China. It is still almost indistinguishable from the populations of Manchuria, northern Mongolia, and southern Siberia.

Ecological Geography in Europe and Asia

In Europe and Asia the following zones of vegetation can be discerned from north to south: tundra, taiga, temperate mixed and deciduous forest, temperate tree steppe, treeless steppe and desert, savanna, and tropical forest. Nearly everywhere the regular sequence is interrupted by mountain systems that have their own zonation from base to summit. No species of *Accipiter* breeds in arctic tundra or in treeless steppe and desert, but each of the other types of habitat has its own species of *Accipiter*. *A. gentilis* and *A. nisus* belong to the fauna of the boreal forests, penetrating into temperate forest in the western Palearctic. Temperate mixed and deciduous forest in the eastern Palearctic is inhabited by *A. virgatus gularis*. The open country south of the forest, being warm and dry in summer and cold in winter, is inhabited by migrant forms of the *badius* group, viz., *A. brevipes*

TABLE 20
VERTICAL ZONATION OF SPECIES OF *Accipiter* ON THE SOUTHERN SLOPES OF THE HIMALAYAS.

Form	Altitudinal range	
Accipiter badius	valley floor	to 1500 m
Accipiter trivirgatus	valley floor	to 2000 m
Accipiter virgatus affinis	600 m	to 2100 m
Accipiter nisus	1200 m	to 4500 m
Accipiter gentilis	2300 m	to 4500 m

and *A. soloensis,* along with *A. badius cenchroides* in Transcaspia. In the savanna and tropical dry deciduous forest we find *A. badius;* in dense humid jungle and tropical rainforest *A. trivirgatus.* A similar zonation of Accipiters with climatic zones is found on the southern slopes of the Himalayas (Table 20). The altitudinal ranges of the species show considerable overlap. This may be due partly to variations in local microclimate and partly to the fact that in the literature the extreme altitudes are much more carefully recorded than the optimum altitudes.

In the various climatic zones the habitats not only are different, but also the prey as well as the hunting behavior. Typical bird hunting sparrow hawks (*A. nisus* and *A. virgatus*) are found in boreal, temperate, and montane forests, but not in tropical lowland forest. A large goshawk (*A. gentilis*) lives in boreal forest, the tropical forest being inhabited by the much smaller *A. trivirgatus.* A generalized type of small sparrow hawk catching not only birds, but also lizards and insects, is restricted to open savannas and steppes (*badius* group).

Obviously a sparrow hawk dependent on lizards and insects is absent from boreal forests, as lizards and large insects are very scarce or nonexistent there. Small mammals are also unimportant prey for *Accipiter* because most of the forest mice and shrews are nocturnal and they are hunted by nocturnal predators such as the Tawny Owl, Long-eared Owl, Ural Owl, and Tengmalm's Owl. Hence small birds remain the only prey available to a small diurnal predator in boreal forest. Farther south there is no typical bird-hunting Accipiter. This I tentatively conclude is because open country with scattered trees is not suited for this type of hunting, probably because it offers too little shelter.

Curiously no small bird-hunter breeds in the tropical lowland of Southeast Asia, although several other rainforest areas of the world are inhabited by species with feet and bills of the *nisus*-type. For example, in the forest of West and Central Africa there is *A. minullus.* It should be remembered, however, that in the northern winter the Oriental rainforest region is visited by numerous migrants of *A. virgatus gularis,* so at least for part of the year this habitat is utilized by a small bird-hunting Accipiter.

A heavy hawk of the *gentilis*-type is found not only in the northern forests, but also in the tropics. The tropical species, however, is much smaller than its northern counterpart, although one still might wonder whether any prey for a large goshawk would be present in the rainforest. Even more notable is the fact that a large goshawk is lacking from the habitat of *A. badius* and its allies. The explanation for this is that in these regions heavy animals presumably are taken by birds of prey of other genera. In the tropical rainforest various species of the genus *Spizaetus* behave more or less like giant goshawks; in dry tropical country *Hieraaetus nanus* and its allies probably occupy a similar ecological niche.

IV

AFRICA

INTRODUCTION

The 10 African species of *Accipiter* are listed in Table 21. Africa, as used in this chapter, refers to the portion of the continent south of the Sahara. In the desert belt Accipiters are only recorded on migration. In northwestern Africa, or the Maghreb, small populations of *A. nisus* and *A. gentilis* are found, which were considered in Chapter III.

Of the 10 species five are endemic to continental Africa and three to Madagascar. The remaining two species, *A. badius* and *A. nisus,* also occur in Europe and Asia and were discussed in Chapter III. In addition to the Accipiters listed in Table 21, *A. brevipes* and Palearctic races of *A. nisus* winter in Africa.

ACCIPITER TACHIRO (DAUDIN)

DISTRIBUTION

Forest and woodland of Ethiopian Africa (Map 7).

SUBSPECIES

cf. White (1965).

The tachiro *group* (*East African*).—*A. t. tachiro* (Daudin), eastern South Africa, intergrading with the next race in eastern Rhodesia and the Zambesi valley; *A. t. sparsimfasciatus* (Reichenow), northern Angola, northern and eastern Zambia, southern Congo savanna, north through East Africa to Uganda and northern Kenya; *A. t. unduliventer* (Rüppell), highlands of Ethiopia.

The toussenelii *group* (*West African*).—*A. t. macrocelides* (Hartlaub), Upper Guinea from the Casamance to west Cameroons; *A. t. lopezi* (Alexander), island of Fernando Poo; *A. t. toussenelii* (Verreaux), Lower Guinea from south Cameroons to central Congo; *A. t. canescens* (Chapin), eastern Congo.

PLUMAGE

Adult.—Upperparts dark gray, dark brown, or almost black. Female generally browner than male of the same race. Underparts barred or plain, varying geographically. Rectrices brown or gray with two or three light spots adjacent to the shaft on the inner webs.

Juvenile.—Dorsum varying from brown with buffish feather edges to blackish with dark rufous edges. Underparts cream or white; breast marked with dark brown spots, tending toward bars on the abdomen

TABLE 21
Species of *Accipiter* in Africa.

SPECIES	DISTRIBUTION
Accipiter tachiro	Africa
Accipiter castanilius	Upper and Lower Guinea and Congo
Accipiter badius	South Asia and Africa
Accipiter francesii	Madagascar and Comoro Islands
Accipiter minullus	Africa
Accipiter ovampensis	Africa
Accipiter madagascariensis	Madagascar
Accipiter nisus	Palearctic and East and South Africa
Accipiter melanoleucus	Africa
Accipiter henstii	Madagascar

and flanks. Light spots on the tail lacking or much less prominent than in adults.

Geographical Variation

Geographical variation (Table 22) is found in body size, intensity of pigmentation, and the pattern on the underparts in adult and juvenile birds. The western African group of forms (*toussenelii* group) differs from the eastern African *tachiro* group by its more saturated colors. An appreciable variation is found within each group.

A. t. tachiro.—Adult male: upperparts blackish brown. Underparts barred rufous brown and white. Sides of face brown-gray. Flanks washed cinnamon-rufous. Tail with bright white spots.

Female: browner on upperside, less rufous on underside than male. Bars dark brown, in some specimens more or less interrupted. Tail spots lacking.

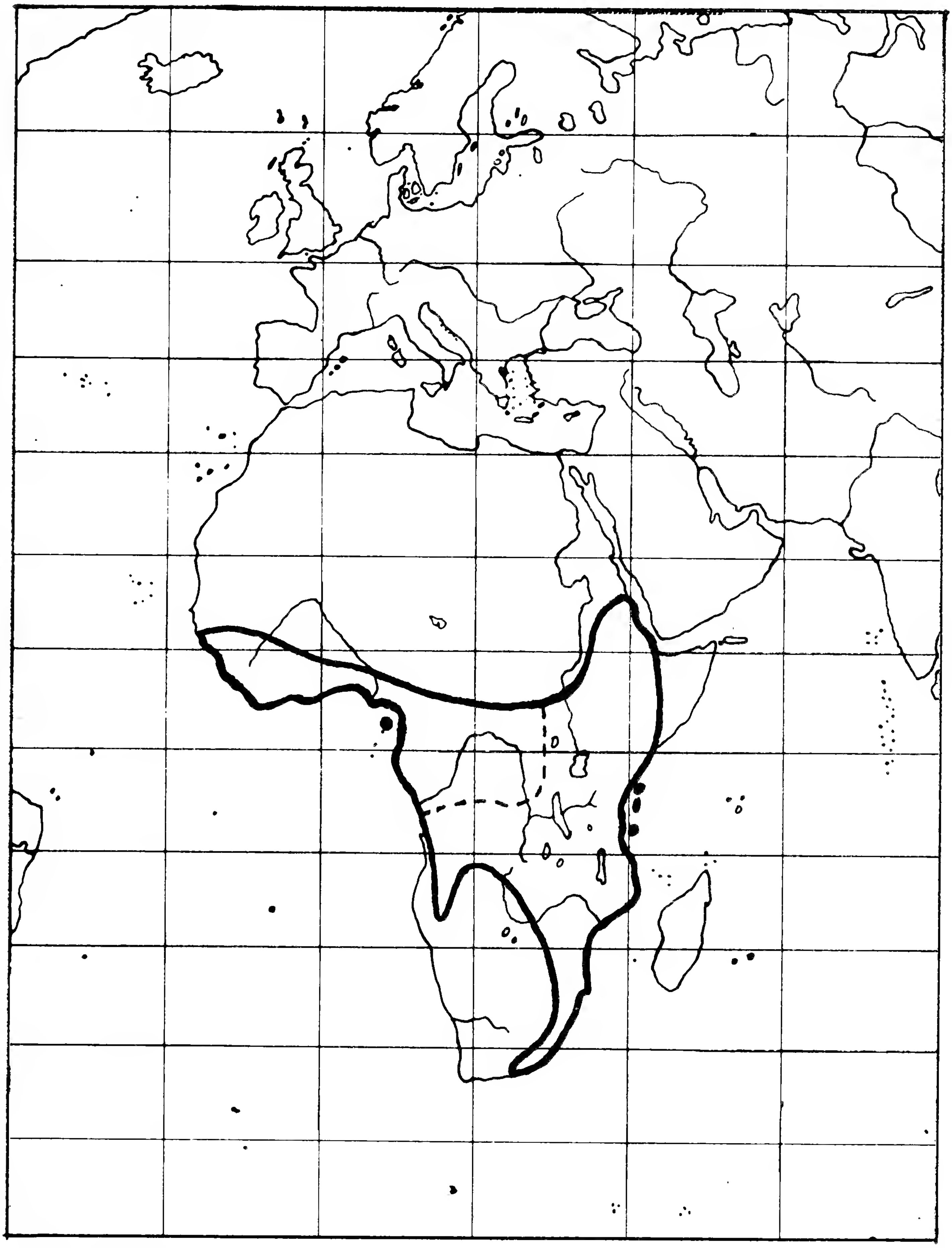
Juvenile: underparts spotted dark brown, flanks and thighs broadly barred.

A. t. sparsimfasciatus.—Poorly differentiated from *tachiro.* Very slightly larger. Bars on underparts more often interrupted. It is interesting that Pemba Island is inhabited by a population of considerably smaller size than *sparsimfasciatus* on the adjacent mainland (Table 22). Birds from Zanzibar do not differ from mainland specimens.

A. t. unduliventer.—Adult: much smaller than nominate *tachiro.* Sexual dimorphism in plumage is not pronounced. Underparts more strongly tinged rufous than in *tachiro.* Thighs plain cinnamon-rufous. Tail with white spots in both sexes.

Juvenile: similar to *tachiro,* but the abdomen is barred rather than spotted.

A. t. macrocelides.—Adult: similar to *unduliventer,* but upperparts are more grayish black and the bars on the underside are almost pure



Map 7. Distribution of *Accipiter tachiro.* Boundary between *tachiro* group and *toussenelii* group indicated by dashed line.

rufous. Sides of the face and bars on the chest are gray. Flanks more rufous than in East African forms. Conspicuous white spots on tail.

Juvenile: upperparts very dark brown, almost black. Underparts white, heavily spotted with dark brown.

A. t. lopezi.—Similar to *macrocelides.* Underparts more strongly marked in adult and juvenile.

A. t. toussenelii.—Adult: upperparts lighter, more gray than in *macrocelides*. Underparts almost plain rufous, at most marked with faint lighter and darker bars.

Juvenile: similar to *macrocelides* but less heavily marked underneath.

A. t. canescens.—Adult: still lighter gray on upperparts than *toussenelii*. Head and interscapular region much lighter than lower back and upperwing coverts. Bars on underparts obsolete. Breast pearl gray, shading toward rufous on abdomen.

Juvenile: similar to *toussenelii*, but still less marked. Many specimens are pure white underneath except for a few spots on the sides of the breast and a few bars on the flanks.

The races *macrocelides*, *toussenelii*, and *canescens* form a cline. In adults a progressive increase in gray tinges on the upperside and a reduction of barring on the underside are found. In juveniles the underparts are progressively less marked. The birds increase in size from west to east (Table 22).

Size and Structure

The size ranges from moderately small to moderately large. The tarsus is long and sturdy, the toes short and heavy, and the claws and bill heavy. The wing is very short and rounded, and the tail very long. Figure 11. Tables 22 and 23.

For the purpose of statistical analysis the data for *sparsimfasciatus* were combined with those for *tachiro*; the data for *toussenelii* and *canescens* were similarly combined. The statistical model was unsatisfactory for the hind claw and wt–6. The difference between the

TABLE 22

Wing length in *Accipiter tachiro*.

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
tachiro	210.4	5.94	2.24	200 - 217	7
sparsimfasciatus	211.2	5.44	1.18	200 - 217	21
sparsimfasciatus, Pemba	193.0	4.36	2.52	188 - 196	3
unduliventer	187.2	6.71	3.35	182 - 197	4
macrocelides	193.5	4.51	1.84	186 - 198	6
toussenelii	191.5	5.96	2.43	185 - 200	6
canescens	195.0	4.46	1.02	185 - 203	19
			♀		
tachiro	241.4	5.40	1.50	232 - 251	13
sparsimfasciatus	245.4	9.78	1.61	231 - 275	37
sparsimfasciatus, Pemba	225	-	-	-	1
unduliventer	219.8	6.15	2.75	211 - 228	5
macrocelides	211.9	5.11	1.81	204 - 218	8
toussenelii	221.2	6.26	2.09	210 - 230	9
canescens	230.3	6.50	1.13	211 - 243	33
				Total	172

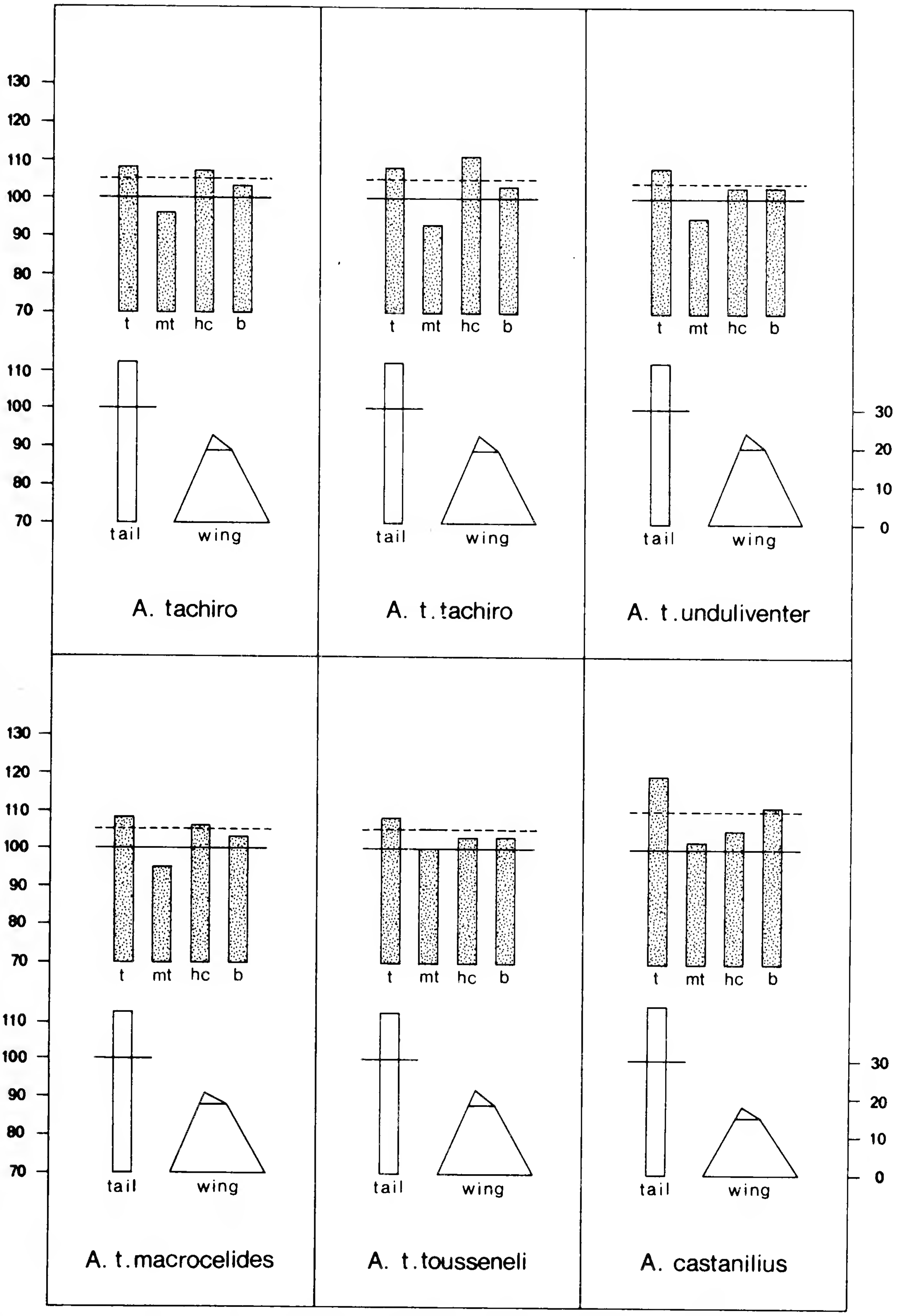


FIG. 11. Structure of *Accipiter tachiro* and *A. castanilius.*

subspecies is significant for the middle toe and wing tip. The difference between the sexes is significant for the tarsus (longer in male), tail (shorter in male), and wing tip (longer in male).

Bill and foot; wing and tail.—These are of the *tachiro*-type. There

TABLE 23

Relative measurements in percent of wing length in *Accipiter tachiro*.

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	29.15	15.33	8.67	7.63	84.99	22.66	3.98
'tachiro'	28.70	14.82	9.10	7.72	84.11	22.99	3.58
unduliventer	28.89	15.30	8.41	7.08	84.91	24.35	4.61
macrocelides	29.81	15.25	8.76	7.92	85.64	21.37	3.61
'toussenelii'	29.18	15.96	8.41	7.80	85.14	21.94	4.12
♂	+1.15	-0.01	-0.25	-0.09	-1.29	+0.95	+0.24
♀	-1.15	+0.01	+0.25	+0.09	+1.29	-0.95	-0.24
Adult	-0.61	-0.44	-0.11	-0.01	-1.75	-0.46	-0.63
Juvenile	+0.61	+0.44	+0.11	+0.01	+1.75	+0.46	+0.63
P model	0.335	0.396	0.033	0.750	0.419	0.334	0.027
P ssp	0.138	0.005	-	0.066	0.368	0.024	-
P sex	0	0.490	-	0.620	0.017	0.008	-
n	51	45	26	44	70	59	26
df	38	32	13	29	55	44	13

is a considerable geographical variation in the bill and foot. In *A. t. tachiro* the middle toe is very small and the hind claw large, whereas in *A. t. toussenelii* the middle toe is relatively larger and the hind claw smaller. *A. t. unduliventer* and *A. t. macrocelides* are intermediate. In the series *tachiro—macrocelides—toussenelii* the bill is progressively heavier in comparison to the hind claw. The wings and tails show only slight differences among the subspecies.

HABITAT

Various types of well-wooded country are the preferred habitat, ranging from evergreen forest to rich woodland and parkland. As in many other Accipiters, alternation of forest and open ground appears to make an area more attractive.

The tachiro *group* (*East and South Africa*).—These forms occur in forest, patches of forest in open country, rich *Brachystegia* woodland, orchard bush savanna, riparian woodland, second-growth, groves of Eucalyptus, and large gardens. The *tachiro* group ranges from coastal lowland up to about 2,100 m in montane forest, but it is apparently absent from the bamboo belt. Benson (1945) observed *unduliventer* in evergreen forest and dry *Juniperus procera* forest at 1,500 m in southern Ethiopia.

The toussenelii *group* (*West Africa and Congo Basin*).—Found in tropical rainforest, forested patches in cultivated parts of the rain-forest belt, dense secondary forest, forest islands in savanna, and in plantations and gardens; rarely "orchard bush savanna" (Serle, 1957). The *toussenelii* group ranges up to 1,000 or 1,200 m in Cameroons and on Fernando Poo, up to 2,000 m in the mountains of the eastern

Congo. In the evergreen forest it is typically a bird of the lowerstories (Chapin, 1932; Marchant, 1953). It is most frequently found along rivers or near swamps.

HUNTING BEHAVIOR

The species practices still-hunting, i.e., swooping suddenly from dense cover and trying to catch its prey in flight. It shows much skill in pursuing its quarry and chases animals driven from shelter by driver ants (Walker, 1939).

FOOD

Its food is middle-sized animals obtained on the ground as well as in trees, viz., mammals, birds, lizards, frogs, large insects, and even crabs. Birds and insects are also taken in flight.

The mammals range in size from shrews to ground squirrels and young monkeys and the birds from nestling song birds to cuckoos and hornbills. When *A. tachiro* lives near human habitation it frequently takes half-grown chicks. Frogs are especially in evidence in the diet of the *toussenelii* group.

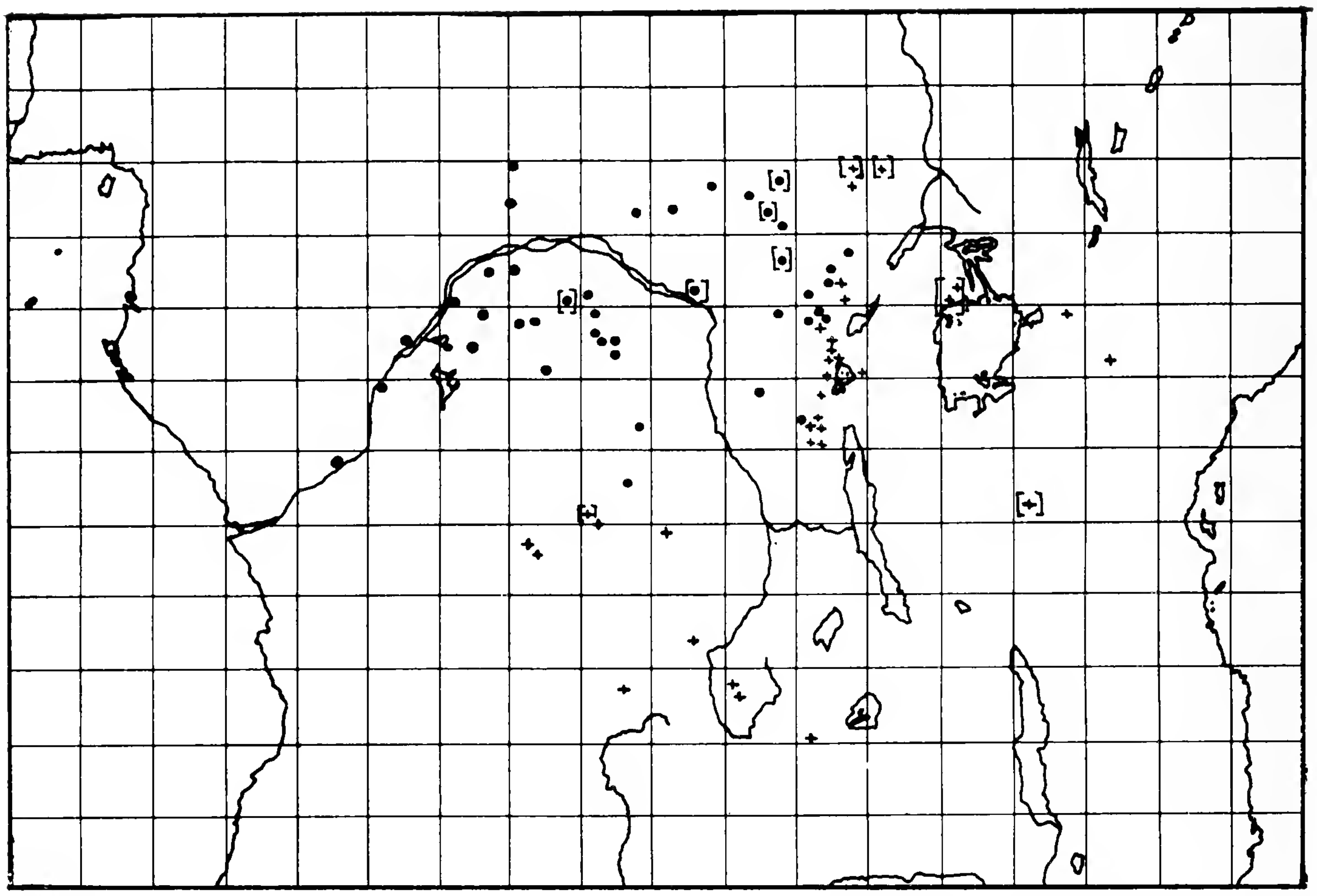
Van Someren (1956) lists 56 prey items brought to the nest by *A. t. sparsimfasciatus* at Ngong, Kenya, viz., 15 mammals, mostly rats; 36 birds, among which were five chicks with the remainder varying from nestling songbirds to cuckoos and young doves and five reptiles.

DISCUSSION

The *tachiro*-type of bill and foot structure is apparently adapted to the taking of a variety of prey in a tropical forest habitat (p. 205). The West African populations have a relatively smaller hind claw than those of East Africa. This may be related to a higher proportion of reptiles, amphibians, and insects in the diet. The short rounded wing and the long tail of this hawk provide excellent equipment for its rapid and skilful flight through dense forest.

A. tachiro has no close relatives outside of Africa. Its relation to the similar species *A. castanilius* is discussed below (p. 76). Like *A. minullus, A. tachiro* has differentiated into East African and West African groups of populations. Several authors regard these groups as separate species (e.g., Chapin, 1932; White, 1965); in fact we are dealing here with a borderline case in the process of species formation. Amadon (1953) discusses the problem at length and I agree with him that both groups should still be treated as a single species.

The boundary between the western and the eastern groups of populations runs along the eastern escarpment of the Congo basin. There *canescens* approaches very dissimilar *sparsimfasciatus* (see Map 8). Although the ranges interdigitate, in no locality have they been found to be sympatric. The reported occurrence of *sparsimfasciatus* at Buta (Uelle) was not confirmed by study of the Tervuren collection; among



MAP 8. Distribution of *Accipiter tachiro* in the Congo Basin and adjacent regions, based on specimens in the collection of the Royal Museum of Central Africa at Tervuren. Specimens of *tachiro* group (+); specimens of *toussenelii* group (●); literature record ([ ]).

32 birds from Buta not a single specimen of *sparsimfasciatus* (*tachiro* group) could be found, all of them being *canescens* (*toussenelii* group).

There is an interesting adult female of *sparsimfasciatus* from Abimva, Uelle, which is distinctly washed rufous on the underparts, especially on the flanks. The existence of this intermediate specimen may indicate interbreeding of *canescens* and *sparsimfasciatus* in northeastern Uelle.

In the pattern of geographical variation in East Africa, *A. tachiro* differs from *A. minullus* by the presence of a well-defined subspecies in the highlands of Ethiopia. *A. tachiro* is much less tolerant of arid conditions than *minullus.* The arid regions which separate Ethiopia from the rest of East Africa act as an effective barrier for the former species but not for the latter.

Geographical variation in the *toussenelii* group is parallel to the situation in *A. minullus* where within the *erythropus* group there exist subspecies both in Upper and Lower Guinea. The boundary between these forms is not situated at the mouth of the river Niger, as it is in *A. minullus,* but more to the east where the Cameroon highlands come close to the sea. Here montane conditions may have existed at sea level during part of the late Pleistocene (Marchant, 1954; Moreau, 1966). At present *toussenelii* does not penetrate the montane forest on the Cameroon highlands, therefore montane conditions are likely to have presented a barrier for the distribution of the species in the Pleistocene.

It is curious that the Upper Guinean form *macrocelides* resembles the remote *tachiro* group, not only in plumage, but also in structure. It is very possible, however, that in a more humid period, probably even quite recently, *A. tachiro* had a continuous range from Ethiopia to West Africa and *macrocelides* was in contact with *unduliventer*. This would account for the similarity of these two forms (see Amadon, 1953). In plumage and structure *macrocelides, toussenelii,* and *canescens* form a cline, which runs from west to east. From the wide divergence between *canescens* and *sparsimfasciatus* it is clear that *A. tachiro* did not colonize the Congo forest from the east.

A. tachiro has developed an endemic subspecies, *lopezi,* on Fernando Poo. The island was probably connected with Africa no more than 11,000 years ago (Moreau, 1966; see, also, Amadon, 1953). It is the only forest Accipiter out of four species on the adjacent mainland that has been found on the island. This is in conformity with the striking, and rather unaccountable, dearth of birds of prey on Fernando Poo (see Moreau, 1966, Table 38).

ACCIPITER CASTANILIUS BONAPARTE

DISTRIBUTION

Forests of west and central Africa (Map 9).

SUBSPECIES

cf. Amadon (1953). *A. c. castanilius* Bonaparte, Ivory Coast (Brunel and Thiollay, 1969) and Nigeria to the western Congo; *A. c. beniensis* Lönnberg, eastern Congo, intergrades with foregoing race in central Congo.

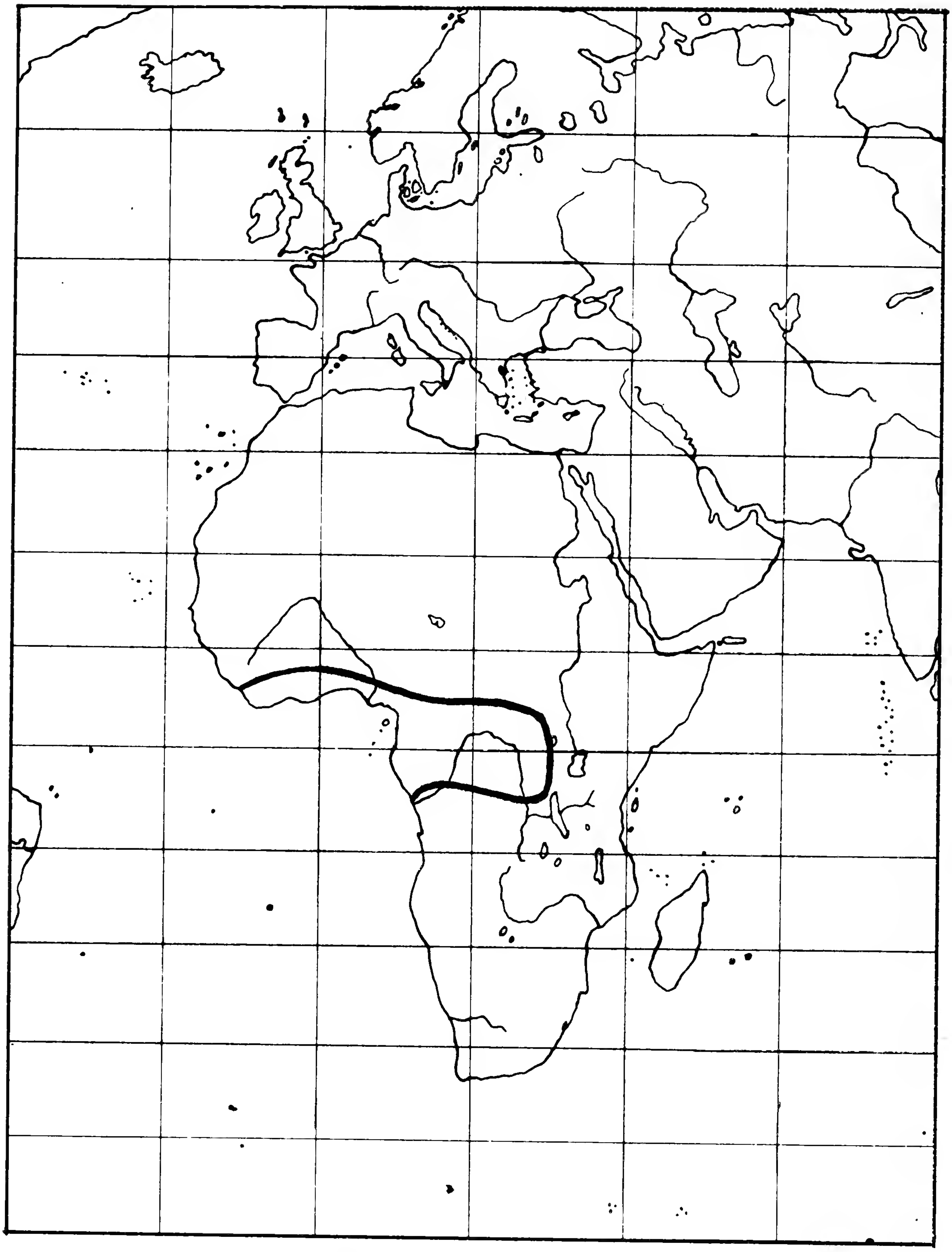
PLUMAGE

Adult male.—Upperparts deep blue-black with a somewhat lighter nuchal collar. Center of breast and abdomen densely barred on white ground, every bar consisting of a rufous and a brown-gray line. Flanks and thighs deep chestnut. Sides of face dark gray. Central rectrices black with bright white spots.

Adult female.—Differs from male by being browner above and less rufous below.

Juvenile.—Upperparts very dark brown with inconspicuous dark rufous feather edges. Underparts white with dark brown spots on breast and abdomen and wide brown bars on the flanks. In some specimens the markings are washed with chestnut. The pattern varies individually; some specimens are heavily spotted, others nearly white. Thighs with brown bars, washed rufous. No white spots on the tail.

Juveniles of *A. castanilius* can be very similar to juveniles of *A. tachiro toussenelii* and *A. t. canescens.* Females of *castanilius* are of



Map 9. Distribution of *Accipiter castanilius*.

the same size as males of *tachiro* and identification of unsexed specimens can be difficult (Stresemann, 1926). Juvenile *A. castanilius* tends to be browner, less black above and more heavily marked underneath than juvenile *A. t. toussenelii* and *A. t. canescens*. The underside of the primaries have light and dark bars in both species. In *A. castanilius* both bars are of equal width, but in *A. t. toussenelii* the light bars are wider than the dark ones. The primaries hardly protrude beyond the tips of the secondaries in *A. castanilius* and somewhat more in *A. t. toussenelii.*

Geographical Variation

A. castanilius shows clinal variation in size, birds from the western population (*castanilius*) being appreciably smaller than those from the eastern population (*beniensis*) (see Table 24). As no specimens from the central Congo were measured, the clinal nature of the variation as described by Amadon (1953) is not apparent in Table 24.

Size and Structure

Size rather small. Tarsus long. Toes short. Claws short and thick. Bill heavy. Wing very short and rounded. Tail very long. Figure 11, p. 69. Tables 24 and 25.

For the purpose of statistical analysis the data for both geographical races were combined. The statistical model was unsatisfactory for the hind claw, tail, and wing tip. The difference between the sexes is significant for the tarsus (longer in male).

Bill and foot.—These are intermediate between the *tachiro*-type and the *trinotatus*-type. In *A. trinotatus* the middle toe and hind claw are considerably shorter; in *A. tachiro toussenelii* the tarsus and bill are

TABLE 24

Wing length in *Accipiter castanilius.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
castanilius	154.0	4.97	2.49	147 - 158	4
beniensis	162.4	2.66	0.84	160 - 168	10
			♀		
castanilius	180.7	2.76	1.38	178 - 184	4
beniensis	189.7	2.66	0.94	185 - 193	8
				Total	26

TABLE 25

Relative measurements in percent of wing length in *Accipiter castanilius.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	32.23	16.40	8.57	8.28	87.13	18.42	2.63
♂	+1.37	+0.07	-0.57	-0.05	-0.59	+0.57	-0.02
♀	-1.37	-0.07	+0.57	+0.05	+0.59	-0.57	+0.02
Adult	-0.24	+0.34	+0.07	+0.03	-0.37	-1.28	-0.53
Juvenile	+0.24	-0.34	-0.07	-0.03	+0.37	+1.28	+0.53
P model	0.050	0.120	0.004	0.502	0.028	0.027	0.303
P sex	0	0.262	-	0.587	-	-	0.556
n	24	21	19	20	24	22	9
df	20	17	14	16	20	18	5

shorter. The structure represents a further stage in the series *tachiro-macrocelides-toussenelii.*

Wing and tail.—These are of the *tachiro*-type with the wing extremely short. The same forms of wing and tail are also found in *A. trinotatus.*

HABITAT

Tropical rainforest, second-growth, and native gardens in the forest. Confined to the lowlands. In virgin forest *A. castanilius* keeps to the middlestory of the trees.

HUNTING BEHAVIOR

The species is very secretive, keeping to dense foliage. This behavior indicates that *castanilius* takes its prey by surprise. It sometimes chases its quarry tenaciously; Bates (1930) records one entering a house in pursuit of chickens.

FOOD

Its prey is various small animals, viz., mice, small birds, lizards, frogs, small snakes, and large insects. Analysis of six stomachs yielded the following results: birds (twice), insects (twice), lizard (once), mouse (once), empty (twice) (data from various literature sources).

DISCUSSION

The bill and foot of *A. castanilius* are intermediate between those of *A. toussenelii* and *A. trinotatus.* In choice of prey it resembles *A. toussenelii,* taking many types of small animals, whereas *A. trinotatus* preys almost exclusively on reptiles and insects. In habitat *A. castanilius* is similar to *A. trinotatus,* being confined to heavy forest. The very short rounded wing is well adapted to this habitat. *A. toussenelii,* on the other hand, is more often found in second-growth and clearings.

A. castanilius resembles *A. tachiro tachiro* in plumage, but is more heavily pigmented. Its distribution is limited to the central African forests. In fact, *A. castanilius* can be regarded as a forest counterpart of the *tachiro* group. Most probably they arose through ecogeographical differentiation when an ancestral group was split into a woodland form (*tachiro*) and a heavily pigmented rainforest form (*castanilius*). This is similar to what seems to have taken place, at a later date, with the subspecies of *A. melanoleucus* and *A. minullus.*

At a later stage, with *A. castanilius* already present in the central African forests, *A. tachiro* again invaded these forests, this time from the west (*toussenelii* group). With reproductive isolation established, *A. tachiro toussenelii* and *A. castanilius* adjusted to slightly different ecological niches and developed into a pair of sympatric sibling species. In this respect it is interesting that subsequent evolution led to heavy pigmentation in *A. castanilius,* in contrast to a pale and unbarred plumage in *A. tachiro toussenelii* and *A. t. canescens.* As no other forms of *A.*

tachiro are so strikingly different from *castanilius* in adult plumage, this situation provides an excellent example of character displacement.

ACCIPITER FRANCESII (A. SMITH)

DISTRIBUTION

Madagascar and Comoro Islands. Not yet found on Moheli; almost extinct on Anjouan (Map 3, p. 25).

SUBSPECIES

cf. Benson (1960). *A. f. francesii* (A. Smith), Madagascar; *A. f. brutus* (Pollen), Mayotte; *A. f. pusillus* (Gurney), Anjouan; *A. f. griveaudi* Benson, Grand Comoro.

PLUMAGE

Adult.—Upperparts gray or brown. Underparts white, with or without bars. Tail plain or faintly barred.

Juvenile.—Above brown with faint rufous feather edges. Underparts white with brown bars, which are wider than in adult. Tail with numerous narrow dark bars.

GEOGRAPHICAL VARIATION

There is a considerable geographical variation of adult plumage in this species. Adult *A. f. francesii* shows pronounced sexual dimorphism, which is absent in *brutus, pusillus,* and *griveaudi.*

A. f. francesii.—Adult male: upperparts dark gray. Underparts white with narrow cinnamon-rufous to grayish brown bars of varying intensity.

Adult female: crown and sides of head gray; back brown, sharply contrasting with head. Underparts white, with regular brown bars, which are wider than in the male.

A. f. brutus.—Adult: upperparts warm dark brown with a lighter nuchal collar. Underparts barred cinnamon-rufous, similar to adult female of *francesii* but more rufous.

Juvenile: exhibits a tendency to spotting instead of barring on the underparts, particularly in the male.

A. f. pusillus.—Adult: resembles adult male *francesii,* but pattern on the underside reduced. Breast and abdomen white, sides of breast washed gray.

Juvenile: resembles juvenile *brutus,* but feathers of dorsum have wider rufous edges.

A. f. griveaudi.—Differs from *pusillus* in being salmon underneath in adult plumage (Benson, 1960).

SIZE AND STRUCTURE

Size very small to small. Tarsus long and slender. Toes and claws short and delicate. Bill heavy. Wing short and pointed. Tail very long

TABLE 26
Wing length in *Accipiter francesii.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
francesii	158.8	3.38	1.13	154 - 164	9
brutus	144	-	-	-	1
pusillus	141.5	-	-	139 - 144	2
			♀		
francesii	175.7	4.86	1.84	172 - 186	7
brutus	160	-	-	-	1
pusillus	163	-	-	-	2
griveaudi	170	-	-	-	1
				Total	23

in *francesii,* relatively shorter in *pusillus.* Figure 6, p. 28. Tables 26 and 27.

For the subspecies *brutus* no data were available for analysis. *A. f. griveaudi* was combined with *pusillus.* The difference between the subspecies is significant for the middle toe, hind claw, bill, and tail. The difference between the sexes is significant for the tarsus (longer in male).

Bill and foot.—Similar to *A. castanilius;* intermediate between *A. tachiro toussenelii* and *A. trinotatus.* In *A. f. pusillus* the middle toe, hind claw and bill are longer relative to the tarsus than in nominate *francesii,* thence in the smaller subspecies the bill and foot are relatively heavier; this was also the case in *A. melanoleucus.*

Wing and tail.—These are of the *minullus*-type, but aberrant in the very long tail and the very short wing. They resemble *A. virgatus*

TABLE 27
Relative measurements in percent of wing length in *Accipiter francesii.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	31.59	16.30	8.63	8.46	81.72	23.48	10.70
francesii	30.88	15.18	8.17	8.07	84.89	23.02	10.13
pusillus	32.30	17.42	9.09	8.85	78.55	23.94	11.27
♂	+1.06	+0.25	-0.13	-0.16	-0.97	+0.11	+0.02
♀	-1.06	-0.25	+0.13	+0.16	+0.97	-0.11	-0.02
Adult	-0.91	-0.44	-0.17	+0.06	-1.14	-0.32	-0.26
Juvenile	+0.91	+0.44	+0.17	-0.06	+1.14	+0.32	+0.26
P model	0.540	0.750	0.264	0.622	0.506	0.877	0.765
P ssp	0.185	0	0.043	0.047	0	0.329	0.311
P sex	0.026	0.382	0.374	0.412	0.112	0.916	0.953
n	21	21	15	15	20	21	16
df	16	16	10	10	15	16	11

affinis and also *A. butleri*. In *A. butleri* the wing is more rounded, however. In *A. f. francesii* the tail is much longer than in both *affinis* and *butleri*.

HABITAT

Occurs in evergreen forest, particularly at edges or along roads. In Madagascar it also inhabits stands of dense and tall forest in arid country, and rarely brush. Altitudinal range from sea level up to 1,800 m (Rand, 1937).

In the Comoro Islands it is also found in cultivated areas in which there are a few remaining tall trees (Benson, 1960), and in secondary forest and mangrove (Nicoll, 1906).

Judging from the large series of specimens that were collected by every expedition visiting Madagascar, *A. francescii* is much more numerous than *A. henstii* and *A. madagascariensis*.

HUNTING BEHAVIOR

Takes small birds and large insects in flight (Schegel and Pollen, 1868), but also arboricolous and perhaps terrestrial prey such as lizards and chameleons. From the fact that it is seen usually sitting on a dead branch or other low perch, it may be deduced that it relies primarily on still-hunting.

FOOD

Various small animals comprise its diet. The stomachs of 38 specimens of different subspecies contained insects (17 times), reptiles (13 times), frogs (7 times), unidentified reptiles or amphibians (3 times), birds (twice), and mammals (twice) (Rand, 1937; Benson, 1960).

DISCUSSION

A. francesii is similar to *A. castanilius* in its choice of prey and in bill and foot. It is, however, less strictly confined to dense tropical forest and the wing is not so very short. It is apparently much more conspicuous in the field.

The adult male of *A. francesii* resembles *A. badius sphenurus*, being about the same size and similar in color pattern. A further similarity is the pointed wing tip. Both forms prey on a variety of small animals, predominantly insects and lizards. Apart from these similarities there are striking differences. *A. francesii* has quite another type of structure than *A. badius sphenurus*, i.e., the tarsus is relatively longer, the bill heavier, the wing tip shorter, and the tail longer. In addition, the juvenile plumage of *A. francesii* differs in that it is entirely barred on the venter. Adult females of *A. f. francesii* and adults of *A. f. brutus* do not resemble *A. badius*. Apparently *A. francesii* inhabits denser forest than *A. badius*.

Pronounced as these differences may be, they hardly exceed the differences which are found within the *badius* complex. The structural peculiarities of *A. francesii* can be regarded as adaptations to life in an insular habitat with luxuriant vegetation. A similar structure is found in *A. butleri,* generally considered to belong to the *badius* complex and inhabiting densely forested islands (Nicobars). In *A. francesii brutus* the barring on the underparts of the juvenile tends to spotting on the breast as in *A. badius.* Within the *badius* complex sexual dimorphism, comparable to that of *A. francesii francesii,* is found in *A. brevipes.* Thus the differences between *A. francesii* and *A. badius sphenurus* accentuate rather than contradict the basic unity, *A. francesii* being the Madagascar representative of the *badius* complex. Because of its aberrant characters it is best regarded as a separate species. Most probably it has colonized Madagascar from Africa in the relatively distant past.

Although it might be surmised that *A. francesii* used the Comoros as stepping stones in reaching Madagascar, the present distribution of the species does not lead to this conclusion. Obviously the Comoro populations are more closely related to *A. f. francesii* than to the African populations of *A. badius.*

In these island races we find a peculiar type of geographical variation. The males and females of *pusillus* and *griveaudi* resemble the male of nominate *francesii,* whereas male and female of *brutus* are like the female of *francesii.* Apparently in each of these populations only part of the genetic potential of the ancestral group has survived. This is in accordance with the general evolutionary tendencies of small populations. The mosaic variation demonstrates, as does the absence of the species on Moheli, that the birds are strongly isolated on each of the islands of the group.

ACCIPITER MINULLUS (DAUDIN)

DISTRIBUTION

Forests of west and central Africa; forests, savanna, and steppe of East and South Africa (Map 10).

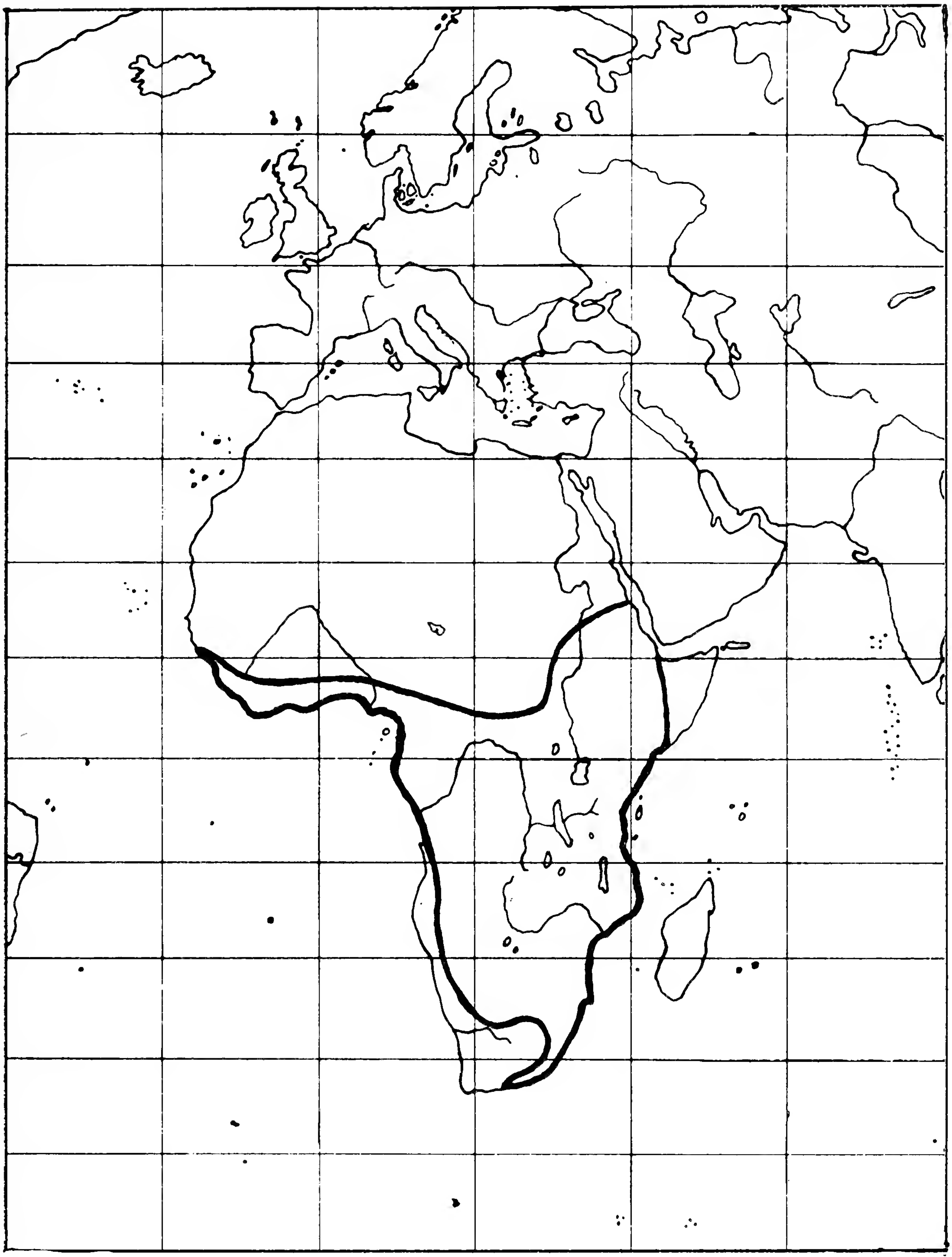
SUBSPECIES

cf. White (1965). *The* minullus *group* (*eastern and southern Africa*).—*A. m. minullus* (Daudin), Cape Province north to Angola and Ethiopia; *A. m. tropicalis* Reichenow, coastal strip from about the Zambesi to southern Somalia.

The erythropus *group* (*western Africa*).—*A. m. erythropus* (Hartlaub), upper Guinea from Gambia to Nigeria; *A. m. zenkeri* Reichenow, Cameroons to the eastern Congo.

PLUMAGE

Adult.—Dorsum dark blue-gray or black with white uppertail coverts. Underparts narrowly barred or plain, varying geographically.



Map 10. Distribution of *Accipiter minullus*.

Flanks washed rufous. In most forms the central rectrices have two bright white spots.

Juvenile.—Upperparts dark brown with narrow rufous or brownish red feather edges. Uppertail coverts white with dark spots. Venter cream with a pattern of spots or bars varying geographically. Tail brown with light bars.

AFRICA

Geographical Variation

The eastern and western African groups of populations differ in the intensity of the pigmentation and in the pattern of the underside.

The minullus *group.*—Adult: upperparts dark gray. Underparts white with narrow, sharply defined bars; each bar consisting of a rufous and a gray line. The amount of rufous pigment varies individually and geographically.

Juvenile: underparts marked with dark brown streaks or spots on breast and abdomen and wide bars on the flanks.

The erythropus *group.*—Adult: dorsum jet black. Underparts varying from light pearl gray to vinous red; plain or faintly barred.

Juvenile: upperparts darker than in the *minullus*-group. Underparts in the Upper Guinea form, *erythropus,* narrowly barred reddish brown, resembling adult *minullus* in pattern and in the Congo form, *zenkeri,* freckled with fine black shaft streaks on the breast and narrow bars on the flanks. Flanks washed rufous in both forms.

Geographical variation within the *minullus* group is slight. *A. m. tropicalis* differs from *A. m. minullus* in being somewhat paler (White, 1965).

In the *erythropus* group the forms are more clearly differentiated. The differences in juvenile plumage have already been mentioned. In adult plumage *A. m. erythropus* lacks the white spots on the tail, which are characteristic of the other races. On the venter *erythropus* shows more gray with less vinous tinges than in *zenkeri,* although gray specimens with faint bars are known from the range of the latter.

Size and Structure

Size very small. Tarsus and toes long and slender. Claws and bill minute and sharp. Wings short and pointed. Tail short. Figure 12. Tables 28 and 29.

The difference between the subspecies groups is significant for the bill and wing tip. The difference between the sexes is significant for the tarsus (longer in male).

TABLE 28

Wing length in *Accipiter minullus.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
minullus & tropicalis	141.7	4.32	0.83	131 - 149	27
erythropus	148.4	2.70	1.02	146 - 153	7
zenkeri	151.2	2.72	0.47	145 - 157	33
			♀		
minullus & tropicalis	160.8	3.92	0.80	151 - 169	24
erythropus	170.0	4.65	1.90	162 - 177	6
zenkeri	172.7	4.00	1.15	164 - 177	12
				Total	109

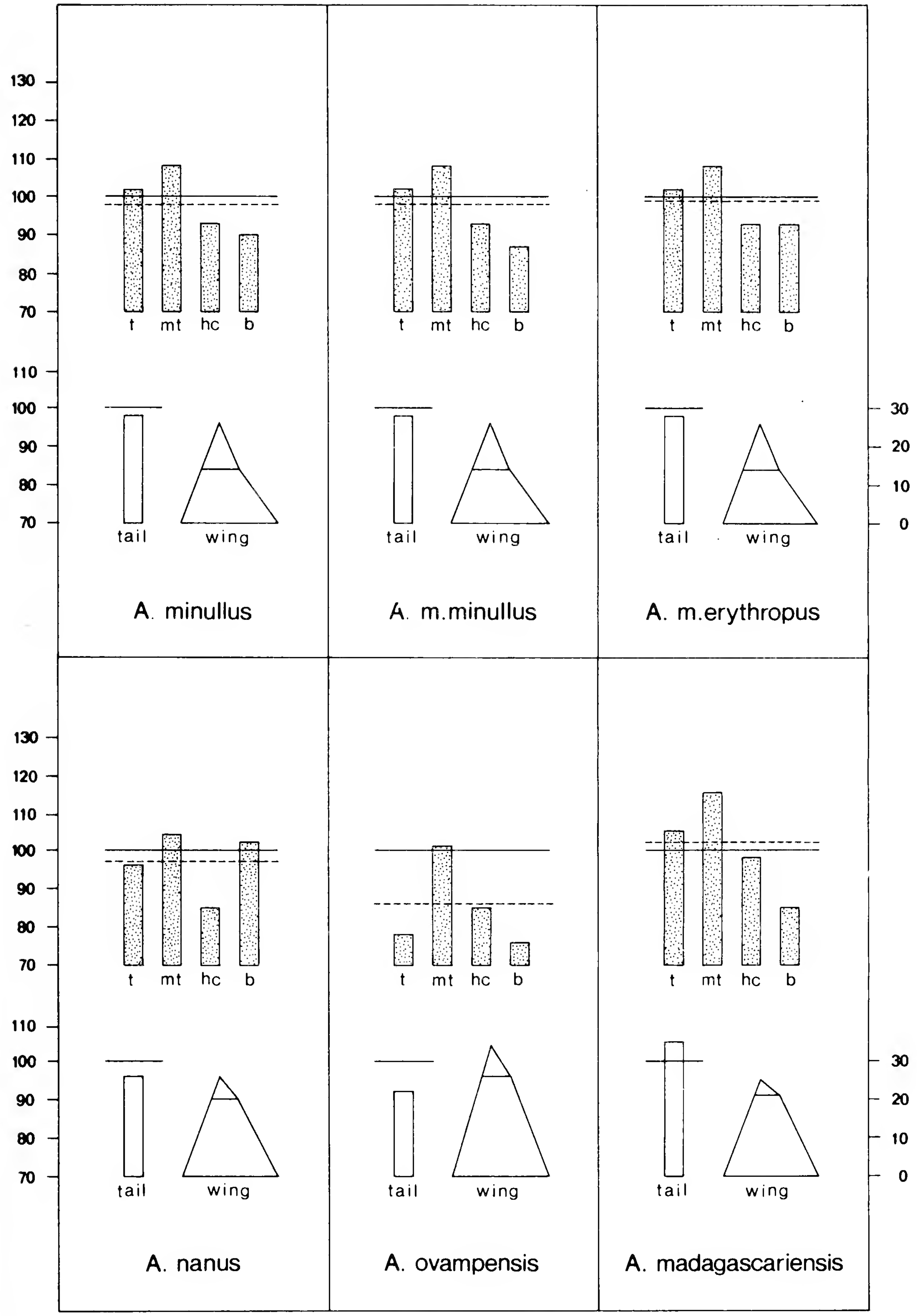


FIG. 12. Structure of *Accipiter minullus, A. nanus, A. ovampensis,* and *A. madagascariensis.*

TABLE 29

Relative measurements in percent of wing length in *Accipiter minullus.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	27.69	17.28	7.60	6.71	74.65	25.85	12.09
minullus-group	27.64	17.20	7.69	6.50	75.54	25.62	11.71
erythropus-group	27.74	17.35	7.51	6.92	73.75	26.08	12.47
♂	+1.00	+0.13	-0.15	-0.09	-0.33	-0.03	+0.46
♀	-1.00	-0.13	+0.15	+0.09	+0.33	+0.03	-0.46
Adult	-0.40	0	+0.04	+0.10	-1.17	+0.24	+0.03
Juvenile	+0.40	0	-0.04	-0.10	+1.17	-0.24	-0.03
P model	0.534	0.278	0.922	0.243	0.996	0.051	0.443
P ssp	0.658	0.366	0.828	0.004	0.126	0.039	0.286
P sex	0	0.304	0.582	0.141	0.926	0.087	0.221
n	45	40	31	33	52	46	29
df	37	32	23	25	44	38	21

Bill and foot.—Of the *nisus*-type. The hind claw and bill are a little larger in relation to the tarsus than in *A. nisus.*

Wing and tail.—Of the *minullus*-type. *A. minullus* is similar to *A. v. virgatus* in both the bill and foot and the wing and tail.

Both groups of subspecies are very similar in structure. In the *erythropus* group the bill is larger in relation to the hind claw than in the *minullus* group. In this respect the *erythropus* group resembles *A. nisus rufiventris.*

HABITAT

Occurs in any type of wooded country from tropical rainforest to dry bush and savanna, usually in the vicinity of water, from sea level to 1,500 m.

The minullus *group.*—Edges of forest, varied parkland, *Brachystegia* woodland, Acacia savanna, dense bush, and various types of cultivation such as open townships, large gardens, and stands of Eucalyptus. *A. minullus* is often found in the vicinity of a river valley, irrespective of the presence or absence of large trees (White, 1945). It inhabits coastal lowland as well as highland, but is absent from typically montane habitats. Benson (1945) met the species in dry thorn scrub at 1,200 m and in *Juniperus* forest at 1,500 m in southern Ethiopia.

The erythropus *group.*—Primary and secondary forest, especially along water courses, roads, or tracks and at the edge of the forest. The species is more frequently found in secondary than in virgin forest. In the forest it keeps to the middlestory; in second-growth it lives mostly in the tree tops (Chapin, 1932). It ascends to about 1,500 m in the mountains of the eastern Congo.

HUNTING BEHAVIOR

In hunting it pursues flying prey with skill, chasing its quarry through scrub and wood. It also practices still-hunting, sitting inconspicuously in dense foliage for a long time. According to Meinertzhagen (1959) *A. minullus* resembles *A. nisus* in hunting behavior.

FOOD

Takes mostly birds and large insects, particularly grasshoppers; more rarely lizards and mammals. Fifty-four prey animals brought to a nest in the southern Cape Province were all birds, with the exception of one mouse (Liversidge, 1962). In Nigeria the species was seen to chase swarming termites.

DISCUSSION

In *A. minullus,* as in several other species, the *nisus*-type of bill and foot is correlated with a *nisus*-like feeding ecology, i.e., the species is a bird hunter in varied terrain. Neither in plumage nor in wing structure is *A. minullus* similar to *A. nisus.* They, therefore, cannot be regarded as close relatives.

A. minullus is a typical African species which must have lived in Africa for a long time, long enough to have become split into two ecologically and geographically different groups of populations. The differences in plumage between the *minullus* group and the *erythropus* group are pronounced. They have often been considered as specifically distinct (e.g., White, 1965).

The boundary between the eastern and western groups runs along the crest of the eastern Congo mountains. For the Semliki valley between Lake Edward and Lake Albert the distributional data are conflicting. Verheyen (1947) asserted that *intermedius* (=*minullus*) has been found in that region, Sassi (1912) identified his specimens from Beni as *erythropus,* whereas Stresemann (1924) considered Sassi's birds to be intermediate between *zenkeri* and *intermedius* (subspecies *sassii*). Stresemann's description, however, may well refer to the normal plumage of juvenile *zenkeri* in the eastern Congo. Mackworth-Praed and Grant (1952) mention *zenkeri* as occurring in the Bwamba forest, which indeed has a typically Congolese lowland fauna (Moreau, 1966). From the above the tentative conclusion may be drawn that the Semliki valley is inhabited by *zenkeri* and that the highlands of Mount Ruwenzori constitute the eastern limit of the *erythropus* group. There are no positive indications of overlap in the ranges of the two subspecies groups.

Although strikingly different in coloration, both groups are very much alike in structure. In addition both have white uppertail coverts, as previously pointed out by Stresemann (1923a). The question of conspecificity cannot be answered conclusively because of the lack of distributional contact. In some plumage characters *zenkeri* is intermediate between *erythropus* and *minullus*. This may indicate past or present gene flow from *minullus* to *zenkeri*. Added to the strong similarity in structure I consider this possible gene flow as an argument for uniting *minullus* and *erythropus* into a single species.

In the African fauna the differentiation of forest versus savanna forms is a common phenomenon. Voous (1966) has given examples for the owls. We have met it already in *A. tachiro* and will find it again in *A. melanoleucus*.

The *minullus* group is tolerant of a wide variety of habitats. Therefore subspeciation through isolation in a particular type of habitat must have been impossible. As a result the existing geographical variation is very slight, probably representing a phenotypical reaction to environmental conditions (birds more heavily pigmented in humid localities?). In the *erythropus* group more pronounced geographical variation is found. The boundary between the forms *erythropus* and *zenkeri* is in Nigeria and reflects the former existence of a gap in the forest near the mouth of the Niger River (Marchant, 1954). From the present distribution of the species it is impossible to deduce whether the ancestral form of *A. minullus* was a forest or a savanna bird.

ACCIPITER OVAMPENSIS GURNEY

DISTRIBUTION

Savanna and steppe of Ethiopian Africa (Map 11).

Believed to be migratory, but no definite information is available.

PLUMAGE

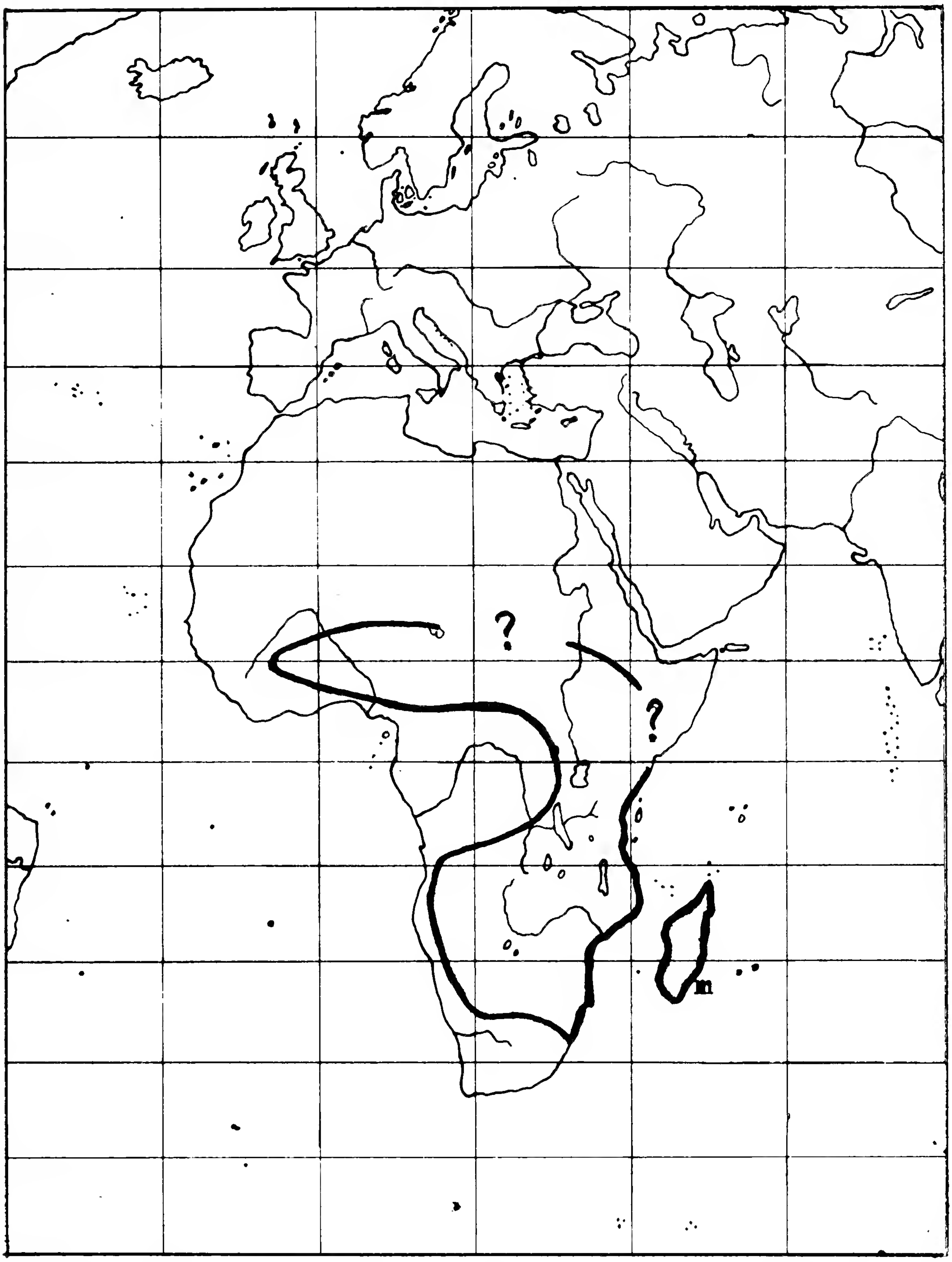
Adult.—Dorsum blue-gray. Underparts densely and narrowly barred gray and white. Uppertail coverts have white spots at the tip. Tail gray with light gray bars. Central rectrices marked with conspicuous white spots at the junction of the shaft and the light bars.

Juvenile.—Upperparts dark brown or gray-brown, usually with wide rufous feather edges. Venter variable, pale cinnamon to cinnamon-rufous marked with more or less distinct brownish bars, in several specimens blending into arrowheads, drops, or shaft streaks, especially on upper breast and throat. In fresh plumage the tips of the feathers may be entirely washed cinnamon-rufous, resembling juvenile. *A. nisus rufiventris*. Uppertail coverts barred white. Central tail feathers with small dirty-white spots near the shaft.

SIZE AND STRUCTURE

Size rather small to medium. Tarsus short and slender. Toes long. Bill and claws small. Wing very long and rounded. Tail short. Figure 12, p. 83. Tables 30 and 31.

The difference between the sexes is significant for the bill (smaller in male).



Map 11. Distribution of *Accipiter ovampensis* and *A. madagascariensis* (m = Madagascar).

Bill and foot.—These are of the *nisus*-type, but aberrant in that the tarsus is very short. No other Accipiter has such a short tarsus.

Wing and tail.—Resemble the *nisus*-type, but the tail is much shorter.

Habitat

Various types of dry woodland and savanna, viz., *Brachystegia* woodland, Acacia savanna, dense bush, sisal plantation, and native farm-

TABLE 30

Wing length in *Accipiter ovampensis.*

SEX	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
♂	224.4	5.23	1.12	213 - 233	22
♀	250.9	4.38	1.22	244 - 262	13
				Total	35

land. *A. ovampensis* avoids evergreen forest and does not go high in the mountains. Benson (1945) records it from moderately dry *Juniperus* forest at 1,500 m in Ethiopia.

Hunting Behavior

A. ovampensis is very elusive, which suggests that it relies mainly on still-hunting. Hoesch (1938) observed it fiercely chasing a glossy starling.

Food

Some authors assume that this species preys primarily on insects (Roberts, 1949; Mackworth-Praed and Grant, 1952; Harwin, et al., 1953), but there is also evidence that it regularly takes birds (Hoesch, 1938; Benson, 1947; labels on skins).

Discussion

A. ovampensis differs from other species showing the *nisus*-type structures by the long wing, the short tail, and the short tarsus. The long wing and the short tail are related to the dry, rather open habitat. It may be presumed also that the short tarsus has something to do with life in this type of country. Unfortunately, the ecology of the species is little-known.

In juvenile plumage *A. ovampensis* resembles *A. rufiventris* and some juvenile specimens of the Palearctic races of *A. nisus.* In adult plumage it is distinguished by the narrow gray barring on the under-

TABLE 31

Relative measurements in percent of wing length in *Accipiter ovampensis.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	21.03	16.22	6.99	5.66	70.30	34.50	8.01
♂	+0.33	-0.27	-0.21	-0.21	-0.35	+0.33	+0.25
♀	-0.33	+0.27	+0.21	+0.21	+0.35	-0.33	-0.25
Adult	-0.18	-0.06	+0.08	+0.02	-0.23	+0.03	-0.32
Juvenile	+0.18	+0.06	-0.08	-0.02	+0.23	-0.03	+0.32
P model	0.478	0.210	0.880	0.359	0.434	0.659	0.264
P sex	0.108	0.097	0.062	0.038	0.359	0.699	0.270
n	22	22	16	15	24	12	13
df	18	18	12	11	20	8	9

side and the pale gray back. In contrast to *A. rufiventris* the rufous pigments have disappeared instead of increased. The male and female are equally gray, so there is no sexual dimorphism. The pale gray plumage with narrow bars is presumably connected with the dry habitat as it is also found in *A. badius polyzonoides* from the steppe and savanna of southern Africa.

The peculiar characteristics of *A. ovampensis* can, therefore, be interpreted as adaptive deviations from the type of *A. nisus. A. ovampensis* probably represents an early African offshoot of the *nisus* group, which has evolved into a typical dry country inhabitant. This evolution may have been caused by the desiccation of large parts of Africa during some stages of the Pleistocene.

In Madagascar *A. madagascariensis* is found, which is also similar to *A. nisus* although showing clearly some characters of its own. If it is supposed that this form reached Madagascar relatively long ago from Africa, this implies that a *nisus*-like species inhabited Africa at an early date in the Pleistocene. This would present an interesting parallel to the situation in the group of *A. gentilis*. From this we may conclude that Meinertzhagen (1951) was correct in suggesting that *A. ovampensis* and *A. madagascariensis* are closely related to *A. nisus*.

In its present distribution *A. ovampensis* is strictly a non-forest species. The center of its distribution appears to be the dry country south of the tropical forest belt. It is unknown whether the species breeds north of the equator or simply visits these regions during the non-breeding season.

ACCIPITER MADAGASCARIENSIS A. SMITH

DISTRIBUTION

Madagascar (Map 11, p. 87).

PLUMAGE

Adult.—Upperparts dark slate gray. Underparts white regularly barred dark gray. Tail gray with many dark bars.

Juvenile.—Dorsum brown with rufous edges to the feathers. Underparts cream marked with streaks on the breast, drops or diamonds on the abdomen. Markings vary in color from pale brown to almost black. In the male they are darker than in the female.

In adult and juvenile plumage *A. madagascariensis* is similar to *A. henstii* though widely different in size and structure. In adult plumage *A. madagascariensis* resembles adult females of *A. nisus,* particularly those with little rufous.

SIZE AND STRUCTURE

Size small to medium. Male much smaller than female. Tarsus and toes long and slender. Claws moderately small. Bill small. Wing short and rounded. Tail medium. Figure 12, p. 83. Tables 32 and 33.

TABLE 32

Wing length in *Accipiter madagascariensis.*

SEX	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
♂	178.0	3.00	1.73	175 - 181	3
♀	225.0	4.58	1.27	219 - 234	13
				Total	16

No statistical analysis of the tarsus, middle toe, hind claw, and wt–6. The difference between the sexes is significant for the bill (smaller in male).

Bill and foot.—These are of the *nisus*-type. Owing to the short wing, the relative measurements appear large. The hind claw is longer in relation to the bill than in *A. nisus.* This is also found in *A. ovampensis,* which has a shorter tarsus in addition. In the general structure of the bill and foot *A. madagascariensis* is similar to *A. virgatus affinis.*

Wing and tail.—*A. bicolor*-type. Resemble *A. henstii,* but the wing tip is longer and the tail shorter.

Habitat

Inhabits evergreen and deciduous forest, as well as brush, from sea level to about 1,000 m. Most numerous in the forests of the dryer parts of western and southwestern Madagascar. Perches where it can be concealed by foliage, or flies rapidly and secretively through the forest as does *A. nisus.* In the stomachs of two specimens only bird remains were found (Rand, 1937).

Discussion

A. madagascariensis represents the structure type of *A. nisus* on Madagascar. It also has a similar ecology. The short wing parallels that of *A. henstii* and may likewise be related to isolation on the island and to the dense habitat.

In this respect it is interesting that the wings and tails of *A. madagascariensis* and *A. henstii* are similar but the bills and feet are quite

TABLE 33

Relative measurements in percent of wing length in *Accipiter madagascariensis.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	28.33	18.36	8.02	6.35	79.76	25.22	4.12
♂	-	-	-	-0.33	+0.43	+0.49	-
♀	-	-	-	+0.33	-0.43	-0.49	-
Adult	-	-	-	-0.04	-1.42	-0.36	-
Juvenile	-	-	-	+0.04	+1.42	+0.36	-
P model		no analysis		0.452	0.293	0.137	no analysis
P sex	-	-	-	0.002	0.403	0.207	-
n	9	8	14	15	16	14	11
df	-	-	-	11	12	10	-

dissimilar. A similar situation is found in the Palearctic where *A. nisus* and *A. gentilis* resemble one another in wing and tail but not in the structure of the foot and bill.

The distributional history of *A. madagascariensis* is parallel to that of *A. henstii* and has been summarized on p. 96. *A. madagascariensis* is believed to represent a colonization of Madagascar by an African branch of the *A. nisus* group. On account of the well-defined differences between *A. nisus* and *A. madagascariensis,* and also on account of the existence of related *A. ovampensis* in Africa, it may be concluded that this colonization dates from a comparatively remote past.

Accipiter melanoleucus A. Smith

Distribution

Forests of Ethiopian Africa (Map 6, p. 55).

Subspecies

cf. White (1965). *A. m. melanoleucus* A. Smith, eastern and southeastern Africa; *A. m. temminckii* (Hartlaub), West Africa and the Congo, the boundary with *melanoleucus* not exactly defined.

Plumage

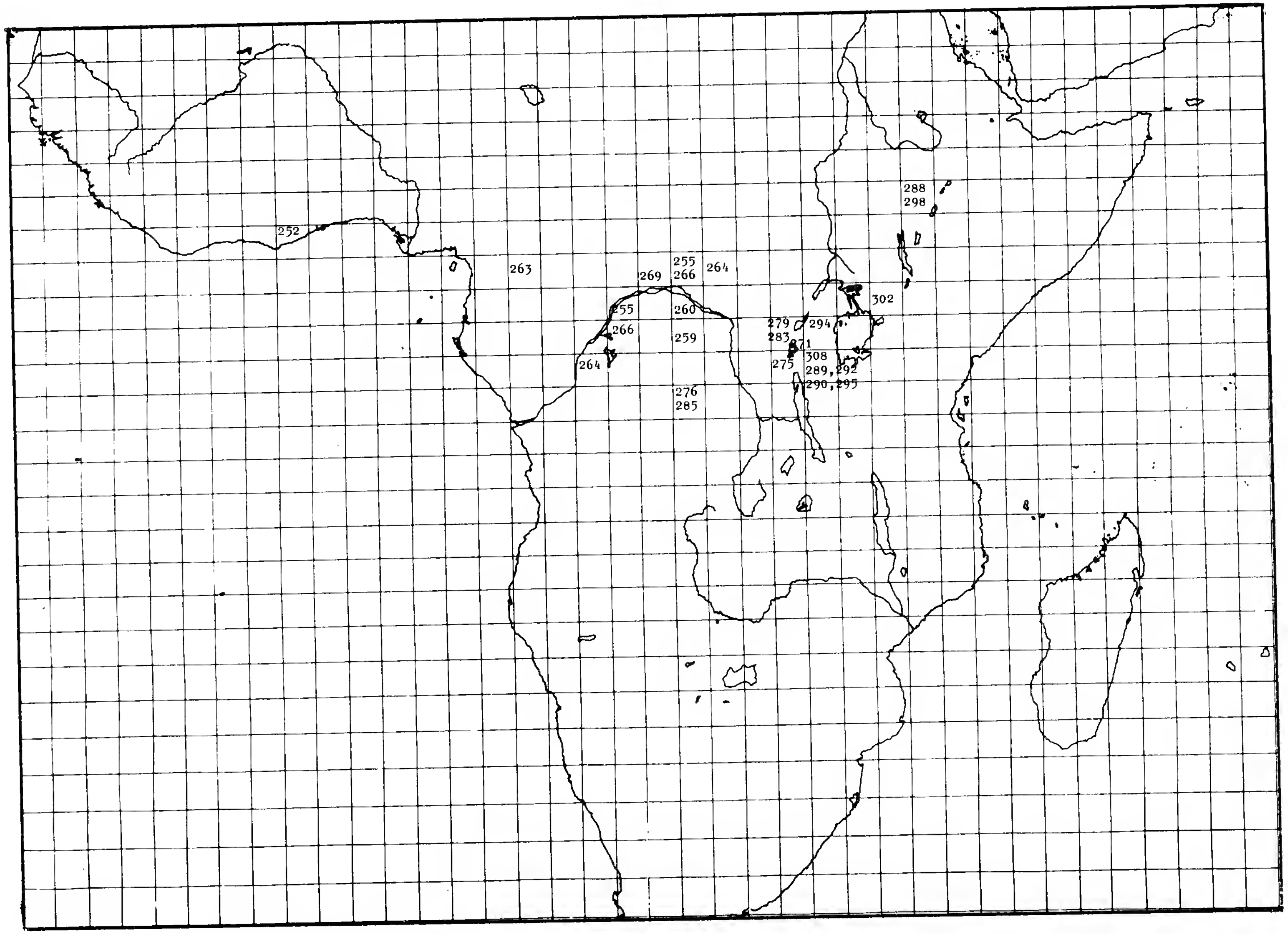
Adult.—Upperparts brownish or grayish black. Venter white. Flanks broadly barred or mottled black and white. A melanistic variant exists in which the entire underparts are black, except for a small white patch at the chin. Tail dark brown with lighter bars in both variants.

Juvenile.—Dorsum dark brown with rufous feather edges. In some specimens these are very wide in the interscapular region. Underparts cinnamon-rufous. Breast and center of abdomen marked with narrow dark brown streaks and the flanks with dark brown spots or bars. Tail distinctly barred light and dark brown.

The juvenile plumage of *A. melanoleucus* is similar to that of juvenile *A. gentilis,* but it is more heavily pigmented, being darker above and more rufous below. Many juveniles of *A. gentilis* are creamy white below, without any cinnamon tinges. Moreover, the dark streaks on the underside are narrow darts in *A. melanoleucus,* rather than broad drops as in *A. gentilis.*

Geographical Variation

Geographical variation is found in body size, the birds from East Africa being larger than those from West Africa. According to Chapin (1932) the wing of the male of nominate *melanoleucus* ranges from 267 to 298 mm, while that of the male of subspecies *temminckii* is from 251 to 273 mm. These values may be compared with those of Table 34. On Map 12 the wing length of 26 males is plotted. From this map it appears that the Congo forest is inhabited by *A. m. temminckii,* the East African highlands by *A. m. melanoleucus* and specimens from the border regions of the forest are intermediate.



MAP 12. Wing length of male *Accipiter melanoleucus* in various parts of its range.

Size and Structure

Size rather large to large. Tarsus and toes heavy, fairly long. Claws and bill heavy. Wing moderate and rounded. Tail long. Figure 13. Tables 34 and 35.

The statistical model was unsatisfactory for the tarsus. The difference between the subspecies is significant for the middle toe, hind claw, and bill. The difference between the sexes is significant for the hind claw (smaller in male) and the tail (shorter in male).

Bill and foot.—Of the *bicolor*-type. *A. melanoleucus* differs from *A. gentilis* by the longer tarsus and middle toe and the smaller hind claw.

The bill and foot in the smaller subspecies, *temminckii,* are larger in relation to the size of the bird than in the nominate race.

Wing and tail.—These are of the *nisus*-type. Differs from *A. gentilis*

TABLE 34

Wing length in *Accipiter melanoleucus.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
melanoleucus	293.3	7.53	2.38	283 - 308	10
transition area[1]	280.4	7.66	2.89	271 - 294	7
temminckii	261.2	5.42	1.63	252 - 269	11
			♀		
melanoleucus	340.7	3.51	2.02	337 - 344	3
transition area[2]	344	-	-	-	1
temminckii	297	-	-	290 - 304	2
				Total	34

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[1] Five specimens from Kivu and two from Sankuru.

[2] Specimen from Kasai.

TABLE 35

Relative measurements in percent of wing length in *Accipiter melanoleucus.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	25.91	16.10	8.49	7.11	76.52	28.99	5.47
melanoleucus	25.35	15.79	8.31	6.81	75.75	29.36	5.33
temminckii	26.47	16.41	8.67	7.41	77.29	28.62	5.61
♂	+0.27	-0.03	-0.22	-0.10	-1.41	+0.84	+1.02
♀	-0.27	+0.03	+0.22	+0.10	+1.41	-0.84	-1.02
Adult	+0.04	+0.05	+0.03	+0.06	-2.00	+0.20	-0.19
Juvenile	-0.04	-0.05	-0.03	-0.06	+2.00	-0.20	+0.19
P model	0.012	0.218	0.207	0.184	0.259	0.629	0.600
P ssp	-	0.038	0.028	0	0.157	0.461	0.749
P sex	-	0.368	0.014	0.070	0.042	0.071	0.126
n	27	25	29	29	31	28	14
df	21	19	23	23	25	22	8

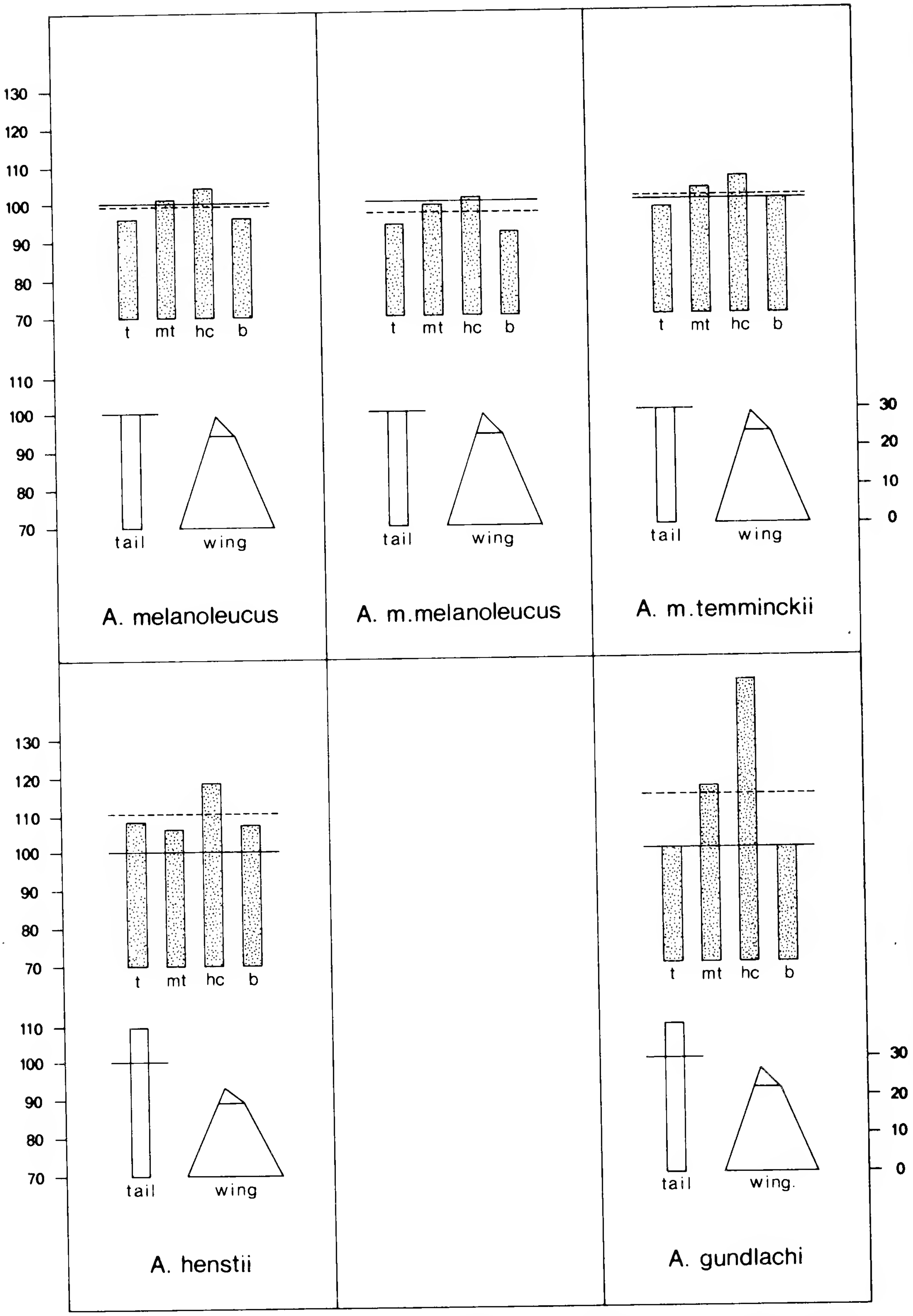


Fig. 13. Structure of *Accipiter melanoleucus*, *A. henstii*, and *A. gundlachi*.

in the shorter wing tip and longer tail. Wing similar to *A. cooperii,* but tail much shorter.

Habitat

Tropical lowland and montane forest, old secondary forest, stands of tall evergreen trees in moist localities, rich *Brachystegia* woodland (Benson and White, 1957), and Eucalyptus plantations (Vincent, 1945).

The species is found in the coastal lowlands, in highlands, and in the mountains, up to 1,500 m in Malawi and Cameroons, to 1,800 m in evergreen mountain forest in Ethiopia (Benson, 1945), and to 1,800 m in the mountains of the eastern Congo (specimen in Koninklijk Museum voor Midden Afrika).

Tall trees are an essential feature of the habitat of *A. melanoleucus.* In the tropical rainforest of the Congo basin it is a species of the tree tops (Chapin, 1932). In Nigeria it prefers remains of virgin forest near villages and old secondary forest to thickets and recent regrowth, where the trees are still small (Marchant, 1953; Elgood and Sibley, 1964). Like *A. gentilis* and *A. nisus* it often hunts in open country in the vicinity of forest.

Hunting Behavior

In hunting it pursues other birds. Searches open country in a low flight, suddenly turning and stooping when sighting prey. *A. melanoleucus* was seen to dislodge a pigeon from shelter with remarkable tenacity. The hunting behavior resembles that of *A. nisus* (Meinertzhagen, 1959).

Food

The diet is little-known, but presumably consists largely of middle-sized birds, such as quail, pigeons, and nightjars. Near human habitation poultry is taken. The smaller subspecies *temminckii* can master chicks up to six weeks old, but as a rule not adult hens (Young, 1946).

Discussion

A. melanoleucus resembles *A. cooperii* in its bill and feet, in size, and in its choice of prey. In comparison to *A. gentilis* it takes lighter prey and a higher proportion of birds in flight; accordingly it has more slender feet and lighter claws.

A. melanolecus is often included in the group of long-toed sparrow hawks (e.g., *A. nisus*), as opposed to the group of short-toed goshawks to which *A. gentilis* belongs (Chapin, 1932). Kleinschmidt (1922-23), however, considered *melanoleucus* as the African representative of *A. gentilis* on account of the striking similarity of the juvenile plumages. Considering that the differences in the bill and feet may well be adaptations to a different type of prey, Kleinschmidt's hypothesis is worth further consideration.

It is true that the adult plumage of *A. melanoleucus* is very unlike that of *A. gentilis,* but pattern reduction on the underside, along with a blackening of the upperside, is also found in other species of the tropical forest (e.g., juvenile *A. tachiro canescens* and *A. bicolor bicolor*), and may be an adaptive character, providing a kind of protective countershading. In this connection it is interesting that in *A. melanoleucus* remains of a barred pattern are found in places where they are not exposed in the sitting bird, as under the wings. Kleinschmidt illustrates a barred feather which he found on the side of the breast of a specimen of *A. melanoleucus* and which is very much like a breast feather of adult *gentilis.* Hence there is good reason to suppose that *melanoleucus* is closely related to a species with a barred pattern on the underparts in adult plumage.

This hypothesis is supported by the presence in Madagascar of *A. henstii,* a large Accipiter which resembles *A. gentilis* in adult and juvenile plumage and more or less in structure. Most probably this species colonized Madagascar from Africa at a time when the African relative of *A. gentilis* was barred underneath in the adult plumage. This implies that the barring in *A. melanoleucus* has disappeared.

From the absence of this species in the western parts of the Upper Guinea forest and from the slight differentiation of the forest subspecies *temminckii,* it may be deduced that *A. melanoleucus* does not belong to the Old African forest fauna. In East Africa the species is older, as shown by the well-differentiated form on Madagascar (*A. henstii*). Like *A. gentilis* it may have been primarily associated with luxuriant woodland alternating with open ground. Presumably it reached Africa during one of the early cold stages of the Pleistocene and has colonized the tropical forest in a subsequent warmer period.

ACCIPITER HENSTII SCHLEGEL

DISTRIBUTION

Madagascar. Most numerous in the humid east and absent in the southwestern subdesert (Map 6, p. 55).

PLUMAGE

Adult.—Upper parts dark slate gray. Underparts white, regularly barred with dark gray. Tail dark gray with narrow, slightly darker bars.

Juvenile.—Dorsum light brown with buffish edges to feathers. Underparts white to cream, heavily streaked or spotted light brown.

A. henstii resembles *A. gentilis* in adult and juvenile plumage. Adults are darker above and more narrowly barred underneath than *A. gentilis.*

SIZE AND STRUCTURE

Size large to very large. Tarsus long. Toes rather long and heavy. Claws and bill heavy. Wing short and rounded. Tail long. Figure 13, p. 94. Tables 36 and 37.

TABLE 36
Wing length in *Accipiter henstii.*

SEX	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
♂	280.7	2.37	0.89	277 - 283	7
♀	322.5	-	-	320 - 325	2
				Total	9

No statistical analysis made.

Bill and feet.—Similar to *gentilis,* but the tarsus and middle toe are relatively longer. Due to the short wing the other measurements appear large. *A. henstii* resembles *A. trivirgatus,* which is also short-winged, but the tarsus and middle toe are longer, the hind claw and bill smaller.

Wing and tail.—Of the *tachiro*-type. Resemble *A. trivirgatus,* but the tail is longer.

Habitat, Hunting Behavior, and Food

Inhabits rainforest and gallery forest in the savanna from sea level up to 1,800 m. Observed to sit quietly on a dead branch or pole along a forest track or to soar high above forest or savanna. In the stomach of three specimens the following prey species were found: lemur (twice), goatsucker (once), and cuckoo (once). Said to take poultry from small native communities at the forest edge (Rand, 1937).

Discussion

A. henstii resembles *A. gentilis* in the structure of the bill and feet and in its choice of prey. The comparatively long tarsus and middle toe may be an adaptation to the taking of arboricolous prey (lemurs). The short wing and long tail can be related to the densely forested habitat and probably also to the species' insular isolation.

In the discussion on *A. melanoleucus* it was pointed out that *A. henstii* is considered to be related to *A. gentilis* and *A. melanoleucus.* The differences in structure between these forms are so large that they are best considered as separate species. Most probably *A. henstii* reached Madagascar from Africa.

Ecological Geography in Africa

In Africa two ecological distinctions are of pre-eminent importance, viz., forest versus non-forest and lowland versus montane habitats (Moreau, 1966). This is reflected in the ecology and distribution of

TABLE 37
Relative measurements in percent of wing length in *Accipiter henstii*
(no analysis of variance).

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	29.20	17.02	9.71	7.94	83.00	22.87	3.44
n	5	5	7	7	9	8	8

the various African Accipiters. Some species range over several habitats, others are restricted within narrow tolerance limits. *A. minullus,* for instance, inhabits all types of country from dry thorn scrub to tropical rainforest, whereas *A. nisus* is confined to montane forest and *A. castanilius* is a typical rainforest form. *A. tachiro* and *A. melanoleucus* are found in tropical rainforest as well as in other habitats, but some type of forest is essential for them, and in the dry districts of southern Africa their distribution is more restricted than that of *A. minullus.* On the other hand, they penetrate montane habitats, which appear unsuitable for *A. minullus. A. badius* and *A. ovampensis* are found only in dry habitats, such as woodland, savanna, and scrub. A survey of the ecology of African species is given in Table 38.

In species which inhabit rainforest as well as other habitats, the rainforest populations are subspecifically different from the others. In *A. minullus* and *A. tachiro* the difference is so great that it is a matter of opinion whether the rainforest forms are conspecific with the other ones or not. In addition to subspecific variation paralleling the habitat diversity, there is also geographic variation indicating the presence of some distributional barriers within the great habitat systems. From the distribution of *A. nisus rufiventris* and *A. n. perspicillaris,* as well as of *A. tachiro sparsimfasciatus* and *A. t. unduliventer,* the conclusion may be drawn that the stretch of excessively dry country in the neighborhood of Lake Rudolf constituted such a barrier for montane species, even at the height of glaciation. The nature of this barrier has not been explained satisfactorily.

Within the confines of the rainforest a barrier was situated in Nigeria, but this barrier may have shifted considerably, and has not always been of the same character (Marchant, 1954). The existence of this barrier is reflected in the distribution of *A. minullus* and *A. tachiro;* it has possibly also slowed the westward penetration of *A. melanoleucus* and *A. castanilius.*

A. melanoleucus, A. minullus, and *A. tachiro* range from northern Kenya to the Cape Province without indications of a zoogeographical barrier anywhere in that region. In *A. badius,* however, we find evidence for the former existence of such a barrier by its splitting into

TABLE 38

SURVEY OF THE ECOLOGY OF AFRICAN SPECIES OF *Accipiter.*

SPECIES	SIZE	MAIN PREY	HABITAT
nisus	medium	birds	montane
ovampensis	medium	birds	dry country
melanoleucus	large	birds	rain forest — dry forest
minullus	small	birds	rain forest — dry scrub
castanilius	medium	generalized	rain forest
tachiro	large	generalized	rain forest — dry forest
badius	small	generalized	woodland — dry scrub

the subspecies *sphenurus* and *polyzonoides*. For *A. ovampensis* the state of affairs is not clear; if the supposition is correct that it does not breed north of the equator, then this barrier would be reflected in the distribution of that species too. Most probably the barrier was formed by montane and forest habitats stretching from the Congo basin to the coast of the Indian Ocean.

The ecological diversity of the African Accipiters is apparently much wider than that of the tropical Asian species. A small bird hunter is found not only in montane forest, but also in lowland forest and in various types of dry woodland. The tropical goshawks (*A. tachiro* and *A. castanilius*) are smaller than Oriental *A. trivirgatus*. A large goshawk taking a variety of heavy prey, comparable to *A. gentilis*, is absent from Africa, as it is from the Orient. The African relative of *A. gentilis* apparently has become adapted to a diet of mainly birds.

Although the Accipiter fauna of Madagascar has as many species as the whole of Europe, in comparison to Africa it can be termed poor. Only those African groups are represented that also range widely in Eurasia, i.e., the groups of *A. badius, A. nisus,* and *A. gentilis*. Typically African species such as *A. tachiro* and *A. minullus* did not reach Madagascar. The Madagascar representatives of *A. badius, A. nisus,* and *A. gentilis* give an impression of antiquity. As far as *Accipiter* is concerned, the fauna of Madagascar is of an impoverished ancient African type.

The ecological diversity of Madagascan species is similar to that of Europe. There is a heavy goshawk preying on birds and mammals, a sparrow hawk taking mainly birds, and another sparrow hawk selecting more generalized prey. In Europe *A. nisus* inhabits forested country, while *A. brevipes* is in more open country. In Madagascar on the contrary, *A. francesii,* which takes a variety of prey, is more confined to forest than the bird-catching species *A. madagascariensis,* which is also found in dry brush areas.

[Note: After the manuscript had been completed an interesting paper on adaptive radiation in southern African Accipiters came to my notice (Black and Ross, 1970). In general the conclusions of Black and Ross support mine, but they show that *A. minullus* is more of a still-hunter and *A. ovampensis* more of a chase-hunter than I had surmised. My suspicion that *A. ovampensis* preys mainly upon birds is borne out by their data.]

V

NORTH AND SOUTH AMERICA

INTRODUCTION

Table 39 lists the Accipiters of North and South America. Two of the three species occurring in North America are closely allied to South American forms. Therefore it appeared desirable to combine the discussion of the Nearctic and the Neotropical Regions. *A. gentilis* has been considered in Chapter III. It is the only species that is widespread outside the Americas.

ACCIPITER POLIOGASTER (TEMMINCK)

DISTRIBUTION

Northern South America, east of the Andes. Collected at widely scattered localities in its range (Map 13). Some of the records may pertain to birds on migration. According to Bertoni (1926) and Laubmann (1939) the species appears in Paraguay only during the season of the heavy rains.

PLUMAGE

Adult.—Dorsum glossy black, fading to blackish brown by wear. Underparts white or very pale gray. Sides of face black or gray. Tail black with inconspicuous dark gray bars.

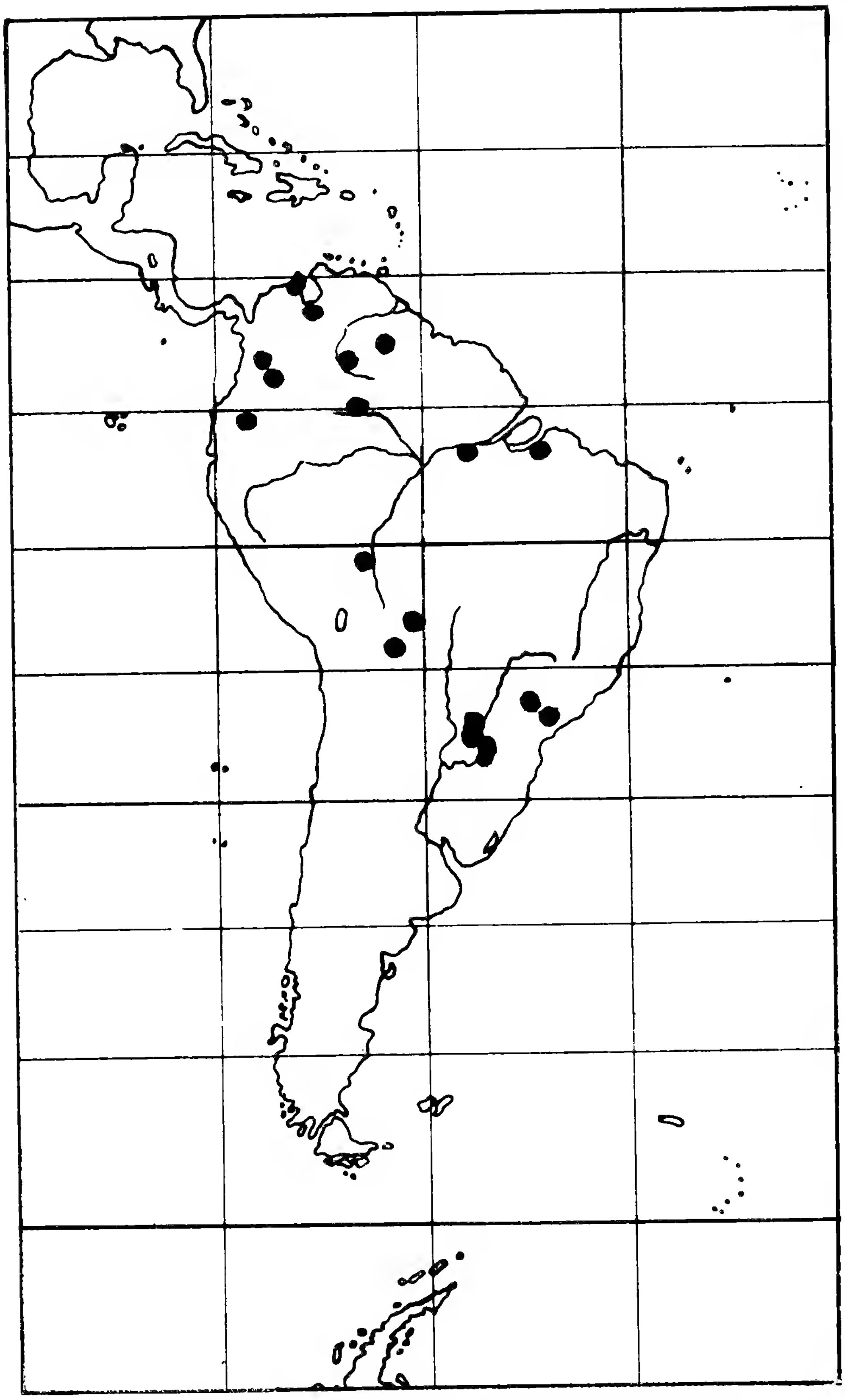
Juvenile.—Upperparts black with a wide rufous collar, with the rufous tinge spreading over the sides of face, throat, and breast. Interscapulars and upperwing and tail coverts with narrow white edges. Crown with inconspicuous black crest. Center of venter white with black streaks on the throat, round spots on the upper breast, and wide bars on the lower breast and abdomen. Tail black with a narrow white terminal line and three distinct gray-brown bars.

It was formerly thought that birds in this plumage represented a distinct species, *Accipiter pectoralis* (Bonaparte). Bertoni (1926) was the first to express the opinion that *"pectoralis"* is the young of *poliogaster.* Laubmann (1939) did not accept this view. It was only as recent as 1961 that Partridge demonstrated that Bertoni was correct.

It has been pointed out by several authors that in its juvenile plumage *A. poliogaster* is strikingly similar to *Spizaetus ornatus.*

SIZE AND STRUCTURE

Size rather large to large. Tarsus and toes short and sturdy. Claws and bill heavy. Wing short and rounded. Tail very short. Figure 4, p. 16. Tables 40 and 41.



Map 13. Distribution of *Accipiter poliogaster.*

TABLE 39

Species of *Accipiter* in North and South America.

SPECIES	DISTRIBUTION
Accipiter poliogaster	Northern South America
Accipiter superciliosus	Middle and Northern South America
Accipiter collaris	Northern Andes
Accipiter striatus	North, Middle, and South America
Accipiter bicolor	Middle and South America
Accipiter gundlachi	Cuba
Accipiter gentilis	Holarctic

TABLE 40

WING LENGTH IN VARIOUS AMERICAN SPECIES OF *Accipiter*.

SPECIES	SEX	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
gundlachi	♀	272.0	3.00	1.73	269 - 275	3
superciliosus	♂	139.2	2.06	1.03	137 - 141	4
	♀	161.2	3.20	1.60	159 - 166	4
collaris	♂	148.5	-	-	148 - 149	2
	♀	172.8	2.95	1.32	168 - 176	5
poliogaster	♂	251.0	-	-	243 - 259	2
	♀	273.7	5.91	2.96	269 - 282	4

No statistical analysis has been made.

Bill and foot.—These are of the *albogularis*-type, although the tarsus is relatively shorter than in *albogularis.*

Wing and tail.—Similar to the *novaehollandiae*-type. Tail shorter than that of any other species with this type of tail.

HABITAT, HUNTING BEHAVIOR, AND FOOD

Inhabits tropical lowland rainforest, subhygrophilous forest (Olivares, 1959), open country near riparian forest and second-growth, and isolated patches of dense woods (Giai, 1951). The fact that it is apparently migratory may indicate that it also lives in deciduous forest, presumably during the rainy season. The species is apparently very shy, which may account for its scarcity in collections. It is probably mainly a still-hunter (Giai, 1951). Nothing has been recorded about its food.

DISCUSSION

A. poliogaster is an aberrant member of the genus. It has relatively very short legs and its juvenile plumage differs greatly from that of

TABLE 41

RELATIVE MEASUREMENTS IN PERCENT OF WING LENGTH IN VARIOUS AMERICAN SPECIES OF *Accipiter* (AVERAGE OF SMALL SERIES OF VALUES, NO STATISTICAL ANALYSIS POSSIBLE).

SPECIES	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
gundlachi	27.20	18.60	11.80	7.43	82.67	27.17	5.30
n	2	2	1	3	3	3	3
superciliosus	29.52	20.19	10.11	8.03	71.87	28.50	14.34
n	5	6	7	7	8	7	8
collaris	28.04	19.32	9.80	8.02	72.14	26.50	12.70
n	5	5	5	6	7	5	6
poliogaster	21.97	15.17	8.10	7.46	70.67	26.70	6.15
n	4	3	3	5	6	5	6

all other Accipiters. The simple adult plumage, with a black dorsum and a white underside, resembles various other species of the tropical forest, e.g., *A. melanoleucus,* juvenile *A. bicolor,* and *A. albogularis,* and may be regarded as adaptive (p. 122). *A. poliogaster,* in common with *A. superciliosus,* is restricted to lowland forest habitats in South America and like that species it may be regarded as a relict not closely related to other species of *Accipiter.*

ACCIPITER SUPERCILIOSUS (LINNAEUS)

DISTRIBUTION

South and Middle America from Nicaragua to northern Argentina (Map 14).

SUBSPECIES

cf. Hellmayr and Conover (1949). *A. s. superciliosus* (Linnaeus), northern South America, east of the Andes; *A. s. fontanieri* Bonaparte, southern Middle America and northern South America, west of the Andes.

PLUMAGE

Adult male.—Upperparts blackish brown, interscapular region tinged gray, crown black. Venter white, narrowly barred with gray. Outerside of thighs almost solid dark brownish gray. Sides of face dark gray mottled with dirty white. Tail fuscous with broad black bars.

Adult female.—Dark colors slightly more brownish than in the male and interscapular region less pure gray.

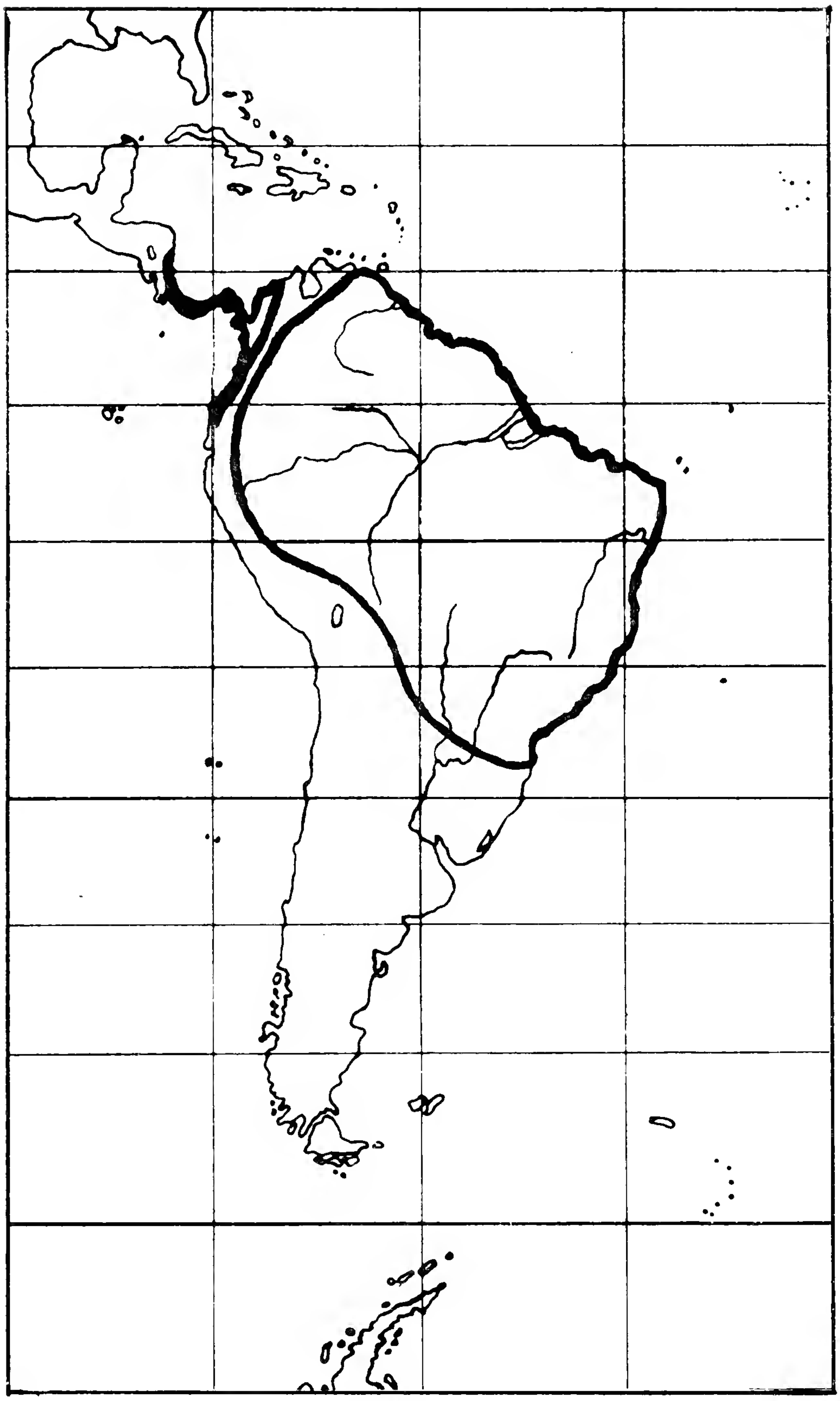
Juvenile.—Strong individual variation, described as two "phases," viz., tawny and brown-backed (Conover, 1946).

Tawny phase: crown blackish, back tawny with dark brown subapical spots on the feathers. Underparts light tawny with narrow dark bars, which are suffused at their margins, less clear-cut than in the adult plumage and the brown-backed juvenile. Tail deep tawny crossed by narrow black bars.

Brown-backed phase: upperparts dark brown with the feathers very narrowly edged with rufous. Underparts white with narrow light brown bars. Tail fuscous with broad, dark brown bars.

A specimen in the Rijksmuseum van Natuurlijke Historie at Leyden, reg. nr. 10.732 (♀ juv., Hausa Humboldt, Santa Catharina) is dorsally dark brown with the feathers narrowly edged with rufous, resembling the brown-backed phase, but beneath it is entirely suffused with tawny. The bars on the underside are tawny brown, darker than in the brown-backed phase and also less sharply defined. This bird is intermediate between the phases suggesting that the gap between the two phases is not so abrupt as has been assumed.

In *A. superciliosus* the tawny juvenile is much rarer than the brown-backed form, as previously noted by Amadon (1964).



Map 14. Distribution of *Accipiter superciliosus.*

It is of interest that the pattern on the underside is similar in adult and juvenile plumages, a feature that is very rare among the species of *Accipiter.*

Geographical Variation

A. s. fontanieri is poorly differentiated. The bars on the underparts are on the average slightly wider and more sharply defined than in the nominate taxon, and in the adult male they are also a little blacker. In addition, *A. s. fontanieri* averages slightly smaller (Hellmayr and Conover, 1949).

Size and Structure

Size very small to small. Tarsus and toes long and rather heavy. Claws heavy. Bill moderately heavy. Wing medium and sharply pointed. Tail very short. Figure 4, p. 16. Tables 40 and 41, p. 103.

No statistical analysis was made.

Bill and foot.—The foot is characterized by the combination of a very long middle toe and a heavy hind claw. The bill and foot resemble the proportions of these structures in *A. gundlachi,* but they are much smaller. In relation to the size of the bird the bill and feet are very heavy.

Wing and tail.—These are of the *minullus*-type. The tail is slightly shorter and the wing tip more pointed than in *A. minullus.*

Habitat, Hunting Behavior, and Food

Inhabits the edges of tropical forest, dense second-growth, open woodland, and plantations contiguous to dense forest in the humid tropical zone, up to about 700 m (Sclater and Salvin, 1879). Does not venture far into dense forest. Keeps to the middlestory of the trees, going higher when coming more into the open (Slud, 1960; 1964). *A. superciliosus* seems to be nowhere common, as it is rather rarely observed and is scarce in collections. From its elusive habits it may be inferred that it is mainly a still-hunter in dense growth. Its prey consists of small birds (Slud, 1964). Carriker (1910) reports a specimen having caught a small antwren (*Rhamphocoenus semitorquatus*).

Discussion

A. superciliosus is aberrant in form in that its bill and claws are comparatively heavy. *A. minullus erythropus,* the small bird-hunting Accipiter of the African forest, is similar in the structure of its wing and tail, but it has a decidedly smaller foot and bill. The significance of this difference between the two small bird-hunters is not clear because of scanty information on their ecology.

A. superciliosus is a typical South American species having no close relatives except *A. collaris.* Morphologically it stands rather apart within the genus. The peculiar barred juvenile plumage is probably an archaic character since the evolution of the juvenile plumage of *Accipiter* appears to be from a barred toward a spotted one. In many species in which the juvenile is spotted below, remains of barring are found at the bases of feathers or in places where they are not exposed, e.g., under the wings.

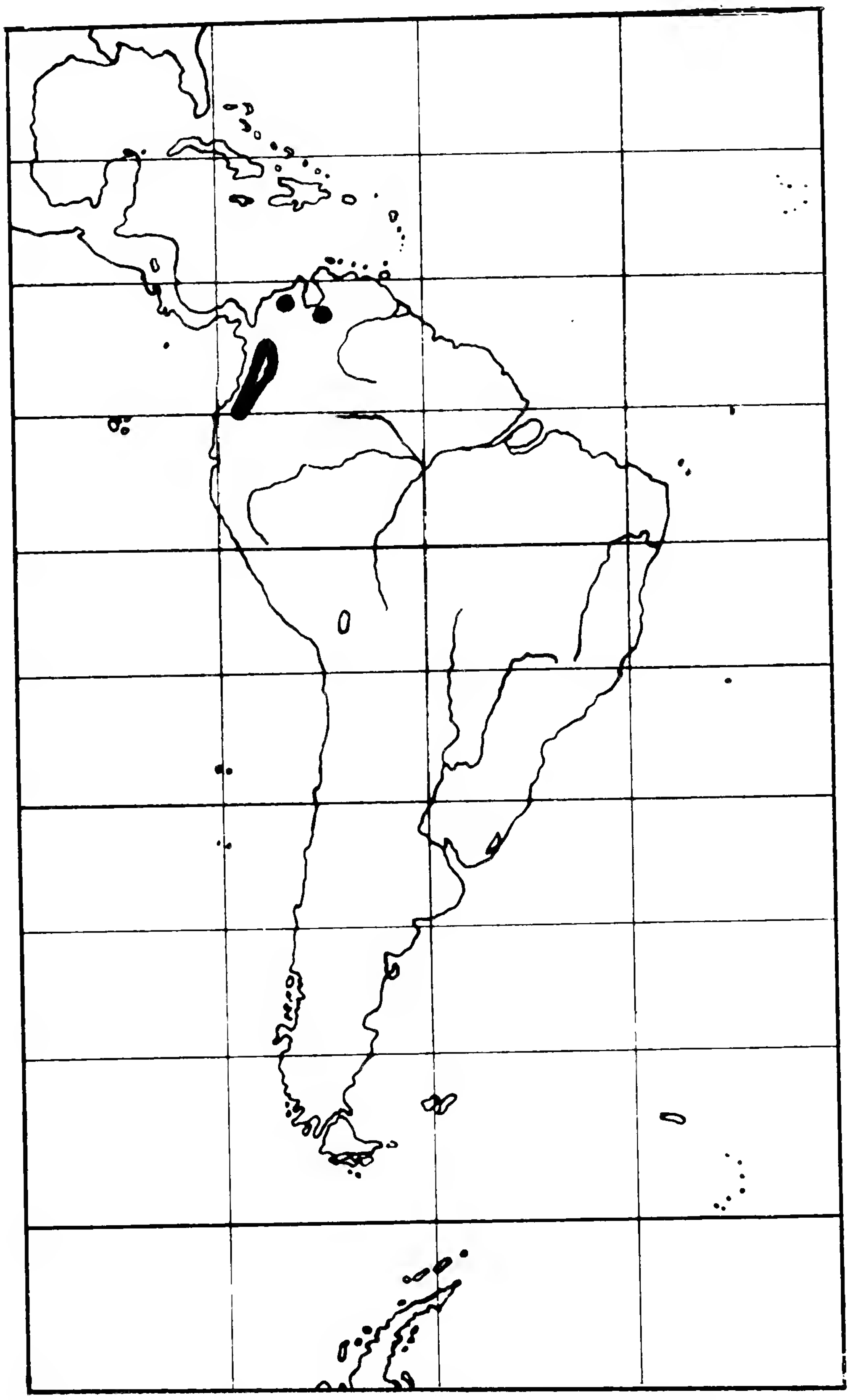
In its distribution *A. superciliosus* is confined to lowland forest. The species is not known from the central tableland of Brazil. The northern Andes separate the Central American and Pacific coast subspecies (*fontanieri*) from Amazonian nominate *superciliosus.* Lowland forest seems to have been a very stable habitat, constituting a suitable refuge for relict species. *A. superciliosus* may be considered to be such a relict, which has been isolated in South America for a comparatively long time.

ACCIPITER COLLARIS SCLATER

DISTRIBUTION

Mountains of northern South America (Map 15).

In addition to the single specimen (juvenile in tawny phase) from Mérida, Venezuela (Swann, 1921) an adult female from the same region is in the Rijksmuseum van Natuurlijke Historie at Leyden.



MAP 15. Distribution of *Accipiter collaris.*

PLUMAGE

Adult.—Dorsum dark brown; crown darker than back, separated by an indistinct white nuchal collar in which the white bases of the feathers may be seen through the brown tips. Underparts cream with broad brown bars. Tail dark brown with gray bars.

Juvenile.—Strong individual variation, described as two "phases": tawny and brown-backed (Conover, 1946), parallel to the situation in *A. superciliosus.*

Tawny phase: upperparts brown with broad tawny feather edges or dorsum wholly tawny. Crown darker than back and separated by a distinct light tawny collar. Underparts light tawny with suffused dark bars. Tail barred tawny and black.

Brown-backed phase (description taken from Conover): upperparts brown, slightly lighter than adult, with inconspicuous rufous edges to the feathers. Crown darker than back and separated by an indistinct white collar. Underparts more narrowly barred than adult, bars lighter and buffish.

Contrary to *A. superciliosus* the tawny phase is much commoner than the brown-backed one. Both Conover (1946) and Amadon (1964) found only one brown-backed specimen among four juveniles. Five specimens studied by me (two of which had also been seen by Conover) all belonged to the tawny phase. Two, however, were browner on the back than the other three, approaching the brown-backed phase and indicating that, as in *A. superciliosus,* individual variation may bridge the differences between the two "phases."

SIZE AND STRUCTURE

Size small to rather small. Apart from being somewhat larger, *A. collaris* is virtually identical to *A. superciliosus* in conformation. Figure 4, p. 16. Tables 40 and 41, p. 103.

No statistical analysis.

HABITAT

Apparently lives in mountain forest, alternating with more or less open ground. Collected at plantations amidst "luxuriant mountain forest and clearings" (Todd and Carriker, 1922, erroneously identified as *A. superciliosus*) and in woodland close to a small farm (Olivares, 1960). Restricted to the upper tropical and subtropical zones from 600 to 2,100 m. Nothing is recorded regarding its food or hunting behavior.

DISCUSSION

The great resemblance between *A. collaris* and *A. superciliosus* led Amadon (1964) to suspect that *collaris* is a subtropical and temperate zone representative of *superciliosus.* Following Amadon I prefer to regard *collaris* as a separate species until it can be proved that intergradation occurs where both forms meet.

NORTH AND SOUTH AMERICA

ACCIPITER STRIATUS VIEILLOT

DISTRIBUTION

Alaska and central Canada south through North and Middle America and along the Andes to Bolivia, and in Brazil, Argentina, Cuba, Hispaniola, and Puerto Rico (Map 5, p. 44).

The northern North American populations are migratory.

SUBSPECIES

cf. Storer (1952). *Accipiter s. perobscurus* Snyder, Queen Charlotte Islands, and possibly adjacent regions of western Canada, and wintering south to Oregon; *A. s. velox* (Wilson), breeding from Alaska and Canada south to the southern U.S.A., but very scarce in southeast, and wintering from British Columbia and the northern U.S.A. south to Panama, the Gulf Coast, and the Bahamas; *A. s. suttoni* van Rossem, mountains of Mexico south to Michoacán and Veracruz, intergrading with *velox* in northern Mexico and descending to lower altitudes in winter; *A. s. madrensis* Storer, Sierra Madre del Sur, Guerrero, Mexico; *A. s. chionogaster* Kaup, Chiapas, Mexico to western Nicaragua; *A. s. ventralis* Sclater (*A. s. salvini* Ridgway considered a synonym), Andes from Colombia and Venezuela to central Bolivia; *A. s. erythronemius* Kaup, southeastern Bolivia and central Brazil south to northern Argentina where said to be common between Loberia and Bahía Blanca (Pereyra, 1938), but this requires confirmation; *A. s. fringilloides* Vigors, Cuba; *A. s. striatus* Vieillot, Hispaniola; *A. s. venator* Wetmore, Monte del Estado, Puerto Rico.

PLUMAGE

Adult.—Dorsum dark bluish gray, slate, or almost black; crown darker than back in several subspecies. Underparts extremely variable, the basic pattern being a rufous or rufous-brown barring on white background. Throat with narrow dark shaft streaks. Sides of face rufous with dark brown shaft streaks. Tail broadly barred dark and light gray. The female is slightly browner on the upperside than the male.

Juvenile.—Upperparts light or dark brown with tawny or rufous edges to the feathers. Underparts white or cream variously patterned with brown markings. Tail broadly barred light and dark brown.

GEOGRAPHICAL VARIATION

Geographical variation occurs mainly in the color and pattern of the venter in both the adult and juvenile. In addition there are differences in size, structure, and intensity of pigmentation on the back.

A. s. velox.—Adult: underparts broadly barred rufous or cinnamon and white. In many specimens the white bars are interrupted by rufous streaks along the shafts of the feathers, leaving only white spots on one or both webs. Rufous pigments are particularly predominant on the flanks. There is pronounced individual variation in the tinge of the pigmentation.

Juvenile: underparts cream with broad cinnamon or brown streaks on the breast, diamonds or arrowheads on the abdomen, and more or less complete bars on the flanks.

A. s. perobscurus.—On the average more heavily pigmented than *velox*. Adults are darker on the upperside, more solidly rufous underneath.

Mexican races.—The races *suttoni* and *madrensis* are characterized by immaculate light rufous thighs. They are slightly larger than *velox*. *A. s. madrensis* is much lighter underneath, approaching *chionogaster* (Storer, 1952). Adult *chionogaster* is pure white on the breast and abdomen, contrasting beautifully with the almost black upperparts. The thighs are uniform light buff. It is smaller in size than *suttoni* and *madrensis* (Friedmann, 1950).

A. s. ventralis.—Adult: venter extremely variable, ranging from pure white with a few dusky shaft streaks ("*salvini*") to sooty black ("*nigroplumbeus*"). The "*salvini*"-type resembles *chionogaster,* although the thighs are deeper rufous. Similar to the "*salvini*"-type are specimens with faint rufous or gray bars. A darker variant has the flanks uniformly rufous and the center of the breast and abdomen heavily barred rufous-gray, every bar consisting of a rufous and a gray line, as in *A. nisus* and several other Accipiters. In the average *ventralis*-type (Hellmayr and Conover, 1949) rufous pigments, in tinges from buff to earthen brown, have spread all over the underside, obscuring the barred pattern which remains as only a few gray lines. Some specimens are mottled dark gray and rufous-brown, being closely similar to the "*nigroplumbeus*"-type. Thus a complete series of variants leading from one extreme to the other can be found.

Juvenile: underparts correspondingly variable, light individuals having only a few cinnamon streaks on the breast, whereas the dark types are marked with large triangular spots on the breast and heavy bars on the flanks and abdomen. Melanistic specimens are black below with deep rufous feather edges; melanistic juveniles occur in both sexes.

According to Hellmayr and Conover (1949) the melanistic mutant of the adult plumage ("*nigroplumbeus*") is restricted to the male. However, because a melanistic juvenile female was present in my material, it remains possible that the melanistic mutant may be found among the adult females too.

A. s. erythronemius.—Adult: underparts narrowly barred rufous-gray, as in certain types of *ventralis,* showing a striking similarity to the adult male of *A. nisus.* Flanks and thighs deep rufous. Upperparts lighter than in *ventralis.*

Juvenile: back much lighter than in *ventralis.* Underparts cream with brown streaks, drops, arrowheads, or bars, more variable than in the adult. In many specimens the flanks are washed with rufous. In a male from Jujuy, Argentina, the entire venter is almost uniformly rufous with faint gray bars, probably indicating gene flow from nearest populations of *ventralis.* Another male from Jujuy does not show this rufous coloration.

West Indian races.—The races *fringilloides, striatus,* and *venator* are narrowly and regularly barred rufous-gray, similar to *erythronemius.* The thighs are "narrowly barred with grayish brown" in *fringilloides,* "uniform or heavily barred with sayal brown" in *striatus,* and rufescent in *venator* (Friedmann, 1950; cf. Wetmore and Swales, 1931). Variation in this character in the Greater Antilles appears to be clinal.

SIZE AND STRUCTURE

Size small to rather small. Tarsus and toes long and slender. Claws and bill delicate. Wing medium and rounded, comparatively shorter in *ventralis* than in *velox* and *erythronemius.* Tail rather long. Figure 9, p. 48. Tables 42 and 43.

The statistical analysis was restricted to the races *velox, ventralis,* and *erythronemius.* The difference between the subspecies is significant for all series of data except the hind claw. The difference between the sexes is significant for the tarsus (longer in male), hind claw (smaller in male) and bill (smaller in male).

Bill and foot.—These are of the *nisus*-type. *A. s. velox* is almost exactly like *A. n. nisus;* in the races *ventralis* and *erythronemius* the middle toe is comparatively longer and in *ventralis* the bill is longer in relation to the hind claw. In this respect *A. s. ventralis* resembles *A. n. rufiventris.*

Wing and tail.—These are of the *nisus*-type in *A. s. velox.* The wing tip is slightly shorter and the tail slightly longer than in *A. nisus.* In *A. s. erythronemius* the wing tip is again shorter. *A. s. ventralis* has the shortest wing tip and the longest tail and resembles *A. bicolor* in this respect.

HABITAT

Found in many types of forest and woodland, not extensive closed forests, but rather forest edges, small woodlots, and places where the

TABLE 42
WING LENGTH IN *Accipiter striatus.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
velox	173.5	4.40	1.27	169 - 183	12
ventralis	171.1	4.05	0.98	162 - 176	17
erythronemius	168.3	2.55	0.85	166 - 174	9
			♀		
velox	207.1	5.87	1.52	200 - 224	15
ventralis	198.6	4.68	1.25	192 - 206	14
erythronemius	193.0	3.83	1.21	187 - 199	10
				Total	77

TABLE 43

RELATIVE MEASUREMENTS IN PERCENT OF WING LENGTH IN *Accipiter striatus.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	26.95	17.51	6.93	6.00	78.57	27.52	4.73
velox	27.43	16.95	6.85	5.86	77.57	29.71	5.89
ventralis	28.00	18.03	6.97	6.29	80.20	24.92	3.46
erythronemius	25.42	17.55	6.96	5.85	77.94	27.94	4.84
♂	+0.77	+0.02	-0.24	-0.13	-0.04	-0.48	-0.06
♀	-0.77	-0.02	+0.24	+0.13	+0.04	+0.48	+0.06
Adult	-0.12	+0.04	+0.07	+0.08	-0.70	0	-0.50
Juvenile	+0.12	-0.04	-0.07	-0.08	+0.70	0	+0.50
P model	0.163	0.155	0.188	0.655	0.253	0.799	0.263
P ssp	0	0	0.176	0.001	0	0	0
P sex	0	0.213	0	0.016	0.333	0.095	0.318
n	76	62	75	74	75	72	74
df	64	50	63	62	63	60	62

forest is broken by a brook or gully, a clearing or a patch of cultivation. *A. striatus* is more frequently found in coniferous and mixed woods than in pure deciduous forest, and more in colder zones than in warmer regions. In the tropics it occurs mostly in the mountains, but it is not entirely absent from tropical lowlands.

In North America *A. striatus velox* is primarily a bird of the coniferous and mixed conifer-birch-aspen forests of the Canadian and Transition life zones. Less commonly it is found in many other types of woodland throughout the USA. In the north it reaches the arctic tree line. In the southwestern USA and Mexico it is confined to the mountains, reaching 3,000 m in New Mexico (Hubbard, 1965). The subspecies *suttoni* is a characteristic bird of the pine-oak woodland at altitudes from 1,400 to 3,000 m in the Mexican mountains (Storer, 1952).

On migration and in winter *A. striatus velox* occurs in almost every type of country where trees or bushes offer some shelter.

In Central America *A. striatus chinogaster* is a bird of pine forests, regardless of the species of pine (Griscom, 1932) or of the altitude (350 to 2,600 m). It occurs under widely different climatic conditions, from arid tropical to humid temperate. The habitat of the South American subspecies *ventralis* is equally variable, ranging from moist tropical forest to temperate mountain savanna, although the species is most numerous in subtropical cloud forest (Chapman, 1917, 1926; Schäfer and Phelps, 1954). The altitudinal distribution extends from sea level to 3,660 m in Peru (Peters and Griswold, 1943).

In the plains of central South America *A. s. erythronemius* inhabits savanna woodland, gallery forest, dense forest alternating with open scrub, and small stands of spiny bush with a few high trees in open country.

HUNTING BEHAVIOR

Two types of hunting have been described, viz., a fast and stealthy searching flight and still-hunting. In searching for prey *A. s. velox* flies quietly along forest paths or hedgerows, seeking shelter behind a bush, fence, or building, capturing its prey by surprise or after a short chase. Sometimes it pursues its quarry on the ground, moving with long jumps, aided by its wings (Brewster, *in* Bent, 1937). A similar hunting flight was observed in *A. s. ventralis* in Bolivia, the bird flying rapidly through dense forest and catching small birds by surprise, quite like *A. nisus* (d'Orbigny, 1835-44).

When still-hunting *A. s. velox* perches on the inner branches of a tree, close to the trunk, and darts out when a small bird comes close enough to permit a successful attack. If it does not catch its prey immediately, it tries to prevent it from reaching the safety of dense cover (Gabrielson and Lincoln, 1959).

FOOD

The diet of this species is birds, ranging from hummingbirds to small pigeons, but predominantly warblers and sparrow-size species. Occasionally it takes mammals, lizards, frogs, and insects.

A. s. velox has been extensively studied, but information on the food of the other subspecies is scarce. Data on *velox* from the studies of Fisher (1893) and McAtee (1935) are summarized in Table 44. Among 869 prey items recorded in the U.S. Fish and Wildlife Service files, the most frequently represented genera are *Dendroica, Melospiza, Turdus, Hylocichla,* and *Spizella.* The mean weight of the prey taken by males was calculated to be 17.6 gms; by females it was 28.4 gms (Storer, 1966).

DISCUSSION

In structure and ecology *A. striatus* can be considered the American counterpart of the Old World bird-catching sparrow hawks. *A. striatus* is closely similar to *A. nisus,* except in the color pattern of the underparts. In the juvenile the underparts are more pronouncedly streaked longitudinally than in *A. nisus;* in adult plumage there is a wide variation, but never distinct sexual dimorphism. The North American subspecies *velox* stands apart in having the white bars underneath more or less reduced to white spots. It may be concluded that *A. striatus* belongs to the same group of species as *A. nisus, A. ovampensis,* and *A. madagascariensis. A. striatus* is more closely similar to *A. nisus* than are *A. ovampensis* and *A. madagascariensis* (in *A. madagascariensis* the juvenile plumage is streaked longitudinally resembling juvenile *A. striatus*).

The question may be raised as to whether *A. striatus* is related to *A.*

TABLE 44
STOMACH ANALYSES OF *A. striatus velox.*

	Number of times a certain type of prey was found	
	I	II
Total number of stomachs examined	159	944
Empty	52	?
Containing prey	107	?
Warblers, Vireos, etc.	16	273
Sparrows, Finches, etc	44	290
Swallows	-	29
Other small birds	7	?
Unidentified small birds	14	?
Total small birds	76	592 +
Thrushes, Mocking Birds, Orioles, etc.	15	116
Woodpeckers and Flickers	4	?
Pigeons and Doves	2	2
Poultry and game birds	6	7
Other birds	1	?
Unidentified birds	5	?
Total birds	103	718 +
Mammals (predominantly mice)	6	30
Insects	5	12
Unidentified prey	1	?

I = FISHER (1893), II = McATEE (1935), ? = not stated.

virgatus, which inhabits the eastern Palearctic and could have colonized the Nearctic. However, there is no morphological evidence supporting a close relationship between these species. The juvenile plumages of *A. virgatus gularis* and *A. striatus velox* are similar indeed, but the adult plumages are very different. The tropical mountain forms of *A. striatus* resemble the *rufiventris* group of *A. nisus* rather than the *virgatus* group of *A. virgatus.* In wing structure *striatus* differs strongly from *virgatus.* Ecologically North American *A. s. velox* is a bird of the boreal forest like eastern Palearctic *A. nisus nisosimilis,* whereas *A. virgatus gularis* belongs to the fauna of warm temperate deciduous forests. Stresemann (1924) also included *striatus* in the *nisus* group of species, arguing that all species of the group have fine black shaft streaks on the throat.

The distribution of *A. striatus* is of a simple north-south type. Being primarily a bird of the colder zones, it is generally an inhabitant of mountains in Central America and northern South America. Where there are no mountains there are wide gaps in the range of this species, as at the Isthmus of Panama. During the height of the Pleistocene glaciations, when the lower limit of montane conditions was much lower than at present, these distributional gaps must have been considerably narrower, thus favoring colonization of South America by this northern group of sparrow hawks.

According to Chapman (1917, 1926) and Griscom (1932) *A. striatus* is at present not limited to montane forests, but occurs also at lower levels, although only in those places bordering high mountains. The species does not occur in the Amazonian or Central American lowland forests. In the savannas and deciduous forests of southern Brazil, however, it approaches the equator to within ten degrees of latitude. Apparently it has been able to colonize the lowlands where the deciduous forests of the Gran Chaco are adjacent to the foot of the Andes. Presumably this colonization took place during a cool period, and by adapting itself to the changing conditions the species persisted in the lowland forests and savannas in a subsequent warmer period. This may be taken as an illustration of how by analogy *A. ovampensis* could have arisen in dry tropical areas in southern Africa through ecological diversification within an African group of sparrow hawks of a northern origin (*nisus* group, see p. 89). In *A. n. erythronemius* the process has not advanced so far as in *A. ovampensis,* the former being not yet specifically distinct from its northern relative.

A. striatus ventralis and the *rufiventris* group of *A. nisus* in Africa present another striking case of parallelism. Both are tropical mountain birds and in both the transverse barring of the underparts of their relatives from higher latitudes has been largely replaced by an entirely rufous coloration. Disappearance of barring and the increase in rufous coloration are both effects of the increase of rufous pigments. Montane forest conditions within the tropics apparently induce such an increase. However, the occurrence of melanistic variants ("*nigroplumbeus*") and others which are immaculately white underneath ("*salvini,*" *chionogaster*) show that increase of pigmentation is not the only phenomenon of plumage change in tropical mountain forests. A large amount of individual variation in the intensity of the pigmentation is also found in Africa in the *rufiventris* group of *A. nisus,* although not on the same scale as in South American *A. s. ventralis.*

The subspecies of *A. striatus* in the Greater Antilles are more closely similar to *A. s. erythronemius* than to any other race. It was noted above that *A. s. erythronemius* resembles the adult male plumage of *A. nisus.* Apparently similar color patterns occur in widely separate areas in the range of this species group. Hence the resemblance of the Antillean forms to *erythronemius* does not imply, of course, that the Antilles were colonized from South America. On the contrary, the existence of a cline in size and coloration of the tibial feathers in the Greater Antilles is an argument for supposing that these islands were reached by a single colonization from North America.

ACCIPITER BICOLOR (VIEILLOT)

DISTRIBUTION

South and Middle America (Map 16). The southern populations are migratory.

SUBSPECIES

cf. Hellmayr and Conover (1949). *A. b. fidens* Bangs and Noble, southern Mexico from central Veracruz to the Isthmus of Tehuantepec; *A. b. bicolor* (Vieillot), Middle America and northern South America from the Isthmus of Tehuantepec to Junín and Loreto, Peru, northwestern Bolivia (Niethammer, 1953) and probably southeastern Bolivia (Hellmayr and Conover, 1949), Amazonas and Pará, Brazil; *A. b. pileatus* (Temminck), Maranhão, northeastern Brazil, where it possibly intergrades with *bicolor,* south through eastern Brazil to Misiones, Argentina, eastern Paraguay, and (once) Uruguay (Cuello and Gerzenstein, 1962); *A. b. guttifer* Hellmayr, southeastern Bolivia, western Matto Grosso, western Paraguay, and northwestern Argentina; *A. b. chilensis* Philippi and Landbeck, southern Chile and Argentina and in winter north to northwestern Argentina and central Chile.

PLUMAGE

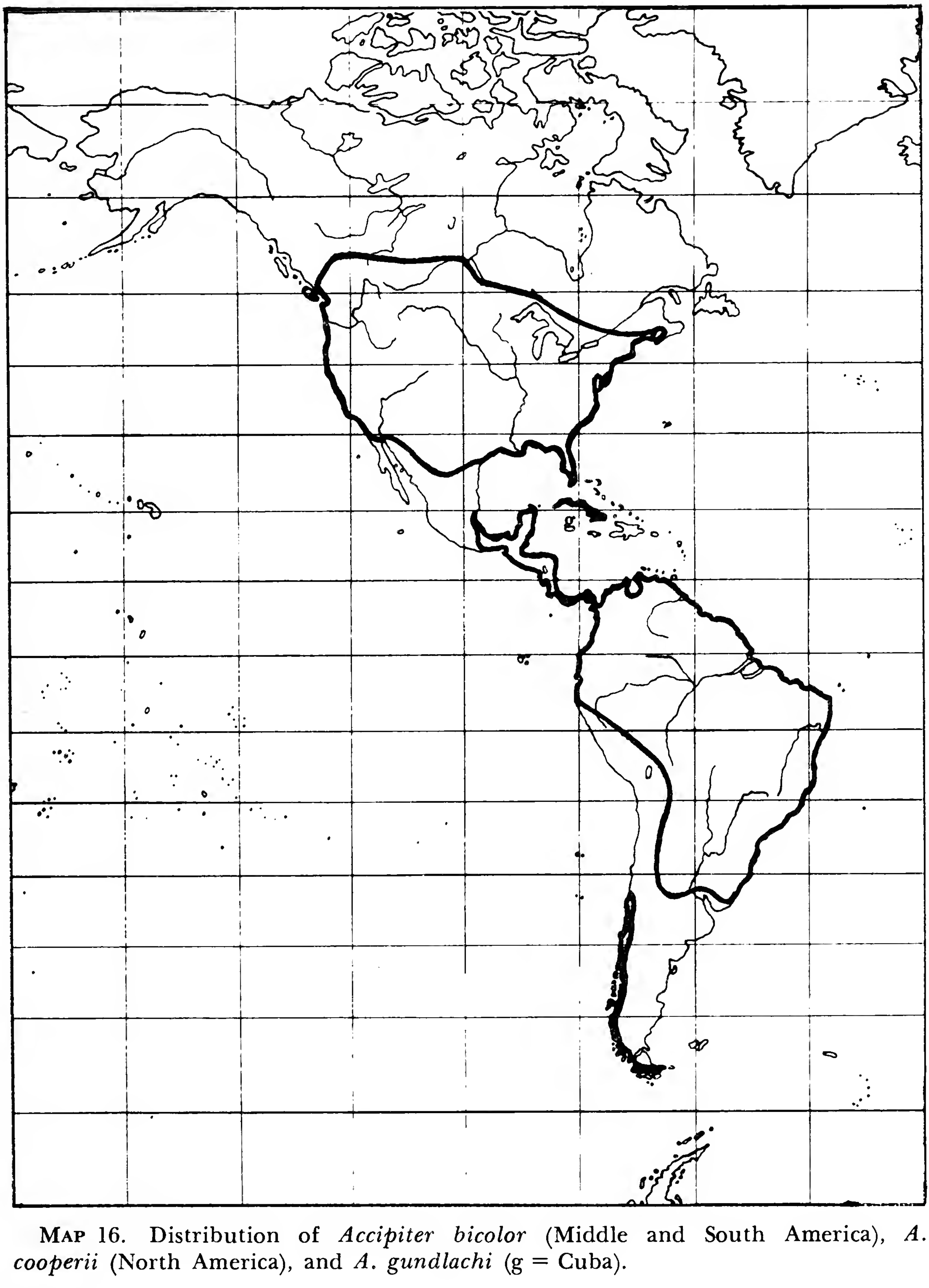
Adult.—Upperparts dark gray or blackish, crown darker than back. Underparts plain gray or mottled gray, rufous, and white, varying geographically. Thighs deep rufous. Tail with a few inconspicuous dark bars.

Juvenile.—Dorsum dark brown with indistinct tawny or cream feather edges and a light nuchal collar. Crown darker than back. Underparts cream to light tawny with a geographically variable pattern of brown streaks or drops. Tail dark brown with wide light brown or almost white bars.

GEOGRAPHICAL VARIATION

Geographical variation is seen in color, in the pattern of the underparts, and in general structure. The races *fidens, bicolor,* and *pileatus* are plain underneath in adult plumage while *guttifer* and *chilensis* are mottled or barred.

A. b. bicolor.—Adult: underparts very pale to rather dark gray. Underwing coverts white or pale tawny. The dark gray variant was



Map 16. Distribution of *Accipiter bicolor* (Middle and South America), *A. cooperii* (North America), and *A. gundlachi* (g = Cuba).

named *schistochlamys* (Hellmayr, 1906), but the occurrence of dark specimens has been found not to be geographically restricted.

Juvenile: underparts plain, white to tawny; thighs more or less strongly marked with dark spots.

The subspecies *fidens* differs from nominate *bicolor* only by averaging slightly larger (Amadon, 1964). *A. b. pileatus* differs in adult plumage by the bright rufous underwing coverts, whereas the juvenile is marked ventrally with dark streaks, and is lighter above and with a wider nuchal collar.

A. b. chilensis.—Adult: underparts barred or mottled white, gray, and rufous, the gray usually dominating, although in some specimens rufous pigments are much in evidence. In these rufous birds the bars consist of two narrow dark gray lines on either side of a wider rufous line, but usually the rufous color is concentrated in drops near the shaft at the tip of the feathers. In some specimens rufous and gray pigments form broad shaft streaks, reducing the white bars to white spots.

Juvenile: tawny white ventrally with dark brown streaks. Thighs broadly barred brown.

A. bicolor guttifer.—Adult: underparts exceedingly variable, ranging from plain gray with inconspicuous white spots, similar to *pileatus,* to a pattern which resembles *chilensis.*

The variant plumages can be grouped into four types: 1. Underparts gray with a faint rufous wash or small white spots or both. 2. Throat and upperbreast plain gray or gray barred rufous; rest of underside either gray heavily washed or mottled rufous, or wholly uniform rufous. 3. Underparts barred rufous and white, with or without a few gray tinges, particularly on the throat or the upper breast. This type can be considered as "typical" *guttifer.* 4. Underparts barred and mottled white, gray, and rufous in almost equal proportions, resembling rufous specimens of *chilensis.*

These types are linked by a series of specimens showing all possible intermediate stages.

Juvenile: underparts cream or pale tawny less heavily spotted or streaked than *chilensis,* being closely similar to juvenile *pileatus.*

Size and Structure

Size medium to rather large. Tarsus and toes long and heavy. Claws heavy. Bill moderate. Wing short to medium and rounded. Tail medium to long. Figure 14. Tables 45 and 46.

On account of their general similarity in structure and their alleged relationship (Amadon, 1964; Bond, 1965), the data for *A. cooperii* were analysed simultaneously with those of *A. bicolor.* The statistical model was unsatisfactory for the tail. The difference between the various forms (including *cooperii*) is significant for all series of data that could be analysed. The difference between the sexes is significant for the middle toe (shorter in male), hind claw (smaller in male), bill (smaller in male), and wt–6 (longer in male).

Bill and foot.—These are of the *bicolor*-type.

Wing and tail.—These structures are of the *bicolor*-type. The wing tip shows a clinal increase in length in the series *bicolor-pileatus-guttifer-chilensis.* The tail is longer in *chilensis* than in the other subspecies.

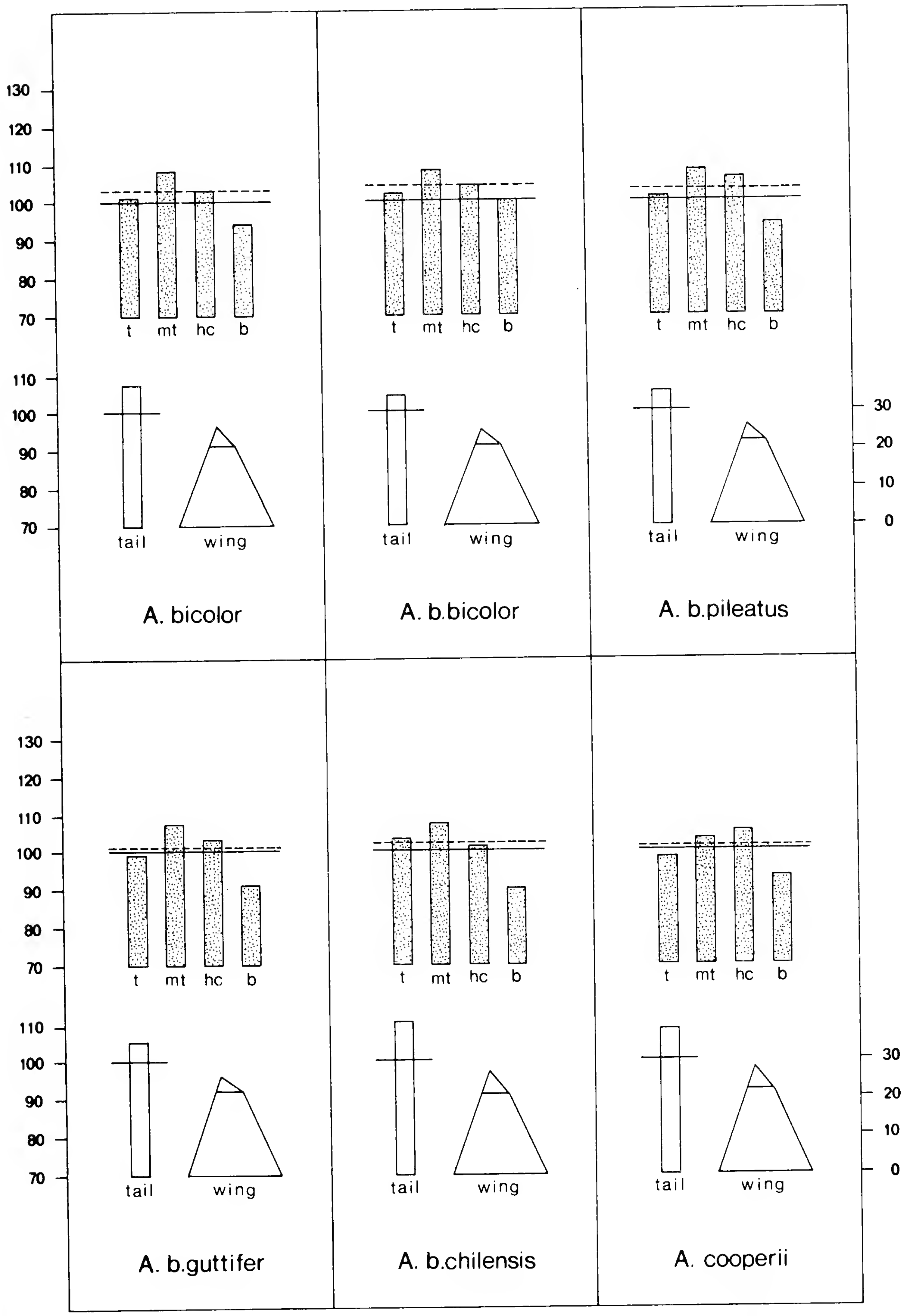


FIG. 14. Structure of *Accipiter bicolor* and *A. cooperii.*

HABITAT

Inhabits forest edges, stands of trees in savannas, scrub, open deciduous woodland, dense gallery forest, second-growth, patches of native

TABLE 45
WING LENGTH IN *Accipiter bicolor* AND *A. cooperii.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
bicolor	206.7	2.55	1.47	204 - 209	3
pileatus	208.5	3.63	1.28	203 - 213	8
guttifer	207.2	3.91	1.29	202 - 215	10
chilensis	209.6	1.90	0.47	207 - 213	16
cooperii	233.2	5.87	1.96	229 - 247	9
			♀		
bicolor	240.0	6.69	3.34	231 - 247	4
pileatus	246.0	6.75	2.76	233 - 251	6
guttifer	248.7	3.74	1.41	244 - 254	7
chilensis	243.2	3.25	0.90	238 - 249	13
cooperii	262.4	7.88	2.63	252 - 272	9
				Total	85

cultivation, plantations, woodland villages, and tropical rainforest. In extensive forest occurs mostly near clearings and water. *A. bicolor* seems to be scarce in the Amazonian rainforest. The vegetation of the habitat varies enormously, ranging from the tropical jungle on the Pacific coast of Colombia and Ecuador to the cold *Nothofagus antarctica* forest of southern Chile and Tierra del Fuego. In the lowlands of Costa Rica it is found high in the understory and in the middle heights of the woodland, nearly always remaining in the shade (Slud,

TABLE 46
RELATIVE MEASUREMENTS IN PERCENT OF WING LENGTH IN
Accipiter bicolor AND *A. cooperii.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	27.25	17.05	8.50	6.96	80.84	26.45	4.81
bicolor	27.55	17.21	8.50	7.43	79.62	24.52	3.21
pileatus	27.40	17.25	8.69	7.02	79.49	25.76	3.86
guttifer	26.74	17.17	8.43	6.78	79.90	26.14	4.51
chilensis	27.94	17.15	8.31	6.65	82.88	27.39	6.29
cooperii	26.63	16.47	8.57	6.94	82.41	28.44	6.17
♂	+0.08	-0.42	-0.29	-0.12	+0.37	+0.42	+0.44
♀	-0.08	+0.42	+0.29	+0.12	-0.37	-0.42	-0.44
Adult	-0.16	-0.07	0	-0.03	-1.63	+0.23	-0.37
Juvenile	+0.16	+0.07	0	+0.03	+1.63	-0.23	+0.37
P model	0.183	0.085	0.082	0.306	0.002	0.491	0.496
P ssp	0.001	0.008	0.012	0	-	0	0
P sex	0.201	0	0	0.006	-	0.081	0.036
n	82	75	82	79	82	82	84
df	62	56	62	59	62	62	65

1960). In more open country the bird may perch high in a tree in order to command a good view of its surroundings.

A. bicolor inhabits a wide altitudinal range, occurring from sea level to over 2,000 m which is well up into the subtropical zone. Some of the highest localities on record are 1,830 m in Ecuador (Chapman, 1926), 2,290 m in Bolivia (Bond and de Schauensee, 1943), 2,500 m in Mérida, Venezuela (Swann, 1921), and 2,745 m in Peru (Taczanowski, 1884).

HUNTING BEHAVIOR

Mainly a still-hunter. Frequently recorded as sitting at some vantage point and then swooping suddenly on its quarry. It flies rapidly and skillfully and may chase songbirds over some distance. The behavior reminded Taczanowski (1884) of *A. nisus.*

FOOD

Its principal diet is birds, mainly of thrush-size, and small mammals and large insects. *A. b. chilensis* is said to take pigeons, *Columba araucana* (Johnson, 1965).

DISCUSSION

A. bicolor resembles *A. cooperii* and *A. melanoleucus* in the structure of its bill and feet, and like them also subsists primarily on middle-sized birds. From tropical to temperate regions the relative size of the bill decreases and the length of the wing tip increases. This is also found in several other species (e.g., *A. striatus*). At least in the race *chilensis* the longer wing tip may be related to the migratory habit.

A series of color-types of the subspecies *guttifer* was described previously (p. 118). The geographical distribution of these types is notable. It is summarized in Table 47, based partly on data from various literature sources, and partly on specimens studied in the course of the present investigation.

Type 3 is the most distinctly barred and at the same time the least gray variant. It is most strongly represented in the populations of the northern Gran Chaco. Types 1 and 2 differ from Type 3 by an increase of gray pigments and a reduction of the barred pattern. They can be regarded as intermediate between Type 3 and *A. b. pileatus.* Type 4 is intermediate between Type 3 and *A. b. chilensis,* but from the fact that *A. b. chilensis* is entirely isolated in the subantarctic *Nothofagus* forests, which have developed in isolation over a considerable period (Vuilleumier, 1967) and from the apparent absence of this type in Tucumán, which is closest to the range of *chilensis,* it is more likely that the resemblance to *A. b. chilensis* is purely coincidental rather than an indication of recent geographical contact between *A. b. guttifer* and *A. b. pileatus.* As Type 4 differs from Type 3 by an increase of gray pigments it may also be considered to be an intermediate between Type 3 and *A. b. pileatus.*

TABLE 47
DISTRIBUTION OF COLOR TYPE IN ADULT *A. bicolor* ACCORDING TO NUMBER OF SPECIMENS EXAMINED.

REGION	COLOUR - TYPE						
	pileatus	1	2	3	4	chilensis	total
Misiones	4	3					7
East Paraguay	2	1					3
West Paraguay		1	2	6	2		11
South-East Bolivia			2	6	2		10
Formosa and Chaco				1	1		2
Jujuy and Salta	1	1	2	1	1		6
Tucuman		6					6
South Argentina and Chile					2[1]	3	5
Total	7	12	6	14	8	3	50

---

1) rufous type of chilensis.

From Table 47 it is clear that intermediate types are found almost everywhere in the range of *A. b. guttifer* (southeastern Bolivia, western Paraguay). The presence of specimens within the range of *guttifer* similar to *A. b. pileatus* caused several authors to consider *guttifer* as a separate species. Conover (1946) demonstrated that the alleged overlap in range is due to the wide individual variability of *guttifer*. In my opinion this variability is the result of interbreeding between *pileatus* and *guttifer*.

The fact that the population of Tucumán belongs to Type 1, being closely similar to *pileatus* indicates that *guttifer* was originally restricted to the region of northern Gran Chaco. When the southern Chaco was colonized, *pileatus* extended west to the Andes, whereas *guttifer* penetrated from the north. The extremely wide individual variation in Jujuy and Salta suggests that there the influence of *guttifer* balances that of *pileatus*. Farther north *guttifer* dominates, to the south *pileatus* is more common.

It is difficult to imagine how *guttifer* was originally isolated in a relatively small area in central South America. Probably this isolation was effected by the Pleistocene transgression of the Rio de la Plata and its tributaries. The subspecies *A. b. bicolor* and *pileatus* are apparently ecologically separated, nominated *bicolor* being the form of the rainforest belt, *pileatus* occurring in the dryer forest types and the savannas of eastern Brazil.

As regards color pattern *A. bicolor* of the South American tropics shows an interesting parallel with *A. tachiro*, widely distributed in Africa. In both species the juvenile plumage of the forms of savanna woodland and open forest have spotted underparts, whereas the forms of the tropical rainforest are white or cream-colored. In the adult plumage the rainforest forms (*bicolor* and *toussenelii/canescens,* respectively) are plain, the remaining forms barred below. This implies that plain underparts were acquired secondarily as an adaptation to the habitat and that the ancestral form of *A. bicolor* was barred. Thus it is not surprising that the southern as well as the northern relatives of *A. b. bicolor* (the races *guttifer* and *chilensis,* and *A. cooperii*) are all barred and resemble each other more than any of them resembles *bicolor.*

ACCIPITER COOPERII (BONAPARTE)

DISTRIBUTION

Temperate North America (Map 16, p. 117).

Migratory, wintering in the southern parts of its breeding range, in Mexico, and in Central America south to Costa Rica. Once recorded from Colombia.

PLUMAGE

Adult male.—Crown blackish brown separated from dark blue-gray back by a faint, light nuchal collar. Underparts white, barred and streaked rufous or cinnamon, closely resembling *A. striatus velox* in pattern. Thighs rufous with narrow white bars. Throat with fine black shaft streaks. Sides of face rufous or cream with dark brown shaft streaks. Tail gray or brownish with wide dark bars.

Adult female.—Tinge of dorsum browner than in male.

Juvenile.—Upperparts brown with feathers edged with cinnamon and a light nuchal patch. Underparts cream with dark brown streaks. Thighs variously patterned with light brown darts, diamonds, or bars. Tail light brown with wide dark bars.

A. cooperii resembles *A. striatus velox* in adult and juvenile plumage. Adults of *cooperii* are lighter on the back than *velox,* whereas *velox* lacks the contrasting dark crown. In juvenile *cooperii* the crown and interscapulary region show more pronounced light feather edges than in *velox.* The pattern of the underparts is simpler, consisting only of dark streaks, much reduced on the abdomen. In *velox* the pattern of the abdomen is rather complex. In addition, the tail of *cooperii* is wedge-shaped while that of *velox* is square. In these characters *A. cooperii* approaches *A. bicolor* rather than *A. striatus.* Adult *A. cooperii* moreover resembles *A. bicolor guttifer,* which may be similarly marked below with cinnamon-rufous and white.

SIZE AND STRUCTURE

Size medium to large. Tarsus and toes long and heavy. Claws heavy. Bill moderate. Wing medium and rounded. Tail very long and graduated. Figure 14, p. 119. Tables 45 and 46, p. 120.

For statistical analysis the data were combined with *A. bicolor* (p. 118).

Bill and foot.—These are of the *bicolor*-type. The middle toe is relatively shorter than in *A. bicolor.*

Wing and tail.—Similar to those of *bicolor*. Wing is longer than in *A. b. bicolor*. In this respect *A. cooperii* approaches the *nisus*-type. In general structure *A. cooperii* is closely similar to *A. bicolor chilensis*.

HABITAT

An inhabitant of various types of mixed and deciduous forest and open woodland, chiefly in Transition and Upper Sonoran life zones (Grinnell and Miller, 1944), more rarely in the Canadian or Lower Sonoran zones. Small woodlots amidst arable land, riparian growth in dry country, river floodplains in the Rocky Mountains, open arid piñon woodland (Johnson, Bryant, and Miller, 1948), and pine-oak woodland (Marshall, 1957). In large forests *A. cooperii* is found near clearings or roads, along rivers, brooks, or lakes, and at the forest edge. In winter it occurs in any type of parkland where trees or scrub afford sufficient shelter, even in pronouncedly arid regions.

A. cooperii ranges from about sea level up to 1,100 m in the Allegheny Mountains (Mengel, 1965), to 2,150 m in California (Johnson, Bryant, and Miller, 1948), to 2,500 m in Coahuila, Mexico (Miller, 1955), and even to nearly 2,700 m in the White Mountains of Arizona (Phillips, Marshall, and Monson, 1964).

HUNTING BEHAVIOR

Hunts in a fashion like that of *A. striatus velox* and *A. nisus*. *A. cooperii* practises still-hunting and has also a characteristic searching flight along fences or through scrub, remaining concealed as long as possible and taking its prey by surprise (see, also, Bent, 1937). It may chase its quarry with persistence and agility through wood or scrub, dashing into dense growth and sometimes driving it from bush to bush until it is exhausted (Smith, 1963). Occasionally small animals are pursued on foot. On rare occasions *A. cooperii* catches birds in mid-air, stooping like a Peregrine Falcon (Mead, 1963).

Leopold (1944) vividly describes the pursuit of a bat over a creek ". . . the bat (twisting) to the right and left with the hawk following every turn. As they passed 50 feet in front of us, the hawk tipped back on its fanned tail, reached an incredible distance forward with both feet, and gracefully picked the bat out of the air. With scarcely a flutter the bird recovered normal flying posture. . . ."

FOOD

Its diet consists predominantly of middle-sized birds, such as thrushes, starlings, jays, quail, flickers, and woodpeckers. Also smaller birds such as sparrows and some larger ones, for example, pigeons, game birds, teal, and the young of other ducks, small owls, and hawks. In addition mammals, mainly squirrels and chipmunks, occasionally also lizards, frogs, and insects, and exceptionally fish from nearly dry watercourses. To a large extent young hawks are fed nestlings and fledglings. In agricultural districts *A. cooperii* is reported to take half-grown poultry, but not so frequently as to deserve the name of farmyard pest, as in the older literature (Meng, 1959). Formerly the Passenger Pigeon was regularly taken (Schorger, 1955). The upper limit of the predation potential lies at half-grown hares, rabbits, and adult ruffed grouse. A summary of the food is given in Table 48.

In comparison to *A. striatus,* on the average *A. cooperii* takes larger birds and proportionally more mammals, lizards, and insects. Storer (1966) calculated the average weight of prey taken by male *A. cooperii* to be 37.6 gms; by the female 50.7 gms. These data pertain mostly to birds shot on migration or in winter.

TABLE 48

Prey of *Accipiter cooperii,* collected at nests. I = Grinnell and Swarth (1913), southern California. II = Errington (1933), southern Wisconsin. III = Fitch, Glading and House (1946), southern California. IV = Hamerstrom and Hamerstrom (1951), southern Michigan. V = Meng (1959), New York State.

	Number of prey items					
	I	II	III	IV	V	Total
Small birds (Warblers, Sparrows, etc.)		19	3	41	15	78
American Robin		4		12	79	95
European Starling				18	241	259
Meadowlark		1		4	118	123
Jays	1	3		16	11	31
Woodpeckers, Flickers, and Cuckoos	3	24	2	22	142	193
Other middle-sized birds				52	70	122
Total middle-sized birds	4	32	2	124	661	823
Pigeons		2		12	18	32
Poultry and game birds		6	5	17	4	32
Unidentified birds				27		27
Total birds	4	59	10	221	698	992
Chipmunks	1	1		24	109	135
Squirrels and Ground Squirrels		7		8	40	55
Mice and Lemmings				3		3
Rabbits			2	1	6	9
Other and unidentified mammals				5		5
Total mammals	1	8	2	41	155	207
Lizards			26			26
Total	5	67	38	262	853	1225

DISCUSSION

A. cooperii is intermediate between *A. gentilis* and *A. striatus* in size, structure of the bill and feet, and choice of prey (Fig. 15). The wing is shorter and more rounded than in *striatus* or *gentilis*.

In structure and plumage *A. cooperii* resembles the southern races of *A. bicolor*. On account of this morphological similarity Stresemann (1924a) considered *bicolor* and *cooperii* as close relatives. Amadon (1964) included *A. cooperii* in a superspecies comprising also *A. bicolor* and *A. gundlachi*. In North America *A. cooperii* is an element of more

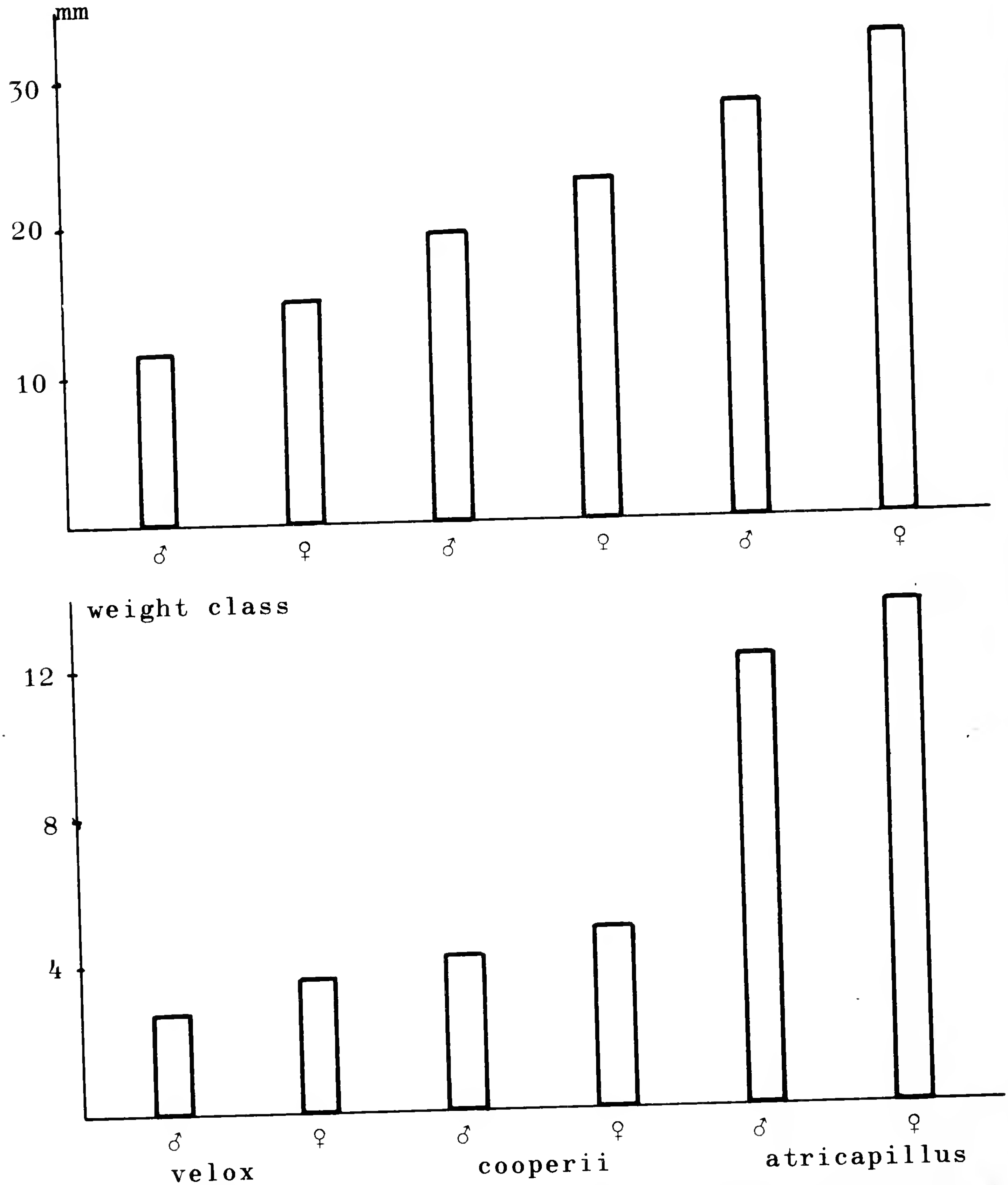


FIG. 15. Upper row: average size of hind claw in *Accipiter striatus velox, A. cooperii,* and *A. gentilis atricapillus*. Lower row: average weight of prey for the same species (in weight classes according to Storer, 1966, Table 2).

southerly life zones than *A. striatus velox*. This is in agreement with a postulated southern origin of *A. cooperii*. A hypothesis concerning the geographical origin of *bicolor, cooperii,* and *gundlachi* will be given in the discussion of *A. gundlachi*.

In adult plumage *A. cooperii* is exceedingly similar to *A. striatus velox*. Here we meet an instance of the very peculiar and puzzling phenomenon that sympatric species of *Accipiter* are similar in color pattern. This phenomenon is also found in *A. henstii* and *A. madagascariensis* in Madagascar, in *A. trinotatus, A. rhodogaster,* and *A. nanus* in Celebes, and in *A. fasciatus* and *A. cirrhocephalus* in Australia.

ACCIPITER GUNDLACHI LAWRENCE

DISTRIBUTION

Cuba (Map 16, p. 117).

This species is very scarce in collections and was thought to be on the verge of extinction. Although certainly not numerous, it has been observed recently, collected in several localities, and appears to be widespread (Bond, 1968).

PLUMAGE

Adult male.—Crown black, remainder of upperparts bluish gray. Chest ashy gray, lower breast and upper abdomen rufous. Flanks gray, more rufous near thighs. Thighs pale rufous, feathers narrowly tipped white. Tail gray with broad dark brown bars (see, Lawrence, 1860; Conover, 1946; Friedmann, 1950).

Adult female.—Above more brownish than male. Chest light gray, lower breast and abdomen spotted and barred white and cinnamon-rufous. Thighs barred (Conover, 1946). A specimen from the U.S. National Museum (No. 117,752; Guantanamo, Feb. 1889) has the throat heavily streaked dusky and the breast and abdomen marked with numerous broad rufous-brown streaks. It has been described by Friedmann (1950) as an adult female, but appears to be an immature bird, retaining part of its juvenile feathers.

Juvenile.—Upperparts dark brown with narrow dark rufous feather edges. Crown darker than back. Underparts cream, heavily streaked dark or rufous brown. Flanks with bars of the same tinge and thighs with diamond spots. The color of the markings is strongly variable. Tail light brown with wide dark brown bars.

SIZE AND STRUCTURE

Size rather large to large. Tarsus and toes long and heavy. Claws very heavy. Bill heavy. Wing medium and rounded. Tail very long. Figure 13, p. 94. Tables 40 and 41, p. 103.

No statistical analysis made. Very few specimens were examined.

Bill and foot.—Very heavy and aberrant, somewhat resembling the *cooperii*-type, but with exceptionally large hind claw. The middle toe is very long in comparison to the tarsus. A more or less similar structure is found in *A. buergersi,* but in that species the tarsus is relatively shorter and the hind claw less impressive.

Wing and tail.—These are of the *bicolor*-type. Resemble *A. bicolor chilensis* and *A. cooperii.*

Habitat, Hunting Behavior, and Food

Inhabits lowland and mountain forest. Gundlach (1871; cf., also, Gundlach's letters, *in* Lawrence, 1860) found a nest in a high tree near a large marsh, with the adult birds hunting in treeless country nearby. "Its flight is rapid and almost in a direct line, never having seen it describe circles, nor does it mount to any considerable height, and is so daring that it seizes young chickens in the farm-yard under the eyes of the husbandman. . . ." In chasing pigeons it ventured quite near houses and even into an open stable. All reports point to a typical sparrow hawk behavior. *A. gundlachi* is apparently very elusive. This may indicate that it also practises still-hunting. Its prey consists of rather large birds. Gundlach observed it chasing pigeons and quail (*Colinus virginianus*).

Discussion

As far as is known the ecology of *A. gundlachi* appears to be similar to that of *A. bicolor* and *A. cooperii.* The presence of extremely heavy claws is noteworthy. Though *A. gundlachi* is smaller than *A. gentilis,* its claws are about as large. As *A. gentilis* is absent from Cuba, it may be surmised that to a certain extent *A. gundlachi* fills the niche of a large goshawk. Probably on the average it takes heavier prey than *A. bicolor* and *A. cooperii.*

Morphologically, ecologically, and geographically *A. gundlachi* belongs to the species group of *A. bicolor.* In plumage it is most similar to Type 2 of *A. bicolor guttifer* (p. 118). A similar resemblance of an Antillean form to one of southern South America is also found in *A. striatus.* As in that species, the resemblance of *gundlachi* to *A. bicolor guttifer* does not imply that these two forms are more closely related to each other than to other forms of their groups, since similar color patterns may arise in different regions within the range of a group of related forms.

A. gundlachi has developed several aberrant characters. This may be interpreted to mean that it has been isolated for a comparatively long period and that Cuba was probably colonized by one of the *bicolor* group early in the Pleistocene. It appears futile to discuss the question whether *A. gundlachi* is more closely related to *A. cooperii* or to *A. bicolor.* All three species have developed from a common stock of tropical American Accipiters.

Taxonomically this group appears to be rather isolated, although less so than *A. poliogaster* and *A. superciliosus.* Tentatively I would venture the hypothesis that it is related to *A. nisus,* on account of a general similarity in ecology. Its ancestors may have belonged to a Holarctic group of species from which originated the *nisus* group in the Palearctic and *bicolor* group in the Nearctic. Subsequently the Nearctic group colonized South America and the Greater Antilles and differentiated into several forms. Possibly early Pleistocene glaciations contributed toward shifting the center of its distribution to the south. At a more recent date the *nisus* group invaded North America, developing into *A. striatus,* which is much more clearly related to *A. nisus* than is *A. bicolor.*

ECOLOGICAL GEOGRAPHY IN NORTH AND SOUTH AMERICA

In North America there is a series of vegetation zones similar to those found in Europe and Asia, but the composition of the Accipiter fauna is rather different. A large goshawk (*A. gentilis*) is present, living in the northern coniferous forest belt alongside a small sparrow hawk (*A. striatus*), exactly as *A. gentilis* and *A. nisus* do in the Palearctic. Unlike the situation in Europe, however, a second and larger *nisus*-like bird-catching species (*A. cooperii*) occupies the more southerly forest zones. During the breeding season *A. striatus* is apparently scarce in the regions where *A. cooperii* is numerous, but in winter many *A. striatus* migrate to the USA and farther south, joining the resident populations of *A. striatus.* Lacking in America is a species of arid savanna country, comparable to *A. badius* and its allies. Thus Accipiters are very sparsely distributed on the wide grassy plains east of the Rocky Mountains and in the southwestern subdeserts, being confined to occasional woodlots or trees fringing water.

The South American Accipiter fauna may be compared with that of Africa, as has been done in Table 49. Apparently it is less diversified ecologically, due to the absence of *badius*-like forms and to the scarcity of tropical goshawks. In Africa, *A. tachiro* is a much more important member of the Accipiter community than *A. poliogaster* is in South America. On the other hand, *A. bicolor* and *A. striatus* seem to be more tolerant of varying habitat conditions than either *A. melanoleucus* or the African forms of *A. nisus.* It may be surmised that in Africa *A. nisus* could not spread into woodland, savanna, and steppe because these habitats were already occupied by *A. ovampensis* and *A. minullus,* whereas when colonizing South America *A. striatus* did not encounter ecologically similar species in the woodlands of southern Brazil. *A. bicolor* inhabits a wider range of habitats than *A. melanoleucus* as it penetrates south to the cold rainswept subantarctic forests, a habitat that is unknown in Africa.

Zoogeographically the American Accipiters fall into two categories: endemic South American species on the one hand and species of Holarctic origin on the other. The *A. bicolor* group may be more or less intermediate, being at present clearly an American element, but probably having originated as an offshoot of the Holarctic group of long-toed bird-catching species.

TABLE 49
Ecological counterparts among African and South American Accipiters.

African species	Ecologically to be compared with:
tachiro (toussenelii-group)	poliogaster
tachiro (tachiro-group)	-
castanilius	-
badius	-
minullus (erythropus-group)	superciliosus
-	collaris
minullus (minullus-group)	striatus erythronemius
ovampensis	-
nisus	striatus ventralis
melanoleucus	bicolor

A. poliogaster, A. superciliosus, and *A. collaris* are ancient South American forms without close relatives in other parts of the world. *A. striatus* probably may be considered to be an early Pleistocene colonist from the Palearctic group of *A. nisus.* Its antiquity in America is indicated by its penetration into South America and by its splitting into several well-defined subspecies. A more recent element in the North America fauna is *A. gentilis.* This species has reached no farther than the boreal forests and the mountains of western North America; geographical variation is slight and the American subspecies are still similar to those of the Palearctic.

Neither *A. virgatus* nor the *A. badius* group ever reached the New World. These groups have a more southerly distribution than *A. nisus* and *A. gentilis.* Apparently only groups with a boreal distribution succeeded in reaching North America during the Pleistocene. This is in accordance with the assumption that Palearctic elements invaded the Nearctic by way of the Bering Sea. In the course of the Pleistocene period this region never had a climate mild enough to permit the passage of warmth-adapted species.

VI

AUSTRALASIA

INTRODUCTION

Sixteen species of *Accipiter* are confined to Australasia, the region from the Moluccas and Lesser Sunda Islands in the west to Fiji and New Caledonia in the east. These sixteen species are listed in Table 50 and will be considered in the present chapter. In addition to these, *A. soloensis* is recorded as a winter visitor as far east as western New Guinea, whereas on Flores a small population of another species, *A. virgatus,* probably breeds in the mountains.

ACCIPITER FASCIATUS (VIGORS AND HORSFIELD)

DISTRIBUTION

Australia and islands to the north and northeast; Christmas Island, Indian Ocean (Map 17).

In Australia the species is apparently more or less migratory. Birds from the southern parts of the continent have been collected in the north, particularly in Western Australia (Condon and Amadon, 1954). An old specimen from Timor in the Leyden Museum belongs to the Australian subspecies nominate *fasciatus,* so it is not impossible that wandering birds sometimes leave the Australian continent.

SUBSPECIES

cf. Stresemann (1925), Peters (1931), Rensch (1931), Mayr (1941b), Rand (1941), Condon and Amadon (1954), and Mayr (1957). *A. f. fasciatus* (Vigors and Horsfield), Australia except northern coastal districts, Tasmania, islands of Rennell and Bellona; *A. f. vigilax* (Wetmore), New Caledonia, Loyalty Islands, Aneiteum (New Hebrides); *A. f. didimus* (Mathews), northern coastal districts of Australia; *A. f. dogwa* Rand, southern New Guinea; *A. f. polycryptus* Rothschild and Hartert, eastern and southeastern New Guinea; *A. f. buruensis* Stresemann, Buru Island, Moluccas; *A. f. wallacii* (Sharpe), northern chain of Lesser Sunda Islands; *A. f. stresemanni* Rensch, islands between the Lesser Sunda Islands and Celebes (probably also population of the Tukangbesi Islands); *A. f. hellmayri* Stresemann, islands of Timor, Semau, and Roti; *A. f. savu* Mayr, Savu Island, between Timor and Sumba; *A. f. tjendanae* Stresemann, Sumba Island; *A. f. natalis* (Lister), Christmas Island, Indian Ocean.

TABLE 50

Species of *Accipiter* in Australasia.

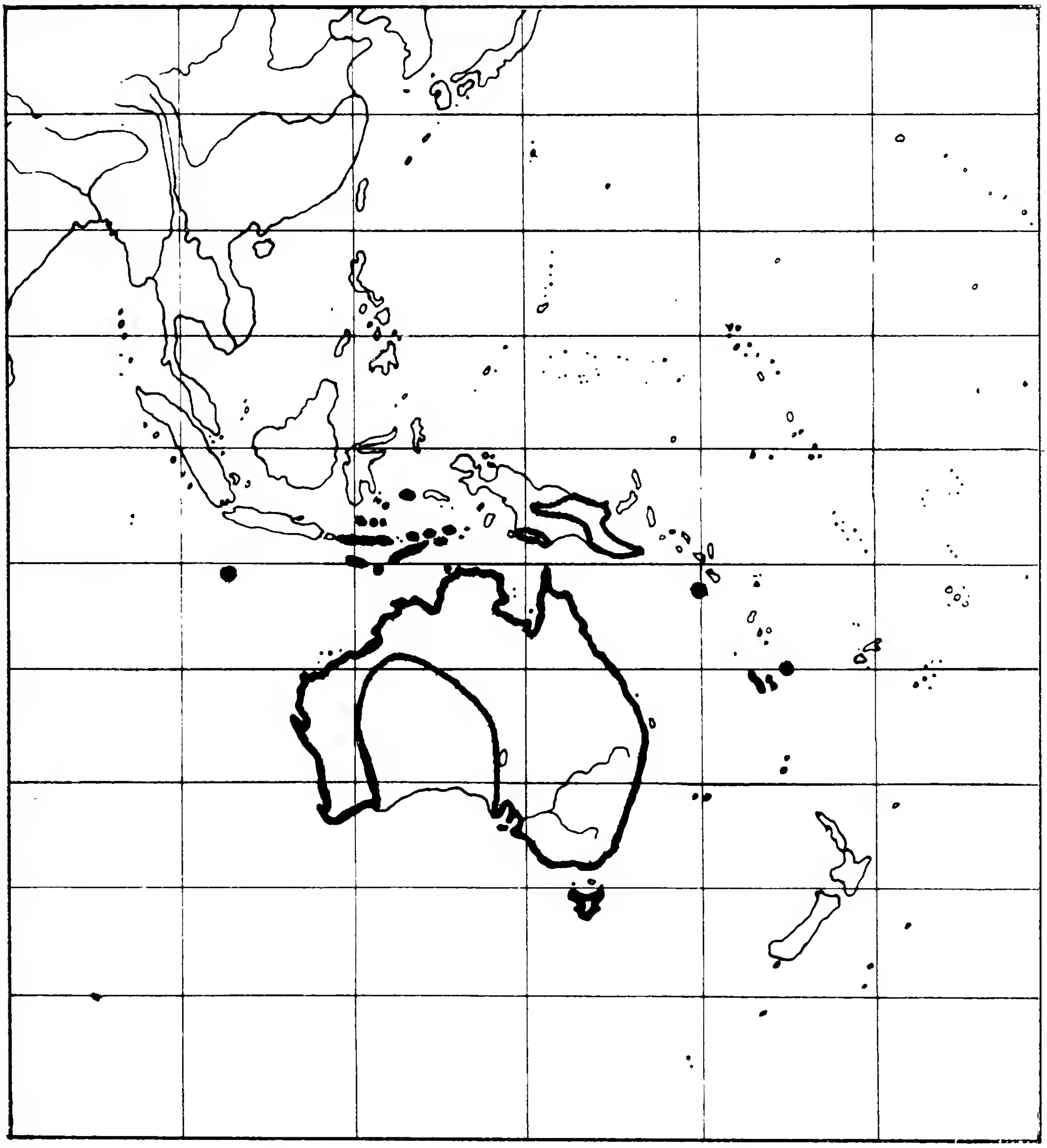
SPECIES	DISTRIBUTION
Accipiter fasciatus	Australia, New Caledonia, Lesser Sunda Islands
Accipiter novaehollandiae	Australia, New Guinea, Moluccas, Melanesia
Accipiter melanochlamys	New Guinea
Accipiter albogularis	Solomon Islands
Accipiter rufitorques	Fiji Islands
Accipiter haplochrous	New Caledonia
Accipiter henicogrammus	Northern Moluccas
Accipiter luteoschistaceus	New Britain
Accipiter imitator	Choiseul and Ysabel, Solomon Islands
Accipiter poliocephalus	New Guinea
Accipiter princeps	New Britain
Accipiter virgatus	South East Asia and East Palearctic (in Australasia: Flores)
Accipiter cirrhocephalus	Australia and New Guinea
Accipiter brachyurus	New Britain
Accipiter erythrauchen	Moluccas
Accipiter meyerianus	Moluccas and Northern Melanesia
Accipiter buergersi	New Guinea

PLUMAGE

Adult.—Upperparts dark gray-brown with a more or less distinct rufous nuchal collar. Venter barred rufous-gray and white, each dark bar consisting of two narrow gray lines with a wider rufous line between. In some forms the underparts are almost solidly rufous-brown with only faint gray bars. Throat gray or mottled gray and white. Tail plain gray-brown above, light gray with numerous indistinct dark bars below.

In Australian nominate *fasciatus,* and probably also in *buruensis* and *tjendanae* (Siebers, 1930), the acquisition of this plumage apparently requires several years. The juvenile plumage is succeeded by a "second year" plumage (Condon and Amadon, 1954), which differs from the adult by the browner upperparts without a collar, the wider and browner bars on the underside, and the more distinctly barred tail.

Juvenile.—Upperparts dark brown with edges of feathers light brown to cinnamon-rufous. Below cream, the breast marked with dark brown streaks, sharply contrasting with the irregular wide rufous-brown bars on the rest of the underside. Thighs buff with wavy light rufous-brown bars. Throat narrowly streaked dark brown. Dorsal side of tail smoky brown with numerous dark bars.



Map 17. Distribution of *Accipiter fasciatus.*

The Australian forms of *A. fasciatus* are strikingly similar to the corresponding forms of *A. cirrhocephalus,* but a "second year" plumage is unknown in *A. cirrhocephalus.* Apart from the points listed by Condon and Amadon (1954), the species differ in the relative length of the middle toe, which is 14.4% of wing in *A. f. fasciatus* (ranging from 13.7-15.6%) and 16.1% in *A. c. cirrhocephalus* (ranging from 15.3-16.9%), and in the shape of the tail. In *A. fasciatus* the tail is wedge-shaped, the outer rectrices being 1½-4 cm shorter than the central ones, whereas in *A. cirrhocephalus* it is square, all feathers being of nearly equal length.

Geographical Variation

A. fasciatus varies geographically in size (Table 51) and in the color of the underparts. *A. f. fasciatus* is the largest subspecies. The races inhabiting northern Australia and the islands to the north are considerably smaller, *hellmayri* of Timor being the smallest. The New Caledonian form, *vigilax,* is intermediate.

In the adult plumage the Australian nominate subspecies has dark bars on the underside. *A. f. vigilax* is closely similar to *fasciatus,* but in the other subspecies the bars have a more reddish tinge. These forms have also a more pronounced nuchal collar than in *fasciatus* and *vigilax.* The Sumba race *tjendanae* shows the closest resemblance to *fasciatus,* with ventral barring being pronounced and more brownish than in the other Lesser Sunda Island populations.

A. f. didimus of northern Australia differs from nominate *fasciatus* in having the bars of the underparts much lighter. The gray lines are lacking and the white interspaces are as wide as the rufous bars or even wider. Several races are similar to *didimus,* viz., *dogwa, buruensis* (Condon and Amadon, 1954), *hellmayri,* and *savu.* In *dogwa, hellmayri,* and *savu* the rufous barring on the lower abdomen, undertail coverts, and thighs is reduced, these parts being immaculate white in some specimens. The population of Timor (*hellmayri*) is greatly different from the population on the adjacent island of Sumba (*tjendanae*).

Different also is the race *wallacii* from the northern chain of Lesser Sunda Islands. In this form the rufous bars on the breast are much darker than in *hellmayri* and show a tendency to merge into a rufous-brown breast shield. The forms *stresemanni* (see Rensch, 1931) and *polycryptus* are similar. In contrast to the situation in *dogwa,* the rufous bars extend over the entire abdomen and the undertail coverts in *polycryptus* (Rothschild and Hartert, 1915; Stresemann, 1935). The difference between *dogwa* and *polycryptus* appears, therefore, to be parallel to the difference between *hellmayri* and *wallacii.*

In juvenile plumage the subspecies *vigilax* and *buruensis* are similar to nominate *fasciatus.* Most other forms have the upperparts lighter brown with narrower rufous feather edges, whereas the bars on the abdomen are lighter and more rufous brown. In *hellmayri* the rufous edges to the brown feathers are rather wide and the pattern on the underside is reduced.

A. f. natalis, of Christmas Island, has a plain rufous breast shield in adult plumage. In the juvenile the breast is heavily barred, not marked with drops as in the other forms. The rufous feather edges on the back are as wide as in *hellmayri* but the general aspect of the upperparts is much darker.

SIZE AND STRUCTURE

Size medium to very large. Tarsus long and heavy. Toes short and heavy. Claws and bill of medium size. Wing long and pointed, shorter and less pointed in *natalis.* Tail long, comparatively shorter in *natalis.* Figures 16 and 17. Tables 51 and 52.

For the purpose of statistical analysis the forms *didimus, dogwa,* and

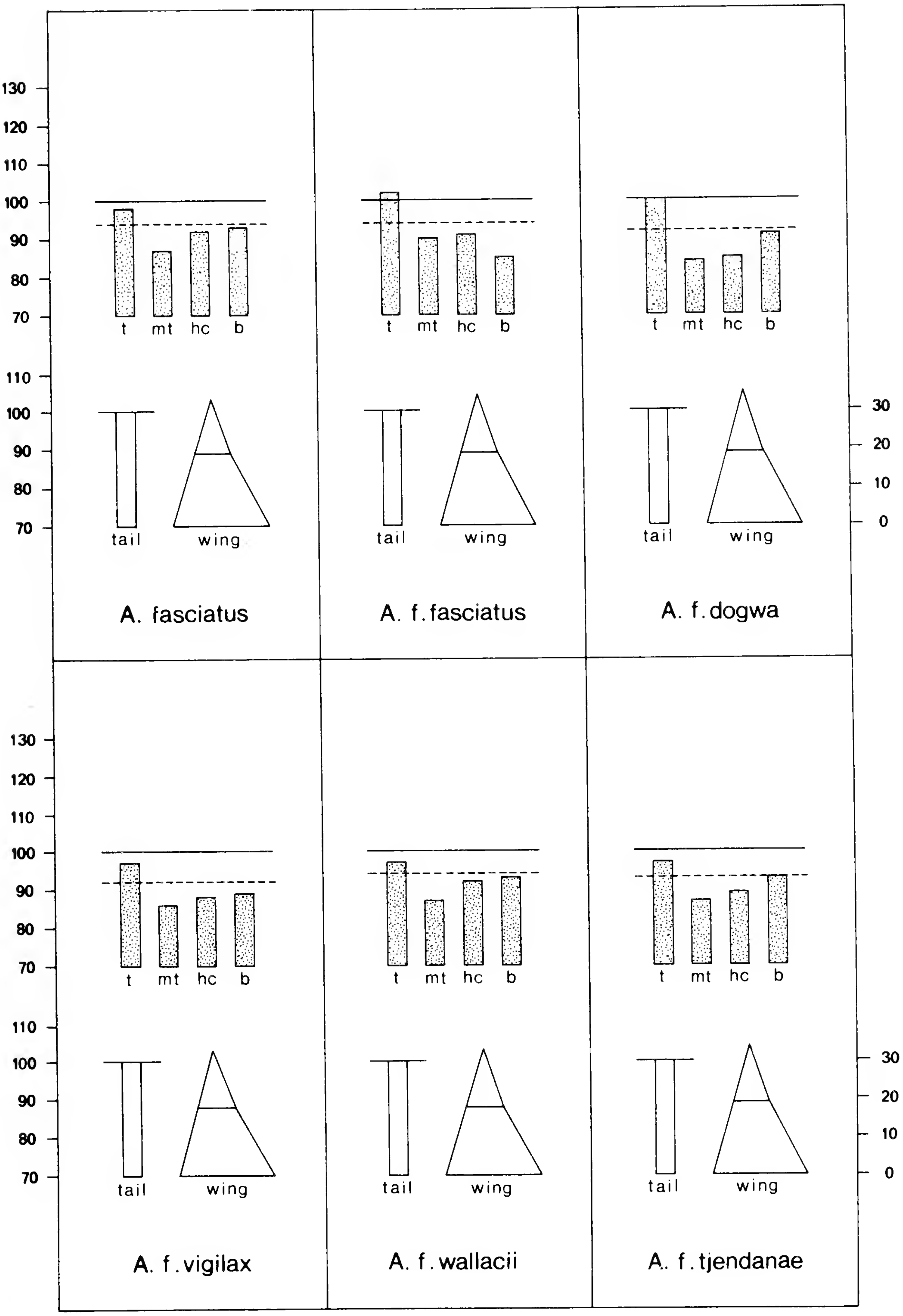


FIG. 16. Structure of *Accipiter fasciatus*.

polycryptus were grouped together. *A. f. buruensis* was excluded from the analysis because too few data were available. Only the hind claw, bill, tail, and wing tip were analysed in *hellmayri*. The difference be-

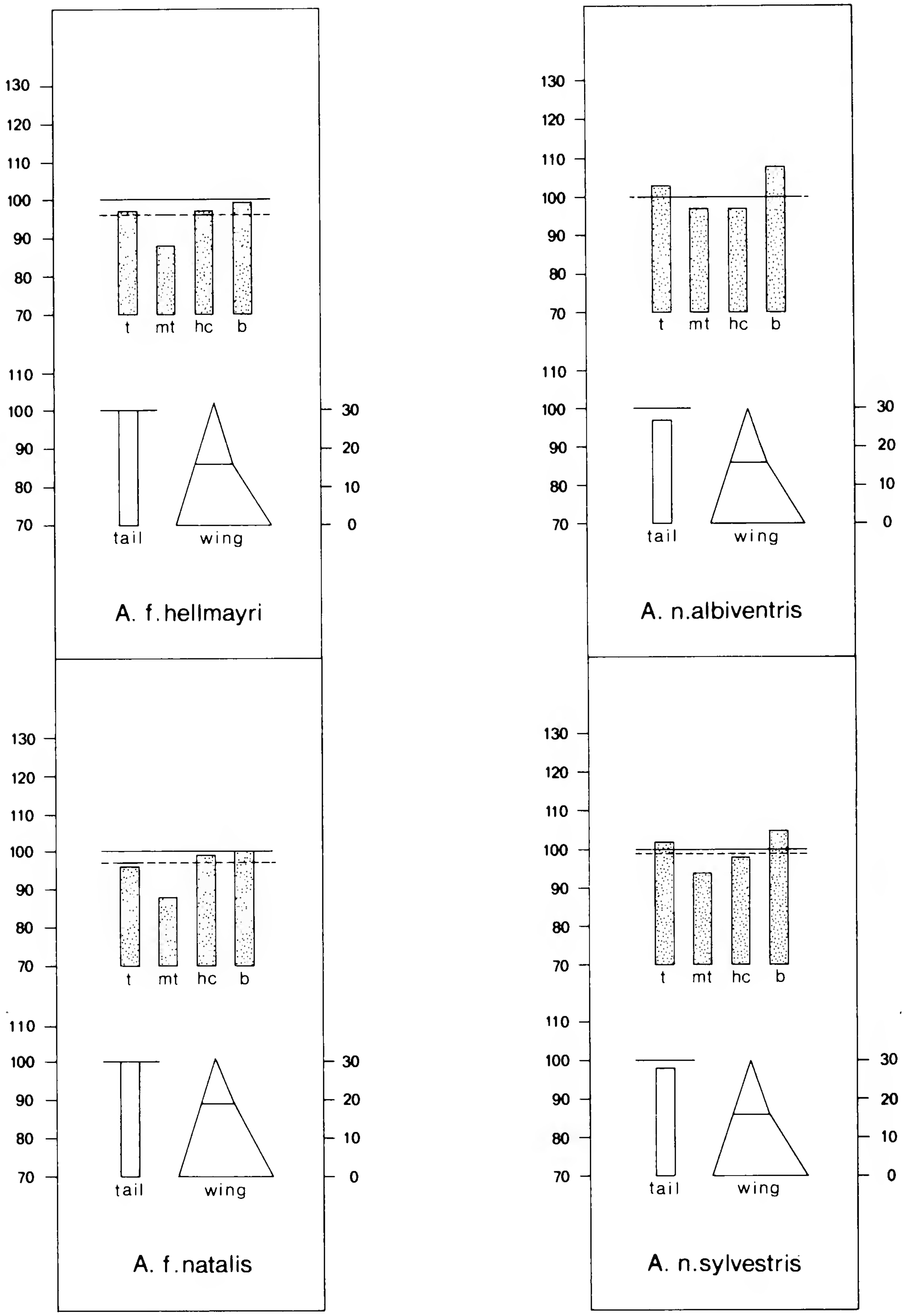


FIG. 17. Structure of *Accipiter fasciatus* and *A. novaehollandiae.*

tween the subspecies is significant for all series of data except the length of tail. The difference between the sexes is significant for the tarsus (longer in male) and bill (smaller in male).

Bill and foot.—Similar to these structures in *A. tachiro.* Owing to

TABLE 51
WING LENGTH IN *Accipiter fasciatus.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
fasciatus	262.1	6.22	1.66	255 - 276	14
didimus	227.0	-	-	223 - 231	2
dogwa	220.6	4.61	2.06	215 - 226	5
vigilax	242.3	11.37	6.56	233 - 255	3
wallacii	225.0	-	-	224 - 226	2
tjendanae	226.0	-	-	223 - 229	2
hellmayri	213.2	4.93	2.46	206 - 217	4
natalis	222.6	2.07	0.93	220 - 225	5
			♀		
fasciatus	302.3	8.91	1.94	287 - 318	21
dogwa	251.2	7.59	3.40	240 - 260	5
polycryptus	258	-	-	-	1
vigilax	279.2	5.12	1.71	270 - 284	9
buruensis	261.0	-	-	260 - 262	2
wallacii	259.5	-	-	255 - 264	2
tjendanae	258.5	-	-	257 - 260	2
hellmayri	245.0	3.36	1.68	241 - 249	4
natalis	267.5	1.92	0.96	266 - 270	4
				Total	87

the much longer wing all relative measurements appear shorter than in *tachiro.* In most subspecies, but not in nominate *fasciatus,* the hind claw is small in relation to the bill. In this respect the tropical races of *A. fasciatus* show more resemblance to *A. tachiro toussenelii* than to *A. t. tachiro.* Particularly in *A. f. hellmayri* and *A. f. natalis* the bill is quite heavy for the size of the bird. In *A. f. fasciatus* and *didimus/dogwa* the tarsus is comparatively long.

Wing and tail.—These are of the *brevipes* type. Closely similar to *A. cirrhocephalus.* In *A. f. natalis* the wing is shorter and more rounded, approaching the *A. minullus* type.

HABITAT

Found in second-growth, more or less open woodland, forest edge, savanna with isolated trees, and cultivated regions, but not in tropical lowland forest.

In Australia it occurs in stands of large trees, sclerophyllous woodland, trees along watercourses and roads. It ranges in New Guinea from lowland savanna through forest edges and mountain grassland with patches of forest or isolated trees up to 1,700 m (Mayr and Gilliard, 1954). On the Lesser Sunda Islands it is found in cultivated parkland with scattered woodlots from sea level up to 500 m (Rensch, 1931) and on the low-lying islands to the south of Celebes it inhabits intensively cultivated country (Meise, 1929). On Christmas Island Gibson-

TABLE 52

Relative measurements in percent of wing length in *Accipiter fasciatus*.

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	26.60	13.93	7.52	6.90	76.00	33.01	14.37
fasciatus	27.58	14.40	7.48	6.34	76.97	33.85	14.62
dogwa1)	27.06	13.50	6.99	6.78	76.28	34.80	16.08
vigilax	26.41	13.80	7.25	6.61	76.84	32.63	14.32
wallacii	26.16	13.87	7.57	6.89	75.33	32.62	14.66
tjendanae	26.36	13.97	7.32	6.89	76.54	34.12	15.08
hellmayri	-	-	7.87	7.38	74.87	32.31	-
natalis	26.04	14.04	8.15	7.42	75.15	30.75	11.46
♂	+0.40	-0.09	-0.22	-0.11	-0.64	+0.29	+0.58
♀	-0.40	-0.09	+0.22	+0.11	+0.64	-0.29	-0.58
Adult	-0.13	+0.06	-0.02	+0.01	-0.54	+0.14	-0.36
Juvenile	+0.13	-0.06	+0.02	-0.01	+0.54	-0.14	+0.36
P model	0.084	0.774	1.000	0.084	0.991	0.593	0.918
P ssp	0	0.039	0.005	0	0.803	0.001	0.024
P sex	0.005	0.721	0.167	0.005	0.766	0.483	0.566
n	58	58	69	76	83	79	60
df	38	38	45	52	59	55	40
No analysis:							
hellmayri	26.20	14.10					15.85
n	1	1					2
buruensis	27.10	13.70	7.30	6.80	80.50	35.12	15.15
n	1	1	1	2	2	2	2

---

1) includes didimus

Hill (1947) reported it in "areas of slightly thinner growth on the edge of thick jungle, or in the borders of clearings."

HUNTING BEHAVIOR

A. fasciatus is a typical still-hunter. Its flight is less agile, but of the same general character as that of *A. gentilis*. In southern New Guinea it was observed waiting for rats to come out when small fires were made (Rand, 1942). Wheeler (1963) describes a harrier-like flight over bushes.

FOOD

Its food consists of small to middle-sized mammals and birds, lizards, snakes and large insects. In the large nominate subspecies young rabbits apparently form a staple food (Dunnet, 1957; Slater, 1961; Wheeler, 1963), but in the smaller races lizards are more in evidence.

Apart from rabbits it also takes birds, from song birds up to the size of a pigeon; poultry, reptiles, and beetles are mentioned as prey of the Australian race. Deignan (1964) found a skink in a stomach of a specimen of *A. f. didimus.* In New Caledonia *vigilax* feeds on birds, lizards, grasshoppers, and other insects (Mayr, 1945a); Layard and Layard (1880) found only lizards in the stomachs of birds also collected there. In New Guinea lizards were recorded from stomachs (Rand, 1942); small snakes, large insects, and occasionally birds were also taken (Rand and Gilliard, 1967). On Christmas Island the prey comprises small birds, rats, and large insects, whereas individual birds are known to raid poultry yards (Gibson-Hill, 1947).

Discussion

In the structure of the wing and tail *A. fasciatus* is typical of a bird of open country. In *A. f. natalis,* the only form from a rather forested island, the wing is clearly shorter than in the other races.

In the discussion of *A. madagascariensis* it was remarked that in Madagascar, as well as in the Palearctic, two species of *Accipiter* are found, viz., *madagascariensis/henstii* and *nisus/gentilis,* respectively, that resemble each other in the structure of their wings and tails while differing strongly in their bills and feet. In Australia the same phenomenon is encountered in *A. fasciatus* and *A. cirrhocephalus.* The resemblance in wings and tails may reflect the similarity of their habitats which is rather open country.

A. fasciatus has no immediate relatives outside Australasia. Its distribution corresponds broadly with the distribution of dryer types of vegetation in the region. Thus in New Guinea it is only a marginal species, and is absent from such heavily forested archipelagos as the Bismarck Islands, Solomon Islands, and Moluccas (with the possible exception of Buru). However, on the comparatively arid Lesser Sunda Islands it has developed a number of geographical races.

In Australia two rather divergent subspecies occur. The northern one, *didimus,* resembles the subspecies of New Guinea and the Lesser Sunda Islands, particularly the form *dogwa* from a small area in southern New Guinea. From this resemblance Condon and Amadon (1954) deduced that in Australia *didimus* is a recent invader from the north.

In New Guinea there is also a more intensely pigmented raced *polycryptus,* which inhabits mountain grasslands. When the sea level was low during glacial periods, a connection existed between Australia and New Guinea. Populations on both sides of the Torres Straits formed, therefore, a single unit on at least two occasions during the Pleistocene (Keast, 1961). The distribution of *dogwa* and its striking resemblance to *didimus* attest to the recent separation of these two forms. *A. f. polycryptus,* on the other hand, represents an older colonization of *A. fasciatus* in New Guinea and may have originated at the time of an earlier connection with Australia. Both its very limited range in New Guinea and the history of the distribution of *dogwa* make it extremely improbable that *didimus* should be regarded as a New Guinea colonist in the Australian avifauna. A more reasonable interpretation is that the race *didimus* originated in a northern Australian savanna woodland refuge during a dry period and subsequently spread to New Guinea.

In addition to *dogwa* the Timor race *hellmayri* is also similar to *didimus*. This form may be considered as an invader from Australia in the Timor avifauna (Mayr, 1944). The colonization of Timor is one of a series of island colonizations. In fact *A. fasciatus* has been very successful as an island colonist where its establishment on the islands was not blocked by unsuitable habitat.

The most recent of these colonizations has resulted in the occupation of Rennell and Bellona Islands by a population that is indistinguishable from *A. f. fasciatus*. In the somewhat more distant past New Caledonia was reached. The population of this island has developed into a separate subspecies, *vigilax*, which is only slightly different from *fasciatus*. The New Hebrides were colonized from New Caledonia.

Far to the west of Australia the species has succeeded in establishing itself on Christmas Island. The recent colonization of Christmas Island by another migratory raptor from Australia, *Falco cenchroides*, serves as proof that migrants from Australia may indeed reach Christmas Island and settle there. In view of the great morphological difference between the races *fasciatus* and *natalis*, the conclusion may be drawn that *natalis* has been isolated for a considerable period. It has become adapted to more humid conditions than any other subspecies of *A. fasciatus*. Correspondingly, the pigmentation of its plumage is much more saturated.

In the Lesser Sunda Islands we can discern three successive waves of colonization. *A. f. hellmayri* on Timor is similar to *didimus* and may be a recent invader to the Lesser Sundan avifauna and not much older than *dogwa* on New Guinea. *A. f. wallacii* and its derivatives, resembling the New Guinea form *polycryptus*, reached the Lesser Sunda Islands at a much earlier date. The resemblance to *polycryptus* may point to a common ancestry of *wallacii* and *polycryptus*, viz., the northern Australian population of *fasciatus*, during some earlier stage of the Pleistocene. The Sumba subspecies, *tjendanae*, resembles the southern Australian form, nominate *fasciatus*. Probably Sumba was colonized independently by birds from southern Australia. The fact that *fasciatus* occasionally reaches the island of Timor (p. 131) is an indication in support of such a colonization from southern Australia. As *tjendanae* is at present clearly distinct from nominate *fasciatus* it may be presumed that this colonization dates further back than that of *hellmayri* on Timor.

The success of *A. fasciatus* as an island colonist is again emphasized by its occurrence on the small islands between Flores and Celebes. Its failure to colonize Celebes proper is probably due to ecological factors, such as unsuitable habitats or the presence of other species of *Accipiter*.

The range of *wallacii* encompasses many islands, of which the group from Lombok to Alor formed a single island when the sea level was lowered during glacial periods of the Pleistocene. Wetar and the islands to the east have always been isolated from this chain. Although they have an avifauna of predominantly Timor affinity (Mayr, 1944), they are inhabited by the Flores subspecies of *A. fasciatus.* There is some difference of opinion about the population on the island of Alor. According to Hellmayr (1914) it is intermediate between the population of Flores and that of Timor. Stresemann (1924a) and Peters (1931) include Alor in the range of *hellmayri,* Rensch (1931) considers birds from the island to belong to *wallacii.* An adult bird in the Leyden collection agrees with *wallacii.* The examination of a sufficiently large series of specimens might reveal that on Alor (and perhaps on Wetar) *hellmayri* and *wallacii* are hybridizing. From the occurrence of *wallacii* farther east I conclude that this is the older form on Alor, whereas *hellmayri* may have colonized the island from Timor recently. This indicates that *hellmayri* is not a very old element of the Timor avifauna, but has reached the island relatively recently from Australia, as was argued above (p. 139) because of the resemblances of *hellmayri* and *didimus.*

Geographical variation in size in *A. fasciatus* provides good examples of "Bergmann's rule." All tropical forms are smaller than the temperate Australian subspecies, nominate *fasciatus.* In addition, *hellmayri* and *dogwa* are smaller than *didimus* from which they are derived, whereas *vigilax* and *tjendanae* are smaller than *fasciatus.*

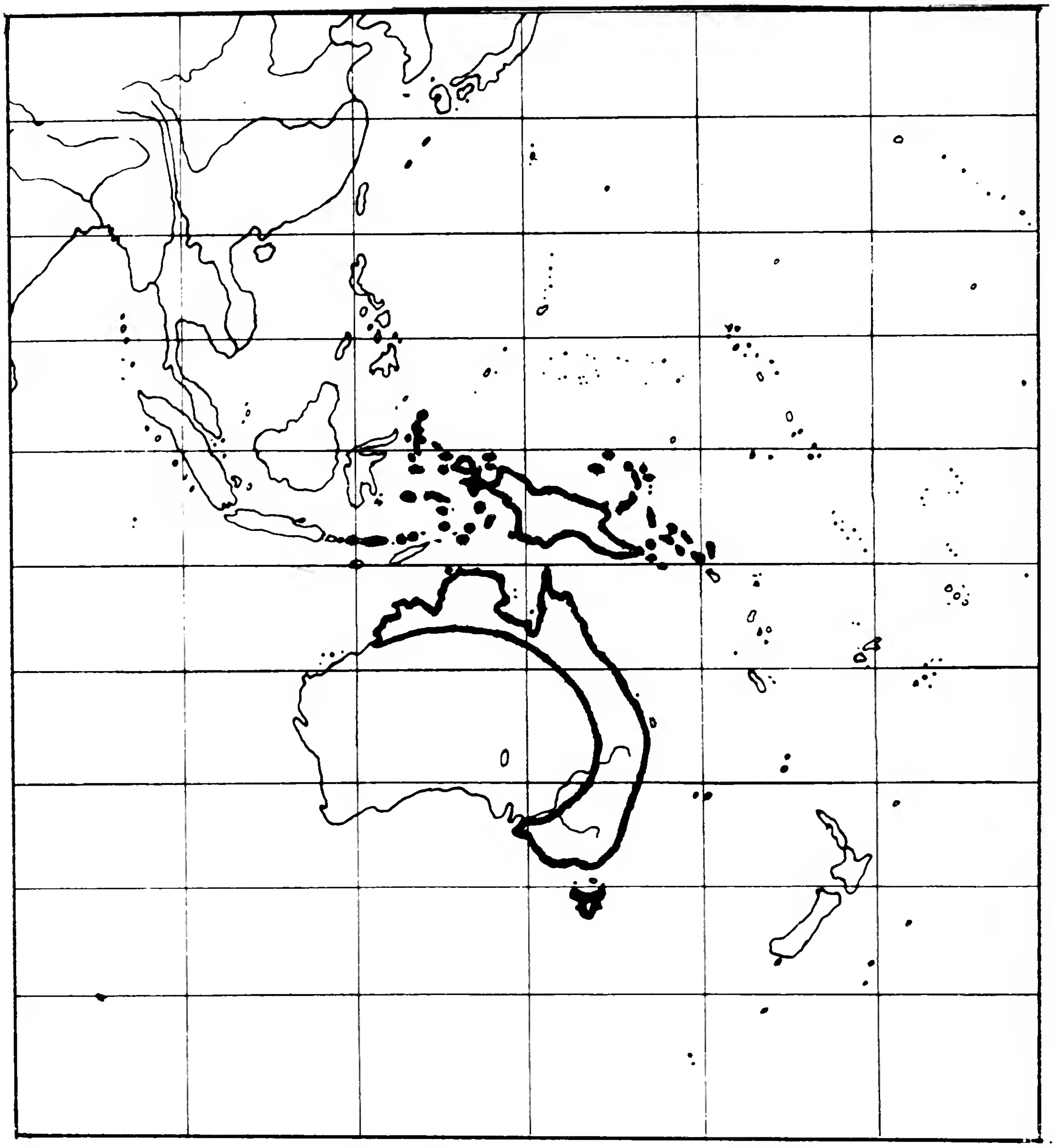
ACCIPITER NOVAEHOLLANDIAE (GMELIN)

DISTRIBUTION

Australia, New Guinea and adjacent islands (Map 18).

SUBSPECIES

cf. Peters (1931), Mayr (1931a, 1940, 1941a, 1945b), and Condon and Amadon (1954). *A. n. novaehollandiae* (Gmelin), eastern and northern Australia and Tasmania; *A. n. leucosomus* (Sharpe), New Guinea, Aru Islands, Waigeu, Misool (Mees, 1965), Salawati, Japen, and Numfoor, and birds from the Trobriand Islands, Woodlark Island, and East Island of the Bonvouloir group, although these may well belong to an undescribed race (Mayr, 1940). *A. n. misoriensis* (Salvadori), Biak; *A. n. pallidimas* Mayr, Fergusson and Goodenough, D'entrecasteaux Archipelago; *A. n. misulae* Mayr, Misima and Tagula, Louisiade Archipelago; *A. n. dampieri* (Gurney), New Britain and Rook; *A. n. lavongai* Mayr, New Hanover and probably the populations of New Ireland and the Tabar group (Mayr, 1945b); *A. n. lihirensis* Stresemann, Lihir group (Lihir, Mahur, Malie, Sinabiet, Masahet) and the Tanga Islands (Boang); *A. n. matthiae* Mayr, St. Matthias; *A. n. manusi* Mayr, Manus, San Miguel, Rambutyo, Los Negros (Ripley, 1947), and Nauna, Admiralty Islands; *A. n. bougainvillei* (Rothschild and Hartert), Bougainville, Shortland group; *A. n. rufo-*



Map 18. Distribution of *Accipiter novaehollandiae.*

schistaceus (Rothschild and Hartert), Choiseul, Ysabel, and Florida; *A. n. rubianae* (Rothschild and Hartert), Vella Lavella, Gizo, New Georgia, and Rendova; *A. n. pulchellus* (Ramsay), Guadalcanal; *A. n. malaitae* Mayr, Malaita and possibly Ulawa (Cain and Galbraith, 1956); *A. n. griseogularis* (G. R. Gray), Halmahera, Tidore, Ternate, Batjan, and Gebe; *A. n. mortyi* Hartert, Morotai Island; *A. n. obiensis* (Hartert), Obi Island; *A. n. hiogaster* (S. Müller), Ceram and Ambon; *A. n. pallidiceps* (Salvadori), Buru; *A. n. albiventris* (Salvadori), Kei Islands; *A. n. polionotus* (Salvadori), Timor-Laut, Babar, Damar, and Banda; *A. n. sylvestris* Wallace, Sumbawa, Flores, Pantar, and Alor.

Plumage and Geographical Variation

A. novaehollandiae is extremely variable. Not only are more subspecies recognized than in any other species of *Accipiter,* but the differences between some of these forms are so extreme that anyone familiar with only two of the most widely divergent ones would not hesitate to allocate them to different species. In surveying the entire group, however, it becomes apparent that all are connected by intermediate forms.

As a consequence of this great variability, no general description of the plumage can be given. The most important characters recurring in all or the great majority of subspecies are summarized by Stresemann (1925) as follows: bright yellow cere (greenish yellow only in females of *griseogularis*), longer bill with higher upper mandible than in *A. fasciatus,* rufous nuchal collar absent or very weakly indicated (distinct in *obiensis, griseogularis,* and *mortyi*), sixth primary longer than second (except in *albiventris, polionotus,* and *sylvestris*), wing tip rounded.

A. n. leucosomus.—The central subspecies of the complex is the New Guinea form *leucosomus.* This is also the form with the widest range of individual variation. A preliminary revision of *leucosomus* is given by Mayr (1940).

Adult male: upperparts dark gray without a nuchal collar, the head being slightly lighter than the back. Underparts darker or lighter vinaceous-rufous, becoming more ochraceous with wear and showing no trace of transverse barring. In specimens from the islands surrounding New Guinea white bars are sometimes present (Mees, 1965). Throat washed more or less with gray, the gray spreading over the upper breast in some specimens. Upperside of tail dark gray without crossbars, underside lighter with inconspicuous bars on the inner webs of the feathers (except on the outermost pair).

Adult female: differs from the male by the brownish tinged dorsum, the smaller amount of gray on the throat, and the less rufous, more ochraceous color below. The majority of the females show a tendency to be lightly barred below. Pronounced white barring is present in some specimens, especially in those from the smaller islands. The conclusion may be drawn that in the *leucosomus* complex a tendency toward barring of the underparts is apparent on the outlying islands (Mees, 1965). Because some females from New Guinea are strongly barred as well, it is impracticable to draw a boundary and to name different subspecies in the range of *leucosomus.*

Juvenile: upperparts brown with narrow pale feather edges which in many cases disappear with wear. Upperside of tail fuscous without bars, underside lighter with numerous dark crossbars. Two types of coloration of the underparts exist, one pale and one rufous (Mayr, 1940; Condon and Amadon, 1954). In the rufous juvenile plumage the entire venter is strongly washed with rufous and vaguely patterned with rufous brown markings on the breast and abdomen. The pale juveniles have a creamy-white to buffish underside, patterned with blackish brown streaks and drops on the breast and more or less regular bars of the same color on the abdomen and flanks. A number of specimens are intermediate. The pale type of juvenile plumage is found mostly in western New Guinea and on adjacent islands.

In *leucosomus* an entirely white leucistic variant is known, which formerly was considered to be a separate species. The white and the pigmented variant interbreed freely, are identical in proportions, and both have a bright yellow cere, yellow irides, and yellow feet. Stresemann (1923b) was the first to conclude that both are variant plumages of one and the same species. The white type has been recorded from New Guinea, Japen, Numfoor, Waigeu, and the Aru Islands, and also from Australia (nominate *novaehollandiae*). A single adult female of a completely blackish-gray melanistic form was reported by Stresemann (1925).

Island races in the New Guinea area.—The population on Biak (*misoriensis*) is similar in plumage to *leucosomus*, but much smaller. The adult is plain rufous below, the juvenile resembles the rufous type of juvenile *leucosomus.*

Birds from the eastern Papuan Islands (*pallidimas* and *misulae*) are large and pale and for the most part strongly barred on the underside in adult plumage. Juveniles from this area resemble the pale type of *leucosomus,* but are more boldly patterned on the underparts (descriptions in Mayr, 1940).

Populations from the Bismarck and Solomon Islands.—Geographical variation in this region has been reviewed by Mayr (1945b) and Hartert (1929). Almost every large island has its subspecies of *A. novaehollandiae* (see pp. 241-242). Adults differ in the tinge of the underside, in the extent of gray on the throat and upper breast, and in the presence or absence of barring on the breast and abdomen. Variation in juvenile plumages primarily affects the pattern of the underside. In addition there is a considerable variation in size (see Tables 53 and 54).

Populations from the northern Moluccas.—Races from the northern Moluccas are similar to one another and differ from the other forms of *A. novaehollandiae* primarily by the presence of a well-defined rufous nuchal collar in adults and a juvenile plumage that is marked with dark streaks and spots on the breast and bars on the flanks and abdomen.

In the population from the Halmahera area (*griseogularis*) the nuchal collar is sometimes indistinct and there is pronounced variation in the barring of the underside and in the amount of gray on the throat. Birds from this region are in general larger than those from New Guinea. Some specimens of *griseogularis* are closely similar to some of those of *leucosomus,* as far as plumage characters are concerned, and an overlap in size has also been found.

Of special interest are two adult males and a female from Gebe, only 80 km from Waigeu and 50 km from Halmahera. On account of their size these specimens can be considered to belong to *griseogularis,* but the males have almost no nuchal collar and are very inconspicuously barred below. The female has a well-developed collar and is distinctly barred below. Adult males from Waigeu (*leucosomus*) are distinctly barred but lack a nuchal collar.

Specimens from Morotai (*mortyi*) and Obi Major (*obiensis*) are smaller than those from Halmahera. *A. n. mortyi* is slightly darker than *griseogularis* while *obiensis* is lighter and has a very wide nuchal collar.

A number of specimens from Halmahera moult from the juvenile plumage into a plumage that, rather than being narrowly barred with rufous on the breast, has quite wide dark brown bars. A similar specimen is also recorded from Misool, within the range of *leucosomus* (Mees, 1965). These birds are strikingly different from other adults of *A. novaehollandiae.* Other juveniles from Halmahera were found to moult into the normal adult plumage. It is not clear whether the specimens with dark brown bars represent a variant or perhaps a "second year" plumage which is replaced by the normal adult plumage at the time of the next moult. I have not seen any specimen in moult from the dark into the rufous plumage.

Populations from the southern Moluccas.—The southern Moluccas are inhabited by small and intensely pigmented representatives of *A. novaehollandiae.* Adults from Ceram and adjacent islands (*hiogaster*) are much darker above than *leucosomus.* The underparts are deep ochraceous chestnut without cross-bars. There is no gray on the throat. These birds show some resemblance to specimens from the Solomon Islands. The juvenile is very dark brown above, the underside being white with small dark brown markings which can be considered the remains of a pattern of narrow and interrupted bars.

Adults from Buru (*pallidiceps*) differ strikingly from all other forms of *A. novaehollandiae* in having the head and the anterior part of the body very pale, the abdomen and undertail coverts deep ochraceous rufous. Apart from the pale head they show greatest resemblance to *hiogaster.* The juvenile is also similar to juvenile *hiogaster,* but lighter brown and more densely marked below.

Populations from the southwestern parts of the range.—These populations differ from other forms by the light gray dorsum and the pointed wing tip. The sixth primary is shorter than the second and lacks the emargination on the outer web. These races differ from each other in size, tinge of the upperside, and pattern of the underside in adult plumage. Birds from the Kei Islands (*albiventris*) and Timor-Laut (*polionotus*) are plain below, those from the Lesser Sunda Islands (*sylvestris*) regularly barred rufous and white. Juveniles from these populations have the upperparts brown with wide pale rufous edges to the feathers and the venter white with light brown drops on the upper breast and irregular bars on lower breast and abdomen.

A. n. novaehollandiae.—The Australian form of *A. novaehollandiae* is not only a giant in proportions, but differs also from the other forms by the absence of rufous pigments. Adult birds are pale gray on the upperside and white below, narrowly barred very pale gray on the breast. In juveniles the bars on the breast are wider and more irregular, in some specimens washed pale brown. A leucistic variant is present in the range of this form. The distribution of both variants is described by Southern and Serventy (1947). In Tasmania the white bird is the only type of *A. novaehollandiae.*

Nominate *novaehollandiae* is very different from all other races. The existence of a leucistic variant in Australia, as well as in New Guinea, however, has kept most authors from separating *novaehollandiae* specifically from the other races (cf. Condon and Amadon, 1954).

SIZE AND STRUCTURE

Size rather small to very large. Tarsus and toes short and heavy. Claws large. Bill heavy to very heavy. Wing rather short and rounded, longer and pointed in *albiventris, polionotus,* and *sylvestris.* Tail medium to short. Figures 17, p. 136, and 18a,b. Tables 53, 54, and 55.

The races *bougainvillei, rubianae,* and *polionotus* were excluded from the statistical analysis, as only a few specimens were available. The statistical model was unsatisfactory for the hind claw. The difference between the subspecies is significant for all series of data that could be analyzed. The difference between the sexes is significant for the tarsus (longer in male), bill (slightly smaller in male), tail (shorter in male), and wt–6 (longer in male).

Bill and foot.—The subspecies of *A. novaehollandiae* show a wide variation in these structures. They may be divided into five groups.

1. Nominate *novaehollandiae* and *leucosomus: gentilis*-type. Hind claw relatively smaller than in *gentilis.* In *leucosomus* the bill is large in comparison to the hind claw.

2. *A. n. dampieri* and *griseogularis: albogularis*-type. Differ from the preceding group in the relatively heavier bill. Continue the ten-

TABLE 53

WING LENGTH IN MALES OF *Accipiter novaehollandiae.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
novaehollandiae	259.6	3.51	1.11	254 - 266	10
leucosomus	213.8	7.06	1.89	202 - 227	14
misoriensis	175.0	-	-	174 - 176	2
dampieri	198.0	2.00	1.00	195 - 199	4
bougainvillei	197.5	-	-	195 - 200	2
rufoschistaceus	205.3	7.50	4.33	198 - 213	3
pulchellus	185.5	-	-	180 - 191	2
griseogularis	228.3	8.14	1.82	217 - 241	20
mortyi	221.0	-	-	220 - 222	2
obiensis	194.5	-	-	191 - 198	2
hiogaster	187.2	5.93	1.98	175 - 195	9
pallidiceps	197.5	-	-	197 - 198	2
albiventris	186	-	-	-	1
polionotus	192.0	-	-	191 - 193	2
sylvestris	184.7	1.70	0.85	183 - 187	4
				Total	79

TABLE 54

Wing length in females of *Accipiter novaehollandiae.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♀		
novaehollandiae	308.4	7.07	2.36	297 - 318	9
leucosomus	241.6	8.91	2.04	229 - 263	19
misoriensis	203	-	-	-	2
dampieri	229.9	5.19	1.96	224 - 237	7
rufoschistaceus	227	-	-	-	1
rubianae	218	-	-	-	2
pulchellus	214.6	4.39	1.66	210 - 222	7
griseogularis	263.9	7.25	1.58	251 - 276	21
mortyi	245.7	5.65	2.31	236 - 251	6
obiensis	240.5	-	-	240 - 241	2
hiogaster	215.0	7.32	2.59	203 - 228	8
pallidiceps	225.0	-	-	224 - 226	2
albiventris	221.6	3.78	1.69	215 - 224	5
polionotus	207	-	-	-	1
sylvestris	209.7	6.95	3.47	205 - 220	4
				Total	96

TABLE 55

Relative measurements in percent of wing length in *Accipiter novaehollandiae.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	27.25	15.33	8.37	8.36	75.09	26.40	7.07
novaehollandiae	26.59	15.50	9.06	7.43	72.48	25.81	5.26
leucosomus	27.71	16.16	9.25	8.20	74.17	25.54	6.05
misoriensis	29.29	15.89	8.73	8.90	75.49	25.69	6.04
dampieri	26.84	15.45	8.52	8.28	72.82	26.56	6.79
rufoschistaceus	26.26	14.15	7.63	8.07	80.34	22.88	5.23
pulchellus	28.41	15.22	7.80	8.57	75.77	23.81	5.00
griseogularis	26.09	15.50	8.72	8.48	76.46	26.09	4.79
mortyi	26.18	14.68	8.17	8.39	76.02	26.89	5.22
obiensis	26.82	15.51	8.68	9.30	76.24	27.30	6.14
hiogaster	27.96	14.95	8.07	8.32	75.14	26.21	7.04
pallidiceps	26.56	15.75	8.54	8.93	72.24	26.69	6.41
albiventris	28.00	15.58	7.76	8.03	74.03	30.11	14.54
sylvestris	27.54	14.96	7.89	7.78	74.96	29.62	13.41
♂	+0.56	-0.05	-0.25	-0.08	-0.70	+0.47	+0.57
♀	-0.56	+0.05	+0.25	+0.08	+0.70	-0.47	-0.57
Adult	-0.32	-0.07	-0.06	-0.02	-0.49	-0.37	-0.42
Juvenile	+0.32	+0.07	+0.06	+0.02	+0.49	+0.37	+0.42
P model	0.234	0.333	0.025	0.073	0.050	0.640	0.664
P ssp	0	0.002	-	0	0	0	0
P sex	0.008	0.356	-	0.027	0.001	0.064	0.019
n	93	79	171	148	156	151	107
df	52	42	106	104	111	107	63

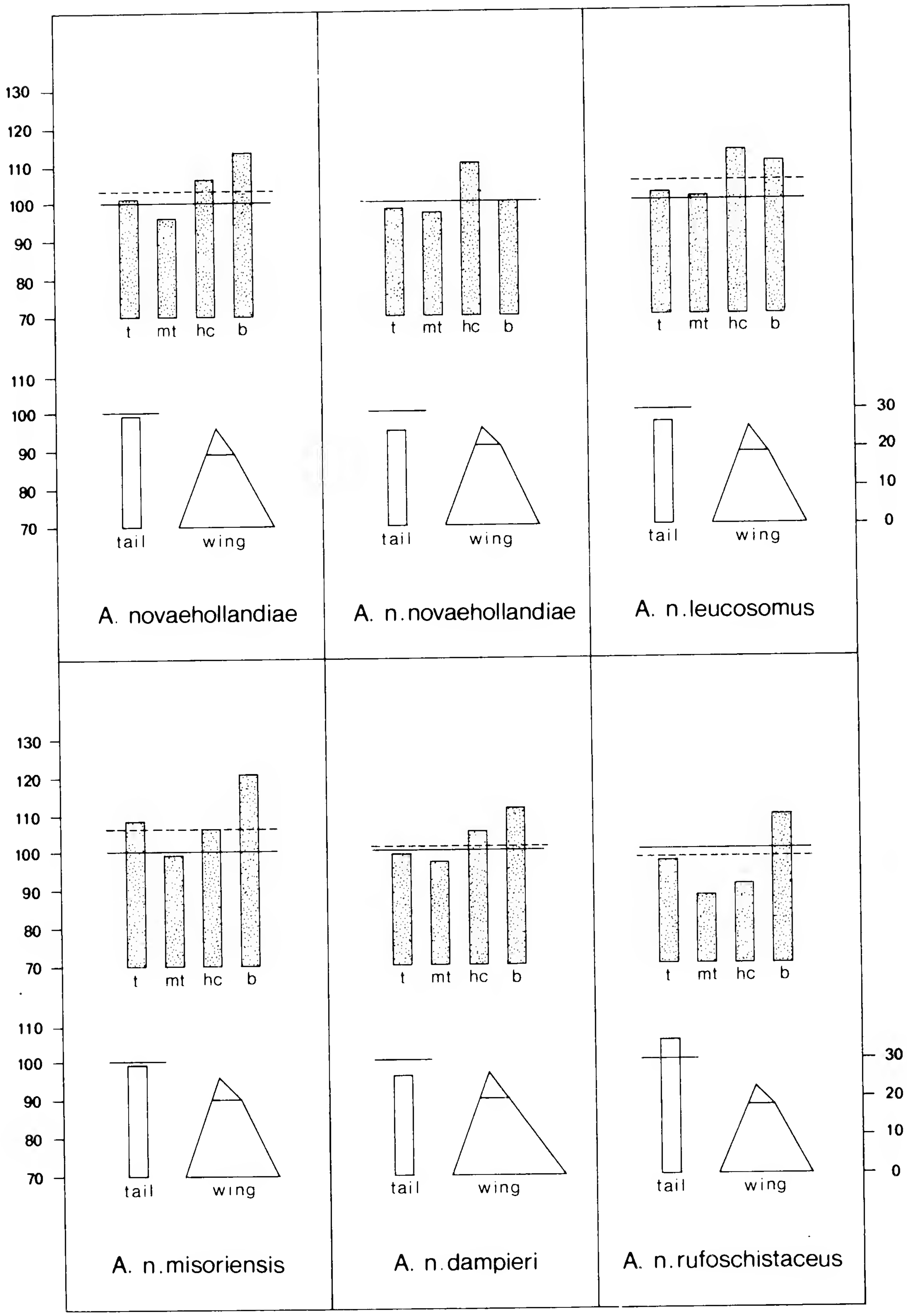


FIG. 18a. Structure of *Accipiter novaehollandiae* (part).

dency to increase the size of the bill which is already apparent in *leucosomus*.

3. *A. n. obiensis* and *pallidiceps:* bill still heavier than in Group 2.
4. *A. n. misoriensis* and *mortyi:* similar to Group 3, but the tarsus

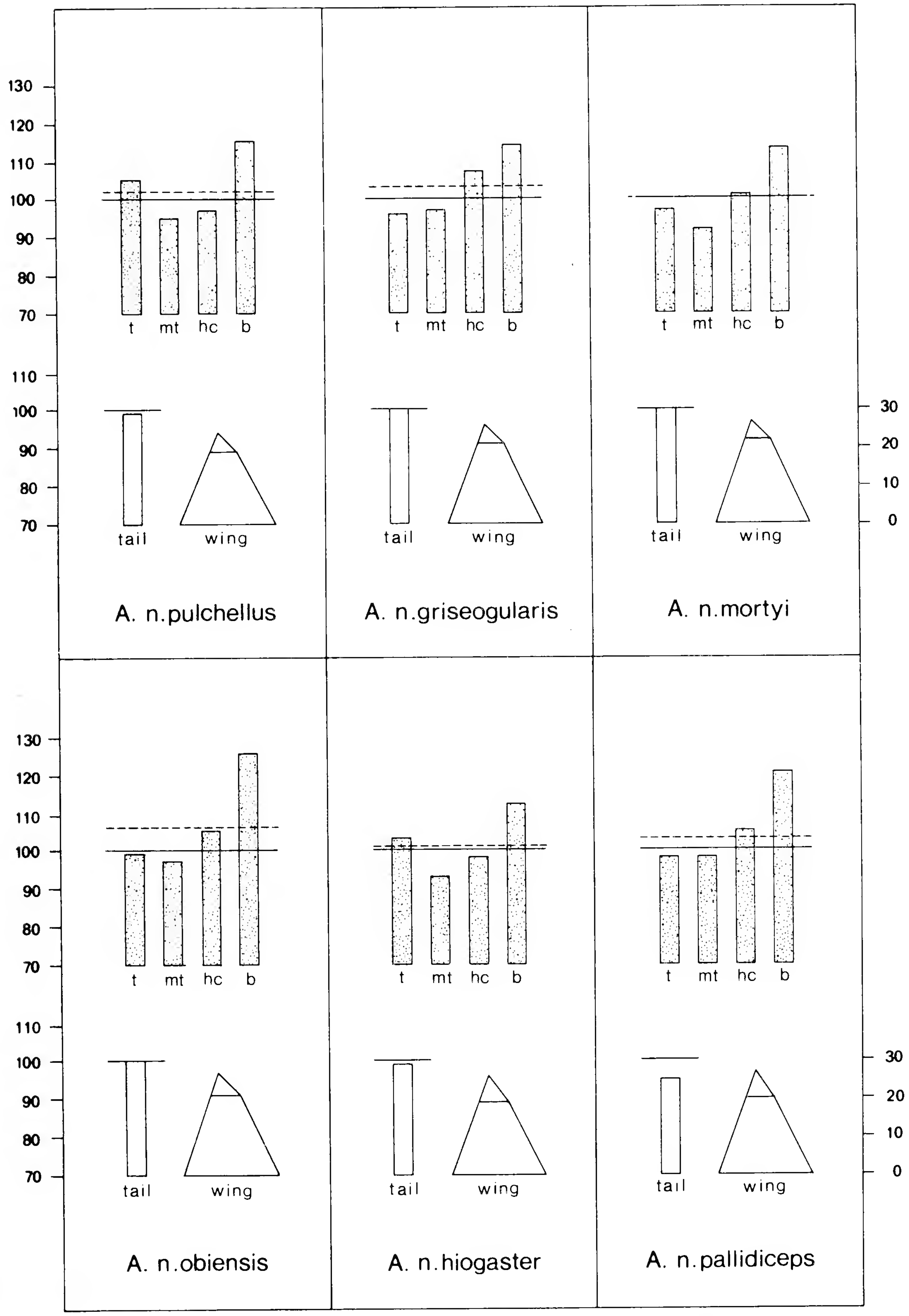


FIG. 18b. Structure of *Accipiter novaehollandiae* (part).

relatively longer. Intermediate between Groups 2 and 3, on the one hand, and Group 5 on the other.

5. *A. n. rufoschistaceus, pulchellus, hiogaster, albiventris,* and *sylvestris:* tarsus still longer in relation to the middle toe and hind claw.

A. n. rufoschistaceus shows resemblance to Group 4, the other forms approach the *trinotatus*-type. *A. n. sylvestris* resembles *A. f. francesii* in proportions, although the relative measurements appear smaller because of the longer wing.

Wing and tail.—These are of the *novaehollandiae*-type. Several subspecies have a relatively long tail, e.g., the northern Moluccan forms *griseogularis, mortyi,* and *obiensis. A. n. rufoschistaceus* has a very long tail and a short wing, resembling the *tachiro*-type. *A. n. albiventris* and *sylvestris* differ from all other races in the pointed wing tip, intermediate between the *brevipes*- and *minullus*-type and resembling the smaller races of *fasciatus.*

Habitat

A. novaehollandiae inhabits a wide variety of habitats, ranging from lowland and mountain forest, second-growth, forest edges and savanna to cultivated areas.

In Australia it is more of a forest bird than is *A. fasciatus,* being recorded mostly from areas with a fairly luxuriant growth of trees. On Cape York Peninsula it breeds in open forest, making its nest in large trees (Barnard, 1911). In southern Tasmania it was found in a region buffeted by storms that had only stunted trees (Green and Mollison, 1961).

In the New Guinea area *A. n. leucosomus* is one of the most common hawks. It is found in lowland and mountain forest, up to 1,600 m, along the edge of the forest, in second-growth, on savanna with isolated trees, along rivers and streams or near the shores of lakes, in grassy marshes, and near native cultivation and plantations. Stein (1936), who collected a fair series on Japen and Numfor, remarks that it was always encountered in more or less open country. On the savannas of southeastern New Guinea Gilliard (1950) noted it perched high on dead trees, whereas *A. fasciatus dogwa* was perched low on living trees in the same locality. Apparently *leucosomus* resembles the European Goshawk and Sparrow Hawk in its preference for varied open country and broken forest.

In the remaining parts of its range the habitat of *A. novaehollandiae* is nearly always described in the same way as in New Guinea. On many islands coconut plantations are favored. On Buru, however, Toxopeus (1922) found the subspecies *pallidiceps* exclusively in dense forest, from sea level to 1,200 m. Apparently the hawk remains in the shade of the canopy.

Hunting Behavior

The species is typically a still-hunter. Dahl (1899) gives an excellent account of his observations on New Britain. The bird conceals itself among the lower leaves of a palm, surprising lizards which are sunning in the neighborhood of its perch. The species was observed hovering over grassy marshes in New Guinea, repeatedly dropping into the grass and trying to catch weaver birds skulking about (Rand, 1942). Its flight is slow and heavy and much less agile than that of the European Goshawk.

FOOD

Its diet is a wide variety of small animals from small mammals to insects. Insects are much more in evidence than in the food of *A. fasciatus.*

In Australia *A. n. novaehollandiae* takes a fair number of birds; small mammals, lizards, and insects are also recorded, and, once a freshwater crab was found in a stomach (Mathews, 1909).

A total of 23 stomach analyses from the New Guinea region yielded the following prey items: small mammals (5 times), small birds (three times), lizards (9 times), snakes (twice), unidentified reptile (once), insects (10 times) that were mainly grasshoppers (data from various literature sources). Stein (1936) also found arboreal Orthoptera, which live high in the crowns of forest trees (Rothschild, Stresemann, and Paludan, 1932).

In the Bismarck Archipelago lizards are the most important item of prey (Dahl, 1899), but many other animals are also taken, such as young megapodes, domestic chickens, quail and other smaller birds, mice, and large insects. The same type of food is reported from other localities. A total of 15 stomachs from various parts of the species' range revealed rats and mice (twice), remains of megapodes (twice), other birds (twice), lizards (5 times), snake (once) and insects (7 times) (data from various literature sources).

DISCUSSION

A. novaehollandiae shows a wide variation in structure, but it is not known whether there is a corresponding variation in ecology. The subspecies *novaehollandiae,* with its bill and feet of the *gentilis*-type, plays more or less the role of a large goshawk. The structurally similar, though much smaller, New Guinea form *leucosomus* takes on the average much smaller prey. There is a tendency in many smaller races, which often inhabit small islands, to have comparatively heavier bills than those of nearby but larger races (cf. *novaehollandiae* and *leucosomus, leucosomus* and *misoriensis, griseogularis* and *obiensis* in Table 55, p. 147). The wing of *A. novaehollandiae* is shorter and more rounded than that of *A. fasciatus,* which may be related to the former's generally more forested habitat. Whether the long-winged forms *albiventris, polionotus,* and *sylvestris* inhabit more open country than the other races is not known, although for *albiventris* and *polionotus* this seems hardly probable because the islands are heavily forested.

The distribution of *A. novaehollandiae* centers in New Guinea, where the species is common. From there it has colonized the smaller oceanic islands to the north, east, and west. It has been very successful as an island colonist, having reached all islands of the Bismarck group, the Admiralty Islands, and the Solomon Islands. It is absent from San Cristoval, the southeasternmost island of the Solomons, which suggests that the species advanced southeastward from the Bismarck Archipelago.

To the west of New Guinea we find three strongly different groups of subspecies, viz., *griseogularis* and its allies in the northern Moluccas, *hiogaster* and *pallidiceps* in the southern Moluccas, and *albiventris* in the Kei Islands. *A. n. griseogularis* and *hiogaster* differ more from one another than either differs from *leucosomus,* so it is evident that the northern and southern Moluccas were reached by two separate colonizations. *A. n. albiventris,* with its pale plumage and aberrant wing formula, shows no close affinities to either of the Moluccan groups, nor to *leucosomus.* It probably represents an old isolate. It is remarkable that the small Banda Islands, close to Ceram, should be inhabited by *polionotus,* which is similar to *albiventris* and occurs also on Timor-Laut, Damar, and Babar. Apparently these widely separated islands were colonized from the Kei Archipelago. Babar and Damar may have served as stepping stones for colonizing the Lesser Sunda Islands. Apart from the barring on the underparts, which is a rather variable character in *A. novaehollandiae,* the Lesser Sundan form *sylvestris* is similar to *polionotus.*

The Australian subspecies *novaehollandiae* is very different from all the island forms and is only linked to *leucosomus* by the occurrence of an all-white variant. In this respect the situation in *A. novaehollandiae* contrasts strikingly with that in *A. fasciatus* and *A. cirrhocephalus.* In the last two species the populations of northern Australia and southern New Guinea are almost identical, reflecting the Pleistocene land connection across the Torres Straits. Not the slightest indication of such a recent connection is found in the distribution of *A. novaehollandiae.* This means that the races *novaehollandiae* and *leucosomus* did not meet, presumably because either in the region of the Torres Straits or more to the south a barrier existed, preventing nominate *novaehollandiae* from penetrating New Guinea or *leucosomus* Australia. In the distribution of *A. fasciatus* and *A. cirrhocephalus* a barrier between northern and southern Australia is reflected in the existence of two separate Australian subspecies. This barrier was probably a stretch of arid country with few trees. If *leucosomus* had penetrated into Australia as far as this continental barrier it was subsequently wiped out, probably by a shift of the arid belt toward the north.

Within the taxon *A. novaehollandiae* a considerable number of forms have been united that nowhere come in contact with one another. Hence it is impossible to verify whether they are races within a single species or represent several allopatric species. Recently Brown and Amadon (1968) raised the *griseogularis* group to specific rank on account of certain resemblances to *A. fasciatus.* They consider it impossible to decide whether *griseogularis* or *A. henicogrammus* is more closely related to *A. novaehollandiae.* It was shown above that *A. n.*

griseogularis is close to *A. n. leucosomus* and that the population of Gebe even displays some intermediate features. Admitting that it is impossible to prove that *griseogularis* and *leucosomus* belong to a single species, I regard it as inconsistent that Brown and Amadon do not discuss the status of several other subspecies. For example, the question may be raised as to whether the presence of a leucistic variant really proves that the species barrier between *leucosomus* and *novaehollandiae* has not been crossed. The forms of the *albiventris* group resemble *A. fasciatus* in wing formula, apparently a rather conservative character. In this case, however, it is certain that the *albiventris* group is specifically separated from *A. fasciatus* because *sylvestris* and *A. fasciatus* are sympatric on Sumbawa, Flores, and Alor and *polionotus* and *A. fasciatus* are on Damar. Weighing the available evidence I prefer to use a wide species concept and to include all these forms in the species *A. novaehollandiae.*

In both geography and in ecology this species is complementary to *A. fasciatus*. As indicated above the distribution of *A. novaehollandiae* centers in New Guinea, the distribution of *A. fasciatus* in Australia. *A. novaehollandiae* is primarily a rainforest species, whereas *A. fasciatus* is a bird of open forest and savanna. Similar complementary forms of forest and savanna Accipiters are also known in Africa, e.g., *A. t. tachiro* and *A. tachiro toussenelii.* In morphology some forms of *A. novaehollandiae* resemble *A. fasciatus.* The most important differences in structure are: shorter tarsus, heavier bill, and shorter wing. A heavy bill and a short wing are characteristic of forest forms in several other species groups. From the complementary character of the ranges and from the existing similarities in morphology, I draw the conclusion that *A. fasciatus* and *A. novaehollandiae* have developed from a common origin. The differences in plumage and structure, and the overlap in range, indicate that they have long been separated specifically.

ACCIPITER MELANOCHLAMYS (SALVADORI)

DISTRIBUTION

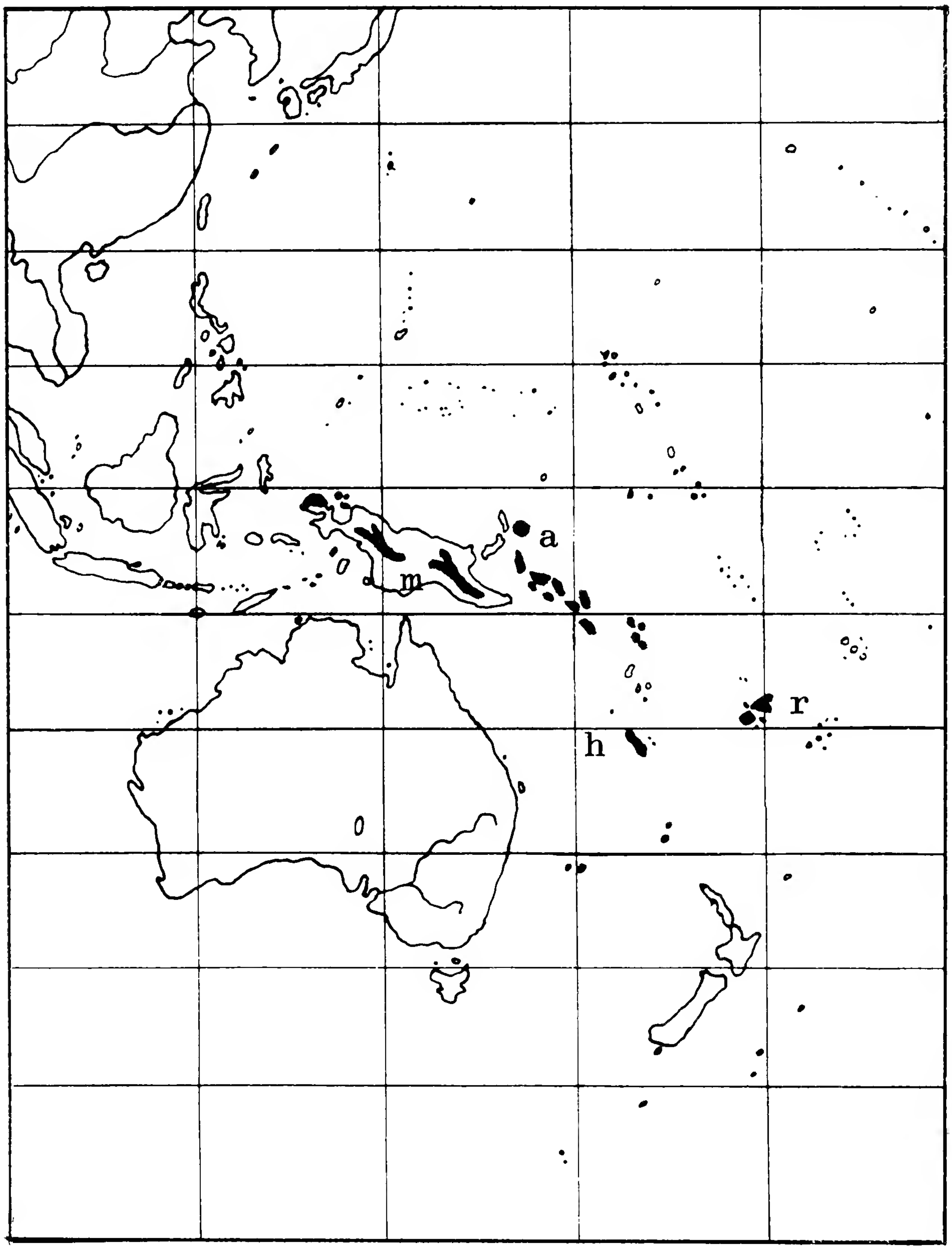
Mountains of New Guinea (Map 19).

SUBSPECIES

cf. Mayr (1941a). *A. m. melanochlamys* (Salvadori), Arfak Mountains, Vogelkop Peninsula; *A. m. schistacinus* Rothschild and Hartert, mountains of the remaining part of New Guinea.

PLUMAGE

Adult.—Crown and back black or very dark gray with a deep rufous nuchal collar. Throat black. Breast and abdomen deep rufous, unbarred or with faint indications of a few transverse bars on the abdo-



MAP 19. Distribution of *Accipiter melanochlamys* (m), *A. albogularis* (a), *A. rufitorques* (r), and *A. haplochrous* (h).

men. Upperside of tail black, unbarred; underside browner with dark crossbars.

Juvenile.—Upperparts very dark brown with tawny feather edges. A light nuchal collar is evident. Underparts whitish with blackish brown streaks and drops. Tail brown with numerous dark bars which are more conspicuous above than below (see Mayr, 1940).

GEOGRAPHICAL VARIATION

A. m. schistacinus is said to differ from nominate *melanochlamys* by being slightly grayer above. Gyldenstolpe (1955), comparing an adult male of *schistacinus* with an adult female of the nominate race, observed that the former also had darker chestnut rufous underparts. Both differences may be due to sexual or individual variation and various authors have expressed some doubt with regard to the subspecific variation within this species. In view of the limited material in collections this question cannot be resolved at present.

SIZE AND STRUCTURE

Size medium to rather large. Tarsus rather long. Toes short. Claws and bill moderate. Wing medium, intermediate in shape. Tail short. Figure 19. Tables 56 and 57.

No statistical analysis made.

Bill and foot.—These structures are of the *tachiro*-type. Hind claw rather small in relation to tarsus, hence similar to *toussenelii.*

Wing and tail.—The moderately pointed wing places this species between *A. fasciatus* and *A. novaehollandiae.* In general structure of the wing and tail *A. melanochlamys* resembles *A. fasciatus natalis.*

HABITAT, HUNTING BEHAVIOR, AND FOOD

Inhabits heavy lichen-clad cloud forest, forest edge, second-growth, and native cultivation at altitudes from 1,400 to 3,000 m. Nothing has been recorded of its hunting behavior. Ripley (1964) observed one quietly hawking through native gardens and secondary stands of *Casuarina,* causing alarm among small birds. The prey apparently consists of various small animals. In five stomachs the following were

TABLE 56

WING LENGTH IN VARIOUS AUSTRALASIAN SPECIES OF *Accipiter.*

SPECIES	SEX	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
meyerianus	♂	300.0	-	-	291 - 309	2
	♀	332	-	-	-	1
buergersi	♂	296.3	4.16	2.40	293 - 301	3
	♀	323.0	-	-	321 - 325	2
brachyurus	♂	173	-	-	-	1
melanochlamys	♂	219.4	5.77	2.58	214 - 227	5
	♀	253.2	4.72	2.11	249 - 261	5
poliocephalus	♂	194.8	4.64	1.47	188 - 202	10
	♀	218	-	-	-	1
luteoschistaceus	♂	191.3	5.51	3.18	185 - 195	3
	♀	211.5	-	-	209 - 214	2
imitator	♀	205.0	-	-	201 - 209	2
henicogrammus	♂	224.2	5.45	2.44	217 - 232	5
	♀	245.4	6.49	1.87	237 - 260	12
nanus	♀	167.3	0.59	0.33	167 - 168	3

TABLE 57

Relative measurements in percent of wing length in various Australasian species of *Accipiter* (averages of small series of values, no statistical analysis possible).

SPECIES	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
meyerianus	24.60	15.77	9.53	8.03	70.33	31.17	6.97
n	3	3	3	3	3	3	3
buergersi	24.32	18.00	10.12	7.34	71.40	32.30	7.50
n	5	5	5	5	5	5	5
brachyurus	31.20	19.70	8.10	7.30	71.00	27.20	13.90
n	1	1	1	1	1	1	1
melanochlamys	27.77	14.87	8.15	7.44	73.67	26.81	9.34
n	8	6	10	10	9	8	9
poliocephalus	26.98	14.57	7.76	8.44	78.37	28.07	12.10
n	11	9	9	7	8	10	2
luteoschistaceus	30.16	13.95	7.16	8.00	77.00	24.40	5.18
n	5	4	5	3	3	5	5
imitator	27.05	13.30	7.15	9.00	77.50	21.50	4.40
n	2	2	2	2	2	1	2
henicogrammus	29.74	13.08	6.77	7.99	84.12	24.00	4.68
n	15	13	16	14	15	15	5
nanus	26.10	16.63	7.00	7.55	73.00	26.20	5.80
n	3	3	2	3	3	3	3

found: small marsupial (once), small birds (twice), frogs (twice), and insects (once) (data from various literature sources).

DISCUSSION

A. melanochlamys is similar to *A. tachiro toussenelii* in preying apparatus and probably also in ecology. Both species take a variety of small animals in heavy forest. Ecologically *A. melanochlamys* represents *A. novaehollandiae leucosomus* at higher altitudes (subtropical and temperate zone).

Mayr (1957) suggested that *A. melanochlamys, A. albogularis, A. haplochrous,* and *A. rufitorques* are closely related, forming a species group, which he called the *rufitorques* group. A general discussion of this group is to be found in the section on *A. rufitorques* (p. 162).

ACCIPITER ALBOGULARIS G. R. GRAY

DISTRIBUTION

Solomon and adjacent islands (Map 19, p. 154).

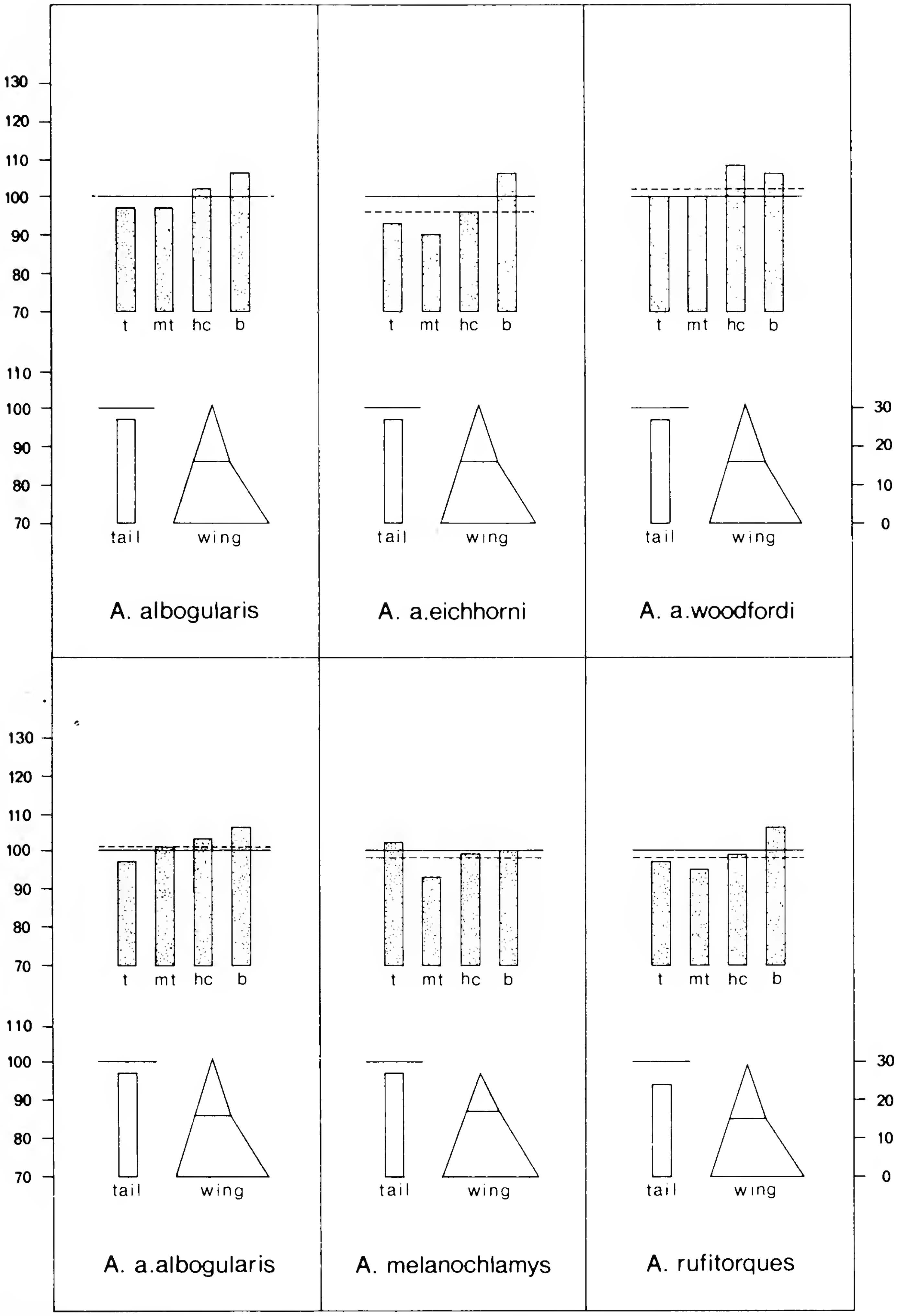


FIG. 19. Structure of *Accipiter albogularis, A. melanochlamys,* and *A. rufitorques.*

SUBSPECIES

cf. Mayr (1945b, and 1957) and Galbraith and Galbraith (1962). *A. a. eichhorni* Hartert, Feni Island, east of southern New Ireland; *A. a. woodfordi* (Sharpe), Bougainville, Treasury, Shortlands, Choiseul, Ysabel, Florida, Guadalcanal, Malaita, and Ulawa; *A. a. gilvus* Mayr, Vella Lavella, Kolombangara, New Georgia, and Rendova; *A. a. albogularis* G. R. Gray, San Cristoval and Santa Ana, and probably on Ugi; *A. a. sharpei* (Oustalet), Santa Cruz Islands.

PLUMAGE

Adult.—Upperparts dark slate gray or slate black, with or without a chestnut-rufous nuchal collar. Underparts white; in many specimens sides of upper breast tinged gray or inconspicuously vermiculated grayish vinaceous. Dorsum of tail plain black or dark gray, underside lighter, the feathers faintly barred with numerous dark crossbars on the inner web. There is a melanistic variant (*"holomelas"*) of *albogularis* and *woodfordi.*

Juvenile.—Blackish brown above with narrow light margins to the feathers. Scapulars and uppertail coverts heavily barred black on rufous-gray background. Underparts creamy white to pale tawny, variously patterned with blackish brown markings. Tail brown with numerous narrow dark crossbars. The juvenile plumage of the melanistic variant has the underparts heavily suffused with rufous.

GEOGRAPHICAL VARIATION

Geographical variation within *A. albogularis* has been described by Mayr (1957). The adult plumages of *albogularis, woodfordi,* and *gilvus* are indistinguishable. In part of the population of *woodfordi,* however, a rufous nuchal collar is present, which is not known to occur in *albogularis* and *gilvus.* The collar is conspicuous and broad in *eichhorni,* but obsolete in *sharpei.* In *eichhorni* the upperparts are lighter than in the three races of the Solomon Islands, whereas *sharpei* is intermediate.

The juvenile plumage differs among races of the Solomon Islands. In *woodfordi* the venter is creamy white with black drops on the breast abruptly changing into hearts or irregular bars on the abdomen; the flanks are barred. In *gilvus* the markings are much reduced and in *albogularis* the ground-color is darker, suffused with tawny, and the pattern is intermediate between *gilvus* and *woodfordi.* The drops and streaks of the breast change gradually into the arrowhead markings of the abdomen (Galbraith and Galbraith, 1962). Juvenile *eichhorni* resembles *woodfordi.* The juvenile of *sharpei* has not been described.

SIZE AND STRUCTURE

Size medium to rather large. Tarsus and toes rather long and heavy. Claws and bill heavy. Wing long and pointed. Tail medium. Figure 19, p. 157. Tables 58 and 59.

No data were available for a statistical analysis of the races *gilvus* and *sharpei.* Data for the tarsus length were insufficient for analysis in the other subspecies. The difference between the subspecies is signifi-

TABLE 58
WING LENGTH IN *Accipiter albogularis.*

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
eichhorni	206.5	-	-	206 - 207	2
woodfordi	212.0	1.73	1.00	210 - 213	3
albogularis	209	-	-	-	1
			♀		
eichhorni	239.3	5.13	2.96	235 - 245	3
woodfordi	247.7	4.54	2.62	242 - 251	3
gilvus	248	-	-	-	1
albogularis	245.3	1.22	0.49	244 - 247	6
				Total	19

cant for the middle toe and hind claw. No significant difference exists between the sexes.

Bill and foot.—These are of the *albogularis*-type. In *eichhorni* the tarsus, middle toe, and hind claw are comparatively shorter than in the other subspecies.

Wing and tail.—These structures are of the *brevipes*-type, but the wing tip is shorter and tail longer than in *A. brevipes* and they are closely similar to Lesser Sunda races of *A. fasciatus.*

HABITAT, HUNTING BEHAVIOR, AND FOOD

Inhabits dense lowland and hill forest, which are interspersed with clearings and second-growth, from sea level to about 1,200 m. In the

TABLE 59
RELATIVE MEASUREMENTS IN PERCENT OF WING LENGTH IN *Accipiter albogularis.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	26.18	15.53	8.38	7.86	73.62	30.80	14.53
eichhorni	-	14.39	7.89	7.62	76.07	30.52	13.10
woodfordi1)	-	16.01	8.82	8.07	73.54	31.10	15.36
albogularis	-	16.18	8.42	7.89	71.26	30.78	15.14
♂	-	-0.29	-0.26	-0.11	+0.38	+0.38	+0.86
♀	-	+0.29	+0.26	+0.11	-0.38	-0.38	-0.86
Adult	-	-0.35	-0.05	+0.15	+0.37	-0.19	-1.03
Juvenile	-	+0.35	+0.05	-0.15	-0.37	+0.19	+1.03
P model	no analysis	0.644	0.730	0.250	0.640	0.185	0.185
P ssp	-	0.049	0.002	0.092	0.206	0.273	0.062
P sex	-	0.518	0.053	0.186	0.698	0.173	0.081
n	15	14	17	18	18	19	18
df	-	5	8	8	8	9	8

---

1) includes gilvus

Solomon Islands *A. albogularis* is more confined to forest than is *A. novaehollandiae* (Cain and Galbraith, 1956), but on the Santa Cruz Islands it is often seen in gardens (Hadley and Parker, 1965). Nothing has been recorded about its hunting technique. Its flight is described as being light and slow, in contrast to that of most other Accipiters (Sibley, 1951). Its prey consists of small birds and their nestlings, lizards, large insects, and probably also larger birds (Cain and Galbraith), including domestic fowl (Sibley).

Discussion

In *A. fasciatus* the long and pointed wing tip was interpreted as an adaptation to a more or less open habitat. The short wing tip of *A. novaehollandiae,* on the other hand, was thought to enable the bird to fly rapidly and skilfully through dense forest. Although *A. albogularis* is allegedly even more strictly confined to forest, its wing tip is much longer than that of the Solomon Islands races of *A. novaehollandiae.* Perhaps this has something to do with the "light and slow" flight, differing in character from that of other Accipiters.

A. albogularis is a typical Solomon Island species that has reached the Santa Cruz Islands to the southeast and Feni to the northwest. According to Mayr (1945) *A. albogularis* should occur only on Vanikoro and Utupua in the Santa Cruz group, but Hadley found it on all the islands that he visited (Hadley and Parker, 1965). Although the Santa Cruz Islands have several bird species in common with the Solomon Islands, the fauna of this archipelago generally has more affinity with southern Melanesia.

Galbraith and Galbraith (1962) have given an outline of the avifaunal geography of the Solomon Islands and it is interesting to compare the distribution of *A. albogularis* and *A. novaehollandiae* with their findings. The division into three main districts, Main Chain (Bougainville to Malaita), new Georgia group, and San Cristoval, is clearly recognizable. *A. albogularis* is represented by a separate subspecies in each district, *woodfordi* in the Main Chain, *gilvus* in the New Georgia group, and *albogularis* on San Cristoval. *A. novaehollandiae* has a well-defined subspecies in the New Georgia group (*rubianae*), and is lacking on San Cristoval. Within the Main Chain Galbraith and Galbraith recognize three zoogeographic sections: Bougainville to Ysabel, Florida and Guadalcanal, and Malaita. *A. novaehollandiae* is present in all of these. Malaita and Guadalcanal each has its own race. Florida, which is included in the Guadalcanal section, shares the race *rufoschistaceus* with Choiseul and Ysabel, combined biogeographically with Bougainville.

It is noteworthy that *novaehollandiae,* although thought to have arrived more recently in the Solomons, shows much more geographic variation than *A. albogularis.* In the Main Chain it is represented by no less than four subspecies, whereas all these islands are inhabited by the same form of *A. albogularis* (i.e., *woodfordi*). It may be concluded that the differentiation of subspecies is very rapid in *novaehollandiae*, which is in accordance with the large number of races described from other parts of its range.

The greater antiquity in the Solomon Islands of *A. albogularis* as compared to *A. novaehollandiae* may be deduced from the much greater morphological gap between *A. albogularis* and its nearest relatives in the *A. rufitorques* group, from the fact that it has colonized San Cristoval and the Santa Cruz Islands, and from the fact that it is apparently being replaced by *A. novaehollandiae*. In most of the islands *novaehollandiae* is numerous and *albogularis* scarce, but on San Cristoval and the Santa Cruz Islands *albogularis* is a common bird (Mayr, 1945a; Hadley and Parker, 1965).

ACCIPITER RUFITORQUES (PEALE)

DISTRIBUTION

Fiji Islands (Map 19, p. 154).

PLUMAGE

Adult.—Upperparts delicate gray with a broad light rufous nuchal collar. Underparts light rufous, less saturated in tinge than nuchal collar and lightly suffused with pearl gray. In some specimens, especially females, faint light crossbars are present on the breast and abdomen. Thighs gray-rufous. Throat white. Tail gray without crossbars.

Juvenile.—Above brown with rufous feather edges, which become obsolete with wear. The edges are very broad in the nuchal region, giving the appearance of a light collar. Underparts creamy white, somewhat variable in tinge, marked with dark brown drops giving way to bars on the flanks. In some birds a few irregular bars are present on the abdomen. Thighs with wavy rufous bars. Tail light brown with faint dark bars.

The juvenile plumage is much lighter, with a more rufous tinge, than in *haplochrous*. It shows a remarkable similarity to the juvenile plumage of *A. fasciatus polycryptus* and *A. f. dogwa*. Generally speaking these forms have the upperparts a little lighter, the streaks on the breast more elongated, and the abdomen more distinctly barred. *A. rufitorques* tends to have fewer bars on the distal half of the primaries than *A. fasciatus*.

SIZE AND STRUCTURE

Size medium. Tarsus and toes of moderate length, rather heavy. Claws medium. Bill heavy. Wing medium and pointed. Tail very short. Figure 19, p. 157. Tables 60 and 61.

The difference between the sexes is significant for the hind claw (smaller in male) and tail (shorter in male).

Bill and feet, wing and tail.—These are very similar to those struc-

TABLE 60
Wing length in *Accipiter rufitorques.*

SEX	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
♂	201.7	4.29	1.29	195 - 207	11
♀	236.7	5.59	2.11	230 - 243	7
				Total	18

tures in *A. albogularis* except for the relatively shorter hind claw, wing tip, and tail.

Habitat, Hunting Behavior, and Food

A. rufitorques is the only Accipiter on Fiji; presumably it inhabits a wide variety of habitats from forest to open country with scattered trees. It feeds upon various small animals such as lizards, large insects, and crustaceans. Numerous hard black seeds were found in the gizzard of a specimen. The stomach of another specimen contained the remains of a small bird as well as a number of insects (Wood, 1926).

Discussion

Mayr (1957) has argued that *A. rufitorques* is not conspecific with *A. fasciatus,* as was formerly thought, but instead belongs to a more easterly group of forms, which he calls the *rufitorques* group. The other species of this group are *A. melanochlamys, A. albogularis,* and *A. haplochrous.* The species of the *rufitorques* group resemble each other in proportions and in juvenile plumage. They have a more eastern distribution than have *A. fasciatus* and *A. novaehollandiae.*

Although I agree with Mayr that *A. rufitorques* is more closely related to the other species of the *rufitorques* group than to *A. fasciatus,* it cannot be denied that it shows a resemblance to *A. fasciatus* in plumage and structure of the wing. Other species of the group also have some features in common with *A. fasciatus,* e.g., the rufous collar, the juvenile plumage, and the pointed wing. In my opinion these

TABLE 61
Relative measurements in percent of wing length in *Accipiter rufitorques.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	26.29	15.13	8.10	7.88	71.42	29.18	13.82
♂	+0.24	-0.27	-0.22	-0.14	-0.89	+0.27	+0.39
♀	-0.24	+0.27	+0.22	+0.14	+0.89	-0.27	-0.39
Adult	-0.65	-0.19	+0.02	-0.05	-1.14	+0.12	-0.21
Juvenile	+0.65	+0.19	-0.02	+0.05	+1.14	-0.12	+0.21
P model	0.093	0.825	0.255	0.595	0.800	0.913	0.251
P sex	0.156	0.126	0.025	0.111	0.045	0.600	0.236
n	13	13	15	15	17	18	18
df	9	9	11	11	13	14	14

resemblances indicate that the *rufitorques* group is related to *A. fasciatus.* This conclusion is supported by geographical arguments. The Melanesian islands were undoubtedly colonized from Australia and New Guinea. There we find at present two species whose ancestors may have taken part in this colonization, viz., *fasciatus* and *novaehollandiae.* Both have proved to be successful colonists. In the discussion of *novaehollandiae* it was shown that they had a common origin. Therefore, by assuming that the *rufitorques* group originated from the same stock, we get a logical explanation for the existence of three largely allopatric groups of more or less similar, medium-sized goshawks in Australasia. The marginal overlap between these groups has arisen secondarily by double colonizations, such as the colonization of New Caledonia by *A. fasciatus* and of the Solomon Islands by *A. novaehollandiae.*

No species of the *rufitorques* group is present on New Britain. Probably a former representative of this group on the island was eliminated by the subsequent arrival of *A. novaehollandiae.* In this respect it is noteworthy that *A. albogularis* flourishes on Feni Island, close to New Ireland, where *A. novaehollandiae* does not occur, and that in the Solomon Islands *A. novaehollandiae* may be replacing *A. albogularis.* Also in New Guinea *A. melanochlamys,* presumably the older form, is a rare mountain bird while *A. novaehollandiae* is numerous all over the lowlands.

ACCIPITER HAPLOCHROUS SCLATER

DISTRIBUTION

New Caledonia and adjacent islands (Map 19, p. 157).

PLUMAGE

Adult.—Upperparts slate black without a trace of a rufous collar. Lower breast, abdomen, and thighs white. Throat and upper breast as black as the back. In some specimens these parts are barred white or plain white (Sarasin, 1913). Upperside of tail plain black.

Juvenile.—Above very dark brown with the feathers narrowly edged lighter. Underparts creamy white with a pattern of dark brown streaks and drops on the breast and transverse bars on abdomen, flanks, undertail coverts, and thighs. Tail brown with numerous narrow dark bars.

SIZE AND STRUCTURE

Size medium. Tarsus long and heavy. Toes short and sturdy. Claws medium. Bill heavy. Wing medium and pointed. Tail short. Figure 20. Tables 62 and 63.

The difference between the sexes is significant for wt–6 (longer in male).

Bill and foot.—These structures are of the *tachiro*-type. The hind

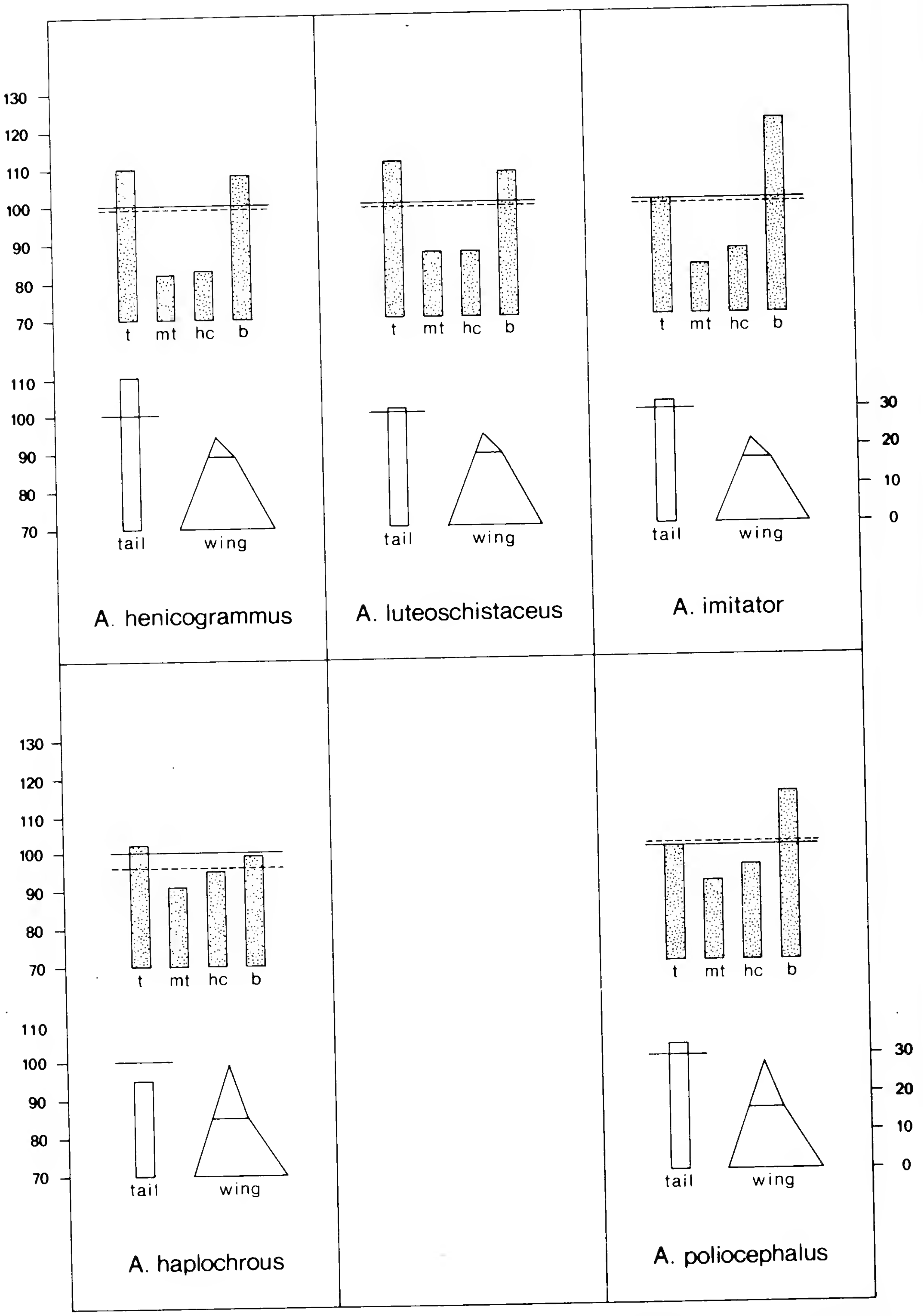


FIG. 20. Structure of *Accipiter henicogrammus*, *A. luteoschistaceus*, *A. imitator*, *A. haplochrous*, and *A. poliocephalus*.

TABLE 62
WING LENGTH IN *Accipiter haplochrous.*

SEX	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
♂	204.0	5.00	1.89	199 - 209	7
♀	236.5	4.93	1.49	228 - 244	11
				Total	18

claw is rather small. Similar to *A. tachiro toussenelii* and particularly to *A. melanochlamys.*

Wing and tail.—Of the *brevipes*-type. Similar to *A. albogularis* but wing tip slightly shorter.

HABITAT AND FOOD

Inhabits lowland and mountain forest up to 1,000 m. The sympatric form *A. fasciatus vigilax* occurs mainly in more open country. The food of *haplochrous* comprises rather large birds, such as parrots, pigeons, and domestic poultry, but also mice, lizards, grasshoppers and other insects (Mayr, 1945a). In the stomach of a juvenile collected by Sarasin (1913), and wrongly identified by him as *A. fasciatus* (specimen examined), grasshoppers were found.

DISCUSSION

As in *A. albogularis,* the long and pointed wing tip is peculiar for an Accipiter allegedly living in the forest. Presumably *A. haplochrous* also has a somewhat aberrant type of flight.

Although more different from the other species of the *rufitorques* group than these are from each other, *A. haplochrous* is clearly related to this group of species (Mayr, 1957). Its place in the avifauna of New Caledonia is similar to that of *A. albogularis* in the Solomon avifauna. In the Solomons *A. albogularis* inhabits the forest and *A. novaehollandiae* the more varied types of country; in New Caledonia *A. haplochrous* is the forest bird and *A. fasciatus* lives in bush and open

TABLE 63
RELATIVE MEASUREMENTS IN PERCENT OF WING LENGTH IN *Accipiter haplochrous.*

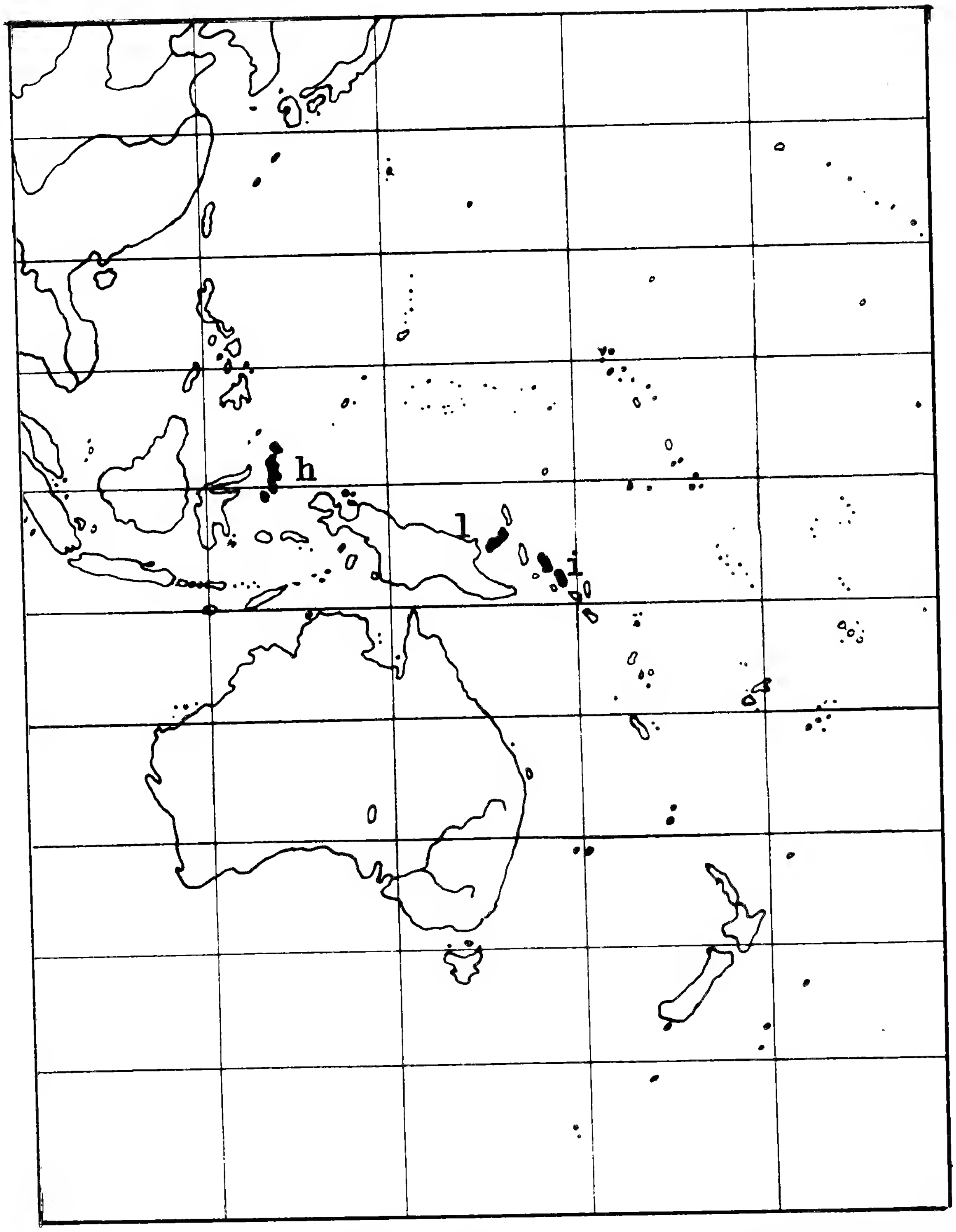
	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	27.51	14.55	7.79	7.35	72.39	29.44	14.44
♂	+0.29	-0.02	-0.02	-0.04	-0.38	+0.20	+0.86
♀	-0.29	+0.02	+0.02	+0.04	+0.38	-0.20	-0.86
Adult	-0.39	-0.19	-0.06	+0.04	-0.89	-0.02	-0.21
Juvenile	+0.39	+0.19	+0.06	-0.04	+0.89	+0.02	+0.21
P model	0.060	0.864	0.807	0.997	0.822	0.883	0.821
P sex	0.102	0.975	0.082	0.811	0.619	0.738	0.002
n	14	13	16	16	18	17	18
df	10	9	12	12	14	13	14

country. The extensive grasslands in the lowlands of New Caledonia are of recent origin, having developed as a consequence of man's presence in the island (Sarasin, 1917). Accordingly, *A. fasciatus* may be considered a recent invader to the island whereas *A. haplochrous* belongs to an old endemic New Caledonian fauna.

ACCIPITER HENICOGRAMMUS (G. R. GRAY)

DISTRIBUTION

Northern Moluccas (Map 20).



MAP 20. Distribution of *Accipiter henicogrammus* (h), *A. luteoschistaceus* (l), and *A. imitator* (i).

PLUMAGE

Adult.—Above dark slate gray; in some females there is a brown wash. Throat dark gray mottled chestnut and white. Sides of upper breast dark slate, as on back. Rest of underparts cinnamon-chestnut, regularly and narrowly barred white. In several specimens the white lines become obsolete on the breast, the chestnut forming an almost solid breast shield. Tail dark gray, with numerous blackish crossbars, inconspicuous above and distinct below.

Juvenile.—Upperparts very dark brown, broadly barred and spotted creamy white or pale brown. The feathers of the back have a narrow terminal rufous line, a subterminal dark brown bar, followed proximally by some white and brown bars. The scapulars and secondaries are regularly barred dark and light brown. Creamy white below; regularly barred from chest to undertail coverts. The bars are blackish brown on the breast becoming more chestnut toward the abdomen. Throat white with blackish spots. Tail light brown with numerous dark bars.

This type of juvenile plumage, which is barred above and below, is very peculiar for an Accipiter and only known in *A. henicogrammus* and *A. luteoschistaceus*. *A. luteoschistaceus* differs strongly from *A. henicogrammus* in adult plumage. The differences between the adult plumage of *A. henicogrammus* and those of paler sympatric *A. novaehollandiae griseogularis* are listed by Kuroda (1954).

SIZE AND STRUCTURE

Size medium to rather large. Tarsus long. Toes short. Claws small. Bill heavy. Wing short and rounded. Tail long. Figure 20, p. 164. Tables 56 and 57, pp. 155-156.

No statistical analysis made.

Bill and foot.—These are of the *trinotatus*-type. Owing to the longer wing, all comparable measurements appear smaller than in *A. trinotatus*. Closely similar to *A. luteoschistaceus*.

Wing and tail.—Similar to the *tachiro*-type.

HABITAT AND FOOD

Observed in forest and at the forest edge from the foot of mountains up to 1,300 m. The stomachs of two specimens contained lizards (twice) and grasshoppers (once) (Heinrich, 1956).

DISCUSSION

The juvenile of *A. henicogrammus* differs from almost all other juvenile Accipiters by being strongly barred above and below. A similar juvenile plumage is only found in *A. luteoschistaceus*. In structure *A. henicogrammus* resembles *A. luteoschistaceus* and *A. imitator*, which are also isolated species with very restricted insular ranges. In addition, some insular races of *A. novaehollandiae* have a structure which is more or less similar to that of *A. henicogrammus,* although with a shorter tarsus and heavy bill. Also, in adult plumage *A. henicogrammus* resembles some Solomon Islands races of *A. novaehollandiae.* Brown and Amadon (1968) are doubtful as to whether *henicogrammus* or *griseogularis* is the northern Moluccan representative of *A. novaehollandiae.* Previously it was argued that *A. n. griseogularis* is allied with *A. n. leucosomus,* but this does not exclude the possibility that *A. henicogrammus* has affinities to *A. novaehollandiae* or to the other species of the *fasciatus-novaehollandiae-rufitorques* complex. Probably it is an old isolate from this complex, living at present side by side with younger *griseogularis.*

It may be noted that these forms apparently occupy different niches, *griseogularis* being a bird of varied country and cultivation, and *henicogrammus* a forest bird. Stomach analyses revealed a rat and a megapode as prey of *griseogularis,* whereas *henicogrammus* presumably takes mainly lizards and insects, as do other Accipiters with bills and claws of the *trinotatus*-type.

ACCIPITER LUTEOSCHISTACEUS ROTHSCHILD AND HARTERT

DISTRIBUTION

Endemic to New Britain Island (Map 20, p. 166).

PLUMAGE

Adult male.—Upperparts black with a brown hue. Underparts pale buff, with narrow and widely spaced faint gray bars on the breast. Sides of face dark gray. Upperside of tail blackish brown.

Adult female.—Differs greatly from male (Stresemann, 1929). Crown and nape blackish brown, sharply contrasting with the back. Interscapular region mottled tawny and dark brown. Balance of upperparts, including wings and tail, smoky brown. Venter buff, slightly paler toward the undertail coverts, with narrow and widely spaced light brown bars on the breast. Sides of face dark gray.

Juvenile.—Crown and nape blackish brown with narrow rufous feather edges, contrasting with the back. Back and upperwing coverts barred with dark brown and tawny, every feather having a narrow terminal rufous edge and a broad subterminal brown bar. Upperbreast spotted dark brown on pale buff ground. Remainder of underparts pale buff with narrow, widely spaced rufous brown bars. Dorsum of tail tawny with narrow brown bars.

SIZE AND STRUCTURE

Size rather small. Tarsus long and slender. Toes short. Claws very small. Bill very heavy. Wing short and rounded. Tail short. Figure 20, p. 164. Tables 56 and 57, pp. 155-156.

No statistical analysis made.

Bill and foot.—Of the *trinotatus*-type. Owing to the longer wing all measurements appear smaller than in *A. trinotatus.*

Wing and tail.—These are of the *novaehollandiae*-type but with a comparatively long tail. Resemble *A. novaehollandiae pulchellus.*

HABITAT AND FOOD

Found in tall open forest, on the ground or perched in a tree. One stomach contained a lizard (Gilliard and Lecroy, 1967).

DISCUSSION

In structure *A. luteoschistaceus* is similar to *A. henicogrammus* and *A. imitator.* In juvenile plumage it resembles *A. henicogrammus;* in adult plumage there is some resemblance to forms of the *A. rufitorques* group that lack the rufous collar. Despite these similarities there are no close affinities to the species mentioned. *A. luteoschistaceus* is a rather isolated species with a very restricted range. It may be considered an old element of the New Britain avifauna. Similar old endemics are found in several other groups of animals.

ACCIPITER IMITATOR HARTERT

DISTRIBUTION

Choiseul and Ysabel, Solomon Islands (Map 20, p. 166).

PLUMAGE

Adult.—Upperparts jet black. Throat and upper breast very dark gray with broad jet black terminal bars to the feathers. Remainder of underparts white. Tail black, without bars. A variant exists in which the throat and breast are white, not black (Mayr, 1957).

Juvenile.—Feathers of crown white with narrow black tips. Hind neck mottled rufous, back fuscous with narrow rufous feather edges. Throat and breast finely barred rufous. Abdomen, lower flanks, and thighs buff, in some specimens with rufous vermiculation, in others unmarked. Tail brownish gray with indistinct narrow black bars. (Description after Mayr, 1957.)

Mayr lists the differences between *imitator* and *eichhorni* showing that they are unrelated, contrary to Hartert's opinion (1926); the latter united both forms in a single species on account of the structure of the legs and feet. *A. imitator* differs from *A. luteoschistaceus* in a number of plumage and structural characters. The upperparts of the adult are jet black, not slate or brownish. The throat and breast are either black or white, not faintly barred. The tail is entirely unbarred, not patterned with faint bars ventrally. In juvenile plumage *luteoschistaceus* has a pattern of streaks on the throat and breast, whereas *imitator* has crossbars up to the throat. The upperparts of *imitator* show nothing of the peculiar crossbarring, which is characteristic of *luteoschistaceus.*

The primaries and tail feathers are much less distinctly barred and on a browner, less rufous background.

Size and Structure

Size rather small. Tarsus of medium length, slender. Toes short. Claws very small. Bill very heavy. Wing very short and rounded. Tail short. Figure 20, p. 164. Tables 56 and 57, pp. 155-156.

No statistical analysis was made because only two adult females were examined.

Bill and foot.—These are of the *trinotatus*-type. The species differs from *A. trinotatus* in having a shorter tarsus and middle toe and a smaller claw. In no other Accipiter is the bill so much larger than the hind claw.

Wing and tail.—These are similar to *A. luteoschistaceus,* but the wing tip is shorter.

Discussion

Nothing has been recorded about the ecology and the habits of *A. imitator,* but from the very short wings it may be guessed that it is a bird of dense forest. Structurally it resembles *A. luteoschistaceus* and *A. henicogrammus.* In adult plumage it is similar to *A. haplochrous* and as in that species has white breasted and black breasted forms. Its juvenile plumage is peculiar. Its range is very restricted and it may be considered a relict.

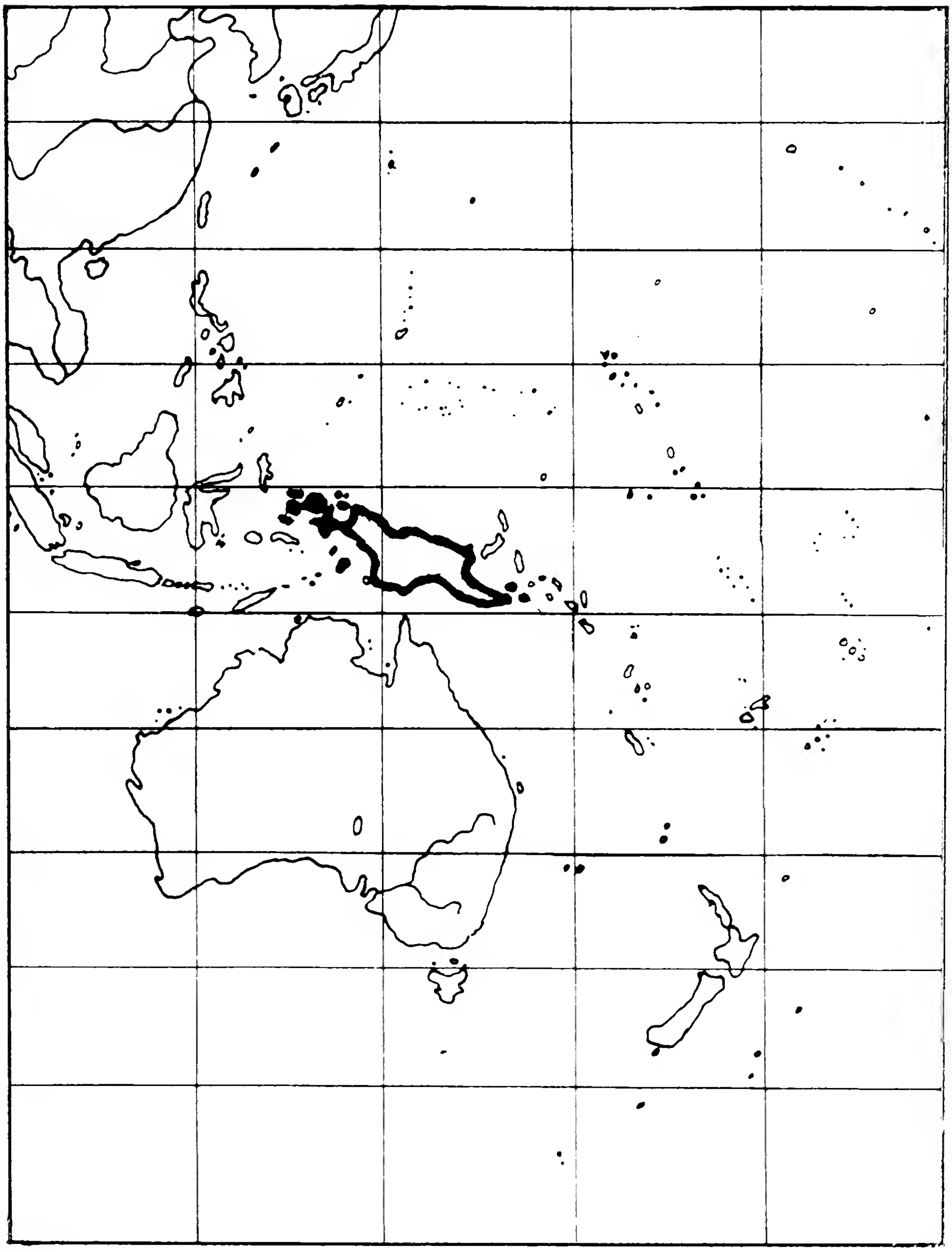
Apparently in the islands surrounding New Guinea a chain of such relict species is found: *henicogrammus-luteoschistaceus-imitator.* All these show distant affinities to the *fasciatus-novaehollandiae-rufitorques* complex. They are probably the scattered remains of a first series of colonizations by this complex into the Australasian island realm. Altogether we can discern three such waves of colonization, the first comprising the three mentioned relict species, the second resulting in the *rufitorques* group, and the third involving the spread of *fasciatus* and *novaehollandiae* to many oceanic islands.

Only on Ysabel and Choiseul islands do we find representatives of all three groups, viz., *A. imitator, A. albogularis woodfordi, A. novaehollandiae rufoschistaceus.* It would be very interesting to study the comparative ecology of these forms. It is remarkable that *A. imitator* and *A. n. rufoschistaceus* resemble each other rather closely in structure, although *rufoschistaceus* is a little larger. If the resemblance in structure is the reflection of a similarity in ecology, one would like to know if there is any competition between these forms or whether they avoid competition by differences in habitat or in local distribution.

Accipiter poliocephalus G. R. Gray

Distribution

New Guinea and surrounding islands (Map 21).



Map 21. Distribution of *Accipiter poliocephalus.*

Plumage

Adult.—Head, hindneck, and interscapulary region pale gray, contrasting with the dark gray of the remainder of the upperparts. Upper breast very light gray, faintly and narrowly barred in some specimens. Remainder of underparts white. Tail dark gray without bars above and lighter with obsolete dark bars below.

Juvenile.—Upperparts dark gray with a slight brownish hue and narrow ochraceous feather edgings, which may be nearly absent. Interscapulary region mottled white. Underparts white patterned with brown-gray darts in the centers of the feathers. On the flanks and the sides of the breast the pattern is more transverse, consisting of dumbbells and arrowheads. Tail gray without bars on the central rectrices and with numerous obsolete dark bars on the outer feathers.

Another type of juvenile plumage is much browner above. All contour feathers and also the primaries are light brown with broad ochraceous edgings. Tail lighter than in the other type.

Two specimens in the Leyden Museum, both from the Aru Islands, show the brown type of juvenile plumage. The other type is represented by a small series from the Vogelkop Peninsula and the island of Batanta. A specimen from Misool is intermediate. Although the material is far too limited to draw definite conclusions, it is possible that the juvenile plumage varies geographically.

Size and Structure

Size rather small to medium. Tarsus long. Toes and claws short. Bill very heavy. Wing medium and pointed. Tail medium. Figure 20, p. 164. Tables 56 and 57, pp. 155-156.

No statistical analysis made.

Bill and foot.—Of the *trinotatus*-type. Tarsus relatively shorter than in *A. trinotatus.* Resembles several races of *A. novaehollandiae,* e.g., *rufoschistaceus* and *hiogaster.*

Wing and tail.—The wings are intermediate between the *brevipes*-type and the *minullus*-type, but the tail is longer than both. General resemblance to *A. albogularis,* although the wing tip is shorter.

Habitat and Food

Inhabits broken country such as clearings near houses, native gardens, second-growth, and, more rarely, primary forest. The altitudinal range is from sea level to 1,000 m. For an Accipiter *A. poliocephalus* is slow in its movements (Mayr and de Schauensee, 1939). It preys mainly on lizards but snakes and insects are also taken. In six stomachs the following prey items were found: lizards (4 times), snakes (twice), and insects (twice) (Rothschild, Stresemann, and Paludan, 1932; Mayr and Rand, 1937).

Discussion

A. poliocephalus does not show a close similarity to any other Accipiter except adult *A. princeps.* A pale gray plumage without rufous pigments is indeed found in *A. n. novaehollandiae,* but this form is quite different in size and structure and in the pattern of the juvenile. On account of the resemblance in adult plumage, Mayr (1934) considers *poliocephalus* and *princeps* as close relatives. As long as the juvenile plumage of *princeps* is unknown this hypothesis remains somewhat speculative.

Regardless of whether or not *poliocephalus* is related to *princeps,* its affinities to other species of the genus are obscure. It is an old New Guinea species which has been isolated so long that its distributional history cannot be reconstructed.

AUSTRALASIA

ACCIPITER PRINCEPS MAYR

DISTRIBUTION

Endemic to New Britain, Bismarck Archipelago. Originally described from three adults taken in the mountains near Wide Bay (Mayr, 1934). Recently Diamond (1971) observed and collected the species on Mt. Talawe.

PLUMAGE

No specimens were available for study, but D. Amadon of the American Museum of Natural History has kindly sent me a photograph of the adult female. The following description is based on the original description by Mayr: upperparts slate gray, sides of head and neck lighter. The sides of the neck are very light, forming an interrupted light nuchal collar. Underparts white with a slight gray wash or indistinct vermiculation on the sides of the upper breast. Tail darker than back, wholly unbarred.

A. princeps resembles *A. poliocephalus* but is much larger. Mayr lists the differences, the most important of which are the fact that the head is not lighter than the back, and the absence of bars on the tail. In addition there are several differences in structure.

SIZE AND STRUCTURE

Size rather large to large. Tarsus of medium length, heavy. Toes short and sturdy. Claws medium. Bill very heavy. Wing short and rounded. Tail short.

Apparently similar to *A. poliocephalus* in the structure of the bill and feet and to *A. novaehollandiae* in the structure of the wing and tail.

DISCUSSION

The adult plumage and the structure of foot and bill suggest that *A. princeps* may be the New Britain representative of *A. poliocephalus* (Mayr, 1934). The much larger size and the structure of the wing and tail throw some doubt on this conclusion, although it is difficult to imagine affinities to any other Australasian Accipiter. Only when the juvenile plumage and the ecology of *A. princeps* become known can its relations to other species be more fully evaluated.

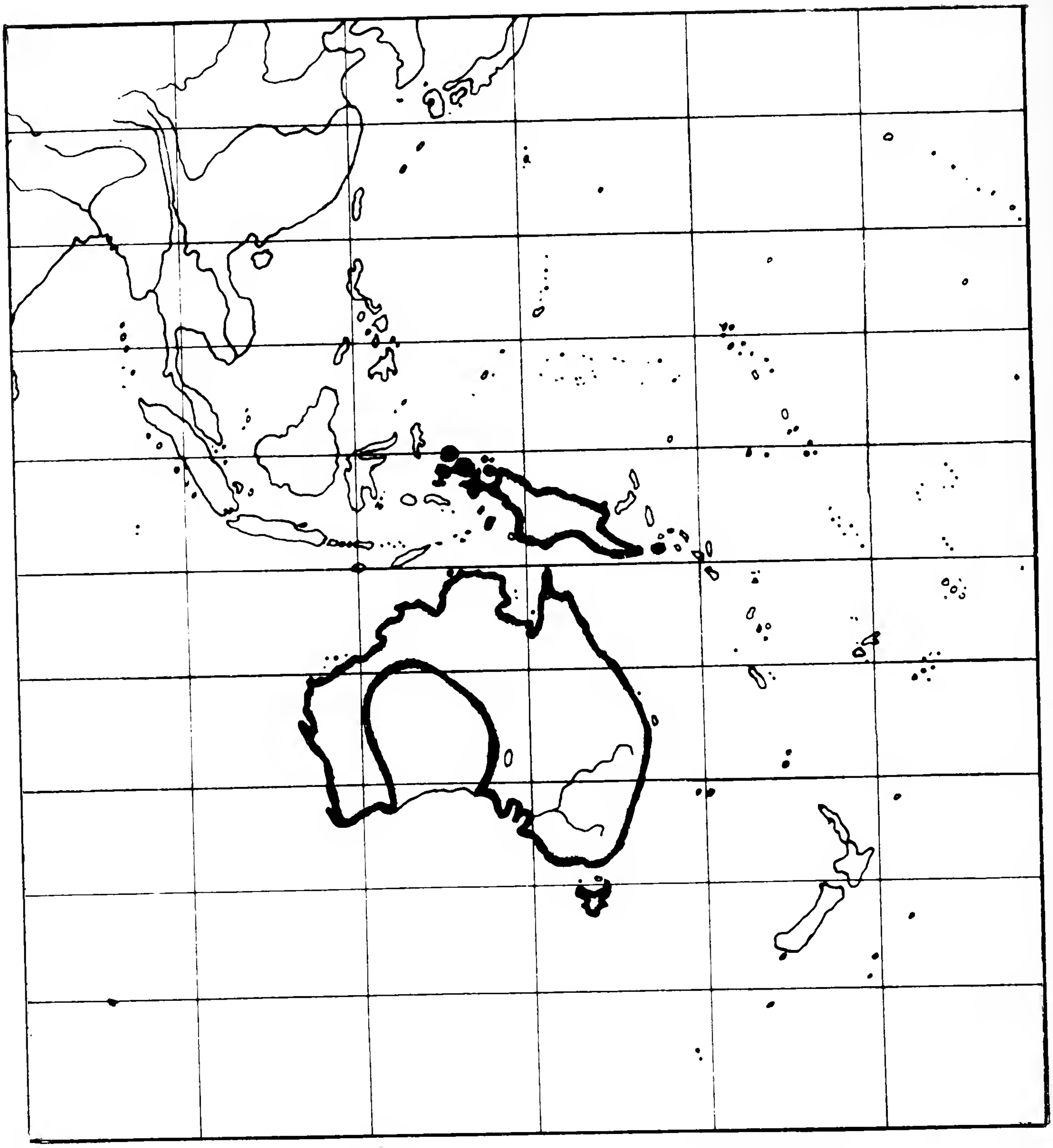
ACCIPITER CIRRHOCEPHALUS (VIEILLOT)

DISTRIBUTION

Australia, New Guinea, and adjacent islands (Map 22).

SUBSPECIES

cf. Condon and Amadon (1954). *A. c. cirrhocephalus* (Vieillot), Australia, except northern coastal districts, and Tasmania; *A. c. quaesitandus* Mathews, northern coastal Australia; *A. c. papuanus*



Map 22. Distribution of *Accipiter cirrhocephalus.*

(Rothschild and Hartert), New Guinea and adjacent islands; *A. c. rosselianus* Mayr, Rossel Island, Louisiade Archipelago.

Plumage

Adult male.—Above slate brown to slate black with an inconspicuous rufous-brown nuchal collar. Below narrowly barred rufous and white. Thighs rufous with faint white lines. Throat mottled gray and white. Tail plain gray-brown above and light gray, with numerous incomplete brown bars, below.

Adult female.—Similar to male, but dorsum paler, more brownish.

Juvenile.—Upperparts dark brown with narrow light brown or rufous feather edges. Below cream with heavy brown spots on the breast and rufous-brown bars on abdomen and flanks. The bars are wider, browner and more irregular than in adult. Thighs buffish with wavy light rufous-brown bars. Upperside of tail brown with numerous faint dark bars, underside light gray with distinct brown bars.

GEOGRAPHICAL VARIATION

A. cirrhocephalus varies geographically in size and in the intensity of the pigmentation (Condon and Amadon, 1954). *A. c. quaesitandus* is smaller and in adult plumage more rufous below than nominate *cirrhocephalus*. *A. c. papuanus* is still smaller and more strongly rufous, the rufous bars being much wider than the white ones. In juvenile plumage *papuanus* is less heavily marked than nominate *cirrhocephalus,* the markings being more tawny. *A. c. rosselianus* was described from juvenile specimens. It is much larger than *papuanus,* being about as large as the nominate subspecies. In plumage it also resembles *A. c. cirrhocephalus,* but the upperparts are darker with wider rufous edges (Mayr, 1940).

SIZE AND STRUCTURE

Size rather small to medium. Tarsus and toes long and slender. Claws fine and sharp. Bill small. Wing long and pointed. Tail medium. Figure 21. Tables 64 and 65.

The data for the closely related species *A. erythrauchen* were analysed simultaneously with those for *A. cirrhocephalus*. A single specimen of *A. c. quaesitandus* was grouped with *A. c. papuanus*. The statistical model was unsatisfactory for the wing tip. The difference between the groups is significant for all series of data that could be analysed except for tail length. The difference between the sexes is significant for the tarsus (longer in male) and hind claw (smaller in the male).

Bill and foot.—Of the *nisus*-type. *A. c. papuanus* has a relatively longer tarsus and bill than nominate *cirrhocephalus*.

Wing and tail.—These structures are of the *brevipes*-type. The wing tip is slightly shorter and the tail slightly longer than in *A. brevipes*.

TABLE 64

WING LENGTH IN *Accipiter cirrhocephalus* AND *A. erythrauchen*.

SUBSPECIES	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
			♂		
cirrhocephalus	208.4	5.01	1.22	197 - 214	17
papuanus	184	-	-	-	1
erythrauchen	166.5	-	-	162 - 171	2
ceramensis	177	-	-	-	1
			♀		
cirrhocephalus	241.0	3.77	0.92	235 - 247	17
quaesitandus	233	-	-	-	1
papuanus	219.0	-	-	217 - 221	2
erythrauchen	201.2	3.40	1.70	197 - 204	4
ceramensis	213.5	-	-	212 - 215	2
				Total	47

TABLE 65

RELATIVE MEASUREMENTS IN PERCENT OF WING LENGTH IN *Accipiter cirrhocephalus* AND *A. erythrauchen.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	28.36	17.43	7.23	6.26	72.64	31.87	15.62
cirrhocephalus	26.66	16.07	6.52	5.38	72.05	33.80	16.54
'papuanus'	27.99	16.08	6.67	6.07	72.07	33.02	16.45
'erythrauchen'	30.43	20.15	8.50	7.32	73.80	28.79	13.86
♂	+0.62	-0.03	-0.29	-0.06	+0.56	-0.52	+0.39
♀	-0.62	+0.03	+0.29	+0.06	-0.56	+0.52	-0.39
Adult	-0.09	+0.04	+0.04	-0.02	-1.35	-0.30	-0.91
Juvenile	+0.09	-0.04	-0.04	+0.02	+1.35	+0.30	+0.91
P model	0.692	0.371	0.839	0.216	0.840	0.023	0.266
P ssp	0	0	0	0	0.209	-	0.001
P sex	0.028	0.494	0.001	0.142	0.287	-	0.126
n	30	26	38	46	47	46	32
df	20	17	27	35	36	35	22

HABITAT

Inhabits forest, woodland, and scrub; varying from rather open country to closed tropical forest.

In Australia occurs generally in more or less open country with scattered trees, such as sclerophyllous woodland, scrub country, and stands of Eucalyptus along seasonal streams in arid country.

In New Guinea it is found in forest and wooded savanna from sea level to 1,800 m (Mayr, 1931b; Junge, 1953). Field notes often indicate that the species is encountered in clearings in the forest.

HUNTING BEHAVIOR

Hunts by either still-hunting or flying low over open country. A searching *A. cirrhocephalus* may attack flying birds or animals on the ground. Apparently it perches more in the open than *A. nisus,* but otherwise the hunting techniques are similar.

FOOD

The diet is predominantly small and middle-sized birds, but also taken are lizards (Mollison, 1961) and small mammals (Rand, 1942).

DISCUSSION

As in other species showing the *nisus*-type of structure, the prey of *A. cirrhocephalus* is mainly birds. The wing, which is more pointed than that of *A. nisus,* may be an adaptation to the more open habitat but *A. c. papuanus* also has a pointed wing, although it occurs on a heavily forested island. In related *A. erythrauchen,* which is a forest species, the wing tip is much shorter. However, *A. c. papuanus* became

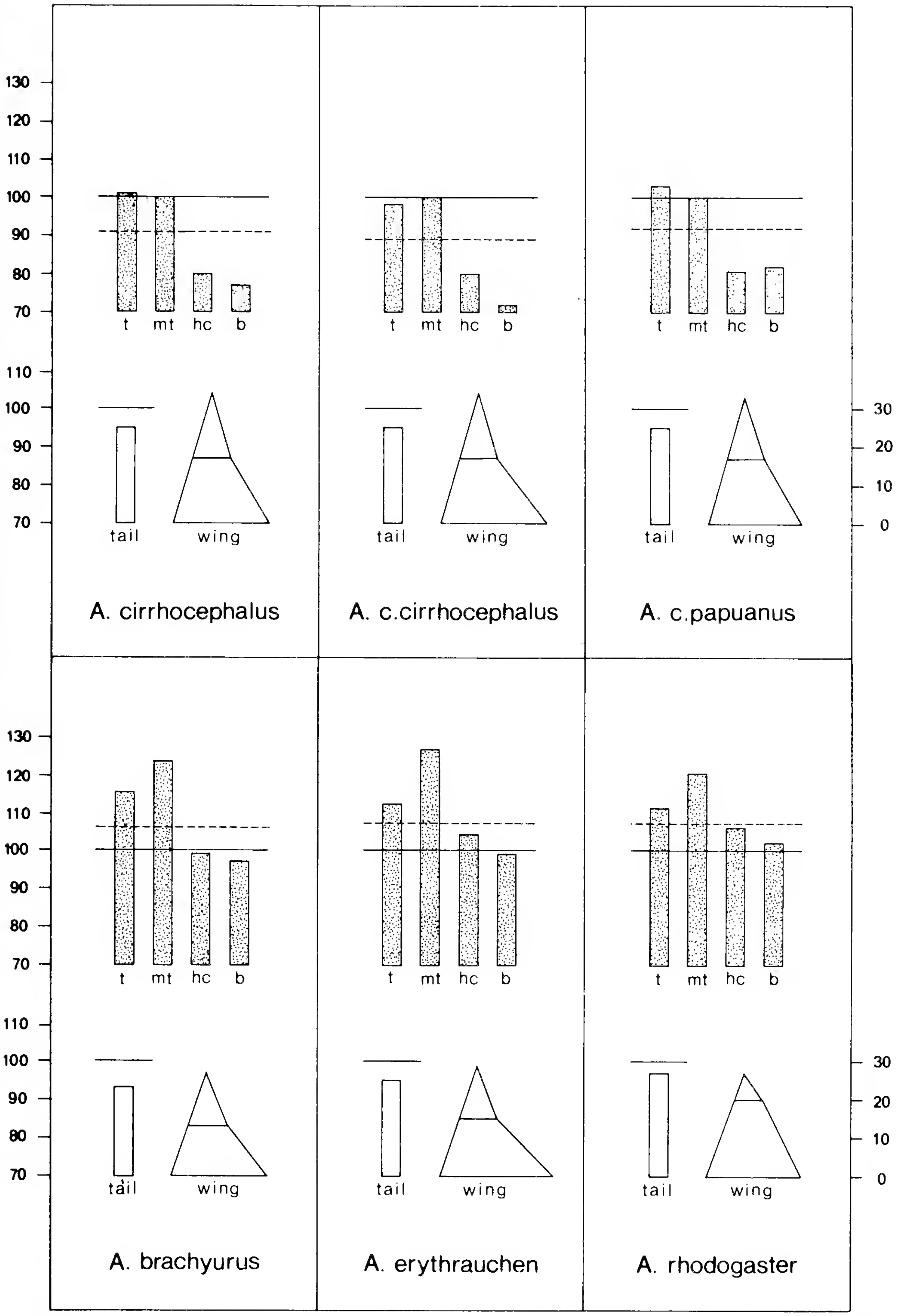


FIG. 21. Structure of *Accipiter cirrhocephalus, A. brachyurus, A. erythrauchen,* and *A. rhodogaster.*

separated from *A. cirrhocephalus* more recently than *A. erythrauchen.* In fact, New Guinea and Australia were united by the lowering of the sea at the height of the glacial periods, probably for the last time about 25,000 to 18,000 years ago. This short period may have been insufficient for adaptive change of the wing tip in *A. c. papuanus.* A full discussion of the geography of *A. cirrhocephalus* and its allies is in the section on *A. erythrauchen.*

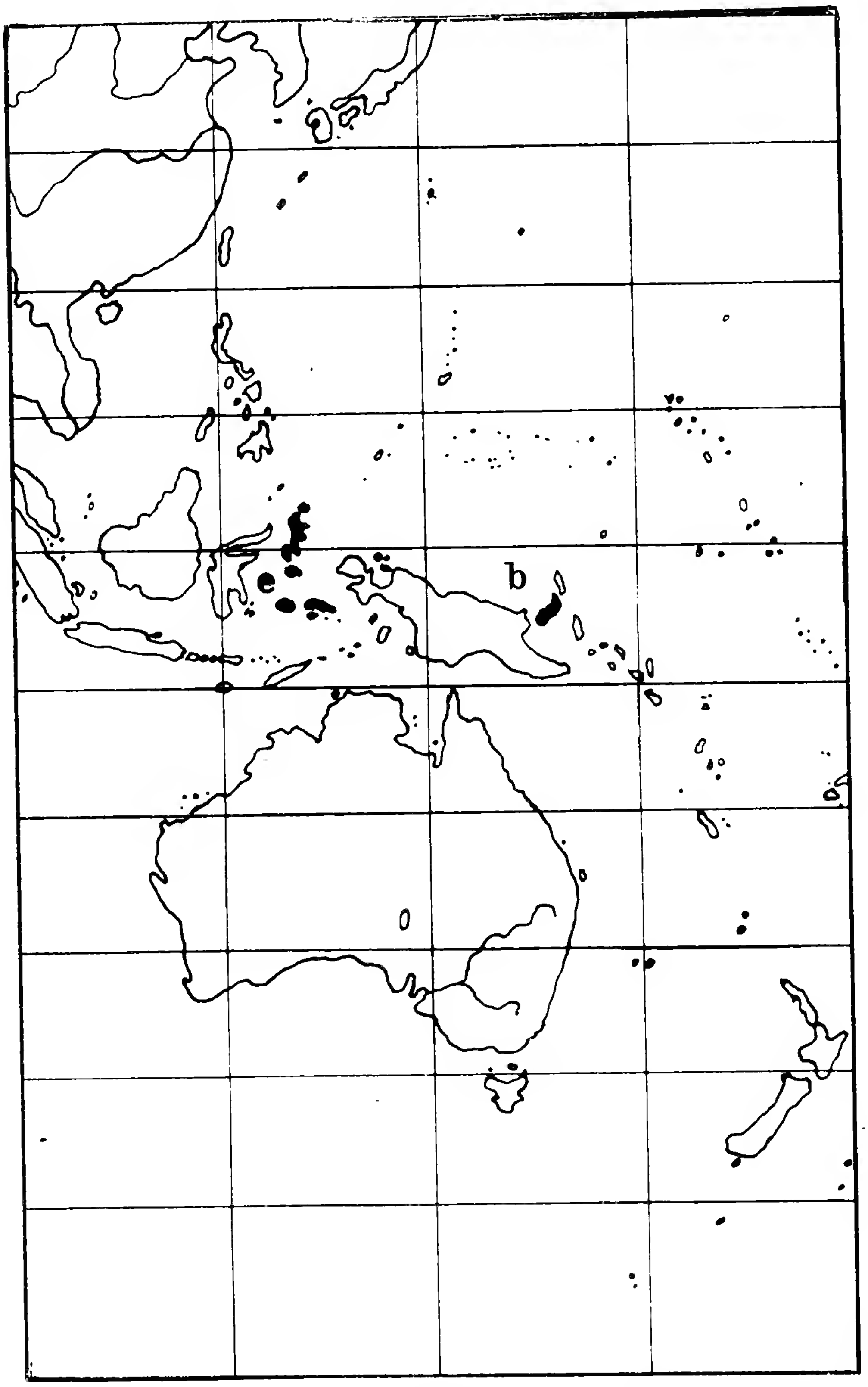
ACCIPITER BRACHYURUS (RAMSAY)

DISTRIBUTION

New Britain, Bismarck Archipelago (Map 23).

PLUMAGE

Adult.—Slate black above, in places with pearl gray lustre. Hindneck with a bright rufous collar. Underparts light pearl gray, shading



MAP 23. Distribution of *Accipiter brachyurus* (b) and *A. erythrauchen* (e).

to white on the abdomen and undertail coverts. Sides of upper breast faintly rufous. Thighs gray. Tail slate gray, lighter below, with no trace of bars.

Juvenile.—Crown black with narrow rufous edges to the feathers. Back and mantle rufous with dark centers to the feathers. Underparts buffy white with brown streaks on upper breast, drops and arrowheads on abdomen. Thighs with wavy brown bars. Tail rufous with numerous narrow dusky bars (Brown and Amadon, 1968).

The adult plumage is similar to adult *A. erythrauchen ceramensis,* but differs in being darker above and lighter below and in lacking the faint bars on the tail.

SIZE AND STRUCTURE

Size rather small to small. Tarsus and toes long and slender. Claws delicate and sharp, rather long. Bill moderately heavy. Wing medium and pointed. Tail very short. Figure 21, p. 177. Tables 56 and 57, pp. 155-156.

Only a single specimen could be studied, precluding a statistical analysis.

Bill and foot.—These are of the *nisus*-type, resemble *A. erythrauchen,* but the hind claw is slightly smaller.

Wing and tail.—Of the *minullus*-type and resembling *A. erythrauchen,* except that the tail and wing tip are shorter.

DISCUSSION

Nothing is known of the habitat and habits of this rare species. As it is similar to *A. erythrauchen* in structure and plumage, it may be presumed that it is a bird-hunter of dense forest. The affinities to *A. cirrhocephalus* and *A. erythrauchen* are discussed in the section on *A. erythrauchen.*

ACCIPITER ERYTHRAUCHEN G. R. GRAY

DISTRIBUTION

Moluccas (Map 23, p. 178).

SUBSPECIES

cf. Van Bemmel (1948). *A. e. erythrauchen* G. R. Gray, northern Moluccas; *A. e. ceramensis* (Schlegel), southern Moluccas.

PLUMAGE

Adult.—Slate black above with a dark rufous nuchal collar. Breast rufous or pearl gray with a rufous wash. Abdomen rufous or rufous and gray with faint white bars.

Juvenile.—Upperparts brown with wide brownish red feather edges. Edges very conspicuous in nuchal region, forming somewhat of a collar.

Below cream boldly streaked with dark brown. Tail brown with numerous dark bars.

Geographical Variation

A. erythrauchen varies in size, the nominate form being smaller than the race *ceramensis*. In addition, *ceramensis* is grayer below in adult plumage and has wider rufous feather edges dorsally in the juvenile.

Size and Structure

Size small to rather small. Tarsus and toes very long and slender. Claws and bill quite heavy. Wing medium and pointed. Tail short. Figure 21, p. 177. Tables 64 and 65, pp. 175-176.

For statistical analysis the taxon is combined with A. *cirrhocephalus* (p. 175).

Bill and foot.—These are of the *nisus*-type, resembling *cirrhocephalus* in proportions, but they are relatively larger. This cannot be attributed entirely to the short wing, as the bill and feet are actually large in relation to the size of the bird itself.

Wing and tail.—Intermediate between the *minullus*- and *brevipes*-types, and resembling the Asiatic races of *A. badius*. The wing tip is decidedly shorter than in *A. cirrhocephalus*.

Habitat, Hunting Behavior, and Food

Inhabits forest from sea level up to 1,400 m (Stresemann, 1914). Presumably its principal prey is birds. Van Dedem (1911) observed it chasing a lory (*Eos bornea*).

Discussion

The long tarsus and toes might indicate that the prey consists of birds, as it is in *A. nisus* and other species with similar structures. The shorter wing than that found in *A. cirrhocephalus* may be related to the forest habitat.

A. erythrauchen, A. cirrhocephalus, and *A. brachyurus* form a group of closely related species that are Australasian in distribution. Morphologically the group is characterized by a dark gray dorsum with a rufous collar, a wing in which the sixth primary is about equal to or shorter than the second, and a bill and feet of the *nisus*-type. *A. brachyurus* and *A. erythrauchen* are the forest representatives of this group, *A. cirrhocephalus* is primarily a species of more open, arid country. In this respect it is interesting that the difference between *A. cirrhocephalus,* on the one hand, and *erythrauchen* and *brachyurus,* on the other, is paralleled in *A. minullus*. In that species the savanna forms (*minullus* and *tropicalis*) are barred below, the forest forms (*erythropus* and *zenkeri*) are plain rufous or gray. A tendency for the bars to merge into a plain rufous venter is also found in the New Guinea race *A. c. papuanus,* which lives principally in the forest.

For the balance, *A. c. papuanus* is most similar to the northern Australian form *A. c. quaesitandus;* previously it was argued that the ranges of these two forms may have been contiguous in the recent past. As neither the Moluccas nor New Britain were ever connected to New Guinea, the ancestors of *A. erythrauchen* and *A. brachyurus* must have reached these islands by overseas colonization. The striking resemblance of *A. brachyurus* to *A. erythrauchen ceramensis* is presumably due to parallel evolution under similar environmental conditions, and certainly is not because of any direct relationship.

Because nearly all races belonging to this group inhabit islands and are, therefore, completely isolated, it is impossible to prove whether any of them has already attained specific status. Owing to their differences in plumage and structure and to their isolation, I have preferred to keep *erythrauchen* and *brachyurus* specifically separated from *cirrhocephalus,* as did Peters (1931) and Brown and Amadon (1968).

ACCIPITER MEYERIANUS (SHARPE)

DISTRIBUTION

Small islands from the Moluccas to the Solomon Islands (Map 6, p. 55). A single specimen is known from the Krätke Mountains in eastern New Guinea (Amadon, 1964). Very scarce in collections.

According to Meyer (1927) the species is not rare on the northern Gazelle Peninsula, New Britain. Among the local inhabitants it is known as the "sparrow hawk of the southeast monsoon," which would imply that it is a dry season visitor in that region. It is possible that *A. meyerianus* shows local migrations, but Meyer could not confirm this.

PLUMAGE

Adult.—Upperparts black to very dark brown-gray. Underparts white with brown-gray bars and narrow shaft streaks. The amount of barring is reduced in some specimens which are much whiter below than others (Amadon, 1964). Other individuals are melanistic, except for faintly lighter bars on the primaries and rectrices. Tail normally plain black above, gray below.

Juvenile.—Above brown with narrow rufous feather edges. Below deep cinnamon with blackish brown streaks or drops on the feathers.

In adult plumage *A. meyerianus* is considerably darker on the upperside, but the remainder of the bird is very similar to *A. gentilis.* Juveniles resemble juvenile *melanoleucus* and rufous types of juvenile *gentilis.*

SIZE AND STRUCTURE

Size very large. Tarsus and toes short and sturdy. Claws and bill heavy. Wing long and rounded. Tail short. Figure 10, p. 57. Tables 56 and 57, pp. 155-156.

No statistical analysis was made, as only three specimens were studied.

Bill and foot.—Of the *gentilis*-type. Middle toe, hind claw, and bill larger in relation to the tarsus than in *A. gentilis*. In the longer middle toe and larger hind claw *A. meyerianus* shows a transition from the structure of *A. gentilis* to that of *A. buergersi.*

Wing and tail.—These are of the *nisus*-type. Tail much shorter than in *A. n. nisus*. In this respect *A. meyerianus* resembles *A. gentilis.*

HABITAT AND FOOD

Inhabits lowland and mid-mountain forest. A large bird was once recorded as prey (Rand and Gilliard, 1967).

DISCUSSION

A. meyerianus is similar to *A. gentilis.* On account of this resemblance Kleinschmidt (1922-23) concluded that the species are closely related and that *A. meyerianus* is a tropical representative of *A. gentilis.* Both are separated, however, by a wide gap in which no species of the *A. gentilis* group occur. This gap spans the great distance between the Palearctic and the Australasian fauna.

A hypothesis that may account for this singular type of distribution is that a group of stragglers of *A. gentilis* settled in Melanesia. If this took place during a glacial period, the difference in climate between northern Melanesia and the Palearctic was probably less than at present. The slight differentiation of *A. meyerianus* may indicate that it has not been isolated for long. It differs less from *A. gentilis* than does *A. melanoleucus,* the tropical African representative of this species group. It is remarkable that a species with such a wide distribution in the islands to the north, west, and east of New Guinea should be virtually absent in New Guinea proper.

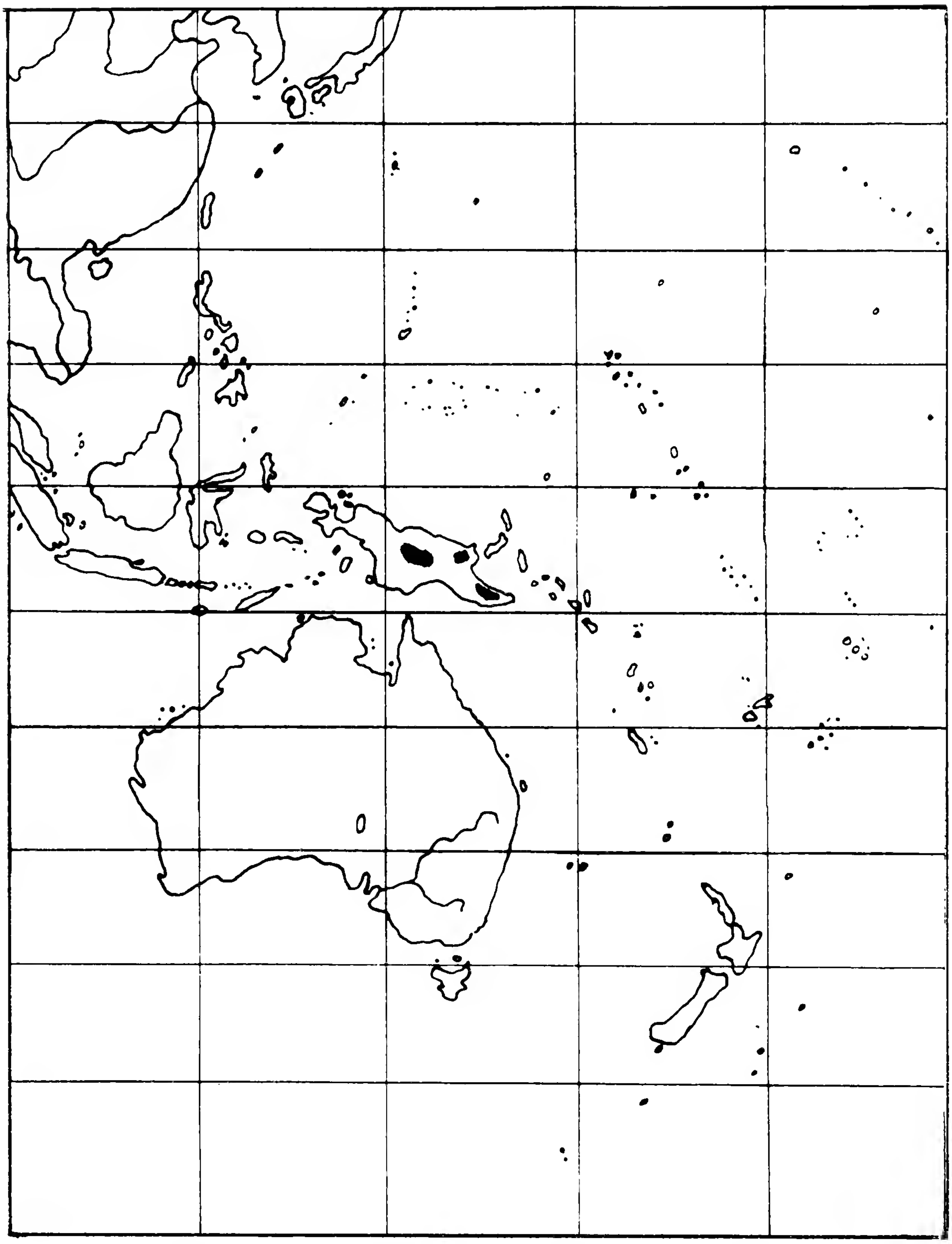
ACCIPITER BUERGERSI (REICHENOW)

DISTRIBUTION

Mountains of eastern New Guinea (Map 24).

PLUMAGE

Adult.—Crown black; feathers on back with black centers and wide chestnut margins; on upperwing and uppertail coverts the chestnut strongly predominates, but in some specimens these parts are nearly wholly black. Underparts white, with broad black streaks on the breast, hearts and bars on the abdomen and the flanks. In some specimens the feathers are widely edged with dark cinnamon. Thighs white with a tendency to black and chestnut barring. Throat white with narrow dark shaft streaks. Dorsum of tail black-brown with numerous light brown bars, which are white on the underside. A melanistic speci-



MAP 24. Distribution of *Accipiter buergersi.*

men studied by me is wholly black with faintly indicated lighter bars on the tail.

Juvenile.—Upperparts with more rufous-brown tinges than in adult. Crown brown with black shaft streaks. Underparts cinnamon with black-brown streaks.

The juvenile plumage resembles juvenile *A. meyerianus,* but is more closely similar to *Erythrotriorchis radiatus,* an Australian species.

SIZE AND STRUCTURE

Size very large. Tarsus short and sturdy. Toes long. Claws very long and heavy. Bill moderate. Wing long and rounded. Tail short. Figure 10, p. 57. Tables 56 and 57, pp. 155-156.

There is no statistical analysis.

Foot.—Characterized by a long middle toe and heavy hind claw. It can be regarded as showing the *gentilis*-type of foot, with an elongated middle toe and hind claw. A gradual increase of the size of toe and claw can be seen in the series *gentilis-meyerianus-buergersi-gundlachi*.

Wing and tail.—These are of the *nisus*-type. Resemble *A. gentilis* and *A. meyerianus*.

Habitat

A. buergersi is said to inhabit luxuriant hill forest from 500 to 1,500 m (Rand and Gilliard, 1967), but the long wing and short tail are characteristic of a species of broken country (such as *A. gentilis*), rather than of a forest species (as *A. tachiro*). Nothing has been recorded about its food or hunting behavior.

Discussion

A. buergersi resembles *A. meyerianus* in size, structure, and juvenile plumage, but differs in the long middle toe and the adult plumage. The long middle toe does not necessarily prove that *buergersi* is a large sparrow hawk rather than a goshawk, as Amadon (1964) supposes. In the discussion of *A. melanoleucus* it was shown that in the *gentilis* group the proportions of the toes and claws may shift, if such a shift provides better adaptation for a particular type of prey.

The adult plumage of *A. buergersi* differs from that of *A. meyerianus* in features which usually characterize a juvenile, i.e., rufous edges to the feathers of the upperside and a longitudinal pattern below. A stronger juvenile aspect of the adult bird is found in the Australian species *Erythrotriorchis radiatus*. This species is included in *Accipiter* by Deignan (1964), but is provisionally kept outside this monograph as a representative of a different genus (see pp. 2 and 211). It is characterized by very long wing tips and by the absence of well-differentiated adult and juvenile plumage.

Whether *A. buergersi* is more closely related to *A. meyerianus*, and consequently to the *A. gentilis* group, or to *Erythrotriorchis radiatus* remains to be determined. At present all three species are so poorly known that a full analysis cannot be made. In my opinion it is not improbable that *A. buergersi* and *E. radiatus* are both old Australasian colonists from the *A. gentilis* group.

ECOLOGICAL GEOGRAPHY IN AUSTRALASIA

In discussing the Accipiter fauna of other parts of the world we dealt mostly with species of major land masses and consequently with hawks which are often wide-ranging. The differences in ecology between the species are comparatively clear-cut, particularly where the species overlap in distribution. In Australasia, on the other hand, the Accipiters occur predominantly on islands. Their ranges are often restricted and several species may have similar ecological requirements.

AUSTRALASIA

Despite the large number of species in Australasia the ecological diversity is no greater than in Africa. The number of long-toed bird-catching hawks is smaller, but species of the structure type of *A. trinotatus* are much in evidence. Hawks of this type apparently are adapted for preying upon small reptiles. A survey of the ecology of the various species is given in Table 66. For several species habitat and habits are entirely unknown; these could not be classified in this table.

The center of distribution of the species of *Accipiter* in this region is New Guinea and Australia. New Guinea and Australia were connected on several occasions during the Pleistocene. Zoogeographically these regions form a unit, although ecologically they contrast with each other, Australia being low and arid, New Guinea crowned with lofty mountains and clad in luxuriant rainforests. To the west of this central part of the Australasian region we find the Moluccas and Lesser Sunda Islands, the transition area between the Oriental and the Australasian faunas. To the east are the islands of Melanesia, which harbor a progressively poorer land fauna of a specialized Australasian type.

In the recent past Australia and New Guinea formed a single continent, with a dry southern half and a moist northern one. These distinctions are reflected in the present distribution of *Accipiter*. *A. fasciatus* and *A. cirrhocephalus,* both species that are widespread in Australia, thrive in savanna and steppe woodland. *A. novaehollandiae,* being more strongly attached to forest, has a restricted distribution in Australia. On the other hand, *A. novaehollandiae* is the most numerous Accipiter in New Guinea, whereas *A. fasciatus* has only a marginal

TABLE 66

Ecological survey of *Accipiter* in Australasia (species occurring mainly in a single habitat type have been marked by broken underlining).

habitat / prey	lowland forest	montane vegetation	open woodland, savanna, etc.	unknown
birds	cirrhocephalus erythrauchen	cirrhocephalus virgatus	cirrhocephalus	
lizards (+insects)	henicogrammus luteoschistaceus poliocephalus		poliocephalus	
generalized	novaehollandiae albogularis rufitorques haplochrous	(novaehollandiae) (fasciatus) melanochlamys	novaehollandiae fasciatus rufitorques	
unknown	meyerianus	buergersi		imitator princeps brachyurus

distribution. *A. cirrhocephalus* is apparently able to live in forest as well as in savanna or steppe. A similar wide ecological tolerance is found in *A. minullus* of Africa. It is noteworthy that similar to the situation in Europe, we find three species of *Accipiter* in Australia, viz., a goshawk (*A. novaehollandiae*), a sparrow hawk (*A. cirrhocephalus*), and a dry country hawk (*A. fasciatus;* cf. *A. brevipes*).

In addition to these three species, New Guinea harbors another three that are all endemic, viz., *A. poliocephalus, A. melanochlamys,* and *A. buergersi*. Only *A. poliocephalus* is a lowland species, the other forms being limited to higher altitudes. *A. melanochlamys* seems to replace *A. novaehollandiae* in the mountains. The state of *A. meyerianus* on New Guinea is uncertain. The virtual absence of this species may be due to the fact that other species absent on the smaller islands occupy a similar niche and prevent *A. meyerianus* from successfully establishing itself on New Guinea.

With five species, among which three are endemic (*A. brachyurus, A. luteoschistaceus,* and *A. princeps*), New Britain has the richest Accipiter fauna of any part of the world. New Guinea, being 24 times as large, has six or perhaps seven species (if *A. meyerianus* breeds there), including three endemics, whereas in Australia, 200 times as large, only three species occur, and no endemics at all. It is discouraging that so little is known about the ecology of the New Britain species; a careful study of the ecological differentiation there might prove very rewarding. As four of these species seem to be rare and *A. novaehollandiae* very numerous, the latter is apparently very successful in New Britain, having forced the others into specialized habitats. Its success is probably connected with the development of primitive human culture on the island, whereas the remaining species are confined to niches in untouched forest. It was previously argued (p. 160) that *A. albogularis* in the Solomon Islands and *A. haplochrous* in New Caledonia might also be restricted to virgin forest by more recent colonists, *A. novaehollandiae* and *A. fasciatus,* respectively.

The impoverishment of the fauna at increasing distance from the continental land mass can be seen by comparing the number of species in several Melanesian Islands (Table 67). When on a given island no more than one Accipiter occurs, its ecological amplitude is very wide (e.g., *A. rufitorques* in the Fiji Islands).

The Moluccas and the Lesser Sunda Islands, both situated to the west of New Guinea, parallel New Guinea and Australia in the diversity of their climate and vegetation, the Moluccas being moist and heavily forested, the Lesser Sunda Islands dry and savanna-like. In addition, the Lesser Sunda Islands are generally intensely cultivated. There *A. fasciatus* is the dominant species, with the local race of *A. novaehollandiae* (*sylvestris*) probably being adapted to arid conditions. In the Moluccas *A. novaehollandiae* is the dominant Accipiter. In addition there are several other species, viz., *A. henicogrammus, A. erythrauchen,* and *A. meyerianus.* Geographically the Moluccas can be

TABLE 67
DIMINISHING NUMBER OF *Accipiters* AT INCREASING DISTANCE FROM AUSTRALIA AND NEW GUINEA.

ISLAND	DISTANCE[1] IN KM	AREA IN KM^2	SPECIES
New Britain	80	22.000	5
Choiseul, Solomon Islands	750	6.035	3
San Cristoval, Solomon Islands	1100	3.840	1
New Caledonia	1350	18.700	2
Viti Levu, Fiji	2700	11.760	1
Savaii, Samoa	4000	1.707	0

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1) distance from nearest point of Australia or New Guinea.

divided into a northern and a southern group. Both are inhabited by clearly different forms of *A. novaehollandiae* and *A. erythrauchen;* the divergence is accentuated by the occurrence of endemic *A. henicogrammus* in the northern Moluccas.

In ecological differentiation the Accipiters of the northern Moluccas show a parallel to those of the African forest. *A. novaehollandiae* takes the larger forest animals and may be compared to *A. tachiro; A. henicogrammus,* preying on lizards and insects, to *A. castanilius* which it resembles also in structure; *A. erythrauchen,* the long-toed sparrow hawk, to *A. minullus;* and *A. meyerianus* to *A. melanoleucus,* although the last appears to be more specialized for catching birds.

A. fasciatus has apparently colonized the island of Buru. Judging from its resemblance to Australian races of that species rather than to Lesser Sunda forms, it may be considered as a recent invader, probably by direct colonization from Australia. The species seems to be barely sustaining itself, probably assisted by the presence of human cultivation in the coastal districts.

In the island arc between the Moluccas and the Lesser Sunda Islands, *A. novaehollandiae* coming from the east meets *A. fasciatus* coming from the west. On the largely forested islands of the Kei and Timorlaut groups only *A. novaehollandiae* is found. This is also the case on Babar, but on the next island to the west (Sermata) we find *fasciatus.* On the small island of Damar both species have been collected. Farther to the west *fasciatus* dominates. It is deserving of mention that Babar and Damar have higher mountains and more forest than the other Southwest Islands.

The Moluccas and Lesser Sunda Islands belong to the transition area between the Oriental and the Australasian regions. Their fauna is a mixed one. In the Lesser Sunda Islands western elements predominate, in the Moluccas eastern elements. *Accipiter* departs from this general rule in showing only eastern elements in both archipelagos, with the single exception of *A. virgatus* on Flores. This deviation is certainly due to the fact that the Oriental region is very poor in species of *Accipiter,* whereas in Australia and New Guinea this group is represented by a large number of species. Celebes has also a good number of species (four) and below we shall see that this fauna is of a typically mixed character, with representatives of eastern as well as western origin. This island has not contributed to the Accipiter faunas of the Moluccas or Lesser Sunda Islands, however.

VII

CELEBES

INTRODUCTION

Celebes is situated between the Oriental and the Australasian regions. Its fauna is a mixture of elements from these two large faunas, together with a number of old endemic elements. In contrast to the situation in Borneo, Sumatra, and Java, the island is very rich in Accipiters, all species being endemic with the exception of *A. soloensis,* a Palearctic migrant (Chapter III). In the present chapter the endemic species *A. griseiceps, A. trinotatus, A. nanus,* and *A. rhodogaster* will be discussed.

ACCIPITER GRISEICEPS (SCHLEGEL)

DISTRIBUTION

Celebes and adjacent islands (Map 25).

PLUMAGE

Adult.—Crown and sides of head gray. Crown inconspicuously crested. Back warm brown. Underparts white with heavy dark brown streaks. Throat with a black mesial line. Thighs narrowly barred dark brown and white. Tail brown with more or less distinct dark crossbars.

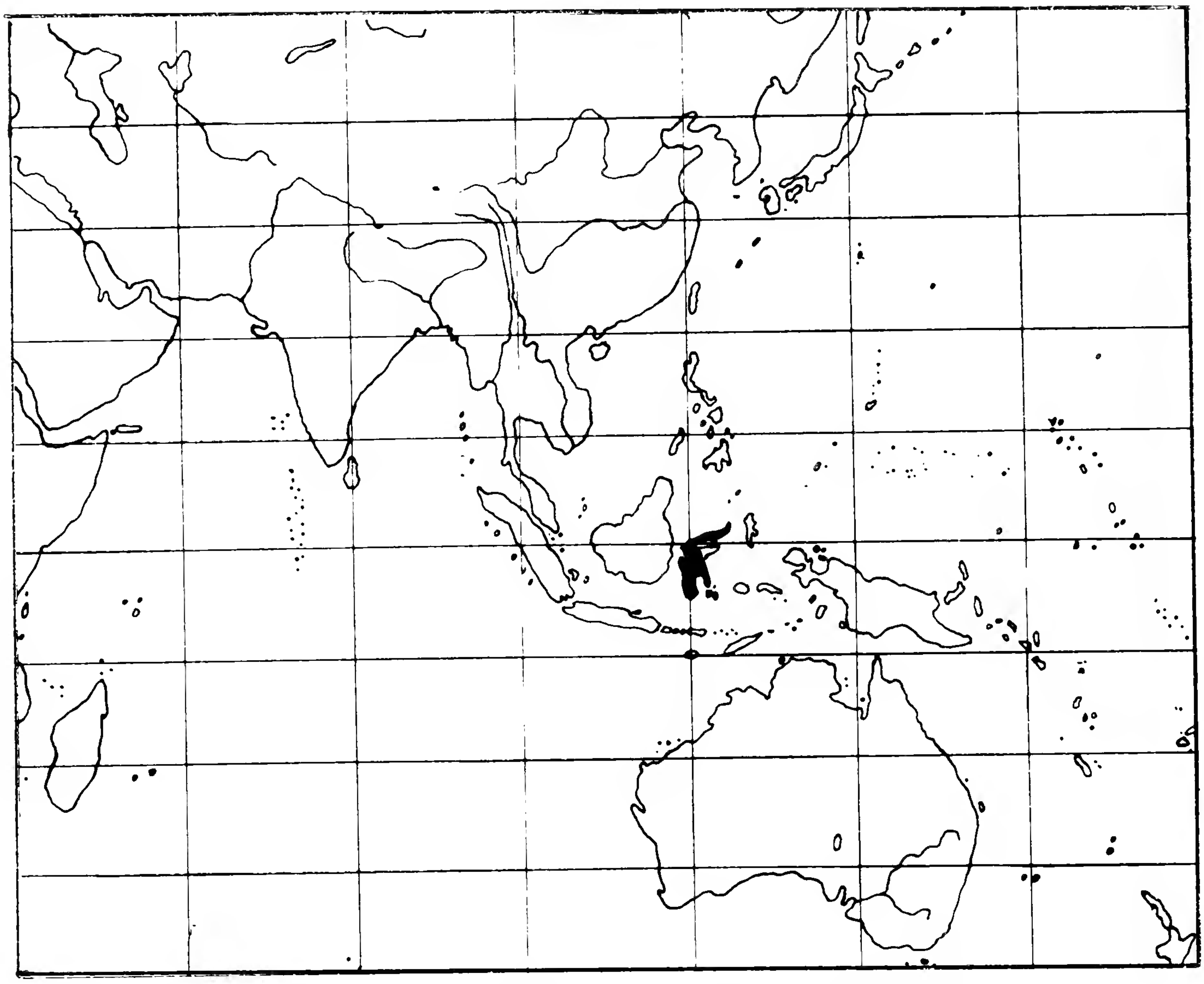
Juvenile.—Crown dark brown, streaked cinnamon buff. Back mottled brown and cinnamon buff, the feathers variously shaded buff with a large brown subterminal spot and a narrow white apical line. Underparts creamy white with buffish brown streaks suffused at their margins and more rufous than in the adult. Thighs barred or spotted. Tail with distinct bars.

SIZE AND STRUCTURE

Size rather small to medium. Tarsus and toes short and sturdy. Claws and bill heavy. Wing short and rounded. Tail medium. Figure 4, p. 16. Tables 68 and 69.

No statistical analysis made of the middle toe, hind claw, and bill. The statistical model was unsatisfactory for the tarsus. In the series of data that could be analysed no significant difference exists between the sexes.

Bill and foot.—These are of the *gentilis*-type. Owing to the short wing the relative measurements appear large. Tarsus and bill are



Map 25. Distribution of *Accipiter griseiceps.*

TABLE 68
Wing length in *Accipiter griseiceps.*

SEX	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
♂	177.1	3.95	1.40	170 - 181	8
♀	201.9	5.56	1.85	192 - 210	9
				Total	17

TABLE 69
Relative measurements in percent of wing length in *Accipiter griseiceps.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	27.60	15.58	10.54	8.97	78.27	23.85	5.32
♂	+0.73	-	-	-	+0.20	+0.87	+0.53
♀	-0.73	-	-	-	-0.20	-0.87	-0.53
Adult	-0.51	-	-	-	+0.87	-0.78	-0.52
Juvenile	+0.51	-	-	-	-0.87	+0.78	+0.52
P model	0.045		no analysis		0.251	0.656	0.547
P sex	-	-	-	-	0.459	0.095	0.205
n	12	13	16	16	17	16	14
df	8	-	-	-	13	12	10

larger in relation to the middle toe and hind claw than in *A. gentilis.* In this respect *A. griseiceps* resembles *A. trivirgatus.*

Wing and tail.—Intermediate between the *bicolor-* and *tachiro*-type and similar to *A. trivirgatus.*

Habitat, Hunting Behavior, and Prey

Inhabits a variety of habitats characterized by alternating trees and open ground, from the coastal plains to approximately 2,000 m. Found in open hilly country with scattered woodlots (Heinrich, *in* Stresemann, 1940), heavy lowland forest and mangrove (Coomans de Ruiter, *in* Van Marle and Voous, 1946), and native villages in the coastal plain (De Haan, *in* Van Bemmel and Voous, 1951). When hunting the bird hides in the foliage and swoops down on the prey, which is frequently taken from the ground. The prey consists of lizards, small birds, insects, and small rodents (Van Marle and Voous, 1946). In native kampongs domestic chicks are taken.

Discussion

Van Marle and Voous (1946) consider *A. griseiceps* to be conspecific with *A. trivirgatus* because of their resemblance in juvenile plumage and in structure. Mayr (1949), on the other hand, believing that *A. griseiceps* is related to *A. trivirgatus,* regards it as a distinct species on account of the peculiar adult plumage with the gray head and the boldly streaked underparts. Indeed, *A. griseiceps* is much more different from all the races of *A. trivirgatus* than these races are from each other. It is certainly related to *A. trivirgatus,* but has been isolated for a long time. Although it is impossible to prove whether *A. griseiceps* is specifically different from *A. trivirgatus,* the available evidence is in favor of such a separation. Therefore, I prefer to follow Mayr and to regard *A. griseiceps* as an endemic Celebes species.

ACCIPITER TRINOTATUS BONAPARTE

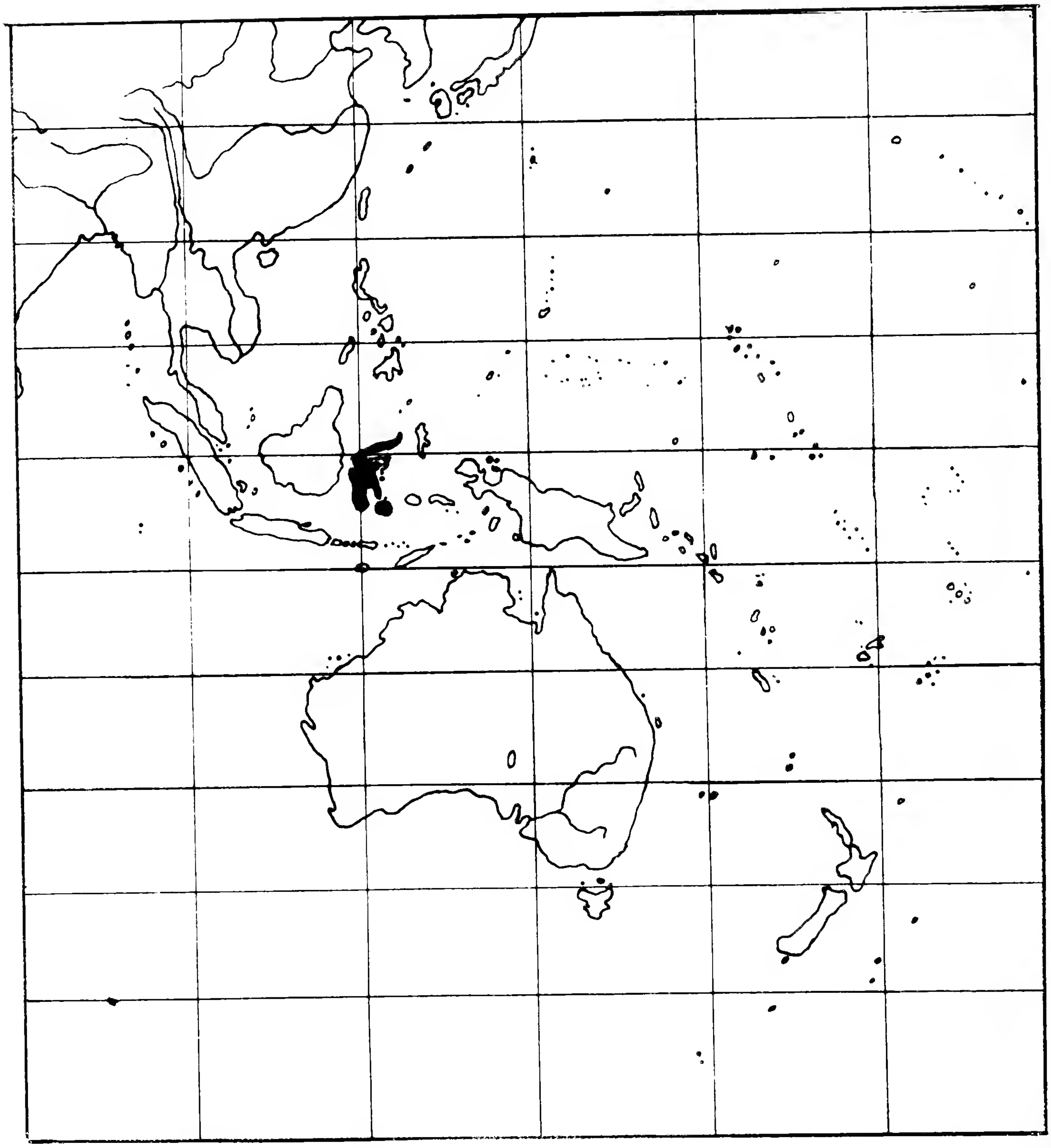
Distribution

Celebes, Muna, Buton (Map 26).

Plumage

Adult.—Upperparts very dark bluish gray. Underparts cinnamon rufous grading into buff and creamy white on the abdomen and undertail coverts. Throat pale gray to dirty white. Sides of face gray, lighter than the back. Dorsum of tail black with two or three white spots.

Juvenile.—Crown dark brown with wide rufous feather edges. Back deep rufous brown, in some specimens inconspicuously spotted with dark brown (Van Marle and Voous, 1946). Underparts fulvous white with heavy dark brown streaks on breast and flanks. Dorsum of tail black with a brown wash and with larger white spots than in the adult.



MAP 26. Distribution of *Accipiter trinotatus.*

GEOGRAPHICAL VARIATION

Some authors follow Hartert (1896) in separating the birds from south and southeast Celebes, Muna, and Buton as *A. t. haesitandus* (Hartert), but the difference apparently is very slight, only affecting the tinge of the crown and the underparts in the junvenile plumage. I prefer to follow Peters (1931) in considering *haesitandus* a synonym of *trinotatus.* According to Stresemann (1940) *haesitandus* (if separable) is confined to mountains in southern Celebes.

SIZE AND STRUCTURE

Size small to rather small. Tarsus long and slender. Toes short. Claws small. Bill heavy. Wing very short and rounded. Tail long. Figure 4, p. 16. Tables 70 and 71.

TABLE 70
Wing length in *Accipiter trinotatus.*

SEX	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
♂	151.3	1.95	0.62	148 - 153	10
♀	164.9	3.64	0.73	157 - 173	25
				Total	35

The difference between the sexes is significant for the tarsus (longer in male) and tail (longer in male).

Bill and foot.—Of the *trinotatus*-type.

Wing and tail.—These are of the *tachiro*-type. The wing is still more rounded than in *A. tachiro* and *A. henicogrammus,* resembling *A. castanilius.*

Habitat and Food

Inhabits forest from sea level to about 1,600 m. Found in mangrove as well as in mountain forest. According to Heinrich (*in* Stresemann, 1940) the species is hardly ever seen outside of dark primeval forest. In northern Celebes *A. trinotatus* has been collected in much larger numbers than the other endemic Accipiters. It is apparently one of the most numerous birds of prey in that region.

It preys mostly on lizards and grasshoppers (Heinrich, *in* Stresemann, 1940), but also on other small animals. Coomans de Ruiters examined 23 stomachs and found lizards (9 times), small snakes (5 times), frogs (twice), and a small bird (once) (data from specimen labels). Heinrich once found three bats in the stomach of a specimen.

Discussion

Although *A. trinotatus* is similar to *A. rhodogaster* and *A. nanus* in adult plumage, it stands quite isolated taxonomically. It is an old endemic element of the Celebes avifauna (Van Marle and Voous, 1946). Its distributional history cannot be reconstructed.

TABLE 71
Relative measurements in percent of wing length in *Accipiter trinotatus.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	32.96	15.73	8.02	8.73	84.27	21.65	2.77
♂	+0.92	+0.13	-0.09	+0.04	+0.87	+0.38	+0.09
♀	-0.92	-0.13	+0.09	-0.04	-0.87	-0.38	-0.09
Adult	-0.47	-0.08	+0.12	+0.14	-0.36	-0.41	-0.29
Juvenile	+0.47	+0.08	-0.12	-0.14	+0.36	+0.41	+0.29
P model	0.206	0.137	0.690	0.776	0.825	0.823	0.833
P sex	0.004	0.197	0.388	0.868	0.049	0.312	0.708
n	33	30	32	30	34	31	32
df	29	26	28	26	30	27	28

In my opinion it is not entirely impossible that *A. trinotatus* is a very old and specialized offshoot of the *A. badius* group. Conformation approaching *A. trinotatus* is found in *A. butleri* and *A. francesii*. *A. butleri* has in addition a markedly rufous juvenile plumage, reminiscent of a juvenile *A. trinotatus*. Hence in some species of the *badius* group plumage and structure trends are present that point in the direction of a bird like *A. trinotatus*. Nevertheless, the indications of a distant relationship between *A. badius* and *A. trinotatus* are weak and inconclusive.

ACCIPITER NANUS (BLASIUS)

DISTRIBUTION

Celebes, but seems to be lacking on the southern peninsula (Map 4, p. 35).

PLUMAGE

Adult female.—Upperparts blackish. Breast cinnamon, abdomen suffused with gray. Thighs gray. Sides of face dark gray, throat white with a few gray streaks. Central rectrices dark gray with slightly darker bars. The second, third, and fourth pairs of rectrices have three white spots on the inner web, causing Blasius (1897) to describe *A. nanus* as a variety of *A. trinotatus*. The outermost tail feathers are unmarked.

Adult male.—Breast vinaceous red, not cinnamon (Blasius, 1897).

Juvenile.—Crown dark brown, back plain cinnamon red, uppertail coverts with dark subterminal bars. Underparts creamy white, breast and flanks marked with dark brown streaks. Dorsum of tail rufous brown with black bars, underside unmarked (cf. Van Marle and Voous, 1946).

The differences between the adult plumages of *A. nanus* and *A. rhodogaster* are listed by Stresemann (1932).

SIZE AND STRUCTURE

Size very small. Tarsus and toes long and slender. Claws small and delicate. Bill heavy. Wing short and rounded. Tail short. Figure 12, p. 83. Tables 56 and 57, pp. 155-156.

No statistical analysis made.

Bill and foot.—Of the *nisus*-type, but modified by the presence of a relatively heavy bill. Differs from all other Accipiters in this respect.

Wing and tail.—These are of the *novaehollandiae*-type. Wing tip more rounded than in *A. rhodogaster*.

HABITAT AND FOOD

Inhabits mountain forest between about 900 and 2,000 m, rarely lower (cf. Coomans de Ruiter, 1947). *A. nanus* is apparently a rather scarce species. Its flight is fast and agile through the forest. Analysis of the stomachs of three specimens yielded insects, always including grasshoppers (3 times) and a small snail (once) (Coomans de Ruiter, *in* Van Marle and Voous, 1946). It attacks domestic fowl, probably usually without success.

Discussion

A. nanus is one of a pair of long-toed Accipiters on Celebes. The other is *A. rhodogaster.* The relationships of both species are discussed by Van Marle and Voous (1946) who conclude that it is impossible to consider either of them as a subspecies of *A. virgatus. A. rhodogaster* was united with *virgatus* by Stresemann (1923a), prior to the rediscovery of *nanus.* Later Stresemann (1932) suggested that *rhodogaster* and *nanus* are of a common origin. In my opinion, on the contrary, *A. rhodogaster* is closely related to *A. erythrauchen* (see p. 198) whereas *A. nanus* is allied to *A. virgatus.*

Both *A. nanus* and the tropical races of *A. virgatus* are small birds living in mountain forests. In adult plumage *A. nanus* is closely similar to adult *A. virgatus confusus* from the southern Philippines. The wing of *A. nanus* is shorter and more rounded than that of the tropical races of *A. virgatus,* but these in turn have a shorter and more rounded wing than the Palearctic subspecies *A. v. gularis. A. nanus* may, therefore, be considered as the end of a series of forms with progressively shorter wings. A more important difference in structure between *A. nanus* and *A. virgatus* is the heavy bill of *A. nanus,* but in several other groups of *Accipiter* forms which have been isolated on islands have relatively heavier bills than forms from adjacent parts of the range (e.g., *A. novaehollandiae leucosomus* versus nominate *novaehollandiae,* see p. 146). The juvenile plumage of *A. nanus* is completely different from that of *A. virgatus.*

Summarizing, we may conclude that there are strong indications of a relationship between *A. nanus* and *A. virgatus,* although there are also several important differences between these species. Probably *A. nanus* is an old colonist from the *A. virgatus* group. The resemblance to *A. rhodogaster* and *A. trinotatus,* both in adult and juvenile plumage, may be regarded as the result of convergent evolution, which for unknown reasons tends to produce a uniform appearance of Accipiters in Celebes (cf. Van Marle and Voous, 1946).

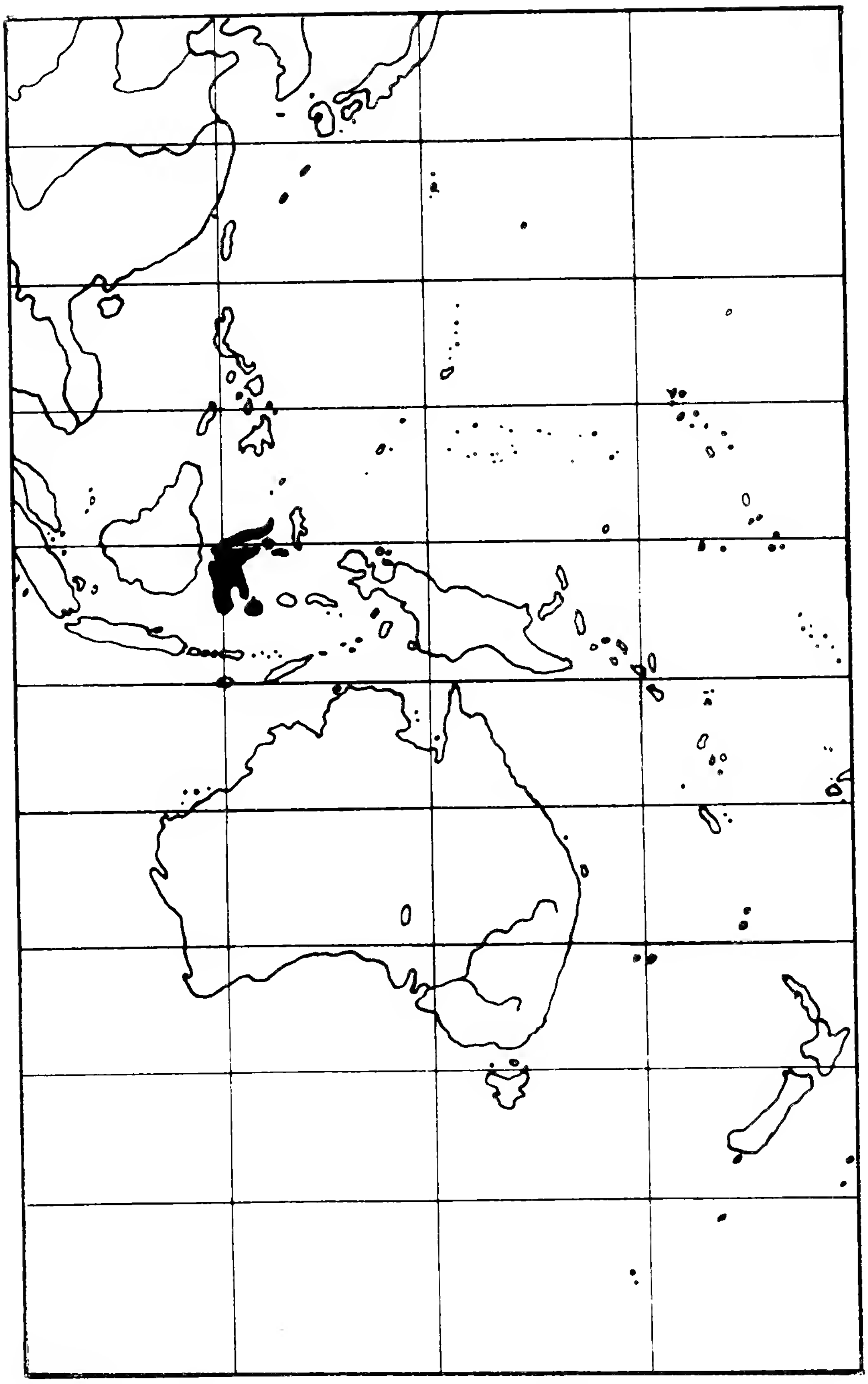
Accipiter rhodogaster (Schlegel)

Distribution

Celebes and adjacent islands and the Sula archipelago (Map 27).

Subspecies

A. r. rhodogaster (Schlegel), Celebes; *A. r. sulaensis* (Schlegel), Sula archipelago, Peling, and Banggai archipelago; *A. r. butonensis* Voous, islands of Muna and Buton.



Map 27. Distribution of *Accipiter rhodogaster.*

PLUMAGE

Adult male.—Deep black above. Sides of face gray. Throat gray or white mottled gray. Breast vividly vinaceous shading into fine pearl gray and white on abdomen and thighs. Tail dark gray with indistinct black bars on the dorsum, lighter with more pronounced bars below.

Adult female.—Above somewhat less deep black than in male, with a brownish wash. Underparts paler.

Juvenile.—Crown dark brown, back deep cinnamon-rufous with large dark brown spots and bars. Underparts fulvous-white with dark brown streaks. Throat with a dark mesial line. Thighs with dark brown spots. Upperside of tail deep rufous with five broad dark brown bars, underside with narrow dark bars.

GEOGRAPHICAL VARIATION

The geographical variation is slight. *A. r. sulaensis* differs from nominate *rhodogaster* in having the sides of the head in the adult tinged with vinous, instead of pure gray (Meyer and Wiglesworth, 1898). In addition *A. r. sulaensis* has a slight vinous wash on the hindneck, suggestive of a faint nuchal collar. The primaries and tail feathers have less dark bars than in *A. r. rhodogaster*. *A. r. butonensis* differs from the other forms in being paler on the underparts, lighter gray on the upperparts (Van Bemmel and Voous, 1951).

SIZE AND STRUCTURE

Size small to rather small. Tarsus and toes long and slender. Claws and bill moderate. Wing short and rounded. Tail short. Figure 21, p. 177. Tables 72 and 73.

For analysis the data from all three subspecies were combined. The difference between the sexes is significant for the tarsus (longer in male), middle toe (shorter in male), and hind claw (smaller in male).

Bill and foot.—These are of the *nisus*-type. Very similar to *A. erythrauchen,* but less heavy in relation to the size of the bird. Although the wing tip is shorter, the relative measurements are about the same as in *A. erythrauchen.*

Wing and tail.—Of the *novaehollandiae*-type. Wing tip slightly less rounded than in *A. novaehollandiae leucosomus,* but otherwise very similar.

TABLE 72
WING LENGTH IN *Accipiter rhodogaster.*

SEX	MEAN	ST. DEV.	ST. ERR./MEAN	RANGE	N
♂	165.0	3.74	1.25	158 - 172	9
♀	203.3	4.70	1.36	194 - 212	12
				Total	21

TABLE 73
RELATIVE MEASUREMENTS IN PERCENT OF WING LENGTH IN *Accipiter rhodogaster.*

	TARSUS	M. TOE	H. CLAW	BILL	TAIL	WING TIP	TIP - P6
Mean	30.04	19.19	8.72	7.60	73.60	26.58	7.73
♂	+0.79	-0.61	-0.50	-0.13	-0.03	+0.60	+0.37
♀	-0.79	+0.61	+0.50	+0.13	+0.03	-0.60	-0.37
Adult	-0.30	-0.18	-0.08	-0.15	-1.05	+0.03	0
Juvenile	+0.30	+0.18	+0.08	+0.15	+1.05	-0.03	0
P model	0.653	0.526	0.233	0.327	0.201	0.582	0.930
P sex	0.049	0.012	0	0.158	0.428	0.112	0.470
n	15	14	18	20	20	21	19
df	11	10	14	16	16	17	15

Habitat and Food

Inhabits forest, forest edges, and broken country. Also found in mangroves (Van Marle and Voous, 1946) and in tamarind trees near native kampongs (Van Bemmel and Voous, 1951). Altitudinal range from sea level to 2,000 m (Heinrich, *in* Stresemann, 1940). The hunting behavior and prey have not been described. In the stomachs of three specimens collected by Coomans de Ruiter a lizard (once) and insects (once) were found (data from specimen labels). The structure of the bill and feet leads one to surmise that *A. rhodogaster* also takes small birds.

Discussion

Van Marle and Voous (1946) discussed the affinities of *A. rhodogaster* and rejected the idea of a close relationship with *A. virgatus,* as proposed by Stresemann (1923a). They also rejected a later suggestion of Stresemann (1932) that *A. rhodogaster* and *A. nanus* were of a common origin. I am in agreement with their conclusions regarding these points.

In my opinion, however, they failed to give due consideration to the possibility that *A. rhodogaster* is related to *A. erythrauchen.* In structure of the bill and feet *A. rhodogaster* and *A. erythrauchen* are similar, and in adult plumage *A. rhodogaster sulaensis* is intermediate between *A. r. rhodogaster* and *A. erythrauchen. A. r. sulaensis* has a faint nuchal collar, the rufous tinges on the breast are less pronounced, and the dark bars on the tail are reduced in comparison to *A. r. rhodogaster.* The peculiar juvenile plumage of *A. rhodogaster* can be considered as the final stage of the series *cirrhocephalus-erythrauchen-rhodogaster* in which the width of the rufous feather edges increases and the pattern of the underparts becomes darker brown and more longitudinal. The shape of the wing tip can be interpreted as an indication that *A. rhodogaster* originates from ancestors with a pointed wing tip which became rounded in the course of its adaptation to forest life. The same phenomenon can be seen in *A. fasciatus natalis* and *A. butleri.* In conclusion, it can be said that *A. rhodogaster* strongly resembles *A. erythrauchen,* and that it can logically be interpreted as a western extension of the *A. cirrhocephalus* group.

This view was proposed by Stresemann in 1914. At that time he included *A. rhodogaster* in the "Formenkreis" of *A. cirrhocephalus.* On the other hand *A. rhodogaster* shows so many peculiarities that it must be regarded as a separate species. It has lived in isolation on Celebes for a considerable time. The intermediate characters of *A. r. sulaensis* point to a colonization of Celebes by using the Sula Archipelago as stepping stones. During the height of the Pleistocene glaciations the straits between the islands were much narrower than at present, although the Sula and Banggai islands were never connected with Celebes.

CELEBES

Ecological Geography in Celebes

The most remarkable feature of the *Accipiter* fauna of Celebes is the wealth of species on a relatively small island. Moreover, this island is for the most part heavily forested and, accordingly, all endemic species are forest hawks. Any differences in ecology must therefore relate to hunting behavior and prey rather than to habitat. *A. nanus* is indeed confined to mountain forest, but *A. griseiceps* and *A. rhodogaster* also occur to heights of 2,000 m, the upper limit for *A. nanus.* Although hunting behavior and the choice of prey are only fragmentarily known, the available data suggest that the species really differ in hunting ecology.

A. trinotatus lives primarily on small forest animals, notably lizards, *A. griseiceps* on larger forms. These two species may be compared ecologically with *A. henicogrammus* and *A. griseogularis* on Halmaheira and with *A. poliocephalus* and *A. leucosomus* on New Guinea. Probably *A. castanilius* and *A. toussenelii* in the African forest exhibit similar ecological relations. *A. nanus* and *A. rhodogaster* show resemblance to *A. nisus* in the structure of the bill and feet, both probably taking prey on the wing. Both show departures from the *nisus*-type, *A. rhodogaster* in having a heavy foot, *A. nanus* in having a heavy bill. This suggests the main differentiation between these species lies in their food ecology, but the scanty information available does not support this supposition. *A. soloensis,* which visits Celebes only in the winter, takes a variety of food, including lizards and insects. It may escape competition by its adaptation to hunting in open country, whereas the resident species live in forest.

Zoogeographically the fauna of Celebes consists of three groups of elements: western elements having reached the island either from the Philippines or from Java; eastern elements invading from the Moluccas; and endemic Celebes elements of unknown ancient origin. In the *Accipiter* fauna we find all these elements represented: *A. griseiceps* is of western origin and probably invaded Celebes by way of the Philippines (Van Marle and Voous, 1946). *A. rhodogaster* represents an eastern element. *A. nanus* is an old Celebes element but shows western affinities, whereas *A. trinotatus* is an endemic Celebes element whose affinities are obscure.

VIII

STRUCTURE AND ECOLOGY

INTRODUCTION

In the genus *Accipiter* structural characteristics are considered to present important indications of taxonomic relationships. An example is the former splitting of this group into two genera, *Accipiter* and *Astur,* in which the relative length of the various toes was thought to be diagnostic. Apart from taxonomic implications, the structure of these birds shows adaptive features. In the present chapter some adaptations will be described and a few principles governing the adaptive variation of structure will be outlined.

The relation between structure and ecology can be tested in two ways, viz., (1) by listing all forms sharing a given structural feature and trying to find common ecological traits, and (2) by comparing structural and ecological characters of one form with those of others. The structure diagrams may serve as a base for comparing the various forms.

BILL AND FOOT

In the following sections the ecological similarities of species with a given type of bill and foot structure will be discussed. In Table 74 the species showing the various types of bill-foot structures are surveyed.

Nisus-TYPE

Small birds constitute the most important prey for nearly all species of the *nisus*-type group of Accipiters. Some also take a fair proportion of insects. A common feature is the tendency to catch the prey in mid-air. Various structural characteristics are considered as adaptations to this type of hunting behavior. The long legs and toes can reach far forward to grasp flying birds and the small, needle-shaped claws will suffice to kill these delicate creatures. The small bill is a precision tool for tearing frail skins and small muscles.

A. nanus exhibits the *nisus*-type of legs and toes, but differs in having a large bill. It probably takes large insects predominantly, and the heavy bill may be adapted to the crushing of chitinous exoskeletons. There are also indications that forms of tropical forest have a relatively large bill (see Table 76) and *A. nanus* is exclusively a species of dense forest.

A. ovampensis differs from the *nisus*-type in having a short tarsus.

TABLE 74

Structure of foot and bill in the species of *Accipiter*.

<table>
<tr><td>Nisus-type
minullus
virgatus
cirrhocephalus
brachyurus
erythrauchen
rhodogaster
madagascariensis
nisus
striatus

modified:
nanus
ovampensis</td><td>Gentilis-type
trivirgatus
griseiceps
novaehollandiae (part)
henstii
gentilis
meyerianus</td><td>Bicolor-type
bicolor
cooperii
melanoleucus

modified:
gundlachi
buergersi</td></tr>
<tr><td rowspan="2">Brevipes-type
badius
brevipes
soloensis</td><td>Trinotatus-type
butleri
trinotatus
novaehollandiae (part)
henicogrammus
luteoschistaceus
imitator
poliocephalus</td><td>Tachiro-type
tachiro
fasciatus
melanochlamys
haplochrous</td></tr>
<tr><td colspan="2">intermediate:
castanilius
francesii</td></tr>
<tr><td>Albogularis-type
poliogaster
novaehollandiae (part)
albogularis
rufitorques</td><td>Other
novaehollandiae (part)
superciliosus
collaris</td><td>Unknown
princeps</td></tr>
</table>

Below we shall see that the tarsus tends to be short in forms taking ground-living prey. As *A. ovampensis* inhabits dry country where grounds birds are plentiful, it may feed commonly on them. Information on its prey is so scanty, however, that this must be considered as merely an assumption.

Gentilis-Type

The diet of species showing the *gentilis*-type of structure is rather generalized, consisting of large and middle-sized birds, mammals, and reptiles. Presumably in this case it is the method of hunting rather than the type of prey that is reflected in the structure of the bill and feet.

Storer (1966) has argued that the momentum of a collision is proportional to the mass and speed of the colliding bodies. When a heavy predator strikes a large prey at high speed a violent collision will be the result. Therefore, the short and sturdy tarsus and toes and the heavy claws of the hawks of this group probably evolved as adaptations to capturing rather heavy prey by pouncing upon it. The speed of predator and prey with respect to each other is much less when the prey is chased in mid-air or picked up in passing. At least *A. gentilis* is known to often pounce upon a prey on the ground, such as a rabbit or a domestic hen.

In support of this hypothesis it may be noted that in Accipiters of similar structure the relative length of the tarsus is related to body size. In all species the male is smaller than the female. In species in which the sexes differ significantly in tarsus length the tarsus is relatively longer in the smaller bird, the male. As the smaller predator will normally capture the smaller prey, the mass of both colliding bodies and the momentum of the collision is reduced in the male. This offers opportunities for the evolution of a more slender and relatively longer tarsus. The same principle is illustrated by comparing the three species of *Accipiter* occurring in eastern Asia: *A. gentilis, A. nisus,* and *A. virgatus* (Table 75).

In some tropical forms with the structural type of *gentilis* the bill is relatively large (*A. trivirgatus, A. griseiceps, A. novaehollandiae leucosomus*). This is in accordance with a tendency toward a heavy bill in many forms of the tropical forest (see Table 76), although it is difficult to speculate upon the adaptive significance of this phenomenon. In the same forms the tarsus is relatively longer. Tentatively

TABLE 75
WING LENGTH AND TARSUS INDEX IN EASTERN ASIAN *Accipiters.*

Form	Mean wing length of ♂	Relative length of tarsus of ♂
gentilis gentilis	323	24
nisus nisosimilis	210	26
virgatus gularis	166	28

TABLE 76

RELATIVE LENGTH OF BILL IN FOREST AND NON-FOREST FORMS OF VARIOUS *Accipiters*.

NON - FOREST		FOREST	
Form	Bill	Form	Bill
tachiro	7.63	castanilius	8.28
badius badius	7.00	butleri	8.40
fasciatus wallacii 1)	6.89	fasciatus natalis	7.42
novaehollandiae novaehollandiae	7.43	novaehollandiae leucosomus	8.20
minullus minullus	6.50	minullus erythropus	6.92
virgatus gularis	6.42	virgatus virgatus	7.29
cirrhocephalus cirrhocephalus 2)	5.38	erythrauchen	7.32
striatus erythronemius	5.85	striatus ventralis	6.29
bicolor guttifer	6.78	bicolor bicolor	7.43
melanoleucus melanoleucus	6.81	melanoleucus temminckii	7.41

---

1) but hellmayri 7.38 !

2) cirrhocephalus papuanus intermediate : 6.07

this may be considered as an adaptation to the taking of arboricolous mammals and reptiles, which are more numerous in tropical habitats than in temperate ones. In addition, a long tarsus may be used in pursuing prey on foot through dense vegetation as was shown for *Micrastur semitorquatus* by Peeters (1963).

Bicolor-TYPE

In structure the species of this group are intermediate between the *nisus*-type and the *gentilis*-type, thereby resembling *A. nisus* in the long tarsus and middle toe and *A. gentilis* in the heavy hind claw. Apparently they take mainly middle-sized birds as prey and a higher proportion of mammals than the species of the *nisus* group. Therefore, in choice of prey they are also intermediate between *gentilis* and *nisus*. Presumably the long tarsus and toe indicate that most of the prey is caught in flight, whereas the heavy claw and the rather large bill are related to the comparatively large-sized prey. Figure 15 shows that the hind claw of *A. cooperii* is exactly intermediate between that of *A. striatus* and *A. gentilis*.

A. gundlachi resembles *A. bicolor* in structure, but appears to have a very large hind claw, although Figure 13 may be somewhat exaggerated because only a single claw was measured. As far as we know *A. gundlachi* preys on middle-sized birds as does *A. cooperii*, thus the ecological meaning of the large claw is not clear. Probably the prey is on the average somewhat larger. *A. buergersi* resembles *A. gundlachi* in structure, but its ecology is unknown. It may take large birds in the New Guinea mountain forests.

The small South American sparrow hawks *A. superciliosus* and *A. collaris* show some resemblance to *A. gundlachi* in structure of their bills and feet. Their ecology is fragmentarily known, and it is obscure why they should differ so strongly from other small sparrow hawks, which all resemble *A. nisus* in structure.

Brevipes-Type

Only three species show the *brevipes*-type of structure and these are closely related taxonomically. They live in a rather dry, open habitat and take a variety of small animals. The hind claw and bill are small as in *nisus,* but the tarsus and middle toe are much shorter than in that species. Previously a long tarsus and middle toe was interpreted as an adaptation to capturing prey in mid-air. In contrast to *nisus* the species of this structural type are slower in hunting and take more of their prey on the ground. This suggests that the short tarsus and toes evolved in relation to the taking of ground animals, as in the *gentilis*-type. It is interesting that in the genus *Falco* the air hunter *columbarius* has a relatively longer tarsus and toe than the ground hunter *F. tinnunculus.*

Trinotatus-Type

Accipiters with the *trinotatus*-type of structure are restricted to tropical islands. Most of the species apparently live in dense primeval forest, *A. poliocephalus* being the only species found on the periphery. The forest species have a very short wing. Lizards and other reptiles predominate in the diet, but in addition many insects are consumed. The short toes and small claws seem to be well adapted for capturing slender agile animals. As the species of the *brevipes*-type also take many lizards and insects, the long tarsus and heavy bill of the *trinotatus*-type may be an adaptation to forest conditions rather than to the type of prey taken. The representatives of other structural types that are forest forms are also characterized by a heavy bill (Table 76) and a long tarsus. The long tarsus may be significant in taking arboreal prey. Apart from the still unexplained correlation with forested habitats, the heavy bill may be useful in tearing tough skins or crushing exoskeletons of insects.

Tachiro-Type

The forms showing the *tachiro*-type of structure constitute a rather heterogenous assemblage with respect to their ecology. The only common feature may be that all prey on a variety of medium-sized and small animals in tropical habitats. Some are birds of rainforest, such as *A. tachiro toussenelii* and *A. haplochrous,* while others live in fairly open habitats, such as *A. f. fasciatus. A. t. tachiro* is intermediate, inhabiting well-wooded tracts in savanna country.

In *A. t. tachiro* and *A. f. fasciatus* the hind claw is heavy. These hawks resemble *A. gentilis* in this respect, differing only in the much longer tarsus. Previously it was suggested that a long tarsus is probably useful in securing arboreal prey. Although this adaptation may be important in *A. tachiro,* it is not for *A. fasciatus* which hunts mostly over open country. In this species the long tarsus may be connected with a special way of hunting, perhaps with picking up prey in passing or with stooping from a very low flight, as harriers do. Published records referring to this type of hunting in *A. fasciatus* are scarce, however. Interestingly, in the dryer localities in Europe the large harrier *Circus aeruginosus* takes many rabbits, whereas for *C. pygargus,* a smaller harrier, lizards are at times an important prey (E. Nieboer, pers. comm.). Analogously, in *A. fasciatus* rabbits are a staple food for the large Australian race (nominate *fasciatus*), while many of the smaller subspecies take mainly lizards.

In the forest forms of *A. tachiro* and in the insular races of *A. fasciatus* the hind claw is relatively smaller than in *A. t. tachiro* and *A. f. fasciatus* and apparently the average prey of these forms is less heavy.

A. castanilius and *A. francesii* are intermediate between the *tachiro*-type and the *trinotatus*-type. In these species the hind claw is still smaller than in *A. tachiro toussenelii.* They take mostly small animals, with insects and reptiles coming into prominence, as in the species of the *trinotatus*-type.

Albogularis-Type

The *albogularis*-type of structure differs from the *gentilis*-type in the heavy bill and from the *tachiro* type in the short tarsus. A heavy bill is characteristic of many tropical Accipiters and may be related to preying on lizards and large insects. It was previously shown that a short tarsus is found in species taking ground animals by pouncing on them. Unfortunately, the ecology of the species showing the *albogularis*-type of structure is virtually unknown. They inhabit various tropical habitats, open country as well as dense forest. Apparently they have a variety of prey, including lizards and insects. The hunting behavior is described for *A. novaehollandiae dampieri,* which was seen to swoop down upon lizards from a high perch. *A. poliogaster* is a mysterious bird, but it probably plays the part of a large goshawk in tropical South America. Its very short tarsus may indicate that it takes heavy prey on the ground.

Conclusions Regarding the Structure of the Bill and Foot

Neither the separation between the various structural types nor the differences in ecology between species with different structures are absolute. Many species are more or less intermediate between two structural types; in fact the *bicolor*-type, the *tachiro*-type, and the *albogularis*-type are themselves intermediate. In addition, the species having the *tachiro*-type of bill and feet represent two very different ways of life. Nevertheless, it is possible to perceive some trends that are apparently indicative of the relation between structure and ecology. A survey of these trends is given in Tables 77, 78, 79, and 80.

TABLE 77

Relation of length of tarsus to ecology in *Accipiter*.

tarsus:	relatively longer	relatively shorter
predator	smaller	larger
prey	smaller	larger
hunting	in mid-air	pouncing on ground
special features	arboreal prey harrier-like hunting pursues quarry on foot	
shown by	nisus-type bicolor-type trinotatus-type tachiro-type	gentilis-type brevipes-type albogularis-type

TABLE 78

Relation of length of middle toe to ecology in *Accipiter*.

middle toe:	relatively longer	relatively shorter
prey	birds, insects	various animals
hunting	in mid-air	on ground or in trees
shown by	nisus-type bicolor-type	gentilis-type brevipes-type trinotatus-type tachiro-type albogularis-type

TABLE 79

Relation of size of hind claw to ecology in *Accipiter*.

hind claw:	relatively larger	relatively smaller
predator	larger	smaller
prey	larger	smaller
shown by	gentilis-type bicolor-type tachiro-type albogularis-type	nisus-type brevipes-type trinotatus-type

TABLE 80
RELATION OF SIZE OF BILL TO ECOLOGY IN *Accipiter*.

bill:	relatively larger	relatively smaller
prey	larger tough-skinned	smaller tender-skinned
special feature	tropical forest habitat	
shown by	gentilis-type bicolor-type trinotatus-type tachiro-type albogularis-type	nisus-type brevipes-type

WING AND TAIL

Having previously discussed the relationship between the structure of the bill and feet and ecology, we may now turn to the structure of the wing and tail. Apart from the difference in shape of the wing tip, which is either rounded or pointed, other variation is gradual and the various structural types described in Chapter III are not rigidly delimited. In the following treatment several structure types will be united when discussing adaptations in wing structure. In Table 81 the species showing the various types of wing-tail structure are surveyed.

SPECIES WITH ROUNDED WINGS

The species with rounded wings constitute a complete series from relatively long-winged birds to very short-winged forms. The long-winged species showing the *nisus*-type are birds of varied country, hunting at the forest edge or in open spaces within the forest. Species with short wing tips showing the *tachiro*-type are, on the contrary, typical forest hunters. Among the species classed under the *nisus*-type, *A. ovampensis* has the longest wing. It is more a species characteristic of open country than are the other taxa. The species of the *novaehollandiae* and *bicolor*-types are intermediate in structure and habitat between those of the *nisus*-type and those of the *tachiro*-type. It is not clear why in the *novaehollandiae*-type the tail is relatively short. Only a close study of the flight of short-tailed and long-tailed forms can elucidate this point. The tail is very long in species of dense forest. It may be surmised that the maneuverability is enhanced by a long tail.

The denser the vegetation in which the prey has to be pursued, the more important it is that the predator be very maneuverable. A comparison of Accipiters and falcons with short and long wings respectively confirms that a long wing is an adaptation to long-sustained flight at high speed, whereas a short and rounded wing and a long tail enable a hawk to perform rapid wheeling flight over a short distance.

TABLE 81

Structure of the wing and tail in the species of *Accipiter*.

Nisus-type	Bicolor-type	Tachiro-type	Novaehollandiae-type
ovampensis	madagascariensis	tachiro	poliogaster
nisus	bicolor	castanilius	novaehollandiae (part)
melanoleucus	cooperii	trinotatus	nanus
gentilis	gundlachi	imitator	rhodogaster
meyerianus		henstii	
buergersi			

intermediate:	intermediate:	intermediate:
striatus	trivirgatus griseiceps	henicogrammus luteoschistaceus

Minullus-type	Brevipes-type
butleri	brevipes
francesii	soloensis
superciliosus	fasciatus
collaris	albogularis
minullus	rufitorques
brachyurus	haplochrous
virgatus (part)	virgatus (part)
	cirrhocephalus

intermediate:
badius
novaehollandiae (part)
poliocephalus
erythrauchen

Apart from variation in the length of the wing tip correlated with the habitat, migratory forms tend to have longer wing tips; this is brought out by comparing migratory *A. nisus nisus* and *A. n. nisosimilis* (wing tip 33.54% and 33.55% of the wing) with the resident races *A. n. wolterstorffi* and *A. n. rufiventris* (30.00% and 31.41%). A similar difference is found between *A. gentilis* and *A. melanoleucus*. Generally tropical forms have shorter wing tips than temperate ones, as is most clearly seen in the races of *A. bicolor*.

Species with Pointed Wings

In species with pointed wings we find nearly as much variation in length of the wing tip as in species with rounded wings, but the majority of the forms is long-winged. The wing tip of maximum length

(*A. soloensis,* 36.51%) is longer than that in the other group (*A. ovampensis,* 34.50%). In general the species of open country have the *brevipes*-type with a long pointed wing. Most of the short-winged species representing the *minullus*-type live in more forested habitats.

The very long-winged species *A. brevipes* and *A. soloensis* are rather slow hunters which hover occasionally. In addition they are strongly migratory. The wing tip is shorter in the tropical species *A. badius,* which is similar to *A. brevipes* in ecology, but the former species migrates over a much shorter distance. Parallel to this case is the example of *A. virgatus gularis* and *A. virgatus virgatus.* Migratory *A. v. gularis* has the structure of the *brevipes*-type, whereas resident *A. v. virgatus* represents the *minullus*-type. *A. v. gularis* has a shorter wing than *A. brevipes,* however, and *A. v. virgatus* has a shorter wing than *A. badius.* This may be related to the more wooded habitat and the bird-hunting habits of *A. gularis* and *A. virgatus.*

Conclusion Regarding the Structure of the Wing and Tail

From the discussion of species with pointed as well as those with rounded wing tips, it appears that in both groups the wing tip is shorter in forest forms, in non-migratory forms, and in forms with a more maneuverable type of flight. Although there is a tendency toward a pointed wing in very long-winged forms, it is not clear why there should be a difference in the shape of the wing. Whether two species with equally long but differently shaped wings, such as *A. virgatus* and *A. striatus,* differ in their modes of flight has not been sufficiently documented.

The division of the genus *Accipiter* into two groups with respect to the shape of the wing may mean either that an intermediate wing tip is aerodynamically unfavorable or that the genus consists of two groups that have become separated in the rather distant past and have since developed independently. On initial consideration the first alternative appears rather improbable. In addition there are several groups in which there is great variation in the length of the wing tip, although the shape remains similar (e.g., *A. brevipes, A. badius, A. butleri*). This would indicate that shape of the wing is a conservative character. On the other hand, *A. novaehollandiae* has some subspecies with a pointed wing, although the majority of the forms has rounded wings. There are no zoogeographical arguments in favor of an ancient splitting of the genus into two groups. Morphologically the species of both groups show no close resemblances, apart from the shape of the wing. From this we may conclude that the second alternative, i.e., an early splitting of the genus into a group with pointed wings and a group with rounded wings, does not hold true. The shape of the wing can, however, give a clue to taxonomic relationship within groups where there are also other grounds to suggest such a relationship (as in the example of the *badius*-group cited above).

IX

CONCLUSIONS

Geography and Taxonomy

As was emphasized in Chapter I, the genus *Accipiter* is a natural unit. There are only a few cases where it is questionable whether a particular species should be included in the genus or not (e.g., *Erythrotriorchis radiatus*). The taxonomic relationships within the genus are not always easily evaluated, however. Some species obviously belong together, e.g., the species of the *badius*-group, *A. nisus* and *A. striatus,* or *A. tachiro* and *A. castanilius.* On the other hand, several species and species pairs are rather isolated and neither morphology nor zoogeography gives any definite clue about their possible taxonomic relationships within the genus (e.g., *A. poliogaster, A. trivirgatus/A. griseiceps, A. poliocephalus/A. princeps, A. superciliosus/A. collaris*).

Leaving aside these puzzling species, the majority of the species in the genus fall into three groups (Table 82): (I) an Old World group of species moderately specialized with regard to their choice of prey and which are found in various types of mainly tropical and subtropical habitats; (II) a cosmopolitan group of long-toed sparrow hawks that capture flying prey in broken forest; and (III) a widespread group of large goshawk-like species, centering in the Palearctic.

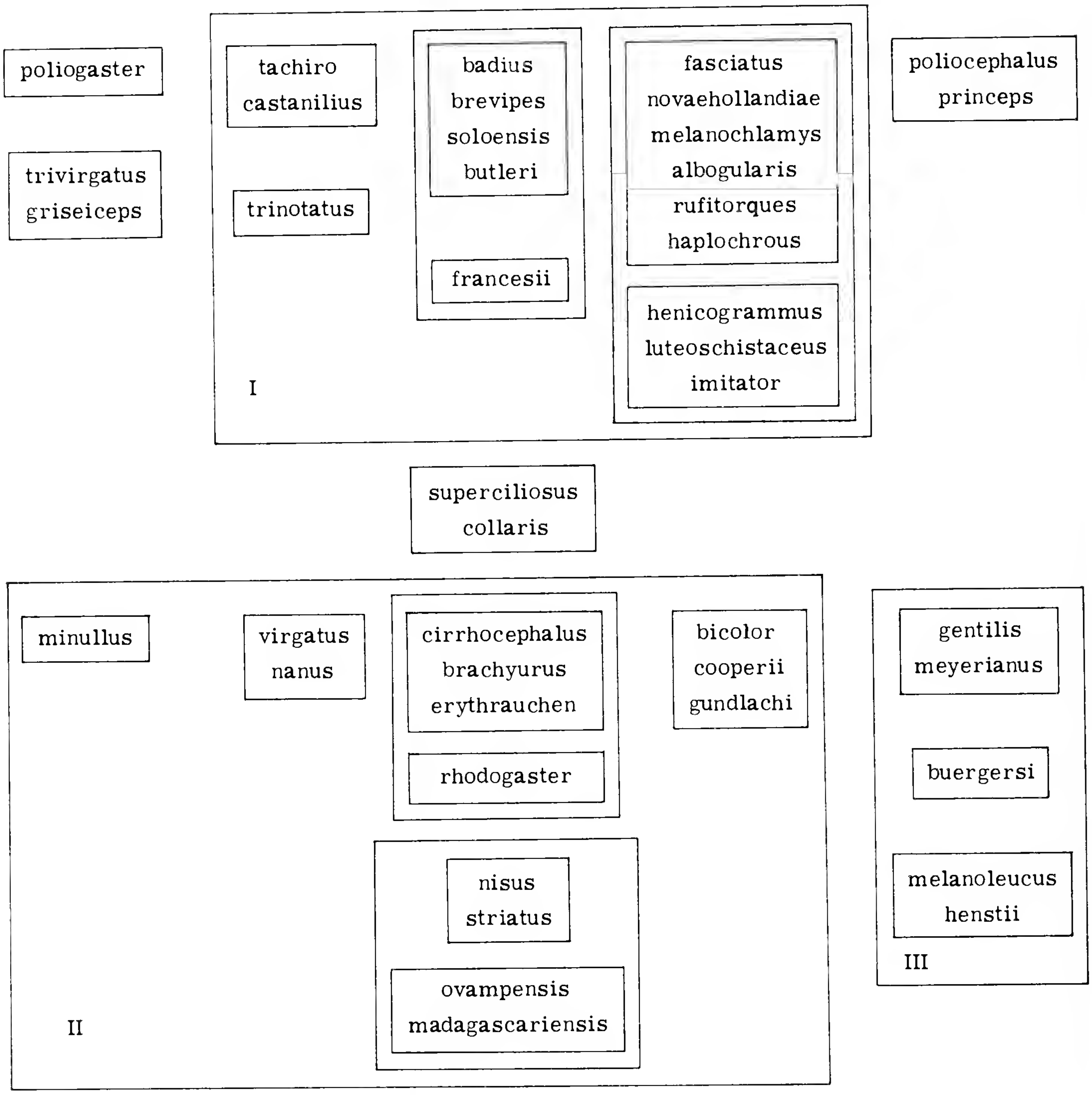
Group I is the least coherent of the three. It consists of a number of taxonomically rather isolated species complexes: *A. tachiro/A. castanilius,* the *A. badius* complex, *A. trinotatus,* and the *A. fasciatus-A. novaehollandiae/A. rufitorques* complex. In the discussion of *A. trinotatus* (p. 194) I attempted to show that this species may have had a common origin with the *badius* complex. In view of the general resemblance of their juvenile and adult plumages the same may be true for *A. tachiro* and the *fasciatus* complex. *A. novaehollandiae sylvestris,* for example, shows a remarkable resemblance to *A. badius* in plumage.

If the above hypothesis is correct, the ancestral form has spread over three continents, invading Africa and Australasia from Eurasia. Similar patterns of distribution are known for many other groups of species. In Africa part of the population has adapted to tropical forest conditions. This has resulted in the evolution of *A. tachiro* and *A. castanilius.* In Australasia the group has undergone a strong secondary radiation, resulting in a wealth of species. Some of these have developed into large goshawk-like types (*A. n. novaehollandiae* and *A. f. fasciatus*), which in Australia occupy an ecological niche similar to that of *A. gentilis* in the Holarctic.

A. poliocephalus/A. princeps and *A. trivirgatus/A. griseiceps* are

TABLE 82

Diagram of presumed taxonomic relations in the genus *Accipiter*.



apparently isolated from this group. The adult plumage of *A. trivirgatus* shows a superficial resemblance to the juvenile plumage of the similarly isolated American species *A. poliogaster*.

Group II consists of the very widespread *nisus* complex, representatives of which are found in Europe, Asia, Africa, and the Americas, and of a number of geographically restricted species or species complexes: *A. minullus* in Africa, the *A. virgatus* complex in eastern Asia, the *A. cirrhocephalus* complex in Australasia, and the *A. bicolor* complex in the Americas. The relation of the *A. bicolor* complex and *A. striatus* is presumably that of a double colonization in the Nearctic. In Africa we find a double colonization within the *nisus* complex (*A. ovampensis* and *A. nisus rufiventris*).

It appears that the present distribution of the species of Group II can be interpreted as the result of two successive "waves" of radiation from a Eurasian, or perhaps Holarctic, center similar to the successive "waves" of radiation in the *A. fasciatus* complex (p. 170). In this concept the geographically restricted species and groups are the remains of an ancient worldwide complex of long-toed bird-hunting Accipiters. In addition, the more recent expansion of the *nisus* complex has added new species of bird-hunting Accipiters to the existing fauna in several parts of the world. In Africa *A. ovampensis* is intermediate in age between *A. minullus* and *A. nisus*. There three successive "waves" of expansion appear to have occurred. Southeast Asia and the regions farther east have not been reached by recent colonizations of sparrow hawks. Whether *A. superciliosus* and *A. collaris* are the remains of an early American colonization of either Group I or Group II, or have a still different origin, cannot be determined with our present knowledge of these species. A coherence of Group I and Group II may be surmised from the fact that some of the old species Group II (notably *A. minullus* and *A. cirrhocephalus*) show a resemblance in plumage to Group I.

Group III consists of a small number of rather closely related species belonging to the *A. gentilis* complex. A discussion of the relationships within this group is given in the sections on *A. melanoleucus* (p. 95), *A. meyerianus* (p. 182), and *A. buergersi* (p. 184). It may be argued that the heavy goshawks of the *gentilis* group represent a specialized offshoot from the main group of bird-hunters.

Bird-hunting Accipiters range in size from very small (*A. minullus*) to large (*A. cooperii*). In the large species, *A. cooperii,* mammals are more important as prey than they are to middle-sized *A. nisus* and *A. striatus.* The tendency toward larger size of both predator and prey may end in a form of *A. gentilis*-like proportions. The feet, being the instrument for obtaining heavy prey, may tend to become very heavy, rather than very long, in the largest species. In this respect it is interesting that among the close relatives of *A. gentilis* we find at least one bird-hunting form (*A. melanoleucus*). *A. melanoleucus,* and *A. cooperii* for that matter, may be considered as ecologically intermediate between the *nisus*-type and the *gentilis*-type of Accipiter. In my opinion it is not improbable that the *gentilis* group (Group III, Table 82) was originally closely connected to Group II. This may provide a justification for the sequence of species in my checklist where the *gentilis* group is placed after the *nisus* group, with the *bicolor* group between.

In Table 82 my views on the taxonomy of the genus *Accipiter* are diagrammatically represented. This scheme has provided the basis for the checklist.

GAUSE'S PRINCIPLE

In order to comply with Gause's principle, sympatric forms of *Accipiter* ought to differ in their ecological demands. From the preceding discussions of ecological geography in various parts of the world it would appear clear that normally this condition is fulfilled. In a number of cases insufficient direct information on ecology is available, but differences in the bill-foot or of the wing-tail structures may attest to differences in choice of prey or style of hunting. The Accipiters of New Guinea exemplify this. *A. novaehollandiae* occurs alongside *A. cirrhocephalus, A. poliocephalus,* and *A. fasciatus* but differs from these in its bill-foot structure. In addition *A. cirrhocephalus* and *A. poliocephalus* are smaller than *A. novaehollandiae.* Finally, *A. fasciatus* prefers dryer habitats. This means that direct competition between any of these four species is highly improbable.

A good example of the applicability of Gause's principle may be found in North America. In contrast to the situation in Europe, where only one species of bird-hunting sparrow hawk lives, two species occur side by side in America. One of these, *A. striatus,* is smaller than European *A. nisus,* the other one, *A. cooperii,* is appreciably larger. It appears that *A. striatus* and *A. cooperii* have diverged from the size of *A. nisus* in different directions (character displacement). It is interesting that females of *A. striatus* are about the size of the males of *A. nisus,* whereas the males of *A. cooperii* are similar in size to females of *A. nisus.* As a consequence of this difference in size *A. striatus* and *A. cooperii* tend to prey on smaller and larger birds, respectively.

Similar examples of Gause's principle can be found in other parts of the world. It may be concluded that information from the genus *Accipiter* supports Gause's thesis. It will be a matter of profound and detailed ecological study to determine how the described effects are brought about.

CHECKLIST OF SPECIES OF ACCIPITER

Accipiter poliogaster (Temminck)
Accipiter trivirgatus (Temminck)
Accipiter griseiceps (Schlegel)
Accipiter tachiro (Daudin)
Accipiter castanilius Bonaparte
Accipiter badius (Gmelin)
Accipiter brevipes (Severtzov)
Accipiter soloensis (Horsfield)
Accipiter butleri (Gurney)
Accipiter francesii (A. Smith)
Accipiter trinotatus Bonaparte
Accipiter fasciatus (Vigors and Horsfield)
Accipiter novaehollandiae (Gmelin)
Accipiter melanochlamys (Salvadori)
Accipiter albogularis G. R. Gray
Accipiter rufitorques (Peale)
Accipiter haplochrous Sclater
Accipiter henicogrammus (G. R. Gray)
Accipiter luteoschistaceus Rothschild and Hartert

Accipiter imitator Hartert
Accipiter poliocephalus G. R. Gray
Accipiter princeps Mayr[1]
Accipiter superciliosus (Linnaeus)
Accipiter collaris Sclater
Accipiter minullus (Daudin)
Accipiter virgatus (Temminck)
Accipiter nanus (Blasius)[2]
Accipiter cirrhocephalus (Vieillot)
Accipiter brachyurus (Ramsay)
Accipiter erythrauchen G. R. Gray
Accipiter rhodogaster (Schlegel)
Accipiter ovampensis Gurney
Accipiter madagascariensis A. Smith
Accipiter nisus (Linnaeus)
Accipiter striatus Vieillot
Accipiter bicolor (Vieillot)
Accipiter cooperii (Bonaparte)
Accipiter gundlachi Lawrence
Accipiter melanoleucus A. Smith
Accipiter henstii (Schlegel)
Accipiter gentilis (Linnaeus)
Accipiter meyerianus (Sharpe)
Accipiter buergersi (Reichenow)

SUMMARY

Although the genus *Accipiter* has fascinated avian taxonomists for a long time, no comprehensive survey of the geographical and ecological differentiation of the group has heretofore been undertaken. In the present study an attempt is made to fill this gap. Data on the ecological differentiation and the distributional history of individual species are brought to bear upon the taxonomy of the group. In addition, Gause's hypothesis, stating that no two species of identical ecology can exist together, is tested. It appears that Accipiters living in the same region always demonstrate definite differences in ecology. On the other hand, species of similar ecology are found in widely separated areas. This is brought out clearly by comparing the Accipiter fauna of the various geographical regions (see concluding sections of Chapters III to VII).

A total of 43 species is recognized in the genus as delimitated in Peters' *Check-list* (1931). In Chapters III to VII these species are grouped by geographical regions and described. In the species accounts

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[1] *Accipiter princeps* Mayr, 1934, Amer. Mus. Novitates, no. 709, p. 3—Balayang (2,500 ft.), Wide Bay, New Britain.

[2] *Erythrospizias trinotatus nanus* W. Blasius, 1897 Fetschrift Herzogl. Technischen Hochschule Carolo-Wilhelmina, p. 292—Rurukan, Minahassa, Celebes.

special attention is paid to adaptive features in the structure of the foot, bill, wing, and tail. For ease in comparing structural characteristics a special diagram was devised. Almost all forms clearly show one of a limited number of structural types. Each of these types appears to represent an adaptation to a particular ecology. A survey of the relationship between structure and ecology is given in Chapter VIII.

Each species account concludes with a discussion of taxonomic affinities and geographical history. The data on taxonomy and zoogeography are summarized and some conclusions are drawn in Chapter IX. A few species, mainly occurring in tropical forest, e.g., *A. poliogaster, A. poliocephalus,* and *A. superciliosus,* stand quite isolated from the remainder of the genus, with neither morphology nor distribution giving any clue to their possible origin. The remaining species can be divided into three groups:

I. An Old World group of moderately specialized species. This group may be considered closest to the original type of the genus *Accipiter* which was a small raptor capturing various small animals by surprise. In Asia this group is at present represented by a single superspecies (*A. badius* and allies), in Africa and the Australian region it shows secondary radiation, which is especially strong in the Australian region. Apparently this group never reached the Americas.

II. A cosmopolitan group of long-toed, bird-hunting species probably representing a more recent development within the genus. This group appears to have colonized all geographical regions from Eurasia, reaching Africa and America in several successive "waves." Geographically and taxonomically the more recent species are closely related to *A. nisus.*

III. A group of heavily-built species, catching large prey, related to *A. gentilis.* This can be interpreted as a specialized offshoot of the foregoing group.

The taxonomic relations within the genus are summarized in Table 82 (p. 212).

X

LITERATURE CITED

ABDULALI, H. 1964. The birds of the Andaman and Nicobar Islands. Journ. Bombay Nat. Hist. Soc., **61**:483-571.

ALI, S. 1949. The Satpura trend as an ornithogeographical highway. Proc. Nat. Inst. Sci. India, **15**:379-386.

ALI, S. 1953. The Birds of Travancore and Cochin. Oxford Univ. Pr., Bombay.

ALI, S. 1954. The birds of Gujarat. Part 1. Journ. Bombay Nat. Hist. Soc., **54**:374-458.

ALI, S. AND S. D. RIPLEY. 1968. Handbook of the Birds of India and Pakistan. Vol. 1. Oxford Univ. Pr., Bombay.

AMADON, D. 1953. Avian systematics and evolution in the Gulf of Guinea. Bull. Amer. Mus. Nat. Hist., **100**:393-452.

AMADON, D. 1964. Taxonomic notes on birds of prey. Amer. Mus. Novitates, no. 2166, 24 p.

ANDERSSON, C. J. 1872. Notes on the Birds of Damara Land and the Adjacent Countries of South-West Africa, Arranged and Edited by J. H. Gurney. John Van Voorst, London.

ARADI, C. 1964. Levant Sparrow Hawk nesting in the Nagyerdö of Debreczen. Aquila, **69-70** (1962-63): 248-251.

AUSTIN, O. L. AND N. KURODA. 1953. The birds of Japan, their status and distribution. Bull. Mus. Comp. Zool., **109**:279-637.

BÄHRMANN, U. 1937. Ein Beitrag zur Rassenfrage des deutschen Hühnerhabichts, *Accipiter gentilis* (L.). Mitt. Ver. Sächs. Ornith., **5**:133-144.

BÄHRMANN, U. 1965. Über das Variieren des Habichts (*Accipiter gentilis gallinarum* Br.). Zool. Abh. St. Mus. Tierk., Dresden, **28**:65-94.

BAKER, E. C. S. 1928. Fauna of British India. Birds. 2d. ed. Vol. 5. Taylor and Francis, London.

BAKER, E. C. S. 1935. The Nidification of Birds of the Indian Empire. Vol. 4. Taylor and Francis, London.

BARNARD, H. G. 1911. Field notes from Cape York. Emu, **11**:17-32.

BATES, G. L. 1930. Handbook of the Birds of West Africa. John Bale, Sons and Danielsson, London.

BENSON, C. W. 1940. Further notes on Nyasaland birds (with particular reference to those of the Northern Province). Part 1. Ibis, **82**:257-298.

BENSON, C. W. 1945. Notes on the birds of southern Abyssinia. Ibis, **87**:366-400.

LITERATURE CITED

Benson, C. W. 1947. Observations from the Kota-kota District of Nyasaland. Ibis, **89**:553-565.

Benson, C. W. 1960. The birds of the Comoro Islands: results of the British Ornithologists' Union Centenary Expedition 1958. Ibis, **103b**:5-106.

Benson, C. W. and C. M. N. White. 1957. Checklist of the Birds of Northern Rhodesia. The Government Printer, Lusaka.

Bent, A. C. 1937. Life histories of North American birds of prey, Order Falconiformes. Part 1. Bull. U.S. Nat. Mus., **167**, 409 p.

Bergman, S. 1935. Zur Kenntnis Nordostasiatischer Vögel. Bonnier, Stockholm.

Bertoni, A. de W. 1926. Apuntes ornitológicos. I. Sobre migración de aves en el Paraguay. Hornero, 3:396-398.

Betts, F. N. 1947. Bird life in an Assam jungle. Journ. Bombay Nat. Hist. Soc., **46**:667-684.

Biswas, B. 1960. The birds of Nepal. Part 1. Journ. Bombay Nat. Hist. Soc., **57**:278-308.

Black, R. A. R. and G. J. B. Ross. 1970. Aspects of adaptive radiation in southern African Accipiters. Ann. Cape Prov. Mus. (Nat. Hist.), **8**:57-65.

Blake, E. R. 1950. Report on a collection of birds from Guerrero, Mexico. Fieldiana: Zool., 31:375-393.

Blasius, W. 1897. Neuer Beitrag zur Kenntniss der Vogelfauna von Celebes, p. 277-395. *In* Festschrift Herzogl. Technischen Hochschule Carolo-Wilhelmina. Friedrich Vieweg und Sohn, Braunschweig.

Bodenstein, G. 1943. Beobachtungen am Kurzfangsperber (*Accipiter brevipes* Sev.) bei Saloniki. Ornith. Monatsb. **51**:158.

Bond, J. 1965. Tenth Supplement to the Checklist of Birds of the West Indies (1956). Academy of Natural Sciences, Philadelphia.

Bond, J. 1968. Thirteenth Supplement to the Check-list of Birds of the West Indies (1956). Academy of Natural Sciences, Philadelphia.

Bond, J. and R. M. de Schauensee. 1943. The birds of Bolivia. Part 2. Proc. Acad. Nat. Sci. Philadelphia, **95**:167-221.

Brown, L. and D. Amadon. 1968. Eagles, Hawks, and Falcons of the World. 2 vols. Country Life Books, Feltham, Middlesex.

Brüll, H. 1964. Das Leben deutscher Greifvögel. Ihre Bedeutung in der Landschaft. 2nd. ed. Gustav Fischer, Stuttgart.

Brunel, J. and J. M. Thiollay. 1969. Liste préliminaire des oiseaux de Côte d'Ivoire. Alauda, **37**:230-254; 315-337.

Butler, A. L. 1899. The birds of the Andaman and Nicobar Islands. Part 3. Journ. Bombay Nat. Hist. Soc., **12**:684-696.

Cain, A. J. and I. C. J. Galbraith. 1956. Field notes on the birds of the eastern Solomon Islands. Ibis, **98**:100-134; 262-295.

LITERATURE CITED

Cairns, J. 1963. New breeding records of Malayan birds. Journ. Bombay Nat. Hist. Soc., **60**:140-159.

Cameron, R. A. D., L. Cornwallis, M. J. L. Percival, and A. R. E. Sinclair. 1967. The migration of raptors and storks through the Near East in autumn. Ibis, **109**:489-501.

Carriker, M. A., Jr. 1910. An annotated list of the birds of Costa Rica, including Cocos Island. Ann. Carnegie Mus., **6**:314-915.

Cave, F. O. and J. D. Macdonald. 1955. Birds of the Sudan. Oliver and Boyd, Edinburgh and London.

Chapin, J. P. 1932. The birds of the Belgian Congo. Part 1. Bull. Amer. Mus. Nat. Hist., **65**, 756 p.

Chapman, F. M. 1917. The distribution of bird-life in Colombia. Bull. Amer. Mus. Nat. Hist., **36**, 729 p.

Chapman, F. M. 1926. The distribution of bird-life in Ecuador. Bull. Amer. Mus. Nat. Hist., **55**, 784 p.

Chasen, F. N. and A. Hoogerwerf. 1941. The birds of the Netherlands Indian Mt. Leuser Expedition 1937 to North Sumatra. Treubia, **18**, suppl., 125 p.

Christison, A. F. P. 1941. Notes on the birds of Chagai. Ibis, **83**:531-556.

Commissie Voor de Nederlandse Avifauna. 1962. Lijst van de in Nederland Waargenomen Vogelsoorten en hun Geographische Vormen. J. Kist and K. H. Voous [eds.]. Brill, Leiden.

Condon, H. T. and D. Amadon. 1954. Taxonomic notes on Australian hawks. Records South Austr. Mus., **11**:189-246.

Conover, B. 1946. Notes on some neotropical hawks. Fieldiana: Zool., **31**:39-45.

Coomans de Ruiter, L. 1947. Roofvogelwaarnemingen in Zuid Celebes. Limosa, **20**:213-229.

Coomans de Ruiter, L. 1954. Trekvogels in Sulawesi (Celebes). Penggemar Alam, **34**:67-96.

Courtois, R. P. F. 1912-18. Les oiseaux du Musée de Zikawei. Mem. Hist. Nat. de l'Empire Chinois, **5**, 121 p.

Cuello, J. and E. Gerzenstein. 1962. Las Aves del Uruguay. Com. Zool. Mus. Montevideo, **6**, 191 p.

Dahl, F. 1899. Das Leben der Vögel auf den Bismarckinseln nach eigenen Beobachtungen vergleichend dargestellt. Mitt. Zool. Samml. Mus. Naturk. Berlin, **1**:107-222.

David, A. and E. Oustalet. 1877. Les Oiseaux de la Chine. 2 vols. G. Masson, Paris.

Dedem, F. K. van. 1911. Lijst van vogels verzameld in Ned. Oost-Indië, gedurende het tijdvak van 15 Mei 1909 tot 16 Maart 1911. Jaarb. Ned. Ornith. Vereen., **8**:45-113.

Deignan, H. G. 1945. The birds of northern Thailand. Bull. U.S. Nat. Mus., **186**, 616 p.

Deignan, H. G. 1964. Birds of the Arnhem Land expedition. Rec.

Amer.-Austr. Sci. Exp. Arnhem Land, **4**:345-425. Melbourne University Press.

Delacour, J. and P. Jabouille. 1931. Les Oiseaux de l'Indochine Francaise. Vol. 2. Exposition Coloniale Internationale, Paris.

Dementiev, G. P. 1937. On the sparrow hawk in Turkestan. Ibis, **79**: 877-881.

Dementiev, G. P. 1938. Sur la distribution géographique de certains oiseaux paléarctiques au point de vue de quelques questions générales de systématique. Proc. 8th Intern. Ornith. Congr., Oxford, 1934, p. 243-259.

Dementiev, G. P. 1951. Order Falconiformes, p. 71-379. *In* G. P. Dementiev and N. A. Gladkov [eds.]. Ptitsy Sovetskogo Soyuza. Vol. 1. Sovetskaya Nauka, Moscow.

Diamond, J. M. 1971. Bird records from west New Britain. Condor, **73**: 481-483.

Diesselhorst, G. 1968. Beiträge zur Ökologie der Vögel Zentral-und Ost-Nepals. Khumbu Himal. Ergebnisse des Forschungsunternehmens Nepal Himalaya. Vol. 2. Universitätsverlag Wagner, Innsbruck-München.

Dombrowski, R. von. 1912. Ornis Romaniae. Staatsdruckerei, Bukarest.

Dunnet, G. M. 1957. Notes on avian predation on young rabbits, *Oryctolagus cuniculus* (L.). C.S.I.R.O. Wildl. Res., **2**:66-68.

Elgood, J. H. 1959. Bird migration at Ibadan, Nigeria. Proc. I Pan-Afr. Ornith. Congr. Ostrich, suppl. 3, p. 306-316.

Elgood, J. H. and F. C. Sibley. 1964. The tropical forest edge avifauna of Ibadan, Nigeria. Ibis, **106**:221-248.

Errington, P. L. 1933. Food habits of southern Wisconsin raptors. Part 2. Hawks. Condor, **35**:19-29.

Fennell, C. M. 1965. Stomach analyses of Korean birds. Misc. Rept. Yamashina Inst. Ornith. Zool., **4**:172-183.

Fisher, A. K. 1893. The hawks and owls of the United States in their relation to agriculture. Bull. U.S. Dept. Agric. Div. Ornith. Mamm., **3**, 210 p.

Fitch, H. S., B. Glading, and V. House. 1946. Observations on Cooper Hawk nesting and predation. Calif. Fish Game, **32**:144-154.

Friedmann, H. 1950. The birds of north and middle America. Bull. U.S. Nat. Mus., **50**, pt. 11, 793 p.

Gabrielson, I. N. and F. C. Lincoln. 1959. The Birds of Alaska. Stackpole Co., Harrisburg.

Galbraith, I. C. J. and E. H. Galbraith. 1962. Land birds of Guadalcanal and the San Christoval group, eastern Solomon Islands. Bull. Brit. Mus. (Nat. Hist.), Zool., **9**:1-86.

LITERATURE CITED

GENENGER, I. AND W. GENENGER. 1968. Ornithologische Beobachtungen in Nord-Persien. Ornith. Mitt., **20**:62-68.

GIAI, A. G. 1951. Notas sobre la avifauna de Salta y Misiones. Hornero, **9**:247-276.

GIBSON-HILL, C. A. 1947. Notes on the birds of Christmas Island. Bull. Raffles Mus., **18**:87-165.

GILLIARD, E. T. 1950. Notes on the birds of southeastern Papua. Amer. Mus. Novitates, no. 1453, 40 p.

GILLIARD, E. T. AND M. LECROY. 1967. Results of the 1958-1959 Gilliard New Britain Expedition. 4. Annotated List of Birds of the Whiteman Mountains, New Britain. Bull. Amer. Mus. Nat. Hist., **135**: 173-216.

GLADKOV, N. A. 1941. Taxonomy of palaearctic goshawks. Auk, **58**: 80-90.

GREEN, R. H. AND B. C. MOLLISON. 1961. Birds of Port Davey and the south coast of Tasmania. Emu, **61**:223-236.

GRINNELL, J. AND A. H. MILLER. 1944. The distribution of the birds of California. Pacific Coast Avif. (Cooper Ornith. Soc.), no. 27, 608 p.

GRINNELL, J. AND H. S. SWARTH. 1913. An account of the birds and mammals of the San Jacinto area of southern California. Univ. California Publ. Zool., **10**:197-406.

GRISCOM, L. 1932. The distribution of bird-life in Guatemala. Bull. Amer. Mus. Nat. Hist., **64**, 439 p.

GUNDLACH, J. 1871. Neue Beiträge zur Ornithologie Cubas. Fortsetzung. Journ. Ornith. **19**:353-378.

GYLDENSTOLPE, N. 1955. Notes on a collection of birds made in the Western Highlands, Central New Guinea, 1951. Arkiv. Zool., ser. 2, **8**:1-181.

HACHISUKA, M. AND T. UDAGAWA. 1951. Contribution to the ornithology of Formosa. Part 2. Quart. Journ. Taiwan Mus., **4**:1-180.

HADLEY, C. J. AND S. A. PARKER. 1965. Field notes on the birds of the Santa Cruz Islands, South-west Pacific. Bull. Brit. Ornith. Club, **85**:154-159.

HAMERSTROM, F. N., JR. AND F. HAMERSTROM. 1951. Food of young raptors on the Edwin S. George Reserve. Wilson Bull. **63**:16-25.

HARRISON, T. 1963. Birds above the Borneo jungle canopy. Ibis, **105**: 403-406.

HARTERT, E. 1896. On ornithological collections made by Mr. Alfred Everett in Celebes and on the islands south of it. Novitates Zool., **3**:148-183.

HARTERT, E. 1910. The birds of Hainan. Novitates Zool., **17**:189-254.

HARTERT, E. 1912-21. Die Vögel der Paläarktischen Fauna. Vol. 2. Friedländer, Berlin.

HARTERT, E. 1926. On the birds of Feni and Nissan Islands, east of South New Ireland. Novitates Zool., **33**:33-48.

LITERATURE CITED

Hartert, E. 1929. Notes on birds from the Solomon Islands. Amer. Mus. Novitates, no. 364, 19 p.

Hartert, E. and F. Steinbacher. 1932-38. Die Vögel der Paläarktischen Fauna. Ergänzungsband. Friedländer, Berlin.

Harwin, R. M. and C. T. A. Maberly. 1953. Field identification of Raptores. Bokmakierie, 5:30-33.

Heim de Balsac, H. and N. Mayaud. 1962. Les Oiseaux du Nord-Ouest de l'Afrique. Encyclopédie Ornithologique. Vol. X. Lechevalier, Paris.

Heinrich, G. 1956. Biologische Aufzeichnungen über Vögel von Halmahera und Batjan. Journ. Ornith., **97**:31-40.

Hellmayr, C. E. 1906. On some new species of South American birds. Bull. Brit. Ornith. Club, **16**:82-86.

Hellmayr, C. E. 1914. Die Avifauna von Timor. *In* C. B. Haniel, [ed.]. Zoologie von Timor. Vol. 1. Stuttgart.

Hellmayr, C. E. and B. Conover. 1949. Catalogue of the birds of the Americas and the adjacent islands. Publ. Field Mus. Nat. Hist., Zool. Ser., **13**, pt. 1, no. 4, 358 p.

Henry, G. M. 1955. A Guide to the Birds of Ceylon. Oxford University Press, London.

Hoesch, W. 1938. Ornithologische Beobachtungen auf einer Fahrt ins Etoscha-Gebiet (S.W. Afrika). Journ. Ornith., **86**:222-233.

Hoesch, W. and G. Niethammer. 1940. Die Vogelwelt Deutsch-Südwestafrikas namentlich des Damara- und Namalandes. Journ. Ornith., **88**, Sonderheft, 404 p.

Höglund, N. H. 1964. Über die Ernährung des Habichts (*Accipiter gentilis* Linn.) in Schweden. Viltrevy, **2**:271-328.

Hollom, P. A. D. 1959. Notes from Jordan, Lebanon, Syria and Antioch. Ibis, **101**:183-200.

Hoogerwerf, A. 1948. Contribution to the knowledge of the distribution of birds on the island of Java, with remarks on some new birds. Treubia, **19**:83-137.

Hoogerwerf, A. 1953. Merkwaardige en zeldzame vogels in Kebun Raya Indonesia te Bogor. Indones. Journ. Nat. Sci., **109**:63-80.

Hubbard, J. P. 1965. The summer birds of the forests of the Mogollon Mountains, New Mexico. Condor, **67**:404-415.

Hume, A. O. 1876. Additional notes on the avifauna of the Andaman Islands. Stray Feathers, **4**:279-294.

Hurrell, L. H. 1961. Migration and movements of birds of prey over Singapore. Bull. Nat. Mus. Singapore, **30**:97-100.

Ishizawa, J. and S. Chiba. 1967. Stomach analysis of 12 species of Japanese hawks. Misc. Rept. Yamashina Inst. Ornith. Zool., **5**:13-33.

Jahn, H. 1942. Zur Oekologie und Biologie der Vögel Japans. Journ. Ornith., **90**:1-302.

Johansen, H. 1957. Die Vogelfauna Westsiberiens, III Teil (Non-

Passeres). 4. Fortsetzung: Aquilinae II (*Accipiter-Aegypius*). Journ. Ornith., **98**:397-415.

Johnson, A. W. 1965. The Birds of Chile and Adjacent Regions of Argentina, Bolivia, and Peru. Vol. 1. Platt Estab. Graf., Buenos Aires.

Johnson, D. H., M. D. Bryant, and A. H. Miller. 1948. Vertebrate animals of the Providence Mountains area of California. Univ. California Publ. Zool., **48**:221-376.

Jordans, A. von and G. Niethammer. 1940. Eine Vogelausbeute aus Fukien. Verh. Ornith. Ges. Bayern, **22**:98-136.

Junge, G. C. A. 1953. Zoological results of the Dutch New Guinea Expedition, 1939. No. 5. The birds. Zoöl. Verh. Leiden, **20**:1-77.

Junge, G. C. A. and J. G. Kooiman. 1951. On a collection of birds from the Khwae Noi Valley, Western Siam. Zoöl. Verh. Leiden, **15**:1-38.

Keast, A. 1961. Bird speciation on the Australian continent. Bull. Mus. Comp. Zool., **123**:302-495.

Kleinschmidt, O. 1922-23. Berajah, Zoographia infinita. Die Realgattung Habicht, *Falco Palumbarius* (Kl.). Gebauer-Schwetschke, Halle a.S.

Kleinschmidt, O. 1923-37. Berajah, Zoographia infinita. Die Realgattung Sperber, *Falco Nisus* (Kl.). Gebauer-Schwetschke, Halle a.S.

Kolthoff, K. 1932. Studies on birds in the Chinese provinces of Kiangsu and Anhwei 1921-1922. Göteborgs K. Vetensk.-o. Vitterhsamh. Handl., Ser. B, 3, 190 p.

Korelov, M. N. 1962. [Birds of Prey], p. 545-564, *in* V. F. Gavrin, I. A. Dolgushin, M. N. Korelov, and M. A. Kusmina (eds.). Ptitsy Kazakhstana. Vol. 2. Akademia Nauk Kazakh. S.S.R., Alma-Ata.

Kuroda, N. 1954. On a collection of birds from Celebes and Halmahera, preserved in the Yamashina Museum of Birds. (Non-Passeres, II.) Misc. Rept. Yamashina Inst. Ornith. Zool., **1**:156-173.

Latouche, J. D. D. 1931-34. A Handbook of the Birds of Eastern China. Vol. 2. Taylor and Francis, London.

Laubmann, A. 1939. *Accipiter pectoralis* (Bonaparte) und seine Verbreitung in Südamerika. Physis Buenos Aires, **16**:109-114.

Lawrence, G. N. 1860. Notes on some Cuban birds, with descriptions of new species. Ann. Lyceum Nat. Hist. New York, **7**:247-275.

Layard, E. L. and E. L. C. Layard. 1880. Notes on the avifauna of the Loyalty Islands. Ibis, **22**:220-234.

Leopold, A. S. 1944. Cooper's Hawk observed catching a bat. Wilson Bull., **56**:116.

Liversidge, R. 1962. The breeding biology of the Little Sparrowhawk *Accipiter minullus*. Ibis, **104**:399-406.

Ludlow, F. and N. B. Kinnear. 1944. The birds of south-eastern Tibet. Ibis, **86**:43-86; 176-208; 348-389.

LITERATURE CITED

McAtee, W. L. 1935. Food habits of common hawks. Circ. U.S. Dept. Agric., no. 370, 36 p.

Macdonald, M. 1960. Birds in my Indian Garden. Jonathan Cape, London.

Mackworth-Praed, C. W. and C. H. B. Grant. 1952. African Handbook of Birds. Ser. 1, Vol. 1. Birds of Eastern and North Eastern Africa. Longmans, Green and Co., London.

McLachlan, G. R. and R. Liversidge. 1961. Roberts' Birds of South Africa. Central News Agency, South Africa.

Marchant, S. 1953. Notes on the birds of southeastern Nigeria. Ibis, **95**:38-69.

Marchant, S. 1954. The relationships of the southern Nigerian avifauna to those of Upper and Lower Guinea. Ibis, **96**:371-379.

Marshall, J. T., Jr. 1957. Birds of pine-oak woodland in southern Arizona and adjacent México. Pacific Coast Avif. (Cooper Ornith. Soc.), no. 32, 125 pp.

Mathews, G. M. 1909. On the birds of North-West Australia, with field notes by the collector, J. P. Rogers. Part 1. Birds from Wyndham. Emu, **9**:1-16.

Matvejev, S. D. 1950. La distribution et la vie des oiseaux en Serbie (Ornithogeographia serbica.). Posebna Izd. Inst. Ekol. Biogeogr., **3**:1-362.

Mayr, E. 1931a. The birds of Malaita Island (British Solomon Islands). Amer. Mus. Novitates, no. 504, 26 p.

Mayr, E. 1931b. Die Vögel des Saruwaged- und Herzoggebirges (N.O.-Neuguinea). Mitt. Zool. Mus. Berlin, **17**:639-723.

Mayr, E. 1934. Notes on some birds from New Britain, Bismarck Archipelago. Amer. Mus. Novitates, no. 709, 15 p.

Mayr, E. 1940. Notes on New Guinea Birds. VI. Amer. Mus. Novitates, no. 1056, 12 p.

Mayr, E. 1941a. List of New Guinea Birds. Amer. Mus. Nat. Hist., New York.

Mayr, E. 1941b. Ueber einige Raubvögel der Kleinen Sunda-Inseln: Ornith. Monatsb., **49**:42-47.

Mayr, E. 1944. The birds of Timor and Sumba. Bull. Amer. Mus. Nat. Hist., **83**:129-194.

Mayr, E. 1945a. Birds of the Southwest Pacific. MacMillan, New York.

Mayr, E. 1945b. Notes on the birds of northern Melanesia. 1. Amer. Mus. Novitates, no. 1294, 12 p.

Mayr, E. 1949. Geographical variation in *Accipiter trivirgatus*. Amer. Mus. Novitates, no. 1415, 12 p.

Mayr, E. 1957. Notes on the birds of northern Melanesia. 4. The genus *Accipiter*. Amer. Mus. Novitates, no. 1823, 14 p.

Mayr, E. and R. M. de Schauensee. 1939. Birds from northwest New Guinea. Proc. Acad. Nat. Sci. Philadelphia, **91**:97-144.

Mayr, E. and E. T. Gilliard. 1954. Birds of central New Guinea. Bull. Amer. Mus. Nat. Hist., **103**:311-374.

MAYR, E. AND A. L. RAND. 1937. The birds of the 1933-34 Papuan Expedition. Bull. Amer. Mus. Nat. Hist., **73**:1-248.

MEAD, R. A. 1963. Cooper's Hawk attacks pigeon by stooping. Condor, **65**:167.

MEDWAY, LORD AND D. R. WELLS. 1964. Bird report: 1963. Malay. Nat. Journ., **18**:133-167.

MEES, G. F. 1965. The avifauna of Misool. Nova Guinea, Zool., **31**:139-203.

MEES, G. F. 1967. Zur Nomenklatur einiger Raubvögel und Eulen. Zoöl. Meded. Leiden, **42**:143-146.

MEES, G. F. 1970. Notes on some birds from the island of Formosa (Taiwan). Zoöl. Meded. Leiden, **44**:285-304.

MEINERTZHAGEN, R. 1920. Notes on the birds of Quetta. Ibis, **62**:132-195.

MEINERTZHAGEN, R. 1951. Some relationships between African, Oriental, and Palaearctic genera and species, with a review of the genus *Monticola*. Ibis, **93**:443-459.

MEINERTZHAGEN, R. 1954. Birds of Arabia. Oliver and Boyd, Edinburgh.

MEINERTZHAGEN, R. 1959. Pirates and Predators. Oliver and Boyd, Edinburgh.

MEISE, W. 1929. Die Vögel von Djampea und benachbarten Inseln nach einer Sammlung Baron Plessens. Journ. Ornith., **77**:431-480.

MENG, H. 1959. Food habits of nesting Cooper's Hawks and Goshawks in New York and Pennsylvania. Wilson Bull., **71**:169-174.

MENGEL, R. M. 1965. The birds of Kentucky. Ornith. Monogr. (Amer. Ornith. Union), no. 3, 581 p.

MEYER, A. B. AND L. W. WIGLESWORTH. 1898. The Birds of Celebes and the Neighbouring Islands. Vol. 1. Friedländer, Berlin.

MEYER, O. 1927. Zur Ornithologie des Bismarckarchipels. Ornith. Monatsb. **35**:112-113.

MILLER, A. H. 1955. The avifauna of the Sierra del Carmen of Coahuila, Mexico. Condor, **57**:154-178.

MISHIMA, T. 1962. A new race of *Accipiter virgatus* and the validity of the race *pullus* of the Common Noddy for Riu Kiu Is. Tori, **17**:219-222.

MOLLISON, B. C. 1961. Notes on Tasmanian birds. III. The Collared Sparrowhawk at the kill. Emu, **61**:58-60.

MOREAU, R. E. 1966. The Bird Faunas of Africa and its Islands. Academic Press, New York.

MUELLER, H. C. AND D. D. BERGER. 1967. Some observations and comments on the periodic invasions of Goshawks. Auk, **84**:183-191.

NICOLL, M. J. 1906. On the birds collected and observed during the voyage of the "Valhalla," R. Y. S., from November 1905 to May 1906. Ibis, **48**:666-712.

Niethammer, G. 1938. Handbuch der Deutschen Vogelkunde. Vol. 2. Akademische Verlagsgesellschaft, Leipzig.

Niethammer, G. 1953. Zur Vogelwelt Boliviens. Bonn. Zool. Beitr., 4:195-303.

Olivares, A. 1959. Cinco aves que aparentemente no habían sido registradas en Colombia. Lozania, **12**:51-56.

Olivares, A. 1960. Algunas aves de Gaitania. Caldasía, **8**:369-382.

d'Orbigny, A. 1835-44. Voyage dans l'Amérique Méridionale. Vol. 4(3). Oiseaux. Bertrand, Paris.

Osmaston, B. B. 1906. Notes on Andaman birds, with accounts of the nidification of several species whose nests and eggs have not been hitherto described. Part 2. Journ. Bombay Nat. Hist. Soc., **17**:486-491.

Owen, J. H. 1932. The hunting of the Sparrow Hawk. Brit. Birds, **25**: 238-243.

Partridge, W. H. 1961. *Accipiter pectoralis,* a synonym of *Accipiter poliogaster.* Condor, **63**:505-506.

Peeters, H. J. 1963. Einiges über den Waldfalken, *Micrastur semitorquatus.* Journ. Ornith., **104**:357-364.

Pereyra, J. A. 1938. Aves de la zona riberena nordeste de la provincia de Buenos Aires. Mems. Jard. Zool. La Plata, **9**:5-304.

Peters, J. L. 1931. Check-list of Birds of the World. Vol. 1. Harvard University Press, Cambridge, Massachusetts.

Peters, J. L. and J. A. Griswold, Jr. 1943. Birds of the Harvard Peruvian expedition. Bull. Mus. Comp. Zool., **92**:281-327.

Peus, F. 1954. Zur Kenntnis der Brutvögel Griechenlands. Bonn. Zool. Beitr. Sonderbd. 1 Teil, 50 p.

Phillips, A., J. Marshall, and G. Monson. 1964. The Birds of Arizona. University of Arizona Press, Tucson.

Phillips, J. C. 1915. Some birds from Sinai and Palestine. Auk, **32**:273-289.

Pleske, T. 1886. Übersicht der Säugthiere und Vögel der Kola-Halbinsel. Theil II. Vögel und Nachträge. Kaiserlichen Akademie der Wissenschaften, St. Petersburg.

Porter, R. and I. R. Willis. 1968. The autumn migration of soaring birds at the Bosphorus. Ibis, **110**:520-536.

Radde, G. and A. Walter. 1889. Die Vögel Transcaspiens. Ornis, **5**:1-128; 165-279. (Also published as: Wissenschaftliche Ergebnisse der im Jahre 1886 in Transcaspien von Dr. G. Radde, Dr. A. Walter und A. Konschin ausgeführten Expedition. Vol. 1. Gustav Fischer, Jena.)

Rand, A. L. 1937. The distribution and habits of Madagascar birds. Bull. Amer. Mus. Nat. Hist., **72**:143-499.

LITERATURE CITED

RAND, A. L. 1941. New and interesting birds from New Guinea. Amer. Mus. Novitates, no. 1102, 15 p.

RAND, A. L. 1942. Birds of the 1938-1939 New Guinea Expedition. Bull. Amer. Mus. Nat. Hist., **79**:425-515.

RAND, A. L. AND E. T. GILLIARD. 1967. Handbook of New Guinea birds. Weidenfeld and Nicolson, London.

REISER, O. AND L. VON FÜHRER. 1896. Materialien zu einer Ornis Balcanica. Vol. 4. Montenegro. Carl Gerold's Sohn, Wien.

RENSCH, B. 1931. Die Vogelwelt von Lombok, Sumbawa und Flores. Mitt. Zool. Mus. Berlin, **17**:451-637.

RICHMOND, C. W. 1903. Birds collected by Dr. W. L. Abbott and Mr. C. B. Kloss in the Andaman and Nicobar Islands. Proc. U.S. Natl. Mus., **25**:287-314.

RIPLEY, S. D. 1947. A report on the birds collected by Logan J. Bennett on Nissan Island and the Admiralty Islands. Journ. Wash. Acad. Sci., **37**:95-102.

RIPLEY, S. D. 1961. A Synopsis of the Birds of India and Pakistan together with those of Nepal, Sikkim, Bhutan, and Ceylon. Bombay Natural History Society.

RIPLEY, S. D. 1964. A systematic and ecological study of birds of New Guinea. Bull. Peabody Mus. Nat. Hist. (Yale Univ.), **19**:1-87.

RIPLEY, S. D. AND D. S. RABOR. 1961. The avifauna of Mount Katanglad. Postilla, Yale Univ., no. 50, 20 p.

ROBERTS, A. 1949. The birds of South Africa. Witherby, London.

ROTHSCHILD, W. AND E. HARTERT. 1915. Notes on Papuan birds. XXXII. Accipitres. Novitates Zool., **22**:46-55.

ROTHSCHILD, LORD, E. STRESEMANN, AND K. PALUDAN. 1932. Ornithologische Ergebnisse der Expedition Stein 1931-32. I. Die Vögel von Waigeu. II. Die Vögel von Numfor. III. Die Vögel von Japen. Novitates Zool., **38**:127-247.

RUDEBECK, G. 1950-51. The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. Oikos, **2**:65-88; **3**:200-231.

SAFRIEL, U. 1968. Bird migration at Elat, Israel. Ibis, **110**:283-320.

SARASIN, F. 1913. Die Vögel Neu-Caledoniens und der Loyalty-Inseln. *In* Nova Caledonia, F. Sarasin and J. Roux, eds. Part A. Zool., **1**: 1-78.

SARASIN, F. 1917. Neu-Caledonien und die Loyalty-Inseln. Reise-Erinnerungen eines Naturforschers. Georg & Co., Basel.

SASSI, M. 1912. Beitrag zur Ornis Zentralafrikas (Exp. Grauer). Ann. Naturh. Mus. Wien, **26**:347-393.

SCHÄFER, E. 1938. Ornithologische Ergebnisse zweier Forschungsreisen nach Tibet. Journ. Ornith., **86**, Sonderheft, 349 p.

SCHÄFER, E. AND W. H. PHELPS. 1954. Aves de Rancho Grande (Las Aves del Parque Nacional "Henri Pittier" (Rancho Grande) y sus funciónes écologicas). Bol. Soc. Venezolana Cienc. Nat., **16**:3-167.

LITERATURE CITED

Schiermann, G. 1925. Wanderfalke und Hühnerhabicht in der Mark Brandenburg. Journ. Ornith. **73**:277-283.

Schlegel, H. and F. P. L. Pollen. 1868. Recherches sur la faune de Madagascar et de ses dépendances, d'après les découvertes de François P. L. Pollen et D. C. van Dam. Pt. II. Mammifères et oiseaux. Steenhoff, Leyde.

Schorger, A. W. 1955. The Passenger Pigeon: its natural history and extinction. University of Wisconsin Press, Madison.

Schüz, E. 1957. Ein Vergleich der Vogelwelt von Elbursgebirge und Alpen. Ornith. Beob., **54**:9-33.

Schüz, E. 1959. Die Vogelwelt des Südkaspischen Tieflandes. Schweizerbart, Stuttgart.

Sclater, P. L. and O. Salvin. 1879. On the birds collected by the late Mr T. K. Salmon in the state of Antioquia, United States of Colombia. Proc. Zool. Soc. London, p. 486-550.

Serle, W. 1950. Notes on the birds of south-western Nigeria. Ibis, **92**: 84-94.

Serle, W. 1957. A contribution to the ornithology of the eastern region of Nigeria. Ibis, **99**:371-418; 628-685.

Sharpe, R. B. 1874. Catalogue of the Birds in the British Museum. Vol. 1. Brit. Mus., London.

Shaw, T. H. 1936. The Vertebrates of China. The birds of Hopei Province. Part 1 and part 2. Gaviiformes—Strigiformes. Zoologica Sinica, series B, **15**:i-xxxiii; 1-528.

Sibley, C. G. 1951. Notes on the birds of New Georgia, central Solomon Islands. Condor, **53**:81-92.

Siebers, H. C. 1930. Fauna Buruana, Aves. Boeroe Expeditie 1921-22. Résultats zoologiques de l'Expédition Scientifique Néerlandaise à l'île de Buru en 1921 et 1922. Vol. 1. Vertebrata. Livr. 3, p. 29-167.

Sládek, J. 1962. Zur Nahrungsökologie des Hühnerhabichtes (*Accipiter gentilis*) in der Slowakei. Sborník Přednášek. Vorträge der II Konferenz der Tschechoslowakischen ornithologischen Gesellschaft in Prag im Juni 1962, p. 125-129.

Slater, P. 1961. Nesting of the Australian Goshawk. Emu, **61**:134-136.

Slud, P. 1960. The birds of Finca "La Selva," Costa Rica: a tropical wet forest locality. Bull. Amer. Mus. Nat. Hist., **121**:49-148.

Slud, P. 1964. The birds of Costa Rica. Distribution and ecology. Bull. Amer. Mus. Nat. Hist., **128**:1-430.

Smith, H. G. 1963. Notes on behavior of a Cooper's Hawk. Wilson Bull., **75**:88-89.

Smith, K. D. 1957. An annotated check list of the birds of Eritrea. Ibis, **99**:1-26; 307-337.

Sody, H. J. V. 1953. Vogels van het Javaanse Djatibos. Met overwegingen over nut en schade voor dit bos. Indones. Journ. Nat. Sci., **109**:125-172.

Southern, H. N. and D. L. Serventy. 1947. The two phases of *Astur novaehollandiae* in Australia. Emu, **46**:331-347.

STEGMANN, B. 1933. Ueber den Kurzfanghabicht (*Accipiter badius brevipes* Severtzow) in der Krim. Ornith. Monatsb., **41**:48-49.

STEGMANN, B. 1936. Die Vögel des nördlichen Baikal. Journ. Ornith. **84**:58-139.

STEIN, G. H. W. 1936. Ornithologische Ergebnisse der Expedition Stein 1931-1932. V. Beiträge zur Biologie papuanischer Vögel. Journ. Ornith., **84**:21-57.

STEPANYAN, L. S. 1958. O rasprostranenii perepelyatnika v Turkestane. Uchen. Zap. Mosk. Gos. Univ., **197**:125-129.

STORER, R. W. 1952. Variation in the resident Sharp-shinned Hawks of Mexico. Condor, **54**:283-289.

STORER, R. W. 1966. Sexual dimorphism and food habits in three North American Accipiters. Auk, **83**:423-436.

STRESEMANN, E. 1914. Die Vögel von Seran (Ceram). Novitates Zool., **21**:25-153.

STRESEMANN, E. 1922. Ueber *Accipiter planes* (Reichenow). Ornith. Monatsb., **30**:109-111.

STRESEMANN, E. 1923a. Ueber einige *Accipiter*-Arten. Journ. Ornith., **71**:517-525.

STRESEMANN, E. 1923b. *Accipiter leucosomus* (Sharpe): eine leucistische Mutante von *Accipiter etorques* (Salvadori)! Ornith. Monatsb., **31**: 127-131.

STRESEMANN, E. 1924a. Raubvogelstudien. Journ. Ornith., **72**:429-446.

STRESEMANN, E. 1924b. *Accipiter minullus sassii* subsp. n. Ornith. Monatsb., **32**:109.

STRESEMANN, E. 1925. Raubvogelstudien XI. Weiteres über indo-australische *Accipiter*-Arten. Journ. Ornith., **73**:319-323.

STRESEMANN, E. 1926. Weiteres über *Accipiter castanilius* Bp. Ornith. Monatsb., **34**:73-76.

STRESEMANN, E. 1928. Die Vögel der Elburs—Expedition 1927. Journ. Ornith., **76**:313-411.

STRESEMANN, E. 1929. Zur Kenntnis von *Accipiter luteoschistaceus*. Ornith. Monatsb., **37**:12-14.

STRESEMANN, E. 1932. Vorläufiges über die ornithologischen Ergebnisse der Expedition Heinrich 1930-1932. VII. Zur Ornithologie von Südost-Celebes. Ornith. Monatsb., **40**:104-115.

STRESEMANN, E. 1935. Die papuanischen Formen von *Accipiter fasciatus*. Ornith. Monatsb., **43**:110-111.

STRESEMANN, E. 1940. Die Vögel von Celebes (Biologische Beiträge von Gerd Heinrich). Teil 3. Systematik und Biologie. Journ. Ornith., **88**:389-487.

STRESEMANN, E. AND G. HEINRICH. 1940. Die Vögel des Mount Victoria. Mitt. Zool. Mus. Berlin, **24**:151-264.

SULKAVA, P. 1964. [On the behavior and food habits of the Sparrow Hawk (*Accipiter nisus*) during the nesting season.] Suom. Riista, **17**:93-105.

LITERATURE CITED

SULKAVA, S. 1964. Zur Nahrungsbiologie des Habichts, *Accipiter g. gentilis* (L.). Aquilo Ser. Zoologica, 3:1-103.

SWANN, H. K. 1921. Notes on a collection of Accipitres from the Mérida district, W. Venezuela. Auk, **38**:357-364.

SWINHOE, R. Notes on the ornithology of Hongkong, Macao, and Canton, made during the latter end of February, March, April and the beginning of May, 1860. Ibis, 3:23-57.

TACZANOWSKI, L. 1884. Ornithologie du Pérou. Tome 1. Friedländer, Berlin.

TAVERNER, P. A. 1940. Variation in the American Goshawk. Condor, **42**:157-160.

TINBERGEN, L. 1946. De sperwer als roofvijand van zangvogels. Ardea, **34**:1-213.

TODD, W. E. C. AND M. A. CARRIKER, JR. 1922. The birds of the Santa Martha region of Colombia: a study in altitudinal distribution. Ann. Carnegie Mus., **14**:1-611.

TOXOPEUS, L. J. (1922). Eenige ornithologische mededeelingen over Boeroe. Hand. Ned.-Indisch Natuurw. Congr., **2**:1-6.

UTTENDÖRFER, O. 1939. Die Ernährung der Deutschen Raubvögel und Eulen. Neumann, Neudamm.

UTTENDÖRFER, O. 1952. Neue Ergebnisse über die Ernährung der Greifvögel und Eulen. Eugen Ulmer, Stuttgart, z.Z. Ludwigsburg.

VAN BEMMEL, A. C. V. 1948. A faunal list of the birds of the Moluccan Islands. Treubia, **19**:323-420.

VAN BEMMEL, A. C. V. AND K. H. VOOUS. 1951. Birds of Muna and Buton. Treubia, **21**:27-104.

VAN MARLE, J. G. AND K. H. VOOUS. 1946. The endemic Sparrow Hawks of Celebes. Limosa, **19**:15-23.

VAN SOMEREN, V. G. L. 1956. Days with birds. Fieldiana: Zool., **38**: 1-520.

VAURIE, C. 1961. The genus *Accipiter*. Amer. Mus. Novitates, no. 2039, 10 p.

VAURIE, C. 1965. The Birds of the Palearctic Fauna. Non Passeriformes. Witherby, London.

VERHEYEN, R. 1947. Liste systématique des oiseaux connus du Parc National Albert. Secteur nord: vallée de la Semliki–contreforts occidentaux du massif du Ruwenzori. Expl. Parc Nat. Albert, Mission S. Frechkop (1937-1938). Fasc. 2. Oiseaux, p. 55-83.

VINCENT, A. W. 1945. On the breeding habits of some African birds. Ibis, **87**:203-216.

VINCENT, J. ET AL. 1962. Foods and feeding. Lammergeyer, **2**:62-71.

VOOUS, K. H. 1950. Geographical variation in the Lesser Sparrow Hawks from Indonesia (*Accipiter virgatus*). Amst. Nat., **1**:95-107.

LITERATURE CITED

Voous, K. H. 1960. Atlas van de Europese Vogels. Elsevier, Amsterdam, Brussel.

Voous, K. H. 1964. Wood Owls of the genera *Strix* and *Ciccaba*. Zoöl. Meded. Leiden, **39**:471-478.

Voous, K. H. 1966. The distribution of owls in Africa in relation to general zoogeographical problems. Ostrich, suppl. no. 6, 499-506.

Voous, K. H. 1969. Predation potential in birds of prey from Surinam. Ardea, **57**:117-148.

Voous, K. H. and H. J. W. Wijsman, 1964. Notes on African Hawk-Eagles. Biol. Jb. Dodonaea, **32**:151-163.

Vorobiev, K. A. 1954. Ptitsy Ussuriiskogo Kraya. Akademia Nauk SSSR, Moskwa.

Vuilleumier, F. 1967. Phyletic evolution in modern birds of the Patagonian forests. Nature, **215**:247-248.

Walker, G. R. Notes on the birds of Sierra Leone. Ibis, **81**:401-450.

Wattel, J. 1966. A specimen of *Accipiter brevipes* from Congo. Revue Zool. Bot. Afr., **74**:273-274.

Westcott, P. 1964. Unusual feeding behavior of a Goshawk. Condor, **66**:163.

Wetmore, A. and B. H. Swales. 1931. The birds of Haiti and the Dominican Republic. Bull. U.S. Natl. Mus., **155**:1-481.

Wheeler, R. 1963. Accipitriformes at the Laverton Saltworks, Victoria, 1950-53. Emu, **63**:8-13.

Whistler, H. 1926. The birds of the Kangra district, Punjab. Ibis, **68**: 724-783.

White, C. M. N. 1943. Field notes on some birds of Mwinilunga, Northern Rhodesia. Ibis, **85**:127-131.

White, C. M. N. 1945. The ornithology of the Kaonde-Lunda province, Northern Rhodesia. Part II. Systematic list. Ibis, **87**:185-202.

White, C. M. N. 1965. A Revised Check List of African Non-passerine Birds. Government Printer, Lusaka.

Winterbottom, J. M. 1960. The zoogeographical affinities of the avifauna of the Western Cape Province. Ibis, **102**:383-393.

Wolfe, L. R. 1950. Notes on the birds of Korea. Auk, **67**:433-455.

Wood, C. A. 1926. A collection of birds from the Fiji Islands. Part III, Field observations. Ibis, **68**:91-136.

Yen, K. Y. 1930. Birds from Yaoshan, Kwangsi. Bull. Dept. Biol. Coll. Sci., Sun Yat-sen Univ., **5**:1-32.

Young, C. G. 1946. Notes on some birds of the Cameroon Mountain district. Ibis, **88**:348-382.

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