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INTRA-INSULAR VARIATION IN THE MASCARENE WHITE-EYE, ZOSTEROPS BORBONICA (AVES)

by
Frank Bennington Gill

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of the requirements for the degree of
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Doctoral Committee:

Professor Robert W. Storer, Chairman
Professor Morris Foster
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ABSTRACT

INTRA-INSULAR VARIATION IN THE MASCARENE WHITE-EYE, ZOSTEROPS BORBONICA (AVES)

by

Frank Bennington Gill

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The nature and evolution of geographic variation in color and size of an endemic white-eye, Zosterops borbonica, on Réunion Island in the western Indian Ocean is of interest because of the rarity of cases of pronounced microgeographic differentiation in birds, particularly within the confines of small oceanic islands. The patterns of color variation are of principal importance. They include a polymorphism for the presence or absence of phaeomelanin (brown) pigments in the feather barbs, distinct geographic groupings of head-color variants of the phaeomelanic morph, and ecogeographic gradients of the intensity of melanin deposition in the underparts. The two color morphs are extensively sympatric in proportions which vary clinally with altitude from pure brown-morph populations in the lowlands to predominantly gray-morph populations in the highlands. Brown morphs in the dry western lowlands and at altitudes above 1400 meters have brown heads, while a gray-headed, brown-backed form predominates in the wet northern and eastern lowlands.

Contact between these two brown forms is abrupt with little evidence of intergradation; two narrow river beds effectively isolate the populations in the lowlands. The intensity of eumelanin deposition in the feathers of the underparts of all color forms varies in relation to altitude, the underparts changing from white in the lowlands to dark gray in the highlands.

The evolution of the differences appears to have taken place entirely within the confines of Réunion Island and in part to have involved the isolation of Zosterops borbonica in pockets of suitable edge habitat before the arrival of man. Expansion and contact of the differentiates probably has been made possible by human destruction of indigenous vegetation. Associated altitudinal expansions apparently have led to differentiation within the past 250 years of steep primary clines in size and the intensity of melanin deposition in the underparts.

The intensity of selection currently maintaining the steep clines in the proportions of the two color morphs is estimated to be on the order of one per cent, which is not very high compared to known values from other natural populations. This suggests that genetic swamping due to interdemal dispersal does not seriously hinder microgeographic differentiation even in small, mobile birds. Explanations for the absence of similar cases of intra-insular variation on other oceanic islands seem to lie in the extremes of

climatic diversity that are required rather than the effects of gene flow. The absence of significant visual predators on Réunion suggests that the selective forces now maintaining geographic aspects of the color variation are related to alternative, physiological functions of the differences in plumage coloration.

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INTRODUCTION

Geographic variation reflects the genetic divergence of conspecific populations through natural selection and thereby serves as primary evidence of the evolutionary process. Because of the theoretical importance of the phenomenon its documentation has occupied the attention of biologists for over a century and forms a substantial portion of the biological literature. Yet, in spite of this amount of attention, our understanding of the dynamics of the process, of its rates, and of the intensity and nature of the responsible selection forces is still surprisingly meager. While theoretical treatments of some of the aspects have been provided by Wright (1943), Fisher (1950), and Haldane (1948), these have seldom been applied to actual situations.

Geographic differentiation is demonstrable on virtually any geographical scale, for every local population differs from adjacent populations with respect to the frequency of some characteristics, albeit inconspicuously. Conspicuous phenotypic differentiation on a microgeographic scale is well-known in such terrestrial and relatively sedentary animal groups as snails (Partula, Cepaea) and lizards (Anolis), but in birds similar cases are certainly

exceptional. In most birds geographic variation is known to be clinal on a continental scale or else to involve isolation as between oceanic islands. Even such famous cases of avian microgeographic differentiation as the San Francisco Bay Song Sparrows have proven to be due to the separation and isolation of the respective populations (Marshall, 1948). Except for cases of secondary intergradation and hybridization, steep (primary) character clines seem precluded by the gradual nature of environmental gradients and the potency of gene flow (Mayr, 1963:382), leading to the hypothesis that nearly all steep zones of intergradation are secondary in origin, i.e. resulting from the contact of many temporary isolates (Mayr, loc. cit.).

Bird species inhabiting small oceanic islands are characteristically homogeneous in their morphology and coloration with respect to any particular species on any particular island. While inter-island differentiation is common, intra-insular variation is certainly exceptional. Until recently the smallest island known to have geographically separated bird populations sufficiently distinct to be considered subspecies was Jamaica (4450 square miles) where the wide-spread endemic red-billed hummingbird (Trochilus polytmus) has a black-billed race (T. p. scitilus) in the wet forests of the northeast. No other island with an area of less than 10,000 square miles was known to have a polytypic species in its avifauna. On the other hand,

many larger islands have differentiated bird populations, the number of which tends to increase with island size. But even on islands as large as Madagascar (240,000 square miles) and Borneo (290,000 square miles) only one or two species have as many as four races. Thus, island size seems to impose some constraints on geographic variation.

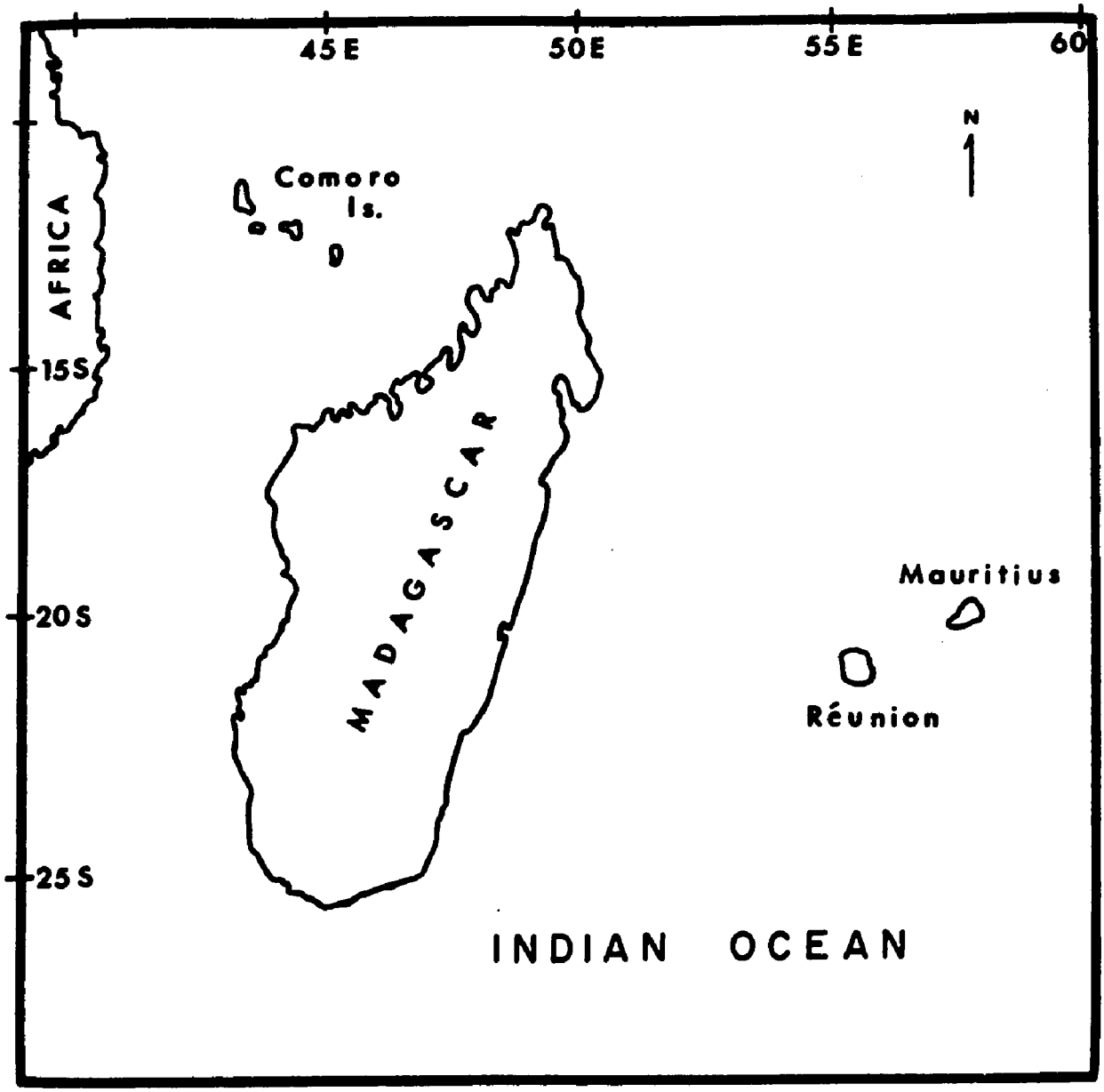
Hence the recognition (Storer and Gill, 1966) of four geographical races of the Mascarene white-eye, Zosterops borbonica, from within the confines of Réunion Island (1000 square miles) was surprising. White-eyes were already well-known for their ability to colonize oceanic islands, as well as for the marked differentiation of local populations, but as in the Song Sparrows of San Francisco Bay, the latter involve either isolated island populations (Mayr, 1942) or montane populations separated by unsuitable "lowland" vegetation (Moreau, 1957). Consequently numerous questions are raised by the Réunion Island situation. Is Zosterops borbonica unusually sedentary or characterized by special qualities conducive to microgeographic differentiation? What is the nature of the variation on Réunion and how does it compare to variation in white-eyes on continents? What was the evolutionary origin of the differences, and what is the approximate magnitude of selection currently required to maintain their geographical separation? What are the responsible selective forces, and are these in some way peculiar to Réunion? The present study was undertaken

to answer some of these questions.

Preceding a listing of materials and methods I describe Réunion and the general biology of Zosterops borbonica in order to familiarize the reader with the location and the species of bird involved. The greater portion of this report is then devoted to an analysis of the patterns of color variation in Zosterops borbonica as these are of principle importance. Size variation is subsequently described in relation to the color differences. In the Discussion I first outline the sequence of events that appears responsible for the evolution of the patterns of geographic variation as we see them today. Consideration is then given to the intensity of selection and the nature of the selective forces which are presently maintaining geographic separation of the differences. Finally, factors contributing to the evolution of geographic variation are considered and in conclusion some problems inherent in the application of subspecific nomenclature to this particular situation pointed out.

FIGURE 1

Location of Réunion Island in the western Indian Ocean


45 E
50E
55 E
60
N
Comoro
Is.
AFRICA
15S
MADAGASCAR
Mauritius
20S
Réunion
25 S
INDIAN OCEAN

RÉUNION ISLAND

Réunion Island is one of the Mascarene Islands, a group of three oceanic islands of volcanic origin in the western Indian Ocean. Situated approximately 400 miles east of Madagascar (Figure 1) at latitude 21° S and longitude 55°30' E, Réunion is closer to Madagascar than is Mauritius, which lies only 90 miles to the northeast, and Rodriguez, the most outlying of the group, 400 miles to the east-northeast. Réunion is elliptical in shape, 39 miles long by 28 miles wide, and encompasses about 1000 square miles, approximately the same area as the state of Rhode Island. It is both larger than either Mauritius (720 square miles) or Rodriguez (42 square miles) and higher, reaching a maximum elevation of 10,068 feet, the highest point in the Indian Ocean.

Topographically Réunion is an extremely rugged island which rises steeply from the sea and has little room for coastal plains (Figure 3). Coral reefs are present, but only in a restricted region along the protected west coast. Actually Réunion is composed of two overlapping shield volcanos (Upton and Wadsworth, 1966), Piton de la Fournaise (Le Volcan; 8342 feet), an active volcano forming the southeastern third of the island, and Piton des Neiges

(10,068 feet), an extinct volcano in the northwest which as a result of extreme development of amphitheatre-headed valley erosion (Upton and Wadsworth, op. cit.) has been dissected up to depths of 2500 meters by deep gorges and three huge basin-like "cirques" arranged like a cloverleaf about the central peak. The youngest lavas erupted from this volcano between 100,000 and 350,000 years ago, or in the late Pleistocene (Chamalaún and McDougall, 1966).

The location of the Mascarene Islands at the southern edge of the tropics ensures a rather stable, mild climate which is divided into a warm rainy season from November through April and a cooler dry season from May through October. During the rainy season, heavy daily rains are normal in the highlands and damaging cyclones are not infrequent. The prevailing winds are from the east-southeast.

Réunion's rugged relief promotes marked local variation in temperature and rainfall. For example, the average rainfall along the west coast, which is in a rain shadow, is less than 1000 millimeters, whereas on the eastern windward slopes it is up to 8000 millimeters. Temperature varies primarily with altitude, decreasing about 7° C with each 1000 meters of increase in altitude, or about 2° per 1000 feet. Thus highlands over 2000 meters are usually 14° C colder than coastal stations where temperatures average about 27° C and 22° C in the summer and winter respectively.

FIGURE 2

Major Réunion Localities

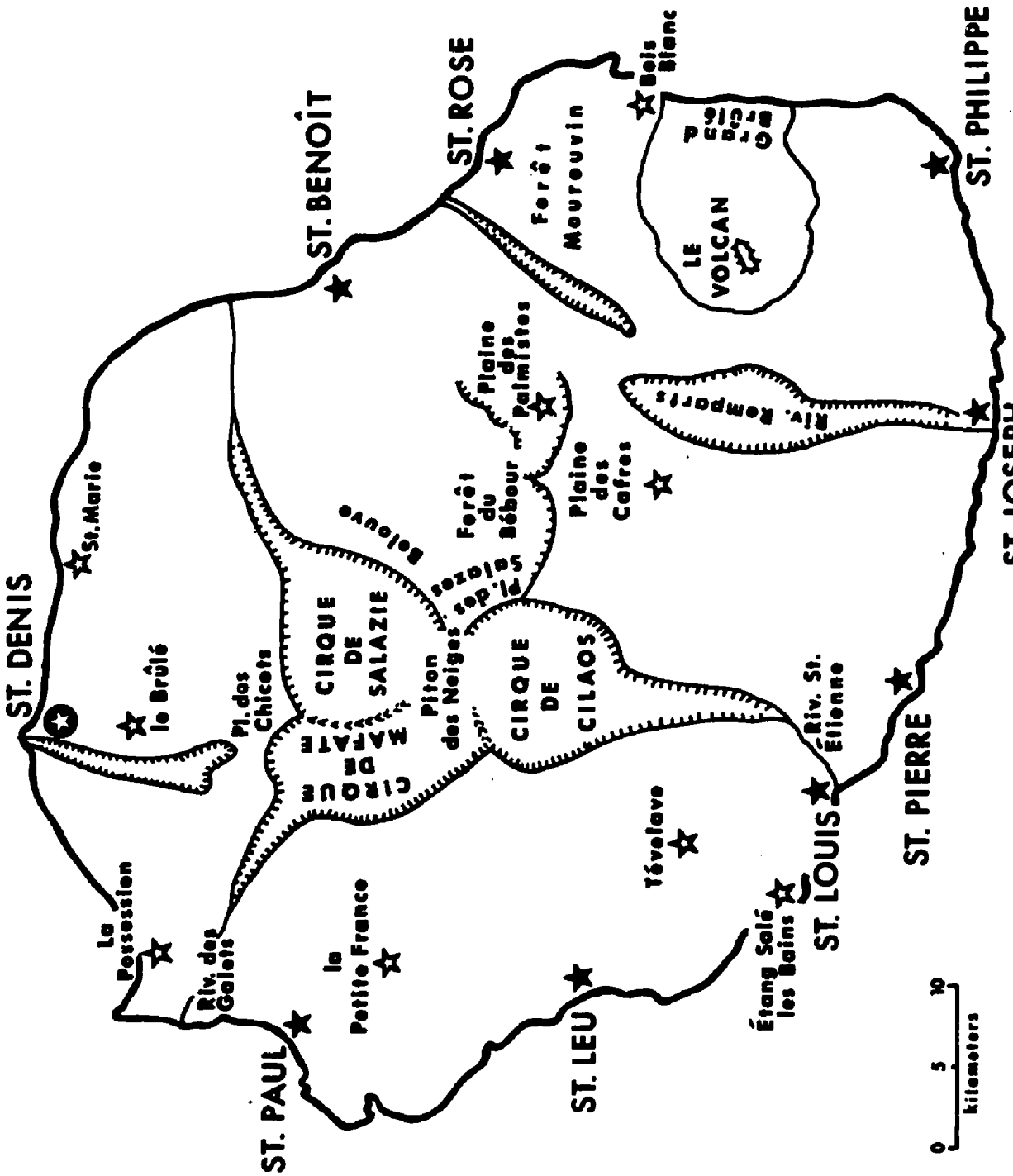
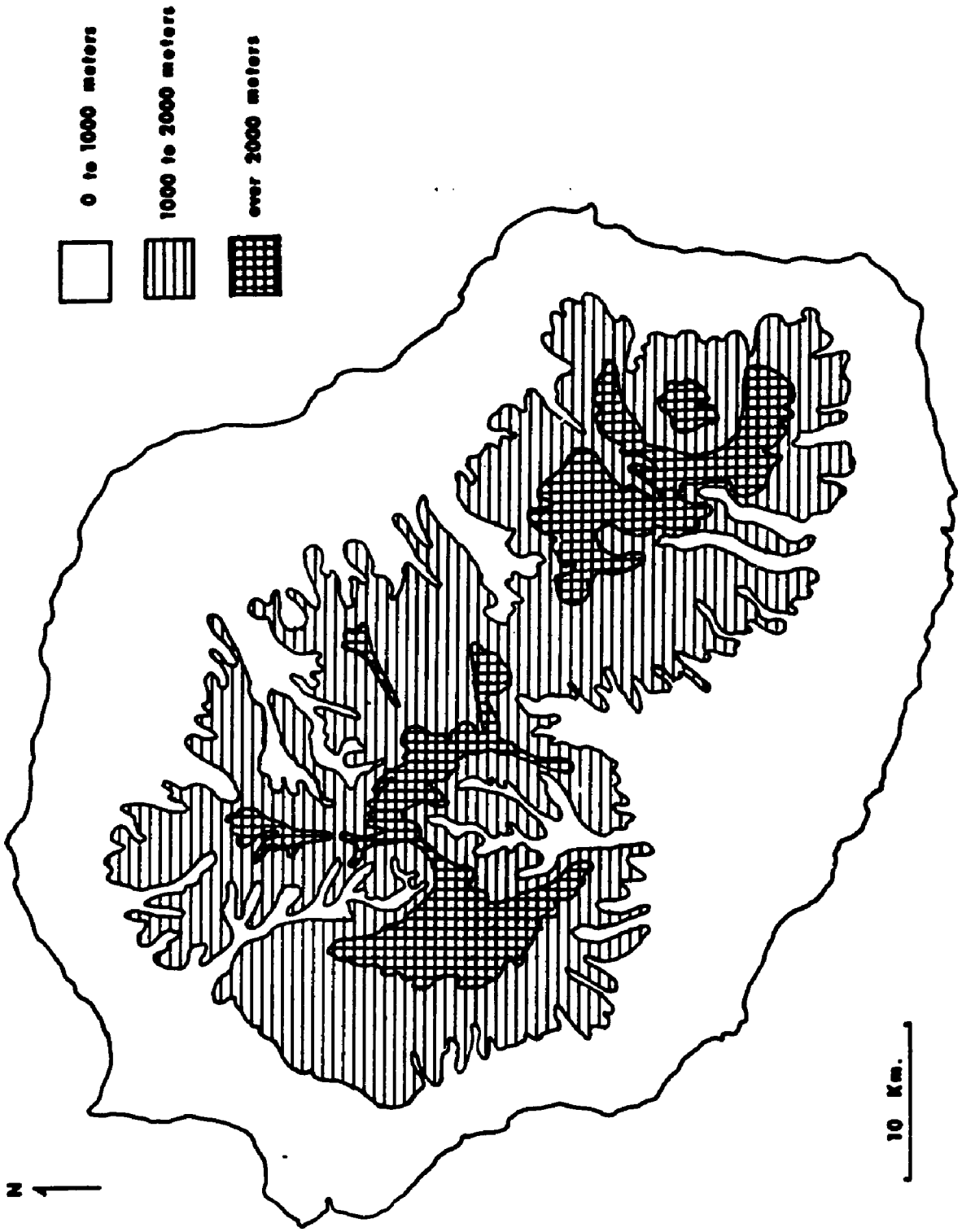

ST. DENIS
St. Marie
le Brûlé
Pl. des Chicots
CIRQUE DE SALAZIE
CIRQUE DE MAFATE
Piton des Neiges
Salazie
Bélouve
Forêt du Bébour
Plaine des Palmistes
Plaine des Cafres
CIRQUE DE CILAOS
ST. BENOÎT
ST. ROSE
Forêt Mourouvin
Bois Blanc
Pas Bras de Pucis
LE VOLCAN
ST. PHILIPPE
Riv. Rempart
ST. JOSEPH
Riv. St. Etienne
ST. PIERRE
ST. LOUIS
Étang Salé les Bains
Tévelave
La Possession
Riv. des Galets
la Petite France
ST. PAUL
ST. LEU
0
5
10
kilometers

FIGURE 3

Topography of Réunion Island


0 to 1000 meters
1000 to 2000 meters
over 2000 meters
N
10 Km.

The absence of latitudinal variation on Réunion renders impossible a distinction between temperature and altitude.

Although hardly comparable to temperature zone fluctuations, seasonal variation is readily apparent in daylength, maximum temperatures, and rainfall. Midsummer days average two and one-half daylight hours longer than winter days and fourteen to sixteen degrees (° C) warmer. On the windward side of the island average monthly rainfalls are about 1100 millimeters higher in the wettest month, March, than in the driest month, August. The difference is less marked on the island's dry side where the difference is on the order of 150 to 250 millimeters.

Corresponding to the climatological variability is a diversity of vegetational types whose original elements have been described in detail by Rivals (1952). A tree savanna once covered the hot dry coast regions on the northwest part of Réunion between Rivière des Pluies and St. Louis (Figure 4). It reached a maximum elevation of 400 meters at La Possession and extended into the cirques of Cilaos and Mafate via the ravine slopes. This forest was nearly completely destroyed by the end of the 17th century because of the high commercial value of the woods. The destruction was also aided by fires and the extremely slow growth characteristic of the species. Today, remnants are found on the massif Montagne St. Denis, on the sides of the Ravine St. Denis and in the Riviére des Galets.

FIGURE 4

Original Vegetation of Réunion Island



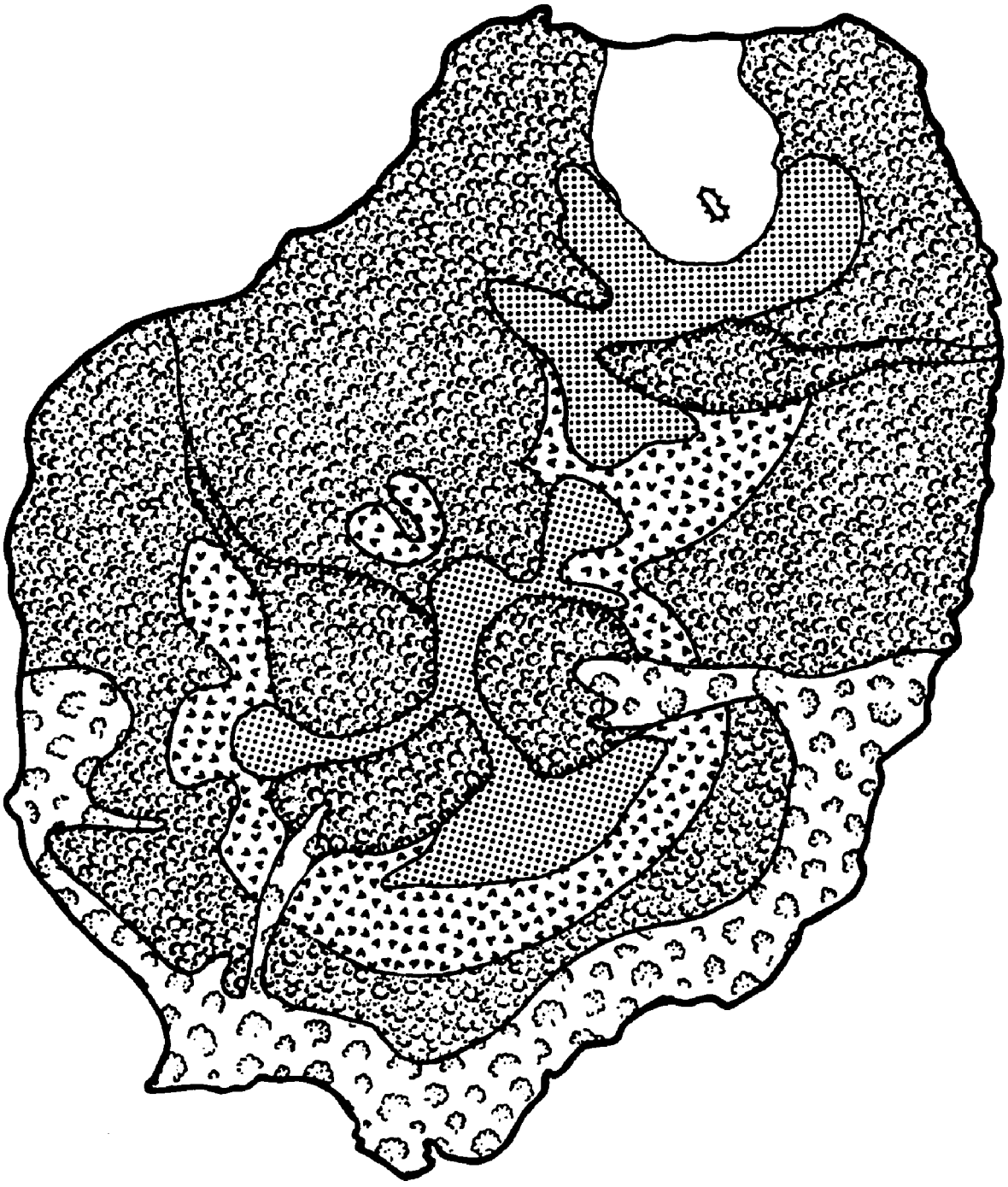
Tree Savanna

"Complex" Evergreen Forest

Tamarin des hauts
(Acacia heterophylla)

Heath

Ash and Recent Lava



Most of the island, however, was covered by complex evergreen forest with trees rarely exceeding 15 meters in height, usually about 10 meters. It included a great many species with irregular, spotty distributions, abundant in a few localities but restricted elsewhere. Several subdivisions based on the predominant species were recognizable.

A belt of "moderately wet forests of low altitudes" was found below the stratocumulus clouds where annual rainfall reached a maximum of 5000 millimeters in no more than 190 days of rain. The upper limit of this forest curved from 300 meters on the southeast side to 700 meters on the northeast, but it reached the sea in tongues on the windward side between St. Marie and St. Pierre. It is now nearly completely destroyed.

At localities where annual rainfall exceeded 6000 millimeters in at least 220 days of rain each year and which were often in the clouds, "moderately wet forests of middle altitudes" were the predominant vegetation. Originally these covered one-fourth of the island, about twice as much area as the complex forest at lower altitudes. Such forests were present from 400 to 1000 meters on the windward side and from 600 to 1300 meters (up to the limit of the tamarins) on the lee side of the island. Extensive but badly damaged patches still persist on both sides of the island, including above St. Denis, Tévelave, and the Forêts Mare à Joseph and Grand Matarum at Cilaos.

Finally "wet forests of high altitudes" occupy the rainy regions on the windward side of the island which are characterized by fine, cold, penetrating rain. Although it has never been measured, the rainfall probably averages 2500 to 3000 millimeters per year which is not much, but in addition there is much dew and mist. There are no more than 15 dry days a year. This forest is distributed between 1000 and 1800 meters, reaching 2000 meters near Le Volcan and Morne d'Mazerin, but includes only 80 square kilometers and has not been exploited or damaged appreciably. It is replaced at higher elevations by the high mountain ericoid vegetation and is the homologue of the Tamarin forests found on the drier side of the island. Localities of interest in this paper include the Forêt du Bébour, Grand Montée de la Plaine des Cafres, near Plaine des Chicots, and the heights of Tévelave.

In places protected from the wind with young, well-drained soil between 1200 and 2000 meters is found the high altitude Tamarin forest, which originally covered about 100 square kilometers. These forests are dominated by the endemic Tamarin (Acacia heterophylla) and dense stands of bamboo (Nastus borbonica) and usually include a rich growth of epiphytes, orchids, ferns, and Usnea.

At high altitudes above the layer of stratocumulus clouds, in an area with intense ultraviolet radiation, variable humidity and frequent frosts, is found the high

altitude ericaceous vegetation or "Brande." Although this vegetation covers one-fifth of the island its continuity is dissected by the cirques and deep valleys. It includes the Plaine des Chicots, Brûlés de St. Paul and St. Leu, Grand Bernard, Piton des Neiges and the high Plaine des Salazes, Coteau Maigre, Plaine des Remparts and the upper parts of the forest covering Piton de Fournaise and Plaine des Sables. Between the forest and 2500 meters, Philippia montana (Ericaceae) and other species of Philippia dominate this vegetation as well as three bright yellow flowering trees, Senecio hubertia (Compositae), Hypericum spp. (Hypericaceae), and Sophora nitida (Leguminosae). Above 2500 meters these are replaced by low clumps of Stoebe passerinoides (Compositae).

It is hardly surprising that after 300 years of human activity on Réunion the original aspect of the island's vegetation has changed greatly. The indigenous vegetation has been nearly completely destroyed below 900 meters on the west side of the island and below 400 meters elevation on the east side, and it has been replaced by sugar cane fields, pasturage for cattle and goats, and the exotic plants that typically surround tropical human habitation. These habitats are broken at regular intervals by ravines containing lush growths of Eugenia jambose (Myrtaceae) on the east side and with Schinus terebenthefolius (Anacardiaceae) and Inga sp. (Leguminaceae) on the dry west side.

On the west coast near Étang Salé les Bains, a large tract of forest, in which Casuarina sp. (Casuarinaceae), Inga, Melia sp. (Meliaceae), and Schinus terebenthefolius are the dominant plant species, replaces the otherwise barren cane fields and goat pasturage of the area. Along the south-eastern coast from St. Rose to St. Joseph on the young volcanic soils, relatively undisturbed forest composed primarily of Mimusops spp. (Sapotaceae) descends to about 200 meters elevation. The recent lava flows and young, poor soils which characterize this area have not encouraged agricultural expansion. Between Tremblet and Bois Blanc, the forests of Grand Brûlé represent a pioneer stage of colonization of the new lava and are composed primarily of Casuarina with a fern (Acrostichum) understory. Just to the north in the vicinity of Bois Blanc and Pointe des Cascades an unusual screwpine (Pandanus) forest is found along the coast.

In many cutover areas, particularly in the lowlands, scrub vegetation or thickets of various mixtures of heath (Philippia), guava (Psittium), Lantana, and Rubus have replaced the original forests. Although the proportions of the component species may vary greatly permitting the distinction of several kinds of scrub (Table 8) based on the predominant species pairs, this vegetation tends to be distinct from other habitats in being relatively open with no overhead canopy as well as low and dense in overall

structure. Physiognomically it is closest to the low ericaceous vegetation of the high altitudes and often includes some of the same plant species.

Much of the indigenous vegetation at higher altitudes is still intact though one is never very far from some human disturbance or exotic species. Between 400 meters and 1400 meters elevation on the western slopes of Réunion the cultivation of geranium (Pelargonium) for its essential oils has caused widespread damage to the forests, in providing firewood for the distillation process as well as cleared plots for planting. In some areas at moderate elevations, e.g. la Petite France (1100 meters), Tampon to Plaine des Cafres, the introduced White Acacia (Acacia latiphylla) is now a predominant element. The wet central forests of Bébour are relatively undisturbed though a dense undergrowth of introduced Fuchsia is established in much of this area. Finally the steep, relatively inaccessible cliffs throughout the island, including the sides of the otherwise heavily-populated cirque basins still retain much of their original vegetation.

The high-altitude heath vegetation is perhaps the least changed of Réunion's original habitats. Some, especially near Plaine des Cafres, has been converted into pasturage and contaminated with Ulex europea (Leguminosae) and much of it has sustained regular fires; nevertheless, the altitude and soil conditions prevent the encroachment

of most exotic species.

Réunion's faunal relationships are with Madagascar and the rest of the islands in the western Indian Ocean. It was almost certainly colonized from Madagascar (Moreau, 1957), though judging from the similarity of their faunas, interchange between Mauritius and Réunion must have been quite frequent. At least eight species of birds became extinct shortly after man's arrival on Réunion. Today the (landbird) avifauna includes eleven indigenous and sixteen introduced species. In the former category are a heron (Butorides striatus), a gallinule (Gallinula chloropus), a harrier (Circus aeruginosus), a swift (Collocalia francica), a swallow (Phedina borbonica), a cuckoo shrike (Coracina newtoni), a bulbul (Hypsipetes borbonicus), a stone chat (Saxicola torquata), a paradise flycatcher (Tchitrea bourbonnensis) and the two white-eyes (Zosterops borbonica and Zosterops olivacea). Most of these species have representatives or relatives on Mauritius Island and/or other land areas in the western Indian Ocean. The introduced species include a variety of finches (Ploceus cucullatus, Foudia madagascariensis, Estrilda astrild, Amandava amandava, Lonchura punctulata, Serinus mozambicus and Serinus canicollis), gamebirds (Turnix nigricollis, Francolinus pondiceranus, Margaroperdix madagascariensis, and Coturnix coturnix), and a pigeon (Streptopelia picturata) as well as the widespread exotics (Acridotheres

tristis, Geopelia striata, and Passer domesticus). Fuller discussions of Réunion's avifauna are to be found in Milon (1951) and Berlioz (1946).

BIOLOGY OF ZOSTEROPS BORBONICA

Zosterops borbonica is an endemic Mascarene species found only on the two main islands, Mauritius and Réunion. While a typical white-eye in proportions and behavior it is somewhat aberrant in plumage coloration, having lost both the familiar white eye-ring and the carotenoid deposition responsible for the characteristic greens and yellows of the Zosteropidae. Furthermore, it has acquired a distinctive white rump patch formed by the white upper tail coverts, as well as elongated white axillary feathers, which are frequently exposed like sunbird pectoral tufts, and white anklets. Zosterops borbonica was once combined in the genus Malacirops with the gray white-eye of the Seychelles Islands, Zosterops modesta, but Moreau (1957) maintained that the few plumage peculiarities distinguishing these species did not merit generic separation and consequently synonomized Malacirops with Zosterops, a change which has been incorporated into the Check-list of the Birds of the World (Moreau, in Paynter, 1967). To date there is no evidence as to the affinities of Zosterops borbonica.

The color variation in Réunion Zosterops borbonica was recognized in early works on Madagascar birds, but its nature was subsequently the source of much taxonomic

confusion and speculation. Pollen and Dam (1868), the first authors to recognize the extent of the color variation, believed it to result from individual but not sexual differences. Shortly thereafter, Hartlaub (1877) restricted the name borbonica to brown-backed, gray-breasted forms and on the basis of two specimens in the Newton collections described a second species, Zosterops E. Newtoni, of which the (presumed) male was all gray and the (presumed) female rich brown on both the breast and upperparts. Gadow (1884) did not recognize Zosterops E. Newtoni on the grounds that there was a perfect gradation between borbonica and this form in the small series of specimens he examined, but considered the all-gray form to be the male, the brown form to be the female and the gray-headed, brown-backed form to be the young of Zosterops borbonica, corresponding to male Z. E. Newtoni, female Z. E. Newtoni, and Z. borbonica of Hartlaub (op. cit.) respectively. Gadow (op. cit.) also suggests that the brown-backed form could be the winter plumage of the species rather than the adult female. Newton (1888) criticized these conclusions and supported Hartlaub's earlier separation of the two species.

Geographic correlations of the color variation were described by Storer and Gill (1966), who delineated four subspecies, Z. b. borbonica, a gray-headed, brown-backed form from the island's northern lowlands, Z. b. xerophila, a form from the dry western lowlands which was entirely

brown above and basically white below, Z. b. alopekion, a brown-backed form with dark gray and brown underparts from the central forests, and Z. b. edwardnewtoni, an all-gray form from the highland heath zone. But, because of the inadequacy of the existing distributional information these four subspecies were not recognized in Moreau's classification of the Zosteropidae in the Check-list of the Birds of the World (Paynter, 1967). Instead the species was divided into the conventional pair of subspecies, Z. b. mauritiana on Mauritius Island and Z. b. borbonica on Réunion Island. The propriety of Storer and Gill's (op. cit.) nomenclature is discussed at the end of this paper (page 193) in the light of the additional information.

Unlike the other remaining endemics which depend in large part on the remnants of indigenous forest, Zosterops borbonica is common over most of Réunion and is well known among the local inhabitants as the "Oiseau (Zo Zo) blanc." The total population on Réunion is estimated to be about 556,000 individuals (Gill, MS). It is abundant in the exotic vegetation of gardens, the forested interior, dry Casuarina plantations along the coast and in the highland heath zone. Indeed, only large cultivated fields, open grass, and expanses of recently formed lava are sufficiently barren to lack these white-eyes, but even in such situations as these, white-eyes inhabit the many dissecting ravines with suitable vegetation. However, despite its

seemingly broad habitat tolerances, Zosterops borbonica is primarily a species of edge and disturbed habitats rather than intact original forest. As mentioned above, most of Réunion's habitats are disturbed, accounting, in part, for borbonica's abundance and widespread distribution, but in the lush central forests which are relatively undisturbed Zosterops borbonica is decidedly scarce except around the edges of clearings and streambeds. One can hike for over an hour on the Plateau de Duverney or along the base of the Coteau Maigre without seeing this white-eye until the path crosses an old clearing or relatively open stream-bed. In the Cilaos forests, Zosterops borbonica is also common along the roads, and extended searching in the forests away from the road on the hillsides usually yields very few individuals.

Like most white-eyes Zosterops borbonica is a social species usually encountered in parties of six to twenty individuals which move cohesively and noisily through the vegetation, feeding, bathing, and resting together. Such flocks are formed throughout the year, though there is a tendency to break up into pairs at the height of the breeding season. Nevertheless the strength of the social bonds overrides the normal rupturing effects of pair formation and territoriality.

Warbler-like foraging for insects, which are captured as they flush, extracted from crevices in the bark,

leaf buds or epiphytes, and gleaned from the undersides of leaves and branches, is the most conspicuous feature of Zosterops borbonica's feeding behavior. Parid-like hanging upside down is also common as is creeping along tree trunks and branches, both horizontal and vertical, in a manner quite like that of the Black and White Warbler (Mniotilta varia). Zosterops borbonica also eats a variety of fruits, particularly during the winter months when they are available and insects are relatively scarce. Frequently these white-eyes do substantial damage to the fruits grown in private and commercial gardens. Finally, although it is not a predominant mode of feeding, Zosterops borbonica visits and extracts nectar from flowers of a variety of species. Flower feeding by this species is most frequently observed where there is an abundance of certain favored flowers, such as Fuchsia sp., Hypericum spp., Sophora nitida, and Eugenia jambose.

Breeding in Zosterops borbonica is seasonal, during the austral summer, as it is in most Mascarene species. After a sudden increase in early August, testicular size continues to increase through August and September until full size, averaging about 7 x 5 millimeters, is reached in early October. Preceding these morphological indications, however, are noticeable changes in behavior. Starting in the last week of July intraspecific chases with repeated displacement became regular in feeding

white-eye flocks. I suspect that these were related in some way to pair formation, as certain individuals (females?) often quiver their wings even when not being chased. In addition, the white axillary tufts and rump patch are prominently displayed by the aggressive individual. Pronounced vocal activity including elaborate singing begins at about the same time as the intraspecific chasing, which lasts into early October, but reaches a peak in mid-September.

Nesting begins in late September and October and continues through December, perhaps into January and February. The first fledged young were noted on 14 October and both fledged young and nestlings were found frequently thereafter up to the last day of field work on 21 December. October and November seem to be the months of peak breeding activity. Breeding is followed by a molt of the entire plumage which is completed by early April. A partial molt of the head feathers takes place in mid-August just prior to the onset of breeding activity. Juveniles molt into the definitive adult plumage in their first prebasic molt.

Although the general timing of breeding is the same throughout Réunion, there were some indications of local variability. Nest-building was first observed at Étang Salé les Bains on 16 September, and nests with eggs were found at about the same time on the wet side of the island at Beaufonds (St. Marie). Yet, in the Tévelave highlands

(1700 meters) directly above Étang Salé les Bains active nest-building was not observed, despite regular checks until 4 October. Similarly in the forests near Cilaos nest-building started about two weeks later than in the lowlands. No early nest-building was observed in the Casuarina forests at St. Paul, which are inhabited by the same morphological type as at Étang Salé les Bains, but these birds were seen carrying nesting material on 30 October. Nest-building and egg-laying at Étang Salé les Bains coincided with an abnormally early flowering adn leafing out of the vegetation and was, in fact, an abortive nesting attempt as all nests and eggs were deserted by early October. The first young noted anywhere on the island were on 14 October at La Possession, a locality inhabited by the form typical of the wet lowlands and just across the Rivière des Galets from the St. Paul Casuarina forests mentioned above. It may be that the actual onset of breeding on the dry west coast depends on suitable rainfall and the corresponding changes in vegetation, and is consequently more variable than in other parts of the island where conditions are not as severe. Birds on the island's wet side may thus be able to start breeding earlier in most years than those on the dry side. By all indications highland birds start nesting at the beginning of October which is later than lowland populations on the island's wet side.

Social elements are evident in Zosterops borbonica's breeding behavior as well as during the winter months.

Intraspecific aggression is rarely observed except for that involved in pair formation and never seems to be associated with territorial or nest area defense. When groups of feeding borbonica pass close to active nests they are joined by the resident individuals, not chased. Nests are sometimes built close together, within fifty feet of each other in a semi-colonial arrangement suggestive of that found in certain cardueline finches, such as Spinus tristis. The only behavior which might be territorial in function is the evening and dawn warbling which is common during the breeding season, but this is confined to such a limited period each day that it seems unlikely to be effective in the exclusion of conspecific individuals from a particular area.

The communality of Zosterops borbonica's breeding behavior extends to the feeding of the young, at least in certain circumstances. The only borbonica nest I watched for an extended period was one in the forests at Cilaos with two young that were almost ready to fledge. At least four adults were observed bringing food to these young and of these, three were collected and proved to be males with ossified skulls and enlarged testes. Following fledging of the young, family groups often join, at least temporarily, the feeding flocks in their area. When feeding by themselves isolated family groups occasionally included an extra male that actively fed the young. Similar cases of cooperative breeding are known in a variety of birds,

particularly sedentary species in the tropics, and usually involve closely related adults (siblings) or young of the previous year (Lack, 1968).

Little information is available as to the nature and extent of movements of Réunion white-eyes, but it appears that they are sedentary. There were no obvious changes in the distributions of white-eye numbers during my 1967 field work which started in late fall and continued to early summer, as locations with many white-eyes in April and May were similarly inhabited in November and December. Furthermore, the local residents who recognize seasonal movements of bulbuls (Hypsipetes) corresponding to the fruiting of certain plants, insist that white-eyes do not move about in similar fashion. There are reports of local and temporary white-eye abundance, e.g. in the fruit gardens near La Possession and at Nez de Boeuf when Sophora nitida is in flower, but these seem to be the effects of local concentrations only.

Resightings of banded birds lend further support to the apparent lack of major movements. Of the 44 borbonica I color-banded near Fôret du Bébour on 30 April and 1 May 1967, four were seen during brief visits to the same location in September and December. At Plaine des Chicots I color-banded 19 borbonica between 2 and 6 May and in the course of two hours of observation on 9 September saw four of these individuals in the same hollow as they were

originally banded. Finally, of the thirty-seven borbonica banded in the Fôret du Grand Matarum between 26 July and 9 August, eleven were seen again on three visits between 16 October and 20 December. These observations all indicate, I think, that while Zosterops borbonica may be quite mobile within a particular area, local populations are, in fact, sedentary.

Consideration of the sources of mortality in Réunion Zosterops borbonica is primarily speculative. So far as is known no owls or small bird hawks have ever existed on Réunion, and they certainly haven't been present in historical times. The only raptor present on the island is a large native harrier, Circus aeruginosus (spilonotus) which now feeds primarily on small introduced mammals, e.g. rats (Rattus), shrews (Suncus), and a tenrec (Tenrec ecaudatus). It hunts primarily over the cirques and ravines, soaring like a buteo, and shows no aptitude for the agile maneuvering required to catch small forest birds. In Europe, it almost always takes prey off the ground and is said to be unable to catch birds on the wing (Bannerman, 1966). At times this hawk does hunt in typical harrier fashion low over the cane fields in the lowlands and similarly over the highland heath and in these situations, particularly the latter, may pose a greater threat to white-eyes, but I seriously doubt whether it constitutes a significant source of predation.

There is undoubtedly some predation on white-eye nests by rats which are common throughout the island including some parts of the upland forests, and by an introduced snake (Lycodon aulis) around houses and gardens in the lowlands. The introduced Indian lizard, Calotes versicolor (Agamidae), which is also common throughout the lowlands, is reported to rob white-eye nests, a likely possibility as they are known to take young birds from the nest in their native range (Lowsley, 1930).

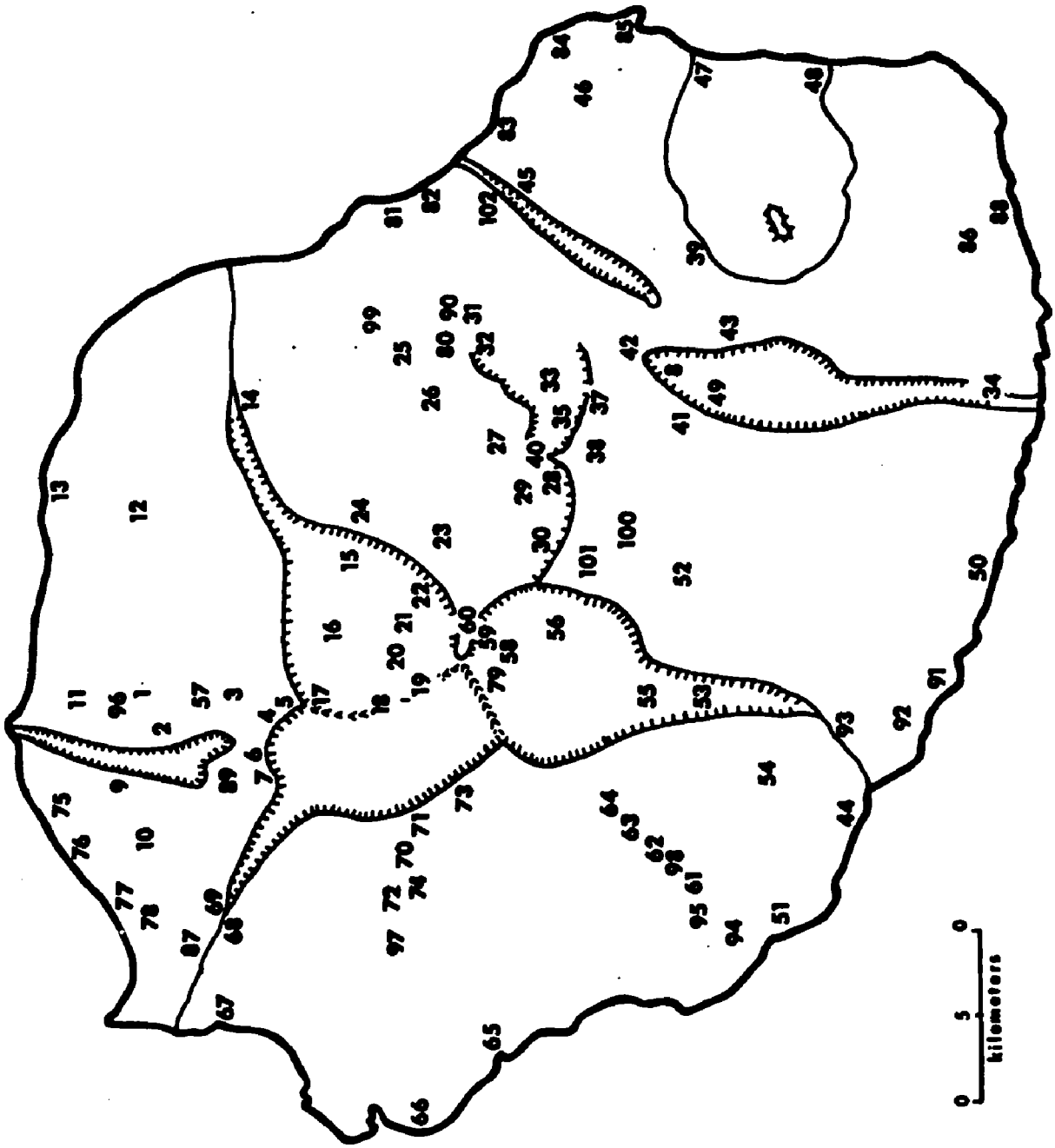
The most important predator on the white-eyes appears to be man himself. Large numbers of Zosterops borbonica are easily captured with long sticks covered with a glue ('la colle') manufactured locally from the fruit juices of Mimusops spp. (Sapotaceae). Experienced bird catchers claim that fifty white-eyes is a normal morning's catch and that 75 to 100 is not an unreasonable goal. Capture of such quantities is made possible, in part, by this white-eye's extraordinary curiosity and tame behavior as well as predictable attraction to the cries and sight of those already captured. At one time, these and other birds provided an important source of protein for the natives of Réunion's rugged interior, but birds now have been replaced by other, more readily available meats. While officially discouraged, birdcatching is still undertaken as weekend sport, and the white-eye bodies, which are fried and eaten whole, are considered a delicacy.

Zosterops borbonica coexists on Réunion with another white-eye, Zosterops olivacea, which is an aggressive, non-social, specialized, flower feeder. Zosterops olivacea feeds primarily at flowers, catches insects by flycatching, and rarely eats fruit. It is usually found in pairs, not flocks, and defends selected flowering plants against both borbonica and other olivacea. This interspecific aggression may have been responsible for the loss of the distinctive white-eye plumage characteristics by borbonica, the subordinate species. Zosterops olivacea also is more closely tied to the complex forests of the central highlands where there is a variety of suitable flowers. It seems on the basis of the degree of ecological specialization and inter-island differentiation that Zosterops olivacea was the first to colonize the Mascarene Islands and that Zosterops borbonica arrived sometime later. The ecological differences between the two species and their evolution are discussed in detail elsewhere (Gill, MS).

FIGURE 5

Sampling Localities on Réunion Island

(see Appendix I)


0
5
kilometers
0

MATERIALS AND METHODS

The material on which this study is based was obtained on expeditions to Réunion Island in November, 1964, when I was accompanied by Dr. Robert W. Storer, and from April to December, 1967. The 1964 field work was a preliminary survey during which small samples of Zosterops borbonica were taken from several widely separated localities, resulting in our original cognizance of the geographic nature of the color variation (Storer and Gill, 1966). In 1967 an effort was made to get samples of specimens from all representative parts of the island and to establish the basic elements of this white-eye's biology through observations of color-banded individuals.

The localities visited total 102 and are listed according to a reference number in Appendix I as well as on an outline map of Réunion Island (Figure 5). The locality names and coordinates were taken from a 1:50,000 topographical map of Réunion published by the Ministère des Travaux Publics et des Transports (Institut Geographic National) of France.

The localities of specimens of Zosterops borbonica have not been fixed more precisely than "Réunion Island" and for this reason had little or no value for the present

study. All specimens referred to in this paper were obtained during the two, above-mentioned expeditions and have been deposited in the U. S. National Museum collections in Washington, D. C. (1964 specimens only) or the collections of The University of Michigan Museum of Zoology in Ann Arbor, Michigan. These include a total of 792 specimens from 76 different localities. I would remind those persons who may feel some concern about taking specimens of an endemic bird species from a small oceanic island that not only is Zosterops borbonica abundant on Réunion, having undoubtedly benefitted from human disturbance rather than suffered, but also that the species continues to flourish despite the annual removal of thousands of individuals by local inhabitants for food.

Except for the month of September specimens were taken continually from May through December. Many of those taken during the breeding season from October to December are badly worn and have consequently been excluded from most analyses as were any other specimens in similar condition. Some minor wear has been tolerated with the conviction that only a small amount of extra variance is introduced into the system without alteration of the basic results. Because all localities in any given region were not sampled simultaneously, no regional bias has been introduced by this procedure. The sedentary habits of this white-eye insure a stability of the patterns

of geographic distribution throughout the year.

Specimen Measurements

All specimens were measured by me. Wing length (arc) was measured to the nearest .5 millimeter; tail length was obtained by inserting a pair of dividers to the base of the middle pair of rectrices and measuring to the tip of the longest rectrix; bill length was taken as the distance from the tip of the upper mandible to the nasofrontal hinge, following the procedure outlined by Moreau (1957); tarsus length was measured from the back side of the middle of the tibiotarsus-tarsometatarsal joint to the lower edge of the lowest undivided scute on the front of the junction of the metatarsus with the base of the middle toe (Baldwin et al. 1931). Weights of fresh specimens from which the cotton was removed from the throat were recorded to the nearest .1 gram. In order to reduce the character's variance and to use a linear rather than a cubic function I have used the cube root of body weight in all analyses. Consequently the term weight is to be understood to be the cube root rather than the raw measure. Since weights increase during the breeding season, particularly in females, only winter specimens taken from May to August were used in analyses involving this character. There is no seasonal variation in weight during this period.

TABLE 1

COLOR CHARACTER STATES AND SPECIMENS USED AS COMPARISON STANDARDS

Character	Character States	Reference Spec. (UMMZ #)
I. Back Coloration	0 - pure gray	213 784
	1 - gray with slight scattered brown	213 524
	2 - heavy suffusion of brown in gray - nearly a 50/50 mixture	213 469
	3 - brown with scattered gray feathers	213 410
	4 - entirely brown	213 779
II. Brown Morph Head Characters		
A. Crown-Forecrown	0 - entirely gray	213 500
	1 - gray with scattered brown	213 601
	2 - 50/50 gray-brown	213 599
	3 - brown with gray wash	213 826
	4 - strong, pure brown	213 343
B. Nape	0 - pure gray	213 493
	1 - gray with scattered brown	213 330
	2 - 50/50 gray-brown	213 609
	3 - brown with gray wash	213 514
	4 - strong, pure brown	213 608
C. Side of Head	0 - entirely gray	213 577
	1 - ocular gray and side of nape gray continuous and broad with only slight brown	213 569

Table 1 cont.

Character	Character States	Reference Spec.
C. Side of Head cont.	2 - well-defined gray above auriculars to eye as well as patch of gray on sides of neck, though separated from ocular gray by a brown collar	213 536
	3 - diffuse gray around auriculars only	213 874
	4 - entirely brown, no discernible gray	214 661
D. Auriculars	0 - pure gray	213 567
	1 - slight brown, esp. below eye	213 470
	2 - 50/50 brown-gray	213 615
	3 - predominately brown but with some gray	213 727
	4 - entirely brown	213 392
III. Underpart Coloration		
A. Underpart Gray	0 - white	213 901
	1 -	213 512
	2 -	213 352
	3 -	213 427
	4 -	213 309
	5 -	213 331
	6 -	213 415
	7 -	213 384
	8 - dark gray	213 419
B. Breast Brown	0 - absent	213 496
	1 - faint brown wash	213 785
	2 - strong but narrow band	213 411
	3 - strong wide band	213 782
	4 - strong and extensive, including parts of throat and belly	213 341
C. Flank Brown (in gray morphs and intermediates)	0 - gray	213 770
	1 - gray with faint brown wash	213 784
	2 - equal proportions of brown and gray	213 363
	3 - strong brown suffused with gray	213 412

Specimen Coloration

All color evaluations were made in Ann Arbor, Michigan against a standard gray background in north sky light on bright to cloudy bright days between 0900 and 1200 hours from March to July, 1968. Each color character was evaluated independently of the others and the specimens were individually compared to a series of standards representing the character states into which each character was subdivided (see Table 1). The standards themselves were chosen so as to span the total variation present in each character and to represent as many intermediate categories as could be consistently distinguished. By doing so a suitable match was potentially possible for every specimen. Each standardized series was checked and completely reevaluated on several successive mornings in order to confirm the validity of the progression and the distinctness of each step within the series.

Climate

Rainfall and temperature records in the form of ten-year summaries for 112 and 30 Réunion localities respectively have been made available by the Service Météorologique de la Réunion. For a few additional localities which have been added to this list only in the past few years I have computed averages from the annual "Bulletins Climatologiques" published by the same service. Most of

my collecting localities are sufficiently far from an actual meteorological station that I have used rainfall values from isohyetical charts based on the ten-year summaries and temperatures regressed from existing altitudinal correlations in preference to values from the nearest station. Two temperatures have been used for each locality, the mean maximum of the warmest month of the year, either January or February, and the mean minimum of the coldest month of the year, usually August. Altitudes were fixed to the nearest 20 meters from either existing altitude markers or from the topographical map (1:50 000).

Botany

Identifications of the plant species mentioned in this paper were generously provided by Theresean Cadet of Ste. Clotilde, Réunion and by Paul Susplugass of St. Denis. The nomenclature of Rivals (1952) has been followed. Representative specimens of most species have been deposited in the University of Michigan Herbarium.

Statistics

The correlation coefficients used in this study are linear product-moment coefficients which have been computed on an IBM 360 computer using The University of Michigan Statistical Research Laboratory programs BMD: 3D and BMD: 3R. Significance of the coefficients was ascertained from

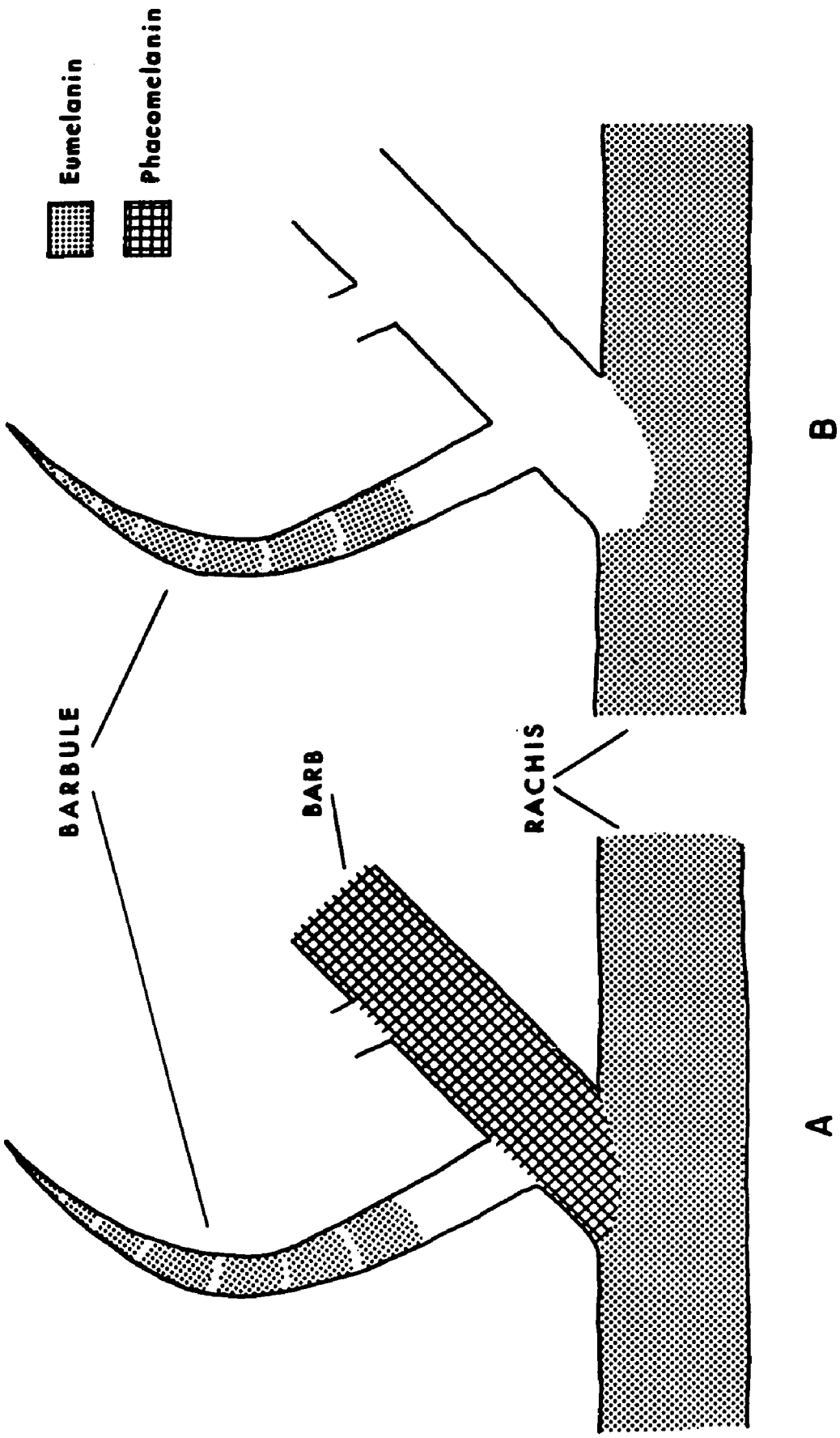
Appendix Table V of Simpson, Roe and Lewontin (1960). Chi-square tests follow the procedures of Bailey (1959). Estimates of sample variances were not calculated for samples of less than five specimens. The .05 level of significance is required for acceptance of null hypotheses and is indicated by a single asterisk (*), whereas the .01 and .001 levels of significance are indicated by double (**) and triple (***) asterisks respectively.

Multiple regression analyses were performed on an IBM 360 computer using the UCLA program for Multiple Regression with Case Combinations as revised and adapted by the Statistical Research Laboratory of The University of Michigan (BMD:3R). Evaluation of the relative importance of the different independent variables with respect to the dependent variable was based primarily on the coefficient of determination, which is a measure of the percentage of the variance in the dependent variable that is accounted for by the total regression, and the standard partial regression coefficients, which are partial regression coefficients converted to the same units, standard deviations. Comparison of the coefficients of determination of different combinations of independent variables permits the selection of the combination of variables that will account for the most variance in the dependent variable. Direct comparison of the standard partial regression coefficients of two or more independent variables, measures

their relative effectiveness in predicting the value of the dependent variable. A close correlation of a variable's contribution to the coefficient of determination and the relative magnitude of its standard partial regression coefficient is to be expected.

FIGURE 6

Pigmentation Differences in a Brown (A) and Gray (B) Feather of *Zosterops borbonica*


Eumelanin
Phacomelanin
BARBULE
BARB
RACHIS
A
B

BASIS OF THE COLOR VARIATION

As in certain other groups of birds, e.g. Junco (Miller, 1941), Parus (Frank, 1938), color variation in Zosterops borbonica involves only the placement and amount of two types of melanins, eumelanins, which are deposited as black or brownish-black granules, and phaeomelanins, which under reflected microscope light appear as tiny reddish or light brown granules (Gornitz, 1923). Aside from the presumed differences in their chemistries these melanins are deposited differently in the feathers of Zosterops borbonica. Eumelanins are found in dense concentrations in the barbules and to a lesser extent in the rachis, but not in the barbs, while phaeomelanins are evident primarily in the barbs (Figure 6).

The eumelanin pigment in Zosterops borbonica corresponds to Type B granules described by Moreau (1957) for African Zosteropidae, rather than Type A in being irregularly shaped, brownish granules instead of black rodlets. This pigment is responsible for the gray in borbonica's plumage coloration. However, buff-colored phaeomelanins, which correspond to Moreau's Type C granules, are responsible for the visual browns. All feathers with phaeomelanin deposition also contain

eumelanins but the reverse is not true. Thus, the basic difference between gray and brown in the plumage of Zosterops borbonica lies simply in the addition of phaeomelanins to produce brown.

Several important aspects of the color variation arise from topographical restriction of phaeomelanin deposition. Other essentially independent aspects of the color variation, particularly the color of the underparts, result from varying concentrations of both melanins. There is no variation in color in relation to sex or age, once the definitive plumage is attained.

FIGURE 7

Variation in Upperpart Coloration of *Zosterops borbonica*

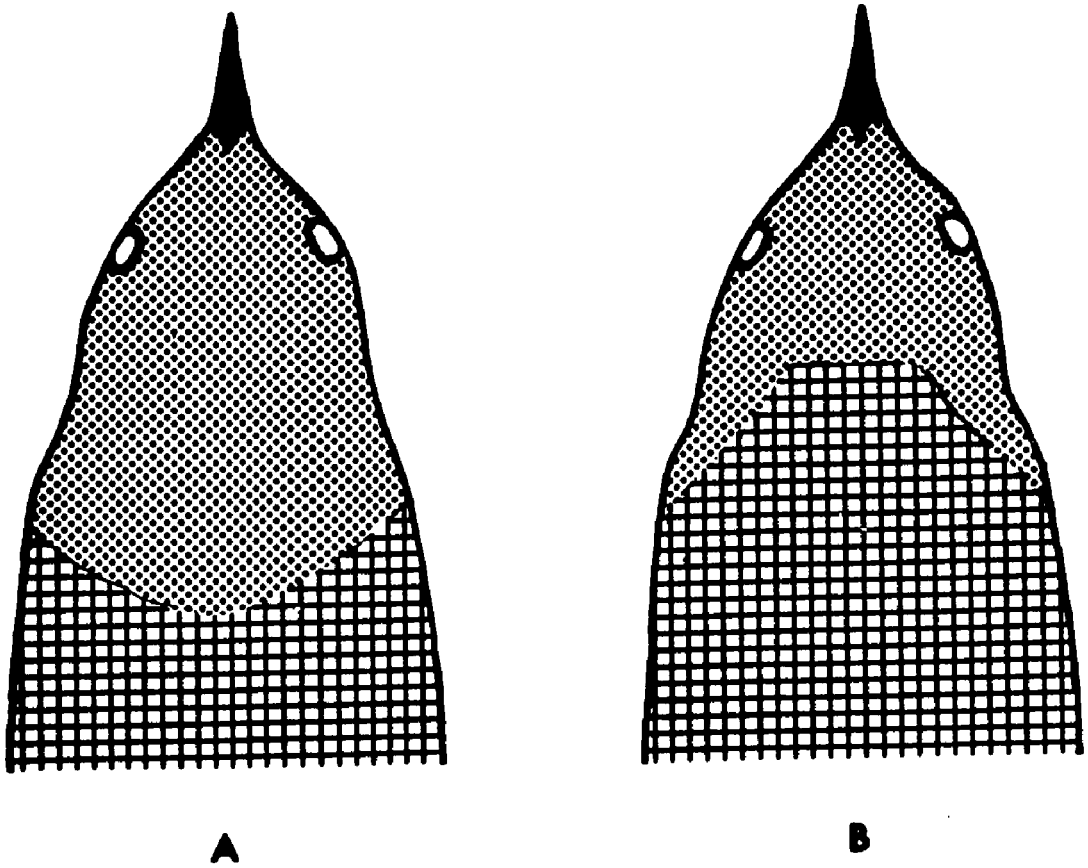
(Stippling indicates gray;
cross-hatching indicates brown)

A. Brown morph - *Zosterops borbonica borbonica* (pure)

B. Brown morph - *Z. b. borbonica* (brown-naped)

C. Brown morph - *Z. b. xerophila*

D. Gray morph - including *Z. b. mauritiana*


A
B
C
D

COLOR POLYMORPHISM IN ZOSTEROPS BORBONICA

Most specimens of Zosterops borbonica from Réunion are assignable to one of two major categories or morphs (see page 84) on the basis of back coloration which is either predominately gray or brown (Figure 7). Intermediates of three types are distinguishable, and consequently I have evaluated the back color of all specimens in terms of the five categories outlined in Table 1. The emphasis placed on an easily discernible mixture of distinct gray and brown elements was necessitated by variation in the intensity of the brown coloration which results from fading and/or wear.

Three hundred one (87.7 percent) of the 343 adult specimens from localities where gray morphs and/or intermediates were known to occur were either pure gray-backed or pure brown-backed, whereas only 42 (12.3 percent) can be considered intermediate (Figure 8). Inclusion of specimens from the remaining localities would only have increased the total in Category 4 by 353 individuals. Thirty of the 42 intermediate specimens were classified in Category 1 and only 7 (2 percent) were strongly intermediate (Category 2). Compared to Category 1 there are relatively few Category 3 specimens, a fact which is underscored by the many

FIGURE 8

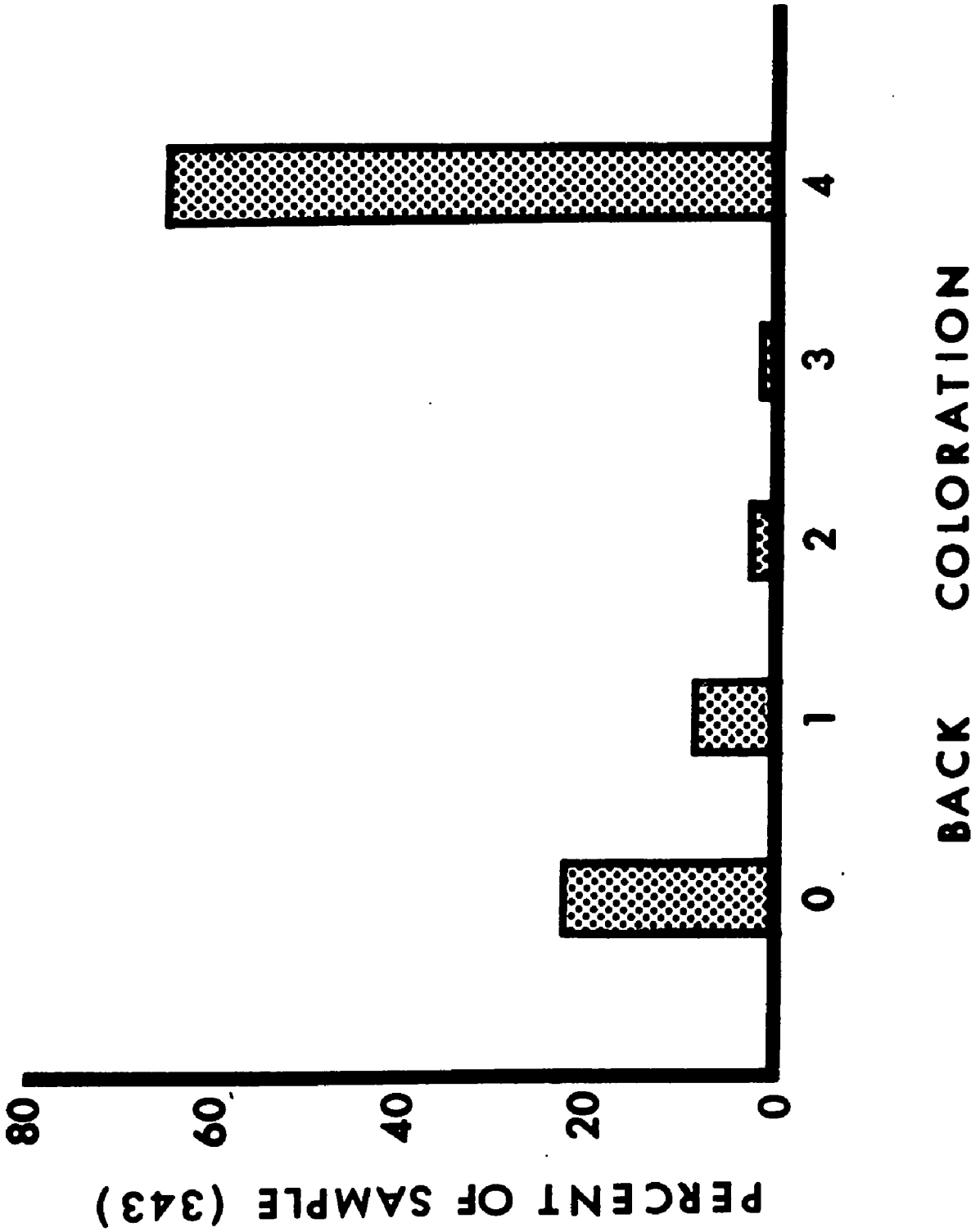
Back Coloration of Adult Specimens (343 Total) from Localities Known to Have Gray Morphs and/or Intermediate Morphs

Category

0 - Pure Gray Morphs

1 - 3 Intermediate Morphs

4 - Pure Brown Morphs


PERCENT OF SAMPLE (343)
80
60
40
20
0
0
1
2
3
4
BACK COLORATION

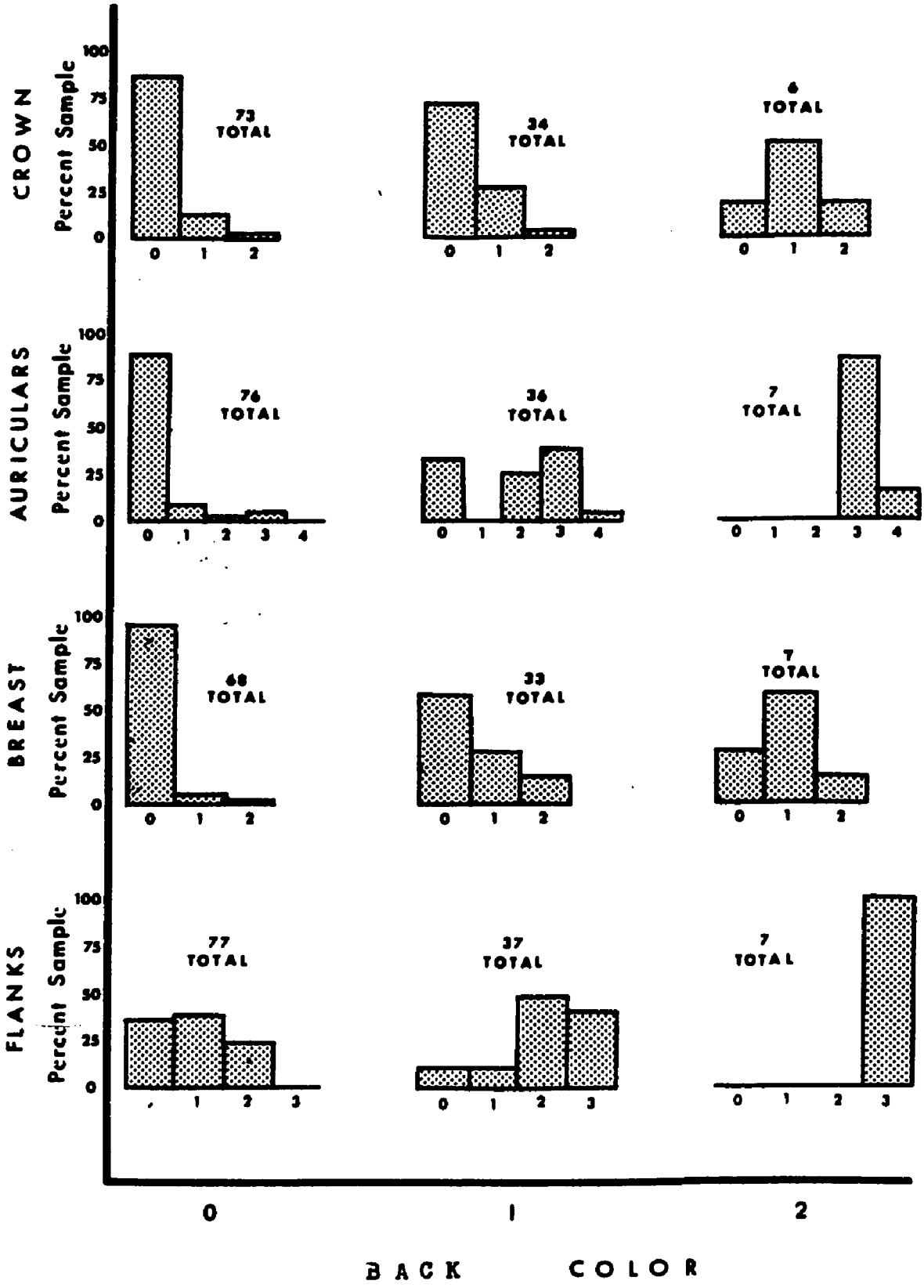
more pure brown-backed specimens in the sample. Notwithstanding a small bias in the ease of detection, there is certainly a greater tendency towards intermediacy or a lower percentage of absolute purity in gray morphs than in brown morphs.

Color Character Correlations in Gray Morphs and Intermediates

Most pure gray-backed individuals (Category 0) have some traces of brown pigmentation. Only 31.3 percent of these specimens are, in fact, completely gray with no discernible brown. In the remaining 68.7 percent, brown may be present on the breast, flanks, or in the region of the auriculars. These characters have each been divided into two or three categories of increasing amounts of brown. Considering each of the characters separately the majority of gray-backed specimens are also pure gray in any one of them (Figure 9). However, brown does appear more consistently in the flanks than elsewhere, and it is this character which is largely responsible for the low percentage of entirely gray individuals. Nevertheless, despite such variation and the emphasis placed on back coloration, gray-backed morphs, including Category 1 intermediates, are distinctly different in aspect from brown-backed morphs, which can also be distinguished by the intense rufous coloration of their flanks.

FIGURE 9

Intermediacy in Characters other than Back Color in Gray Morphs and Intermediates


CROWN
AURICULARS
BREAST
FLANKS
Percent Sample
100
75
50
25
0
73 TOTAL
34 TOTAL
6 TOTAL
76 TOTAL
36 TOTAL
7 TOTAL
68 TOTAL
33 TOTAL
7 TOTAL
77 TOTAL
37 TOTAL
7 TOTAL
0 1 2 3 4
0
1
2
BACK COLOR

Increased variability in these other characters is evident in specimens assigned to Category 1 (Figure 9). In this group of specimens the mean flank coloration has shifted strongly to the right while the other three characters have means close to the central category. In Category 2 intermediates two of the three characters have shifted completely to the strongest intensity found in this series. However, this "extreme" intensity of phaeomelanin pigmentation is still decidedly grayer than the dullest expression in pure brown-backed specimens. The retained variability in breast coloration reflects the normal high variability of this character in highland brown-backed populations (see page 142). Category 3 intermediates have not been included in this figure. Their expressions are all equivalent to pure brown-backed specimens.

Juvenal Plumages

Young borbonica in juvenal plumage show range and pattern of upperpart coloration similar to that of the adults. Some are entirely gray corresponding to the pure gray-morph adults and with similar variations in the presence of brown in other parts of the plumage. Others are very brown and equivalent to brown-morph adults, either those with brown heads or those with gray heads.

A series of seven fledglings from Nez de Boeuf (Plaine des Cafres), a locality with a relatively high

percentage of pure gray morphs, are all basically gray above, though in one a distinct brown wash is present. A pair of fledglings the same age, presumably siblings, that I collected together above Le Brûlé (at Locality 1) includes one pure gray type and one with an intensely brown back and a gray head with some brown wash.

Most of my specimens in juvenal plumage were taken with presumed parents in the Cilaos study area where both brown and gray morphs are common, the former predominating about 3:2. A total of thirteen juvenals from this locality includes pure grays, pure browns, and some intermediates, the variation reflecting the categories found in adult plumages. I have placed these specimens in a series of color categories believed to be equivalent to those used for the evaluation of back color in adults (Table 2). Category 3 is omitted as I doubt that it is discernible in this plumage.

TABLE 2. Back Coloration of Juvenal *Zosterops borbonica* from Cilaos

Category	0	1	2	4
Number of Spec.	2	2	2	7

The two specimens in Category 0 are pure gray and lack any discernible brown wash while in Category 1 a definite, but subtle brown component is present. The

Category 2 specimens are decidedly brownish and intermediate between brown and gray morphs. Specimens in Category 4 are rich brown in color like the adults.

In an attempt to get young of known parentage I collected some pairs of fledged young and the attending adults in the Cilaos forests (Table 3). Large groups including several families were avoided because of the impossibility of determining relationships, and instead I concentrated on finding isolated groups. After establishing that the adults present were feeding the young, I collected the entire group or as many as I could. In two of the seven such family groups an extra adult male was helping the presumed parents feed the young. Each of these "helpers" was the same in plumage color as a presumed parent and thus does not affect the parent-young color relationship.

TABLE 3. Back Color Relations of Adult *borbonica* and Their Presumed Offspring

Parents ♂	♀	No. of Pairs	Offspring 0	1	2	4
0	1	1	2			
1	0	1			1	1
4	1	1		1	1	
4	2	1		1		
4	4	5				8

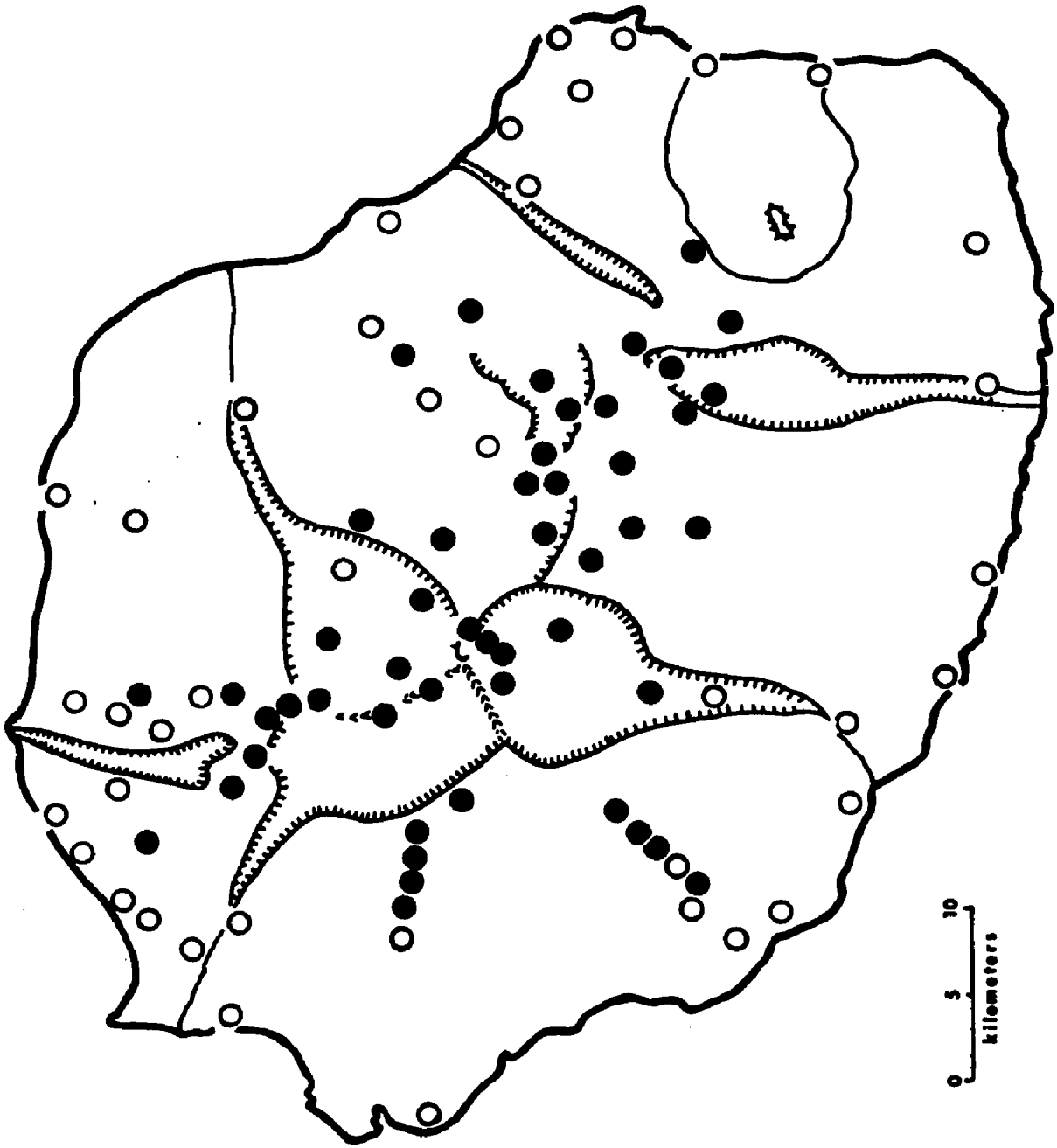
Although the production of mixed broods demonstrates a genetic basis of this aspect of the variation these data

FIGURE 10

Réunion Localities from which Gray Morphs and/or Intermediates have been Recorded

Closed Circles: Present

Open Circles: Absent


0
5
10
kilometers

are inadequate in themselves to establish the nature of the allelic system that is responsible. The production of a brown morph young by gray parents but consistent production of brown young by brown parents, suggests that gray may be dominant over brown. However, modifiers are presumably involved as well.

Distribution of Gray and Brown Morphs

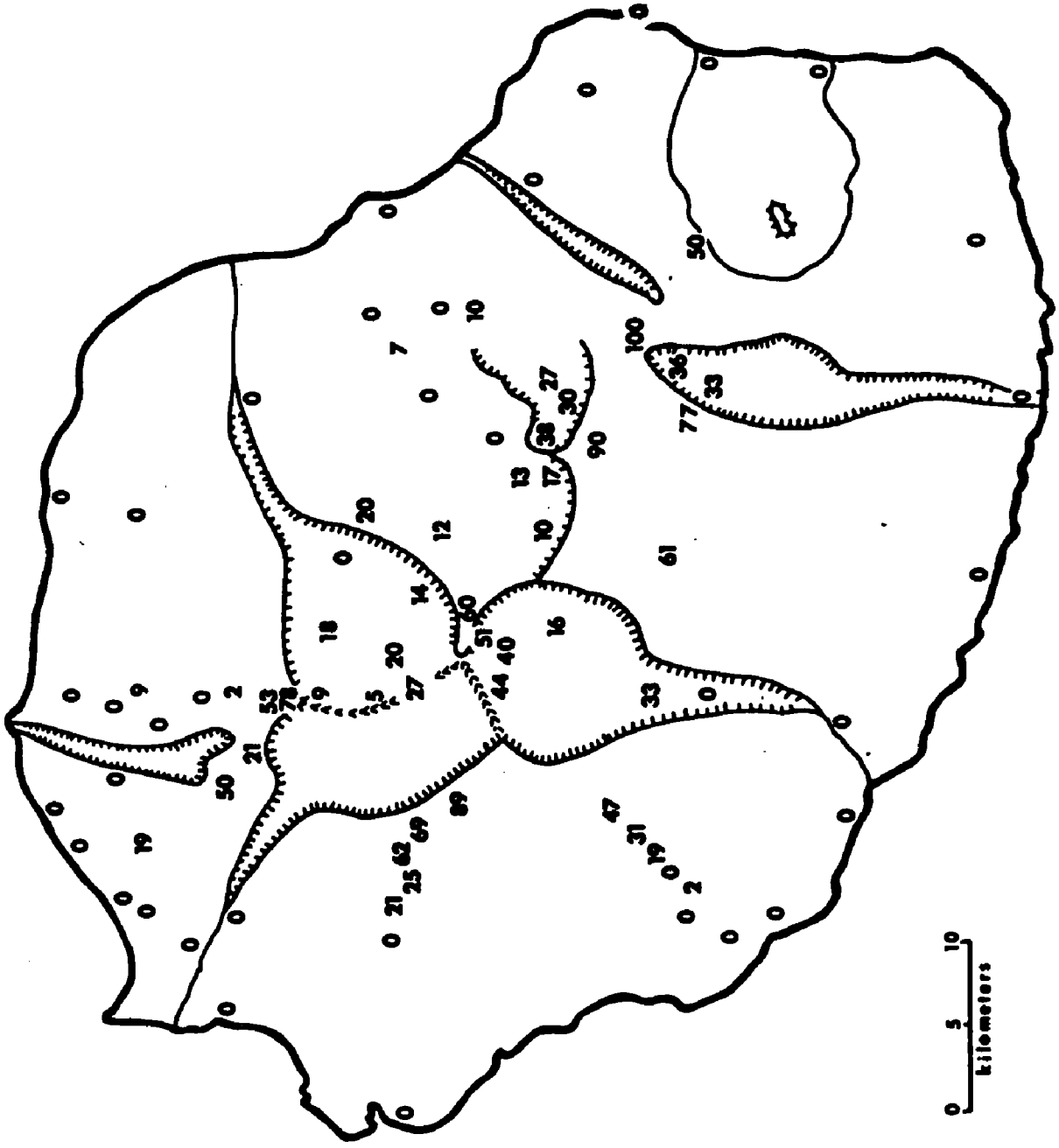
Gray morphs and/or intermediates were recorded at 48 of the 102 localities I visited on Réunion. These comprise a large continuous region in the center of the island but exclude the coastal areas (Figure 10). In contrast to the many lowland localities which have only brown morphs, few populations consist entirely of gray morphs, the one exception being locality 42 at 2300 meters.

When pure gray morphs and intermediates are distinguished there is a significant ($P < .001$) altitudinal segregation in their distributions, pure gray morphs tending to be found at higher elevations (mean altitude = 1744 meters) than intermediates (mean altitude = 1503 meters).

Gray and brown morphs are easily distinguished in the field, making possible counts of the proportions of the two simply by observation. However, Category 1 intermediates and Category 3 intermediates cannot be distinguished through field glasses from gray and brown morphs

FIGURE 11

Frequency (per cent) of Gray Morphs
(including Category 1 intermediates)
at each Réunion Locality Sampled


0
5
10
kilometers

respectively. In order to maximize sample sizes for analysis of the distribution of morph frequencies I have consequently combined Category 1 intermediates with pure gray morphs and Category 3 intermediates with brown morphs. Category 2 intermediates have been excluded. This procedure permits the use of sight records as well as specimens from each locality.

Counts of the numbers of gray and brown morphs were obtained at several localities both during the early winter and again at the beginning of the breeding season (Table 4). Some variation on the order of ± 12 per cent, due primarily to sampling error, is present and to be expected in these data, but the high level of repeatability of such counts militates against major seasonal shifts in morph ratios.

TABLE 4. Repeatability of Morph Ratio Counts
(Per cent gray morphs)

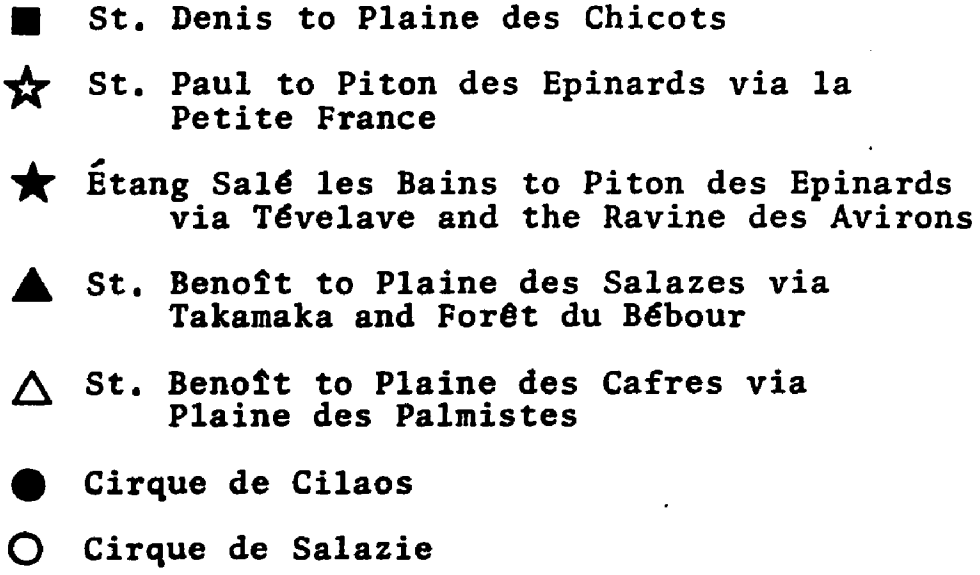
Locality	1	2	3
4	58.8 (4-6 May)	47.7 (9 Sept)	
5	84 (7 June)	73.3 (9 Sept)	
16	22.7 (20 June)	14.3 (3 Nov)	
27	0 (12 May)	0 (26 Nov)	
40	34.1 (28-30 April)	41.6 (6 Sept)	
58	42.7 (15 June)	41.4 (26-29 July)	41.6 (17 Oct)
73	91 (25 May)	92.8 (5 Nov)	

Several factors affect the distribution and relative abundance of gray morphs. High gray morph frequencies (over 60 per cent) were not recorded below 1300 meters and in most cases only over 1600 meters elevation (Table 5). A regular altitudinal increase in the percentage of gray morphs occurs along transects from the coast to the highlands in areas of relatively continuous, undissected topography (Figure 12). On three of the five transects gray morphs were recorded in low frequencies at elevations well below those of sustained increasing occurrence, indicating the occurrence of occasional gray morphs below the elevations normally inhabited by this form. On four of the five transects the sustained appearance of gray morphs was first noted above 1300 meters, i.e. between 1350 and 1450 meters on three and at 1580 meters on the fourth. On the fifth transect grays first appeared at 720 meters elevation and continued to increase in relative abundance with altitude. The factors responsible for this variation may be related to the predominance of open scrub rather than forest at low altitudes on the St. Benoît - Plaine des Palmistes transect (see below).

Topography also affects the proportions of gray morphs. This can be seen inside the deeply-eroded cirques where disruption of altitude-distance relationships is maximum. The data available for the Cilaos and Salazie

FIGURE 12

Transect Groupings of Réunion Sampling Localities



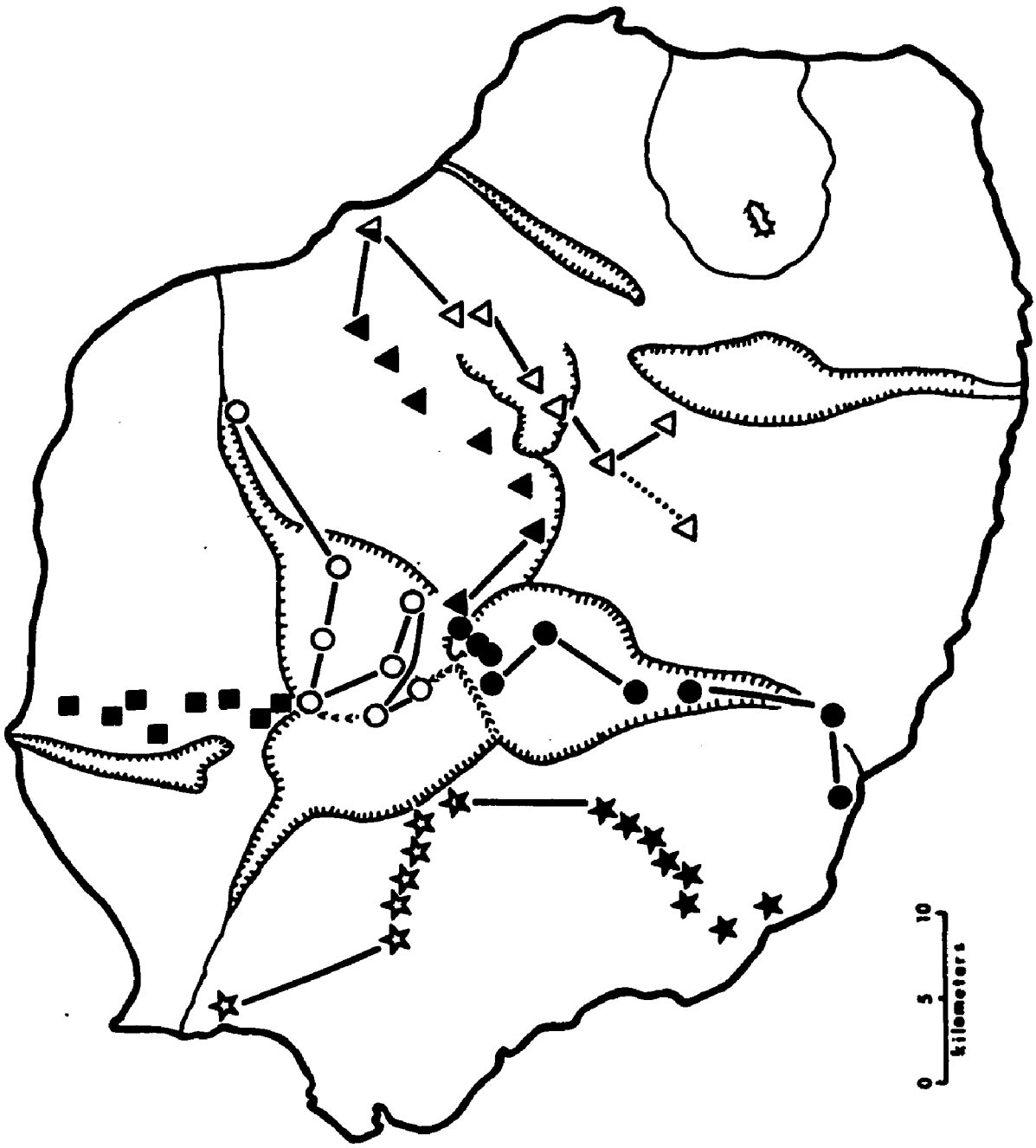

0
5
10
kilometers

FIGURE 13

Altitudinal Relationships of Gray Morph Frequencies

I. West Slope Transects

☆ St. Paul to Piton des Epinards via la Petite France

★ Étang Salé les Bains to Piton des Epinards via Tévelave

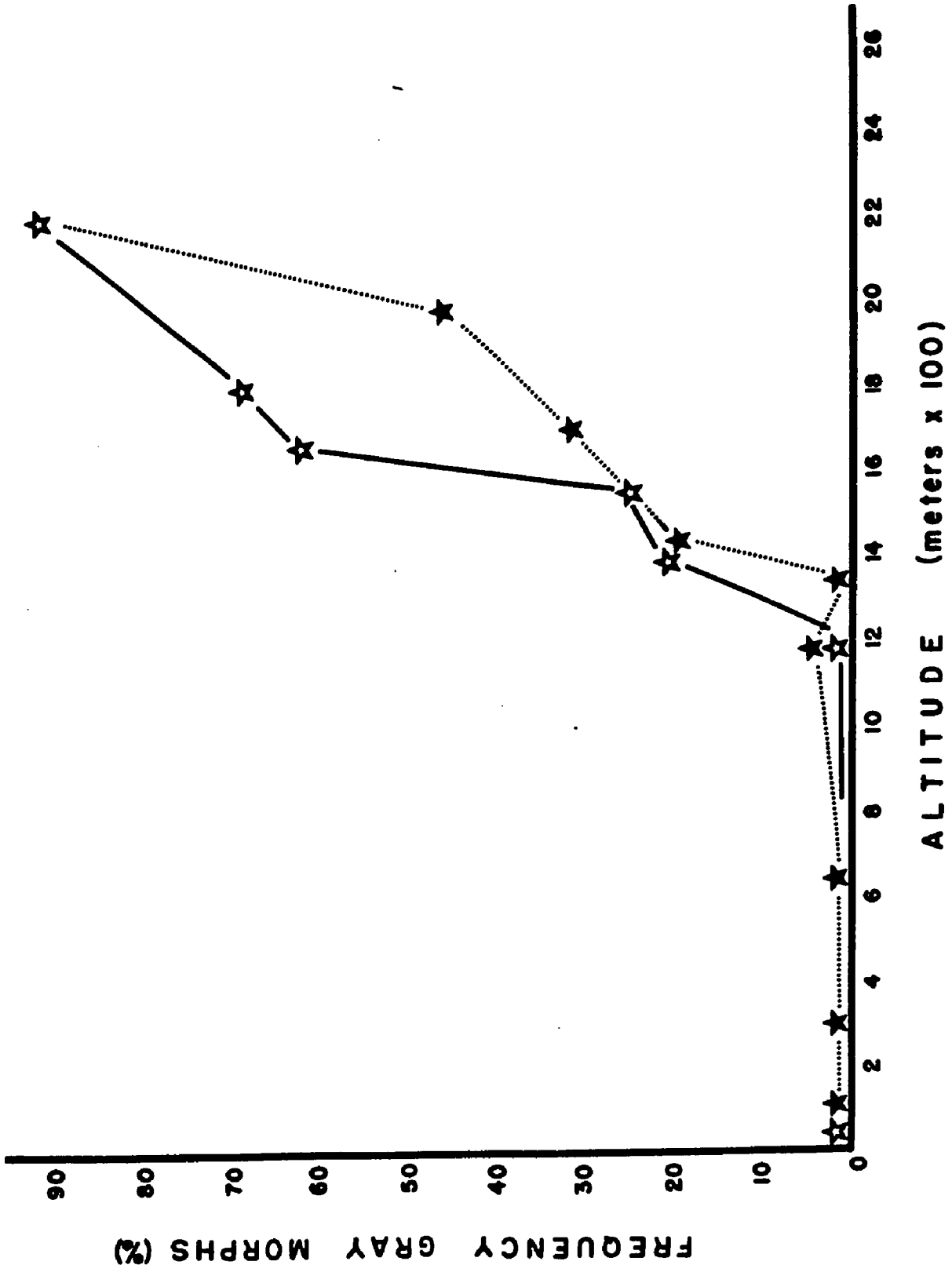

FREQUENCY GRAY MORPHS (%)
90
80
70
60
50
40
30
20
10
0
2
4
6
8
10
12
14
16
18
20
22
24
26
ALTITUDE (meters x 100)

FIGURE 13

Altitudinal Relationships of Gray Morph Frequencies

II. North and East Slope Transects

■ St. Denis to Plaine des Chicots

▲ St. Benoît to Plaine des Salazes via Takamaka and Forêt du Bebour

△ St. Benoît to Plaine des Cafres via Plaine des Palmistes

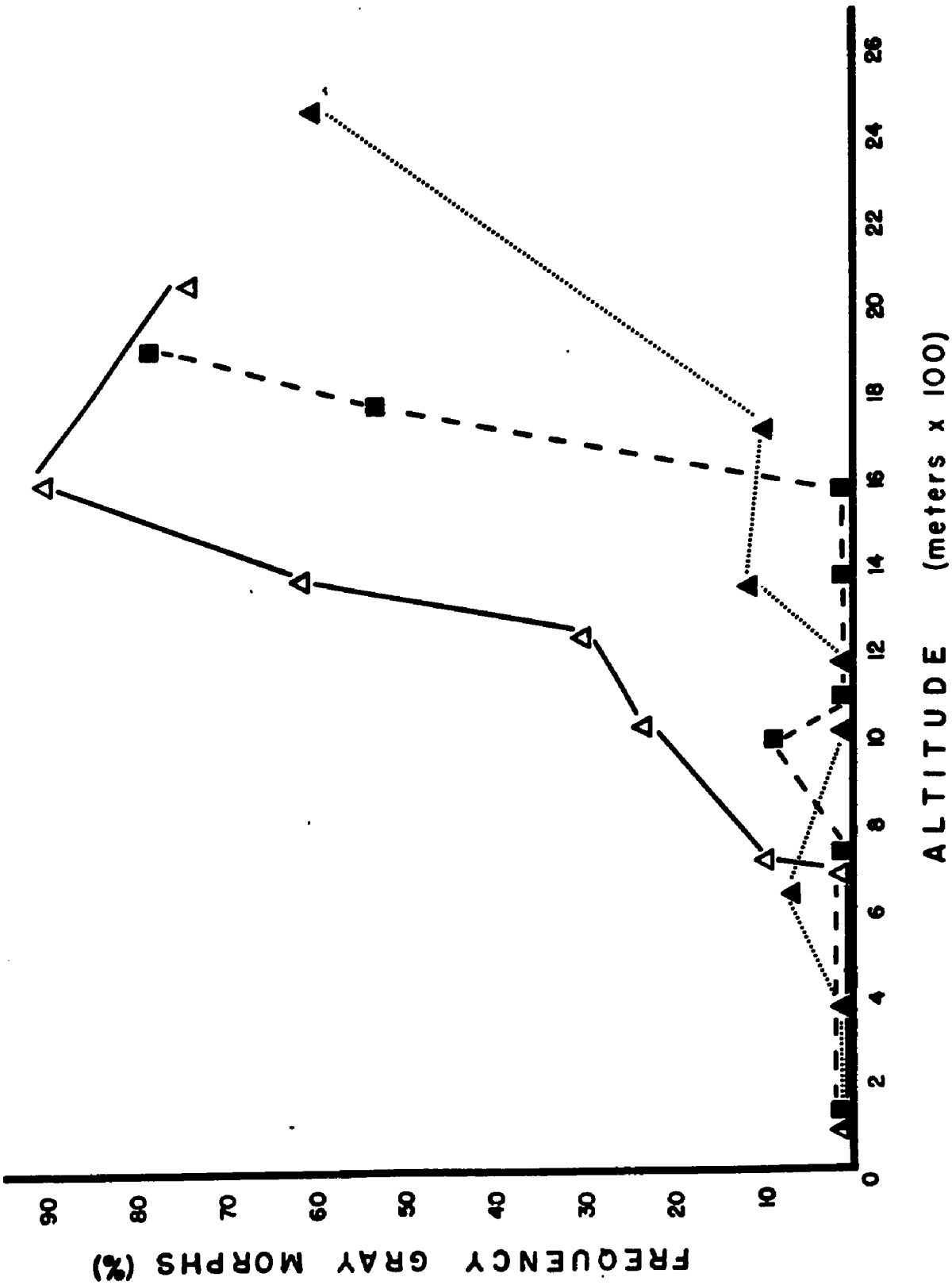

FREQUENCY GRAY MORPHS (%)
10
20
30
40
50
60
70
80
90
0
2
4
6
8
10
12
14
16
18
20
22
24
26
ALTITUDE (meters x 100)

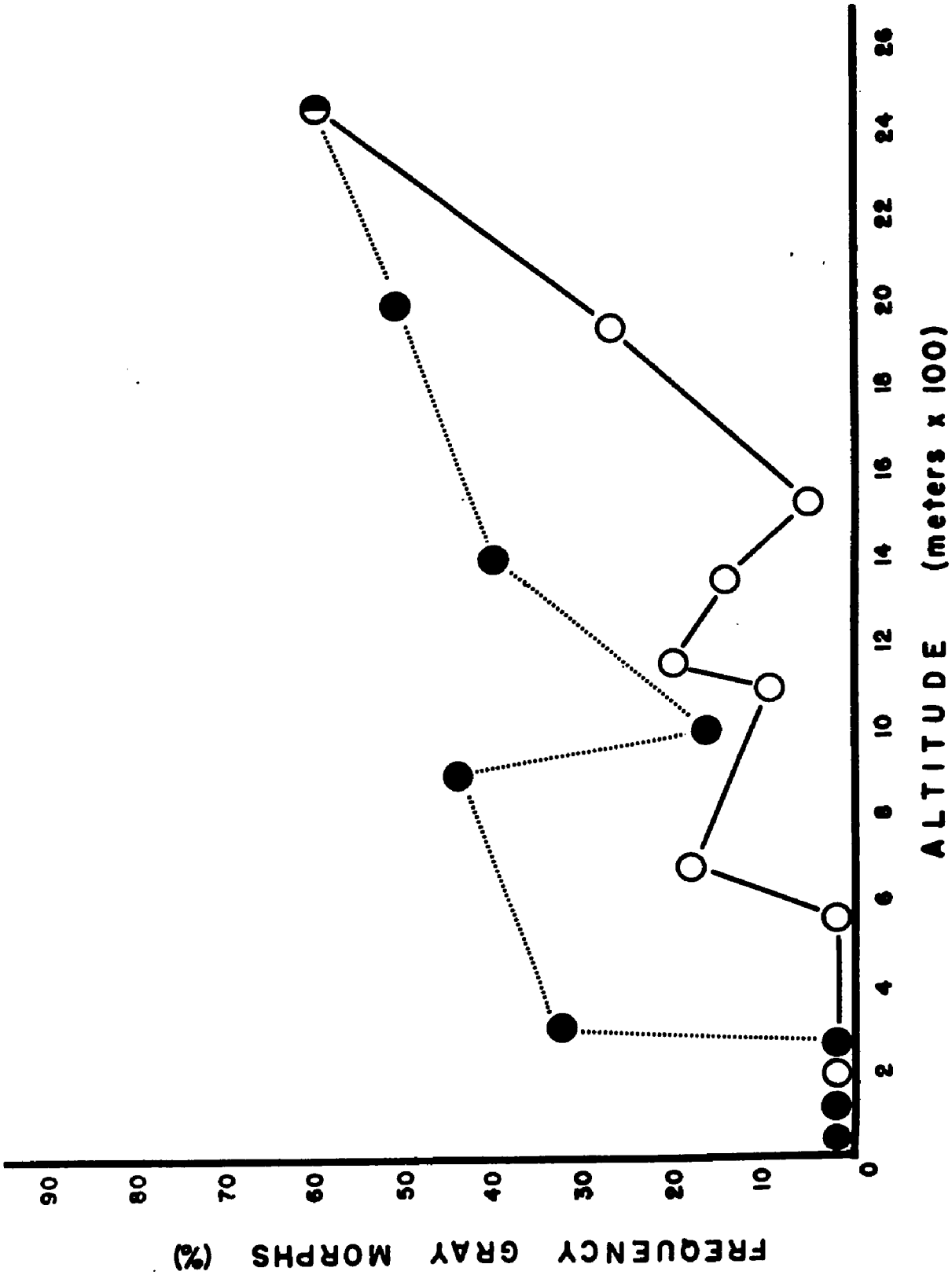
FIGURE 13

Altitudinal Relationships of Gray Morph Frequencies

III. Cirque Transects

○ Cirque de Salazie

● Cirque de Cilaos


FREQUENCY GRAY MORPHS (%)
90
80
70
60
50
40
30
20
10
0
2
4
6
8
10
12
14
16
18
20
22
24
26
ALTITUDE (meters x 100)

cirques differ from the other transects in having high gray morph frequencies at relatively low elevations and strong irregular fluctuations in the correlations of morph ratios with altitude. A characteristic feature of cirque topography is the separation of high altitudes, where gray morphs are common, from very low altitudes, where they are normally absent, by sheer cliffs. By drastically reducing the distances separating extreme altitudes such relief certainly promotes unpredictable morph mixtures as any movement up or down the cliffs by white-eyes would quickly disrupt existing correlations with altitude.

Some evidence of local movements and changes in the proportions of gray and brown morphs is provided by an unusual situation at Nez de Boeuf (Plaine des Cafres) at 2060 meters elevation on the edge of the Ravine de la Rivière des Remparts. In the protected gullies of this area an endemic leguminous tree, Sophora nitida, whose flowers seem especially attractive to white-eyes, grows in abundance. Indeed, the heights above Plaine des Cafres are the center of this tree's distribution (Rivals, 1952). Surrounding the pockets of Sophora trees is nearly pure heath, which is continuous with the Plaine des Cafres at lower elevations in the north.

In 1964 this was predominately a gray-morph locality as virtually all birds that we watched were gray and only

two of the nine specimens we collected were brown morphs. When I revisited the locality on 6 August 1967 many brown morphs were present and a count the following day revealed that they constituted about 70 per cent of the borbonica population. The Sophora nitida was flowering at this time and these white-eyes were feeding heavily at the flowers. By way of contrast, at a locality about three kilometers up the road at nearly the same elevation, but where there was very little Sophora, only two brown morphs were recorded in a count of 20 birds.

By September 5 the Sophora had nearly finished flowering and only a few large trees with flowers remained in the area. On this visit I counted a total of 35 gray morphs and 14 brown morphs and was impressed by the fact that the brown morphs were found almost exclusively near the still productive Sophora, whereas if one wandered through the heath away from the Sophora only grays were encountered. On 23 October after all Sophora flowers had disappeared 35 grays and seven brown morphs were recorded. On 19 December 30 gray morphs and 10 brown morphs were counted indicating a stabilization of about 77 per cent gray morphs, a figure comparable to that found in November 1964.

The explanation of this shift from a predominance of brown morphs to gray morphs in about two months lies in the probable attraction of brown morphs to this highland

area by the abundance of suitable nectar-producing flowers. Furthermore it would seem that they were drawn up from lower elevations and in particular the valley of the Rivière des Remparts, which, 1000 meters directly below Nez de Boeuf, is well populated by brown white-eyes. Such an hypothesis is supported by my observations that early in the morning white-eyes came to the Sophora groves from the cliff edge and in the evening would leave in its direction. Even during the day there was active movement by these white-eyes between the edge of the cliff and the Sophora.

Such marked local movements, although involving the effects of topographical disruption presented above, are exceptional rather than exemplary. Not only are such obvious concentrations of food as dense stands of flowering Sophora unusual, but also they are rarely on the edge of a major cliff as seems to be necessary for significant alteration of the morph ratios.

It was suggested above that the difference in the occurrence of gray morphs at localities on the Takamaka-Bébour and St. Benoît-Plaine des Palmistes transects might be due to the difference in vegetation of the two, i.e. the predominance of scrub, which is physiognomically similar to heath, rather than forest on the latter. The occurrence and in most cases predominance of scrub vegetation at all non-cirque localities below 1300 meters elevation where gray morphs were recorded (Table 5) strongly supports this

conclusion. Furthermore the lowland locality (Locality 25, 640 meters elevation) on the Bébour transect at which a gray morph was recorded was the only one on this transect at which scrub was the predominant vegetation.

At middle elevations gray morphs occur with brown morphs in the indigenous forest but high proportions of gray morphs occur primarily where heath is the predominant vegetation, including relatively low localities (Nos. 38, 52, 35, 100) on or near the Plaine des Cafres which is an extensive heath-covered plateau. No significant correlation is detectable between the occurrence of gray morphs and of heath at middle elevation localities where heath is sometimes present as a minor element or understory in the vegetation.

In this connection it is of interest to note that gray morphs closely match in color the grays characteristic of the stems and interior branches of the heath, Philippia montana, as well as the lichen-covered bark of Sophora nitida, a heath associate which is especially common in the Plaine des Cafres region, whereas the upper part coloration of brown morphs contrasts noticeably against these same backgrounds. In the hardwood forests at lower elevations, brown and green colors tend to predominate rather than grays and the relative advantage in color matching of one or the other is less apparent.

I have analyzed several behavioral features to

determine whether non-random elements are involved in the mutual behavior of brown and gray morphs (Table 6). On September 9 on the Plaine des Chicots, at a time when white-eyes were coming into breeding condition but prior to actual nesting many isolated foraging pairs of white-eyes were encountered and the morphs included in each recorded. Similarly all intraspecific chases were recorded at Cilaos as were established pairs of breeding adults. Finally, huddling pairs of white-eyes noted at Cilaos have also been analyzed. Both the associated pairs of white-eyes at Plaine des Chicots and the mated pairs at Cilaos prove to be random with respect to plumage type. However, huddlings and prebreeding aggressive activity were recorded more frequently between like morphs than was to be expected if the partners had been chosen randomly from the total population. Unfortunately the lack of consistency of these results obviates meaningful interpretation, though a lack of importance of morph discrimination in relation to mating and thereby the maintenance of the polymorphism is suggested by the random pairing associations.

In the course of the 1967 field work I developed the impression that gray morphs fed more frequently in the creeping fashion of the Black and White Warbler than did brown morphs, but this is not borne out statistically (Table 7). No other differences in behavior or sympatric ecology were noted.

TABLE 5. Synopsis of Gray Morph Localities

Locality (No.)	Altitude (meters)	Vegetation	Per cent Gray Morphs
60	2460	Heath	60
39	2300	Heath	50
42	2300	Heath	100
73	2200	Heath	92
41	2060	Heath	65
59	2000	Heath	51
64	1980	Heath	47
1	1940	Heath	27
5	1910	Heath	78
71	1780	Tamarin	62
4	1780	Tamarin + Heath	53
30	1720	Forest	10
63	1700	Tamarin	31
8	1700	Forest	36
70	1660	Tamarin	62
6	1650	Forest	21
38	1600	Heath	90
23	1590	Forest	12
3	1580	Forest	2
74	1550	Tamarin	25
18	1530	Forest	5
62	1440	Forest	19
72	1400	Acacia + Forest	21
58	1400	Forest	40
24	1400	Forest	20
40	1400	Forest	38
52	1380	Acacia + Heath	61
89	1360	Forest	50
28	1360	Forest	16
22	1350	Forest	14
29	1350	Forest	13
35	1250	Forest + Scrub	50
20 (C)	1160	Scrub	20
17	1100	Gardens + Scrub	9
61	1080	Forest + Scrub	2
33	1060	Acacia + Scrub	27
49	1060	Scrub	33
1	1000	Scrub	9
56 (C)	1000	Casuarina	16
79	900	Scrub	44
10	820	Scrub	19
31	720	Scrub	10
16 (C)	680	Scrub	10
25	640	Scrub	7
55 (C)	300	Casuarina	33

(C) Cirque locality

Association		A. Gray x Gray	B. Brown x Brown	C. A. and B. (Combined)	D. Gray x Brown	X^2
Prebreeding Associations (Pl. des Chicots)	Observed	6	2	8	4	.0003
	Expected			7.26	4.69	
Prebreeding Chasing (Pair Formations?) (Cilaos)	Observed	3	12	15	4	5.514*
	Expected			9.89	9.12	
Mated Pairs (Cilaos)	Observed	3	8	11	4	2.735
	Expected			7.8	7.2	
Huddling Pairs (Cilaos)	Observed	6	17	23	3	13.848***
	Expected			13.52	12.48	

* P = .05

*** P = .001

TABLE 6. Analysis of Morph Associations

TABLE 7. Analysis of Foraging Behavior by Gray and Brown Morphs in Cilaos Forests

	Gray Morphs	Brown Morphs	
Warbler	28	55	83
Creeper	15	26	41
	43	81	124

X^2 = .0128 with one degree of freedom

P > .05

In summary, the discontinuous phenotypic variation in back color and associated characters of Zosterops borbonica on Réunion conforms to a classical genetic polymorphism, which has been defined as "the occurrence together in the same locality or habitat of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation" (Ford, 1940). The sympatric occurrence of gray and brown morphs at numerous upland localities, the formation of mixed pairs and the production of mixed broods all substantiate this conclusion. It would seem that genes which play an important role in the synthesis and/or deposition of phaeomelanin pigments in the feather barbs are involved.

FIGURE 14

Distribution of Brown Morph Specimens over Range of Head Character Indices (pure gray head = 0; pure brown head = 16)

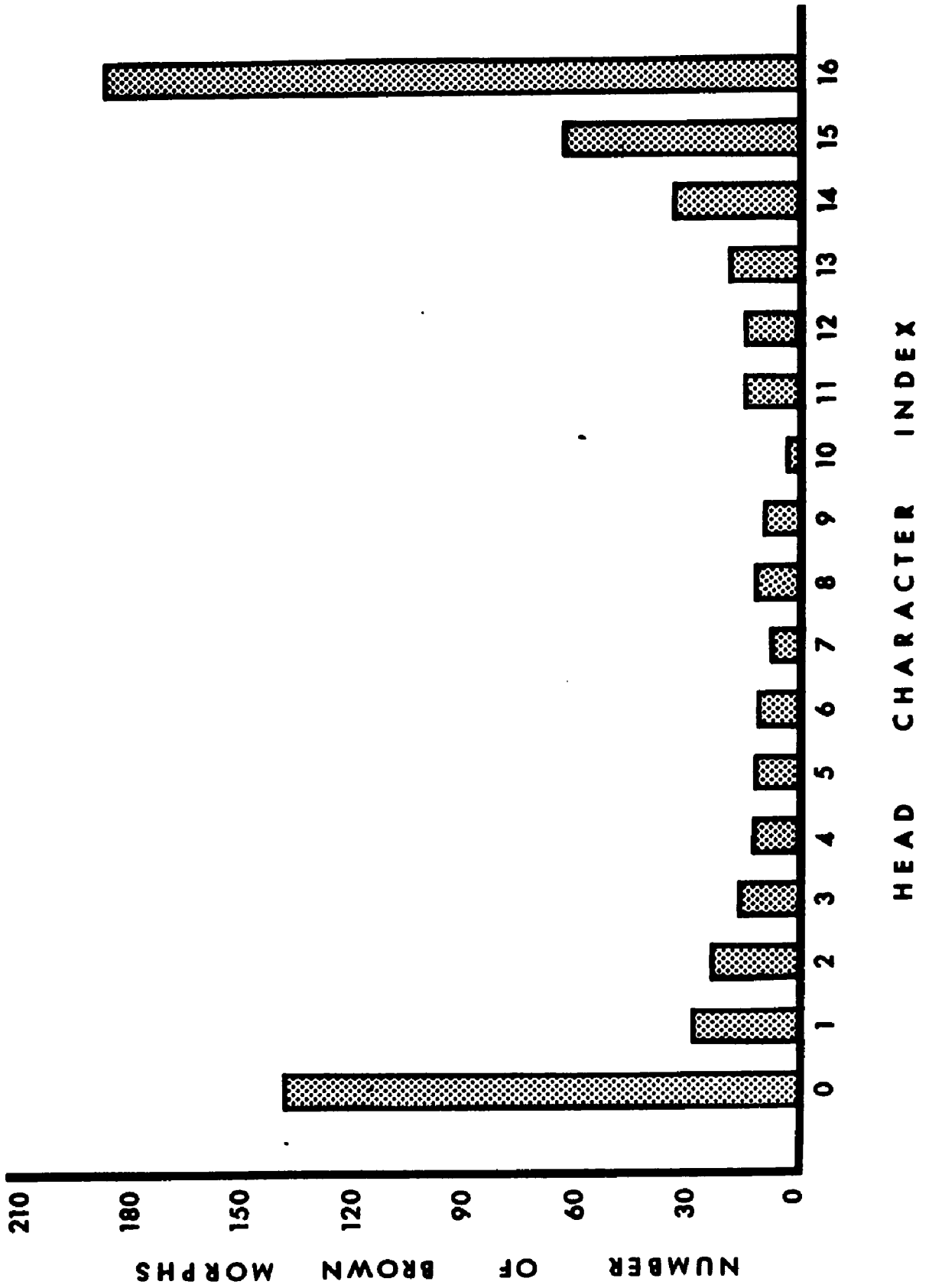
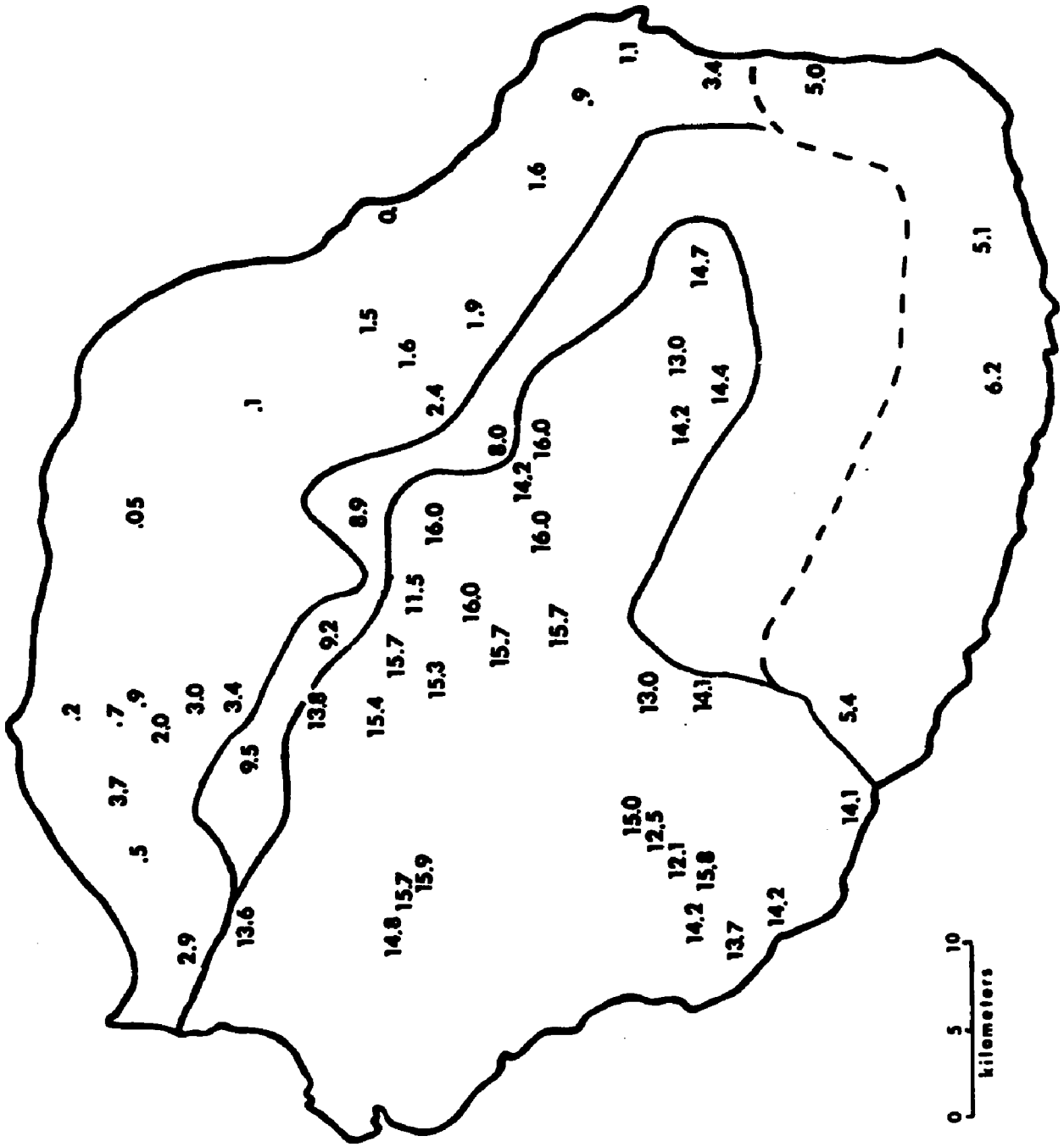

NUMBER OF BROWN MORPHS
0
30
60
90
120
150
180
210
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
HEAD CHARACTER INDEX

FIGURE 15

Distribution of Mean Locality Adult
Head Character Indices
(Brown Morphs Only)


.2
.7
.9
2.0
3.0
3.4
3.7
.5
.05
.1
1.5
1.6
2.4
1.9
.9
1.1
3.4
5.0
5.1
6.2
14.7
13.0
14.4
14.2
8.0
16.0
14.2
16.0
16.0
16.0
11.5
15.7
15.3
15.7
15.7
9.2
13.8
15.4
9.5
13.6
2.9
14.8
15.7
15.9
13.0
14.1
5.4
15.0
12.5
12.1
15.8
14.2
13.7
14.2
14.1
0
5
10
kilometers

HEAD COLORATION IN BROWN MORPHS

I have diagnosed the head coloration of brown morphs, which varies from entirely gray to entirely brown, in terms of four characters, e.g. nape, crown, side of the head, and auriculars. Each character was evaluated in terms of five character states representing increasing amounts of phaeomelanin pigmentation (Table 1). To obtain a single Head Character Index (HCI) for each specimen I then summed the values of the four character states producing a range of seventeen indices from the entirely gray-headed form (HCI 0) to the entirely brown-headed form (HCI 16). The resulting parabolic distribution of specimen numbers over the range of indices is illustrated in Figure 14. Over one-half (54.7 per cent) of the 592 brown morph specimens were scored either 0 or 16, while the remaining 45.3 per cent were distributed among the fifteen intermediate character indices.

Distribution

The geographic distribution of mean adult Head Character Indices of each locality is illustrated in Figure 15. Indices at the brown end of the spectrum characterize the western side of the island from Rivière

des Galets to the Rivière St. Étienne, the cirques of Cilaos and (probably) Mafate and the island's central highlands. Indices at the gray end of the spectrum characterize localities below 1380 meters elevation on the island's north and east sides. A narrow, but distinct band of intermediate mean locality indices of 8 to 10 connects the ranges of the two types. It extends from Plaine d'Affouche and Plaine des Chicots across the Cirque de Salazie, Plateau de Belouve, Plaine des Marsouins and Plateau de Duverney to La Plaine des Palmistes and probably the Rivière de l'Est. The island's southern coast is characterized by intermediate but distinctly lower (5.0 - 6.2) mean indices.

On the northwest coast, the region of contact, which is about five kilometers in width across most of the island, is reduced to the rocky bed of the Rivière des Galets, about one-half kilometer across. Here, the mean index changes abruptly from 13.6 on the river's south side (Locality 65) to 2.9 on the north side (Locality 87). On the southwest coast across the Rivière St. Étienne, there is also a sharp break in the Head Character Index from 14.1 on the north side of the river (Locality 44) to 5.4 on the south side (Locality 93).

Throughout the island the mean locality Head Character Index tends to increase with altitude, reflecting an increase in the amount of brown in the head pattern.

FIGURE 16

Brown Morph Head Color Patterns

(stippling = gray; cross-hatch = brown)

A. "pure" *borbonica* (HCI 0)

B. "brown-naped" *borbonica* (HCI 1-9)

C. brown-faced intermediate (HCI 10-13)

D. "pure" *xerophila* (HCI 16)

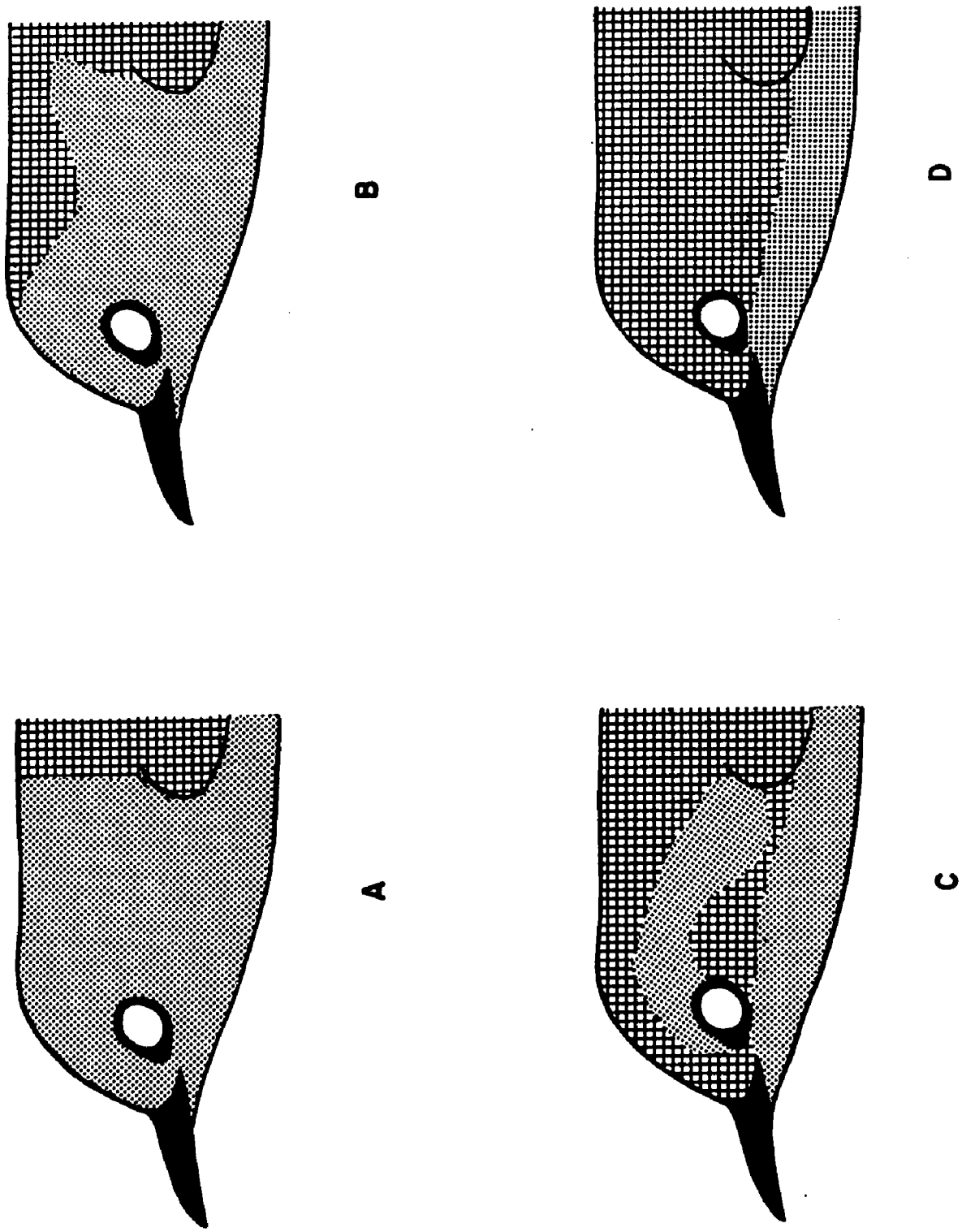
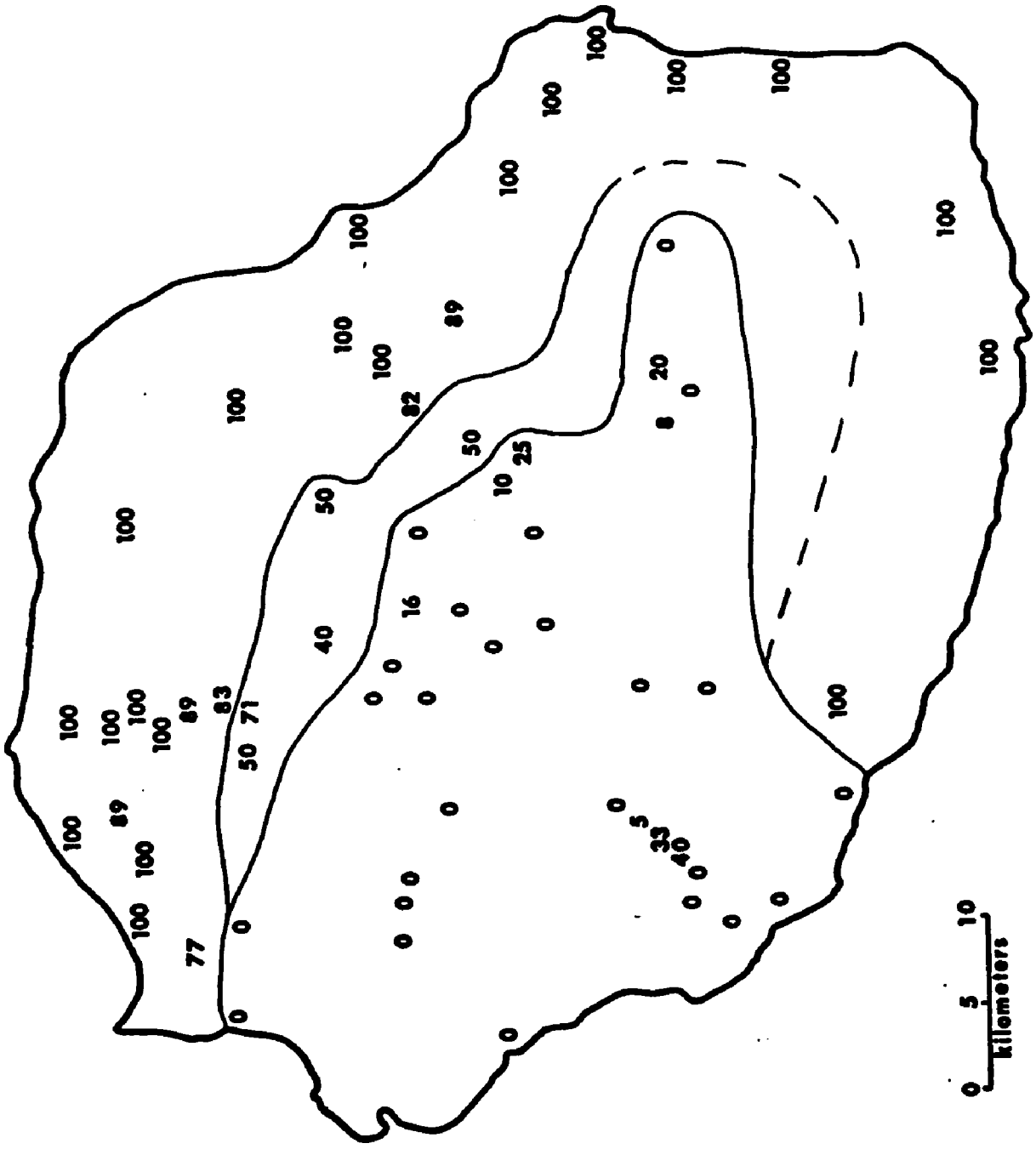

B
D
A
C

FIGURE 17

Relative Distribution of *Z. b. borbonica*
(Head Character Indices 0 - 9)
and *Z. b. xerophila* (Head Character Indices 10 - 16)
in Terms of Per Cent *borbonica* in Each Brown Morph Sample


0
5
10
kilometers

On the west coast some gray is present on the side of the face of otherwise brown-headed types and throughout the eastern lowlands brown is present in the napes of some gray-headed individuals. The frequency of brown-naped individuals increases with altitude and also along the coast just south of Bois Blanc. Observations just to the north of Locality 47 revealed primarily gray-headed birds, whereas two kilometers south of Locality 47 in the Casuarina forests of Grande Brûlé on the southern side of a recent (1954) lava flow that reached the sea, all borbonica had discernible brown on the nape. Locality 47 seems to be in a zone of contact of these two forms. Brown-naped forms predominate at all coastal localities between Rivière St. Étienne and Grand Brûlé. They also appear in minor but significant numbers at Localities 98 and 62 above Tévelave, resulting in a lower Head Character Index than surrounding localities.

Brown pigment appears in the nape before it does in the other regions of the head and, as it increases in intensity, is gradually added to the crown. The appearance of brown in the auriculars is correlated with its appearance in the crown, but the side of the head becomes brown only in those specimens with strong brown on the top of the head. Despite the apparent continuity of the variation in head color therefore, this correlation permits the separation of two groups of brown morphs, those with gray

faces and variable amounts of brown on the top of the head (HCI 0 - 9) and those with considerable brown in the face as well as on the top of the head (HCI 10 - 16). In order to facilitate the remaining discussion I shall use the subspecific name xerophila to refer to brown morphs at the brown-headed end of the spectrum (HCI 10 - 16) regardless of their underpart coloration and borbonica to refer to brown morphs at the gray-headed end (HCI 0 - 9). For the purposes of some of the analyses the distinction of "pure" borbonica (HCI 0) and "brown-naped" borbonica (HCI 1 - 9) will be necessary (Figure 16).

Specimens in these two groups predominate at localities in different parts of the island, corresponding to the basic divisions indicated by the mean Head Character Indices (Figure 17). Borbonica is the predominant form (constituting over 75 per cent of the brown morphs) in the northern, eastern and southern lowlands below 1380 meters, while xerophila predominates along the dry west coast and into the central highlands. Mixing of the two forms occurs in the belt distinguished by intermediate mean Head Character Indices. The significant proportions (40 and 33 per cent respectively) of "brown-naped" borbonica can be seen at Localities 98 and 62.

Environmental Correlates of Brown Morph Distribution

There are no conspicuous differences between brown

morph color variants in their choice of the habitats available on Réunion. The geographic range occupied by either one, i.e. in which it is the predominant color form, comprises a continuous portion of the island's area (Figure 17) including a wide range of habitats rather than a mosaic pattern that would correspond to the distribution of a particular habitat. Many vegetation types are occupied by each form (Table 8), and the differences which do exist correspond to non-casually related incongruities in the distributions of the vegetation and the color variant. For example, dry Casuarina forest is present only on the west side of the island in the range of xerophila, but borbonica does occur in wetter Casuarina at various localities on the island's east side.

The primary correlate of the east-west distributional separation of borbonica and xerophila is a difference in rainfall, as the average rainfall recorded at 31 localities below 500 meters elevation between St. Denis and St. Rose is 2697 millimeters per year compared to an average of 926 millimeters per year for 21 localities below 500 meters elevation between Rivière des Galets and St. Louis (Table 9). There is also a corresponding difference in the lushness of the vegetation of these two coastal regions. Although inhabited by borbonica rather than xerophila, the lowlands between St. Denis and the Rivière des Galets (as represented by the two meteorological stations at

TABLE 8. Relation of Brown Morph Distribution to Locality Vegetation (Based on the Predominant Color Variant at each Locality)

	borbonica	*xerophila*
Intact Forest		
Middle Elev.	57,80,45,46,26	58
High Elev.	26	98,61,62,18,30, 28,29,40,8
Mimusops	86	
Forest Remnants	14,22,48	22,35,36
Tamarin		
Mature		74
Young		70,71,73
Heath		
Low		73,60,42,43
Lush		64,59,19,38
Sophora		41,39
Gardens, etc.	87,83,34	
Ravines		
Schinus	93	68,94,95,54
Eugenia	96,81,99,12, 82	

TABLE 8 cont.

	borbonica	xerophila
Scrub		
Psittium-Heath	10,1,2,25,9,12	20,49
Lantana	16	79
Psittium-Pandanus	31,32	
Casuarina		
Dry Forest		66,67,51,44, 53,55,56,65
Wet Ravines	11,15	
Pandanus	84,85,47,88	
White Acacia		97,72

TABLE 9. Rainfall and Temperatures of Brown Morph Coastal Localities

Locality	Annual Rainfall	January Max. Temp.	August Min. Temp.
"pure" A. Borbonica			
St. Denis	1072.5	30.0	18.8
Gillot	1530.7	29.9	17.1
St. Benoît	2999.3	30.2	16.4
St. Rose	3639.8	31.4	16.1
Mean	2697	30.4	17.1
La Possession	836.6	-	-
Le Port	685.8	31.3	23.5
Mean	761		
B. Xerophila			
Savannah	848.6	31.6	15.7
St. Leu	713.2	32.4	18.0
St. Gilles	570.4	30.7	16.0
Étang Salé les Bains	712.8	32.0	13.1
St. Louis	844.5		
Mean	926	31.7	15.7

TABLE 9 cont.

Locality	Annual Rainfall	January Max. Temp.	August Min. Temp.
C. Brown-naped Borbonica			
Pierrefonds	732.4		
St. Pierre	956.6	29.4	16.8
St. Joseph	1923.3	30.1	15.8
St. Phillippe	4274.7	28.8	17.8
Tremblet	4483.3		
Bois Blanc	4461.4		
Mean	2332	29.4	16.8

Le Port and La Possession) are more similar climatologically to the arid west coast than to the east coast lowlands. The break in the Head Character Index across the Rivière des Galets occurs without any climatological correlations. The coastal regions between Bois Blanc and the Rivière St. Étienne receive an annual rainfall that varies from very wet (4461 millimeters per year at Bois Blanc) to very dry (732 millimeters year at Pierrefonds). Again the break in Head Character Index across the Rivière St. Étienne takes place without a change in climate.

These subdivisions of the Réunion lowlands do not differ greatly in prevailing temperatures (Table 9) though the west coast averages slightly warmer than the other two subdivisions and the southern coast slightly cooler.

The difference in rainfall is relevant only in relation to the coastal populations of brown morphs, for inland at higher elevations xerophila occupies some of the wettest parts of the island. Furthermore, borbonica is limited in its altitudinal distribution, for it does not predominate at any locality over 1380 meters elevation. Thus xerophila occupies a wide variety of environmental extremes from the driest parts of the island to the wettest and from sea level to the highest elevations in contrast to borbonica which is relatively restricted to the humid lowlands.

Reviewing again the distribution of "brown-naped"

borbonica, they increase somewhat in frequency with altitude in the northeastern parts of the island, but they are the exclusive inhabitants of the southern coastal regions from localities of very high rainfall (Bois Blanc to Tremblet) as well as very low rainfall (St. Pierre to Pierrefonds) and appear in relatively isolated pockets such as at Localities 98 and 62 above Tévelave and at Locality 8 in the ravine of the Rivière des Remparts. These disjunct pockets are localities with heavy rainfall and lush forests, which taken in conjunction with the sudden shift to this form just south of Bois Blanc suggests that it has some advantage in areas of high rainfall. If this is so, then their presence in the relatively dry coastal region between St. Joseph and Rivière St. Étienne is paradoxical (see below).

Physiological Differences

The relative distributions of xerophila and borbonica on Réunion seems to be a function primarily of their physiological tolerances. The replacement of borbonica by xerophila above 1400 meters elevation even on the wet side of the island is evidence of a relatively broad tolerance of environmental temperatures in xerophila and rather limited tolerance in borbonica. The east-west coastal division of lowland populations of these two color variants strongly suggests a difference in their dependence

on available water or relative ability to withstand drought. This also seems reasonable in relation to their original distribution and differentiation (see page 175), as borbonica was presumably a bird of the streamsides and ravines of the west side, most of which have running water throughout the year. Xerophila, on the other hand, being restricted to the tree savanna, was undoubtedly subjected to extended periods during the dry winter months when drinking water was very scarce.

Some support for this hypothesis was inadvertently obtained when I shipped twenty live Zosterops borbonica from Réunion to Ann Arbor, Michigan, by airplane. The trip which lasted forty-eight hours proved to be an experiment in tolerance of water deprivation, since the water drinkers in the shipping box became clogged and their contents not available to the white-eyes. Of the twenty borbonica in the shipment, six were gray morphs, six were borbonica, and eight were xerophila. Only two gray morphs and two borbonica survived the trip whereas seven of the eight xerophila were alive upon arrival at Detroit and have continued to live for over a year in Ann Arbor. Combining the gray morphs and borbonica to permit testing of the data by a X^2, the high survival of xerophila is almost significant at the .05 level (Table 10).

If such physiological tolerances are the primary difference between xerophila and borbonica, the predominance

TABLE 10

Differential Survival of Z. borbonica color variants under conditions of extreme water deprivation

	Gray Morphs and borbonica	xerophila	
Lived	4	7	11
Died	8	1	9
	12	8	20

$X^2 = 3.71$ $P_{.05} = 3.84$

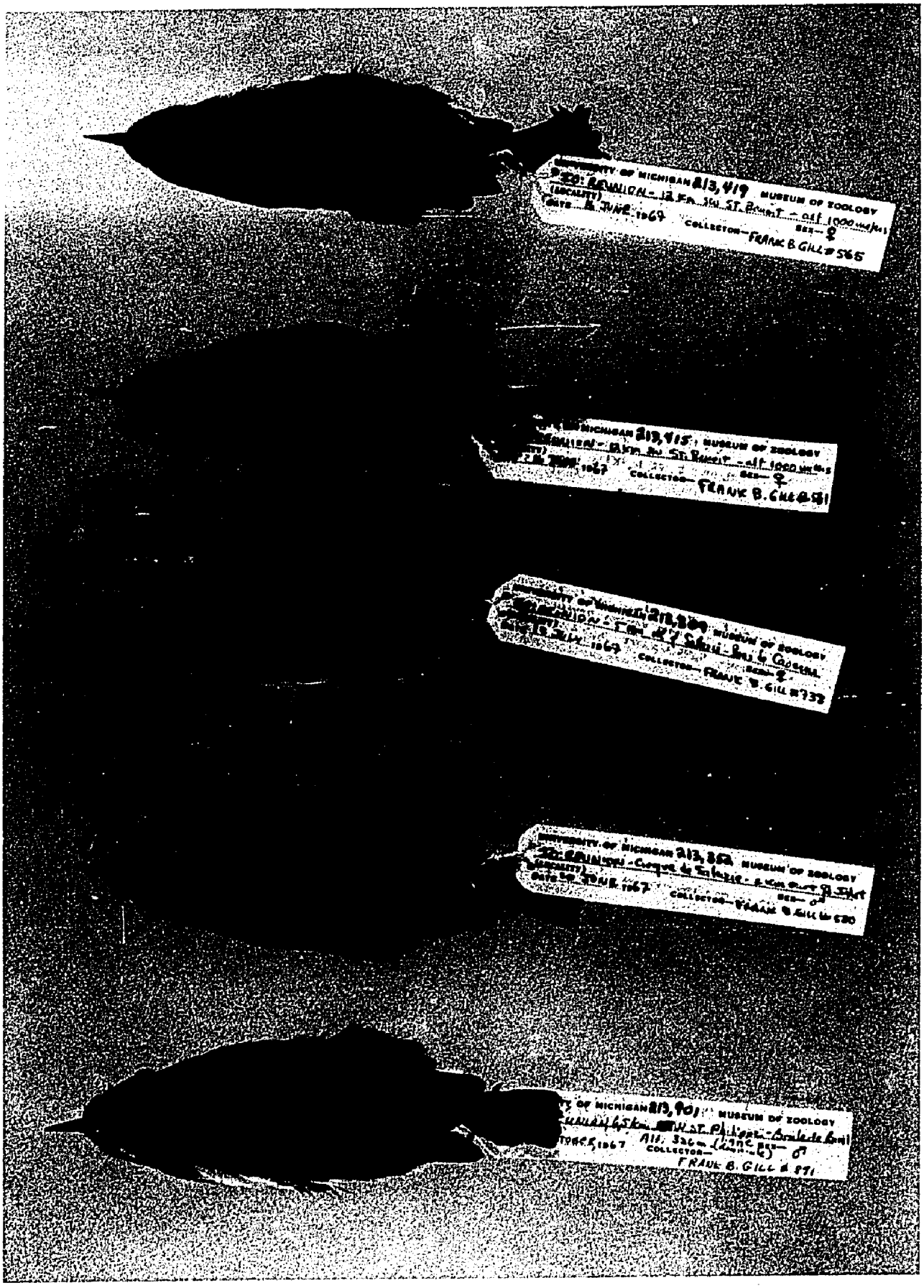
$P_{.10} = 2.71$

of borbonica in the dry lowlands north of the Rivière des Galets requires explanation, although the places at which I observed borbonica in this region were either in irrigated gardens or in ravines with some running water. The fact that the change from one form to the other coincides with as obvious a barrier as the Rivière des Galets, in the absence of any climatological shift, strongly suggests that borbonica's occupation of a seemingly suboptimal region results from swamping from the remainder of the population. Xerophila has an advantage over borbonica in physiologically extreme environments but in the lowlands, at least, seems

to depend on the restriction of gene flow in borbonica and therefore reduced competition from that form. Additional information as to the nature of the contact between these two forms in the Cirque de Salazie would be particularly interesting. A similar competitive situation probably exists along the south-west coast near St. Pierre between "brown-naped" borbonica and xerophila, which again is resolved only in the presence of a geographic barrier, the Rivière St. Étienne.

FIGURE 18

Selected Specimens Used as Standards for
Comparison of Underpart Gray Coloration
(From left to right - Visual Indices 0, 2, 4, 6 and 8)


UNIVERSITY OF MICHIGAN 213,419 MUSEUM OF ZOOLOGY
FRANK B. GILL # 565
UNIVERSITY OF MICHIGAN 213,415 MUSEUM OF ZOOLOGY
FRANK B. GILL # 561
UNIVERSITY OF MICHIGAN 213,901 MUSEUM OF ZOOLOGY
FRANK B. GILL # 571

UNDERPART COLORATION

Variation in the color of the underparts involves both phaeomelanin and eumelanin deposition, but unlike the dorsal aspects of the color variation in Zosterops borbonica, underpart coloration varies in a continuous fashion. Eumelanins are distributed over the entire plumage of the underparts and vary in concentration to such an extent that individuals of Zosterops borbonica range from nearly pure white to lead gray below (Figure 18). In most specimens, but particularly those with light underparts, the breast tends to be slightly darker than either the throat or the belly. Phaeomelanins are more restricted in their placement and are confined primarily to the flanks and breast. While all brown morphs have intensely pigmented reddish-brown flanks, the phaeomelanin deposition in the breast plumage varies greatly. In some specimens there is also a patch of brown on the side of the throat between the flank coloration and the auriculars, but because of its close association with auricular color this character has not been analyzed separately.

Eumelanins

Evaluation

To evaluate the eumelanin deposition in the underparts I compared the specimens to a series of nine selected specimens representing graded intensities of melanin deposition from pure white (Character State 0) to lead gray (Character State 8) (Figure 18). Although the total aspect of the underparts was included in this single evaluation, slightly greater value was given to the belly coloration than to the breast due to higher variability of the latter and the disruptive influence of phaeomelanin deposition in some specimens. Following the initial sorting each category was surveyed for homogeneity and incongruous specimens reevaluated. Then the remaining specimens were compared back to their standards and to the standards one step lighter and one step darker.

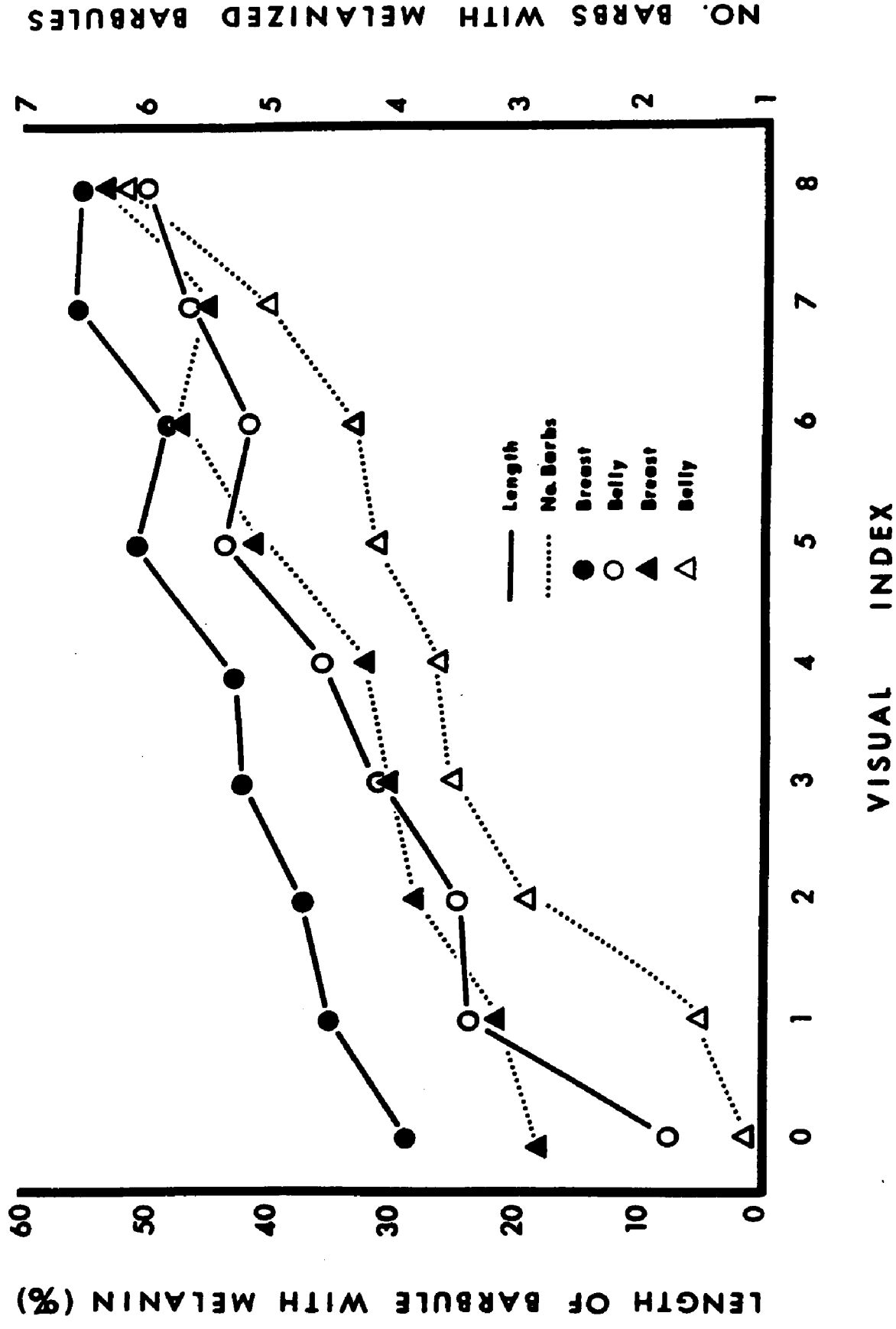
To check the repeatability of these evaluations I randomly drew 107 specimens or 13 per cent of my total sample and reevaluated these on a single morning completely independently of the original determinations; 59 per cent were reassigned to the original category, 41 per cent were within ± 1 cateogry and a single specimen was two steps from the original. Of the 44 specimens which were evaluated differently the second time, 21 were from categories 3 and 4 and were evaluated as one step lighter. Because of the

apparently high percentage of error in these two categories I reevaluated all specimens in them and in doing so confirmed the original determinations in 16 of 21 cases. Thus 73 per cent of the original determinations can be considered repeatable and 99.5 per cent are within ±1 step. In view of the fine distinctions between categories and the numerous variables affecting such color determinations (see Bowers, 1956), I believe this amount of error to be acceptable and unlikely to affect significantly the major results which follow.

Differences in the visual aspect of the intensity of gray melanins correspond at the microscopic level to differences in the extent of melaninization of the barbules. This was evaluated in terms of two criteria. First, the number of barbs on one side of the rachis with melanin-bearing barbules at their base was counted from the tip of the feather inwards. The count was terminated when downy barbules replaced those of contour feather structure. Secondly, the length of the barbule that contained melanin was measured and expressed as a per cent of the total barbule length. This was done by arbitrarily picking a full-length barbule on the proximal side of the base of the next to outermost barb of each feather. By applying such a procedure to each feather, the variance due to location and wear was reduced to a minimum. These criteria were evaluated for feathers plucked from four or five randomly

FIGURE 19

Relation of the Extent of Eumelanization in Feather Structure to Intensity of Underpart Gray Coloration


NO. BARBS WITH MELANIZED BARBULES
7
6
5
4
3
2
1
LENGTH OF BARBULE WITH MELANIN (%)
60
50
40
30
20
10
0
VISUAL INDEX
0
1
2
3
4
5
6
7
8
Length
No. Barbs
Breast
Belly
Breast
Belly

chosen skins from each visual category and for a minimum of six feathers, three from the breast and three from the belly, taken from each skin.

A reasonable correlation of these criteria with the visual categories is evident (Figure 19).

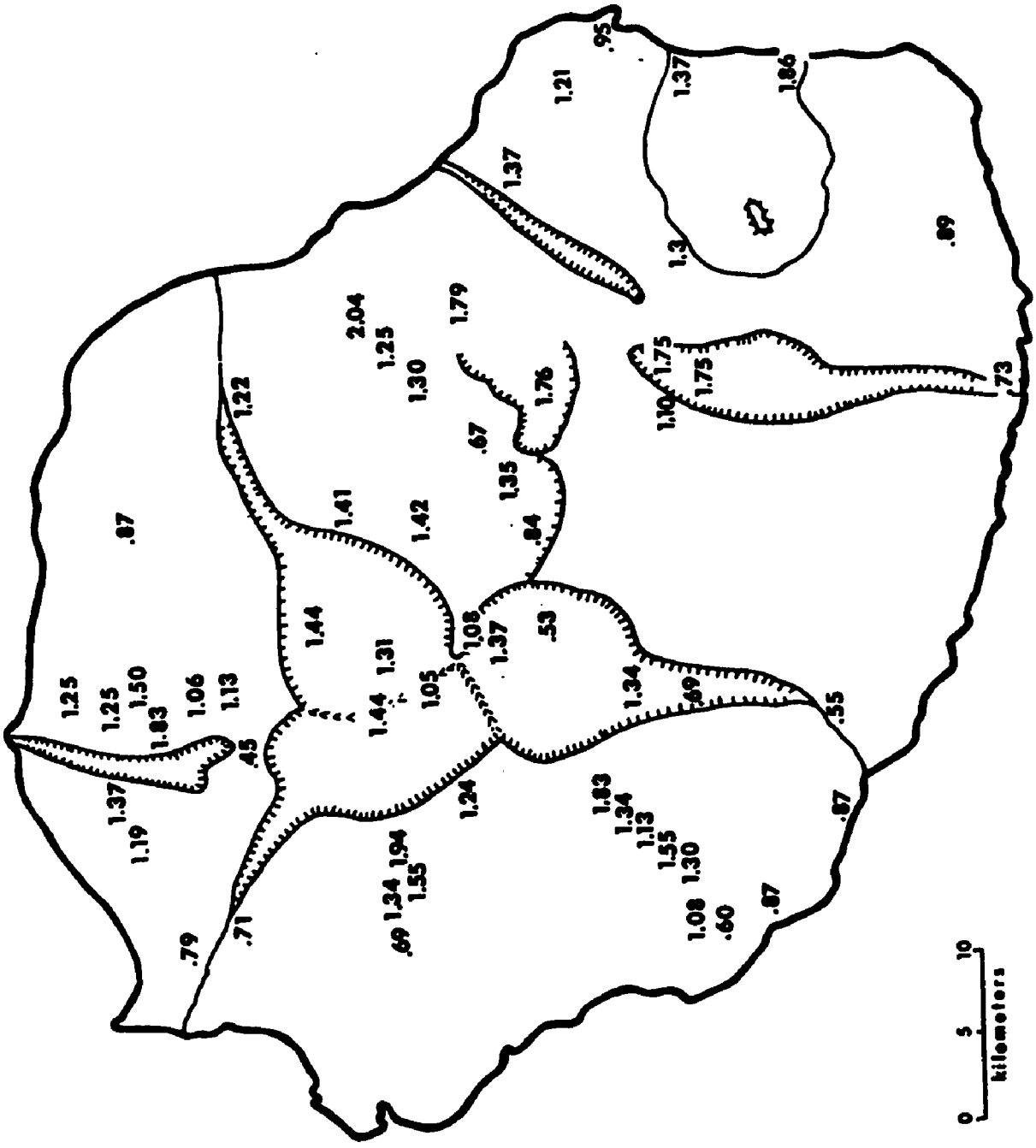
Intralocality Variance

The amount of intralocality variance in underpart gray coloration is presented in Figure 20 in terms of the standard deviation calculated for each sample. Low standard deviations (less than 0.95) characterize the western and southern coasts from La Possession to St. Pierre, a central region that includes part of the Forêt du Bébour, Plateau de Duverney and also a locality in the Cirque de Cilaos and at Beaufond (St. Marie). High standard deviations (over 1.75) are found only at scattered localities, e.g. Locality 2 above Le Brûlé, Localities 70 and 64 high on the western slopes, and a belt, perhaps only artificially continuous, from the region of St. Benoît on the east coast up to Plaine des Palmistes and the upper end of the Ravine des Remparts and then to Tremblet on the southeast coast.

At three localities, e.g. 98, 62, and 55, there was a significant difference between the underpart colorations of coexisting color variants. At Localities 98 and 62 I found many "brown-naped" borbonica with nearly pure white underparts, significantly lighter than the rest of the

FIGURE 20

Locality Variance in Underpart Gray Coloration
(in terms of one standard deviation of the mean visual index)


.95
1.21
1.37
1.86
1.37
1.3
.89
2.04
1.25
1.30
1.79
1.22
1.76
1.10
1.75
1.75
.73
.67
1.35
.87
1.41
1.42
.84
1.44
1.08
1.37
.53
1.25
1.25
1.50
1.83
1.06
1.13
.45
1.44
1.31
1.05
1.34
.69
.35
1.37
1.19
1.24
1.83
1.34
1.13
1.55
1.30
.87
.69
1.34
1.94
1.55
.71
.79
1.08
.60
.87
0
5
10
kilometers

gray-bellied xerophila at these two localities. Inclusion of these specimens increases the standard deviations to 2.11 and 1.79 for localities 98 and 62 respectively, but because of the exceptional nature of the differences they will be considered separately from the general patterns. Similarly the sample from Locality 55 (300 meters elevation) in the Cirque de Cilaos includes gray morphs that are significantly darker-bellied than the brown morphs (xerophila) at this locality. The standard deviation when both morphs are combined is also high, i.e. 1.79, and is not included.

The mean indices of eumelanin deposition for coastal localities below 500 meters separate into three groups which correspond to the coastal divisions of Head Character Indices (Figure 21). Borbonica populations from La Possession to Bois Blanc average darker than xerophila populations on the west side. The difference in means between localities 68 and 87 on the opposite sides of the Rivière des Galets is significant at the 0.01 level. The island's southern coast is occupied by "brown-naped" borbonica which have paler underparts than either of the other two forms. High indices (greater than 4.4) characterize a large central region above 1400 meters on the west side of the island and above 1010 meters on the north and eastern slopes. Mean indices as high as 6.4 and 6.6 occur at a variety of widely-separated highland localities. Indices at moderate elevations are intermediate in value.

FIGURE 21

Mean Locality Indices of Underpart Gray Coloration

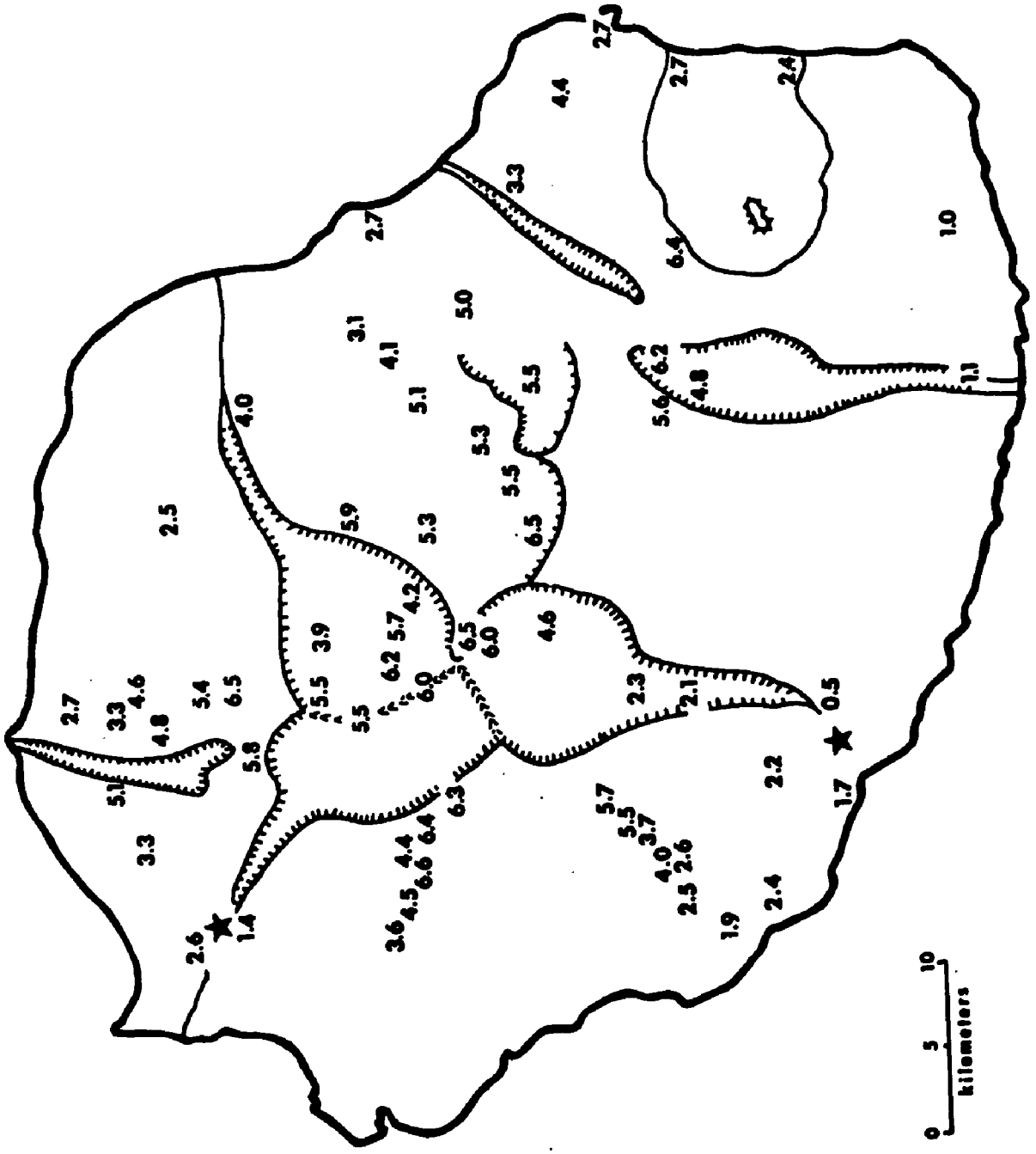

2.7
4.4
2.7
2.4
3.3
2.7
1.0
6.4
3.1
4.1
5.1
5.0
5.5
5.3
5.5
4.0
6.2
4.8
5.6
1.1
2.5
5.9
5.3
6.5
4.2
5.7
6.5
6.0
3.9
15.5
6.2
6.0
5.5
4.6
2.3
2.1
0.5
2.7
3.3
4.6
4.8
5.4
6.5
5.8
5.1
3.3
6.3
5.7
5.5
3.7
4.0
2.6
2.5
2.2
1.7
4.4
6.4
6.6
3.6
4.5
1.4
2.6
1.9
2.4
0
5
10
kilometers

FIGURE 22

Altitude Relationships of Underpart Gray Coloration
(in terms of the mean index of the sample
from each locality)

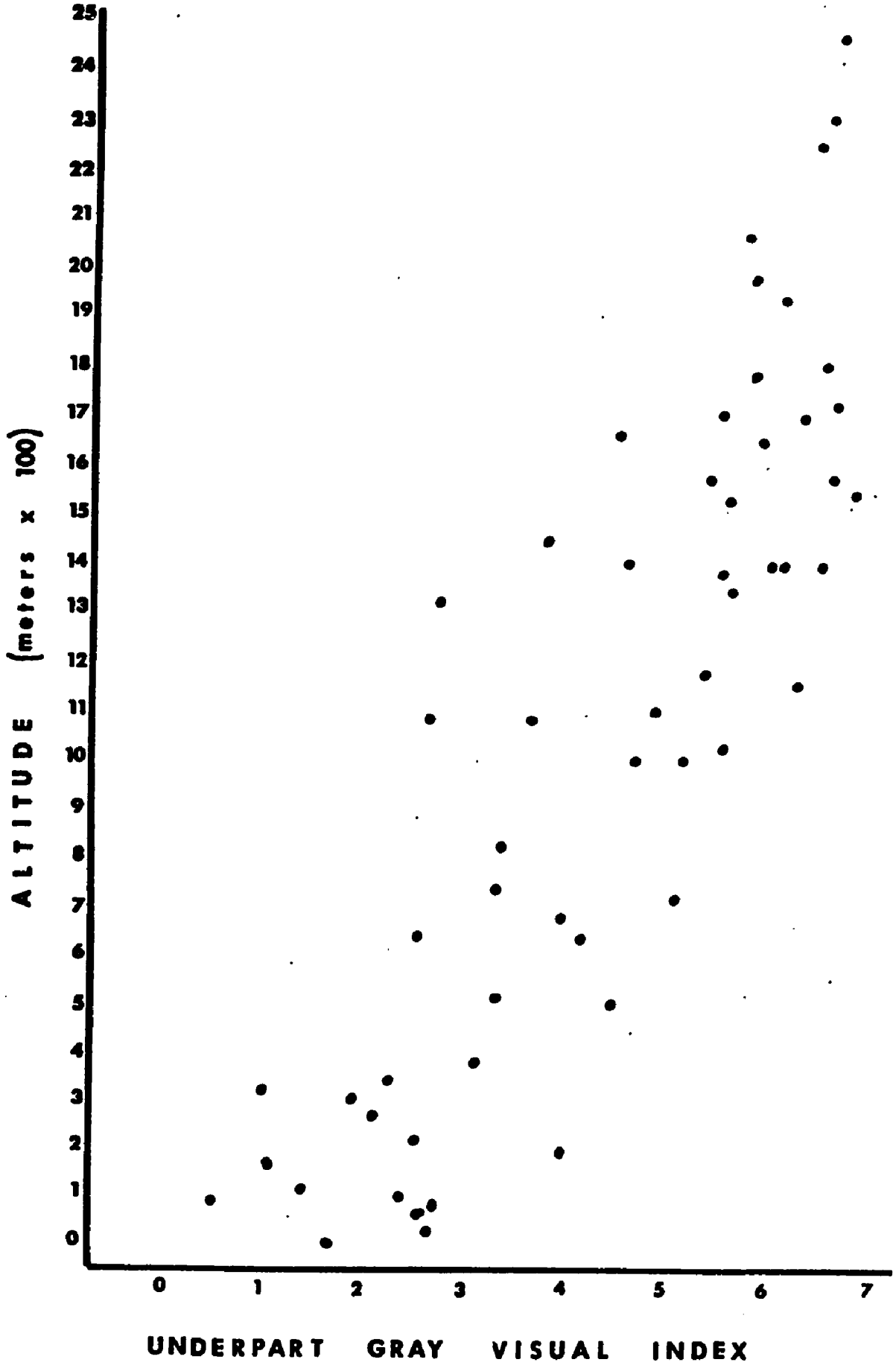

ALTITUDE (meters x 100)
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
0
1
2
3
4
5
6
7
UNDERPART GRAY VISUAL INDEX

FIGURE 23

Altitudinal Correlations of the Intensity of Underpart Gray Coloration

I. "Pure" *borbonica* (Head Character Index 0)

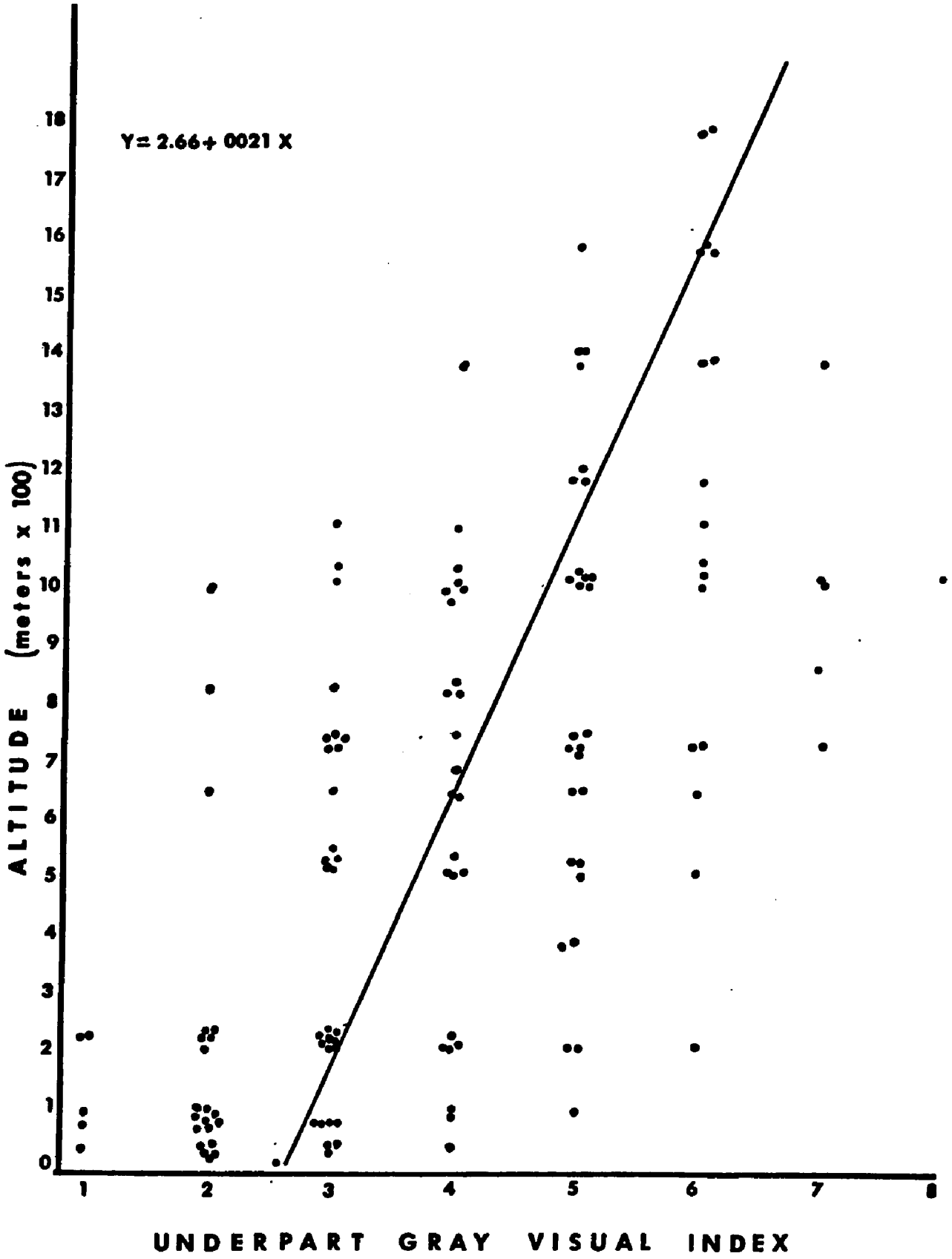

Y= 2.66+ 0021 X
ALTITUDE (meters x 100)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
1
2
3
4
5
6
7
8
UNDERPART GRAY VISUAL INDEX

FIGURE 23

Altitudinal Correlations of Intensity of Underpart Gray Coloration

II. "Brown-Naped" *borbonica* (Head Character Indices 1 - 9)

(Specimens from Localities 98 and 62 are encircled and have not been included in the regression analysis)

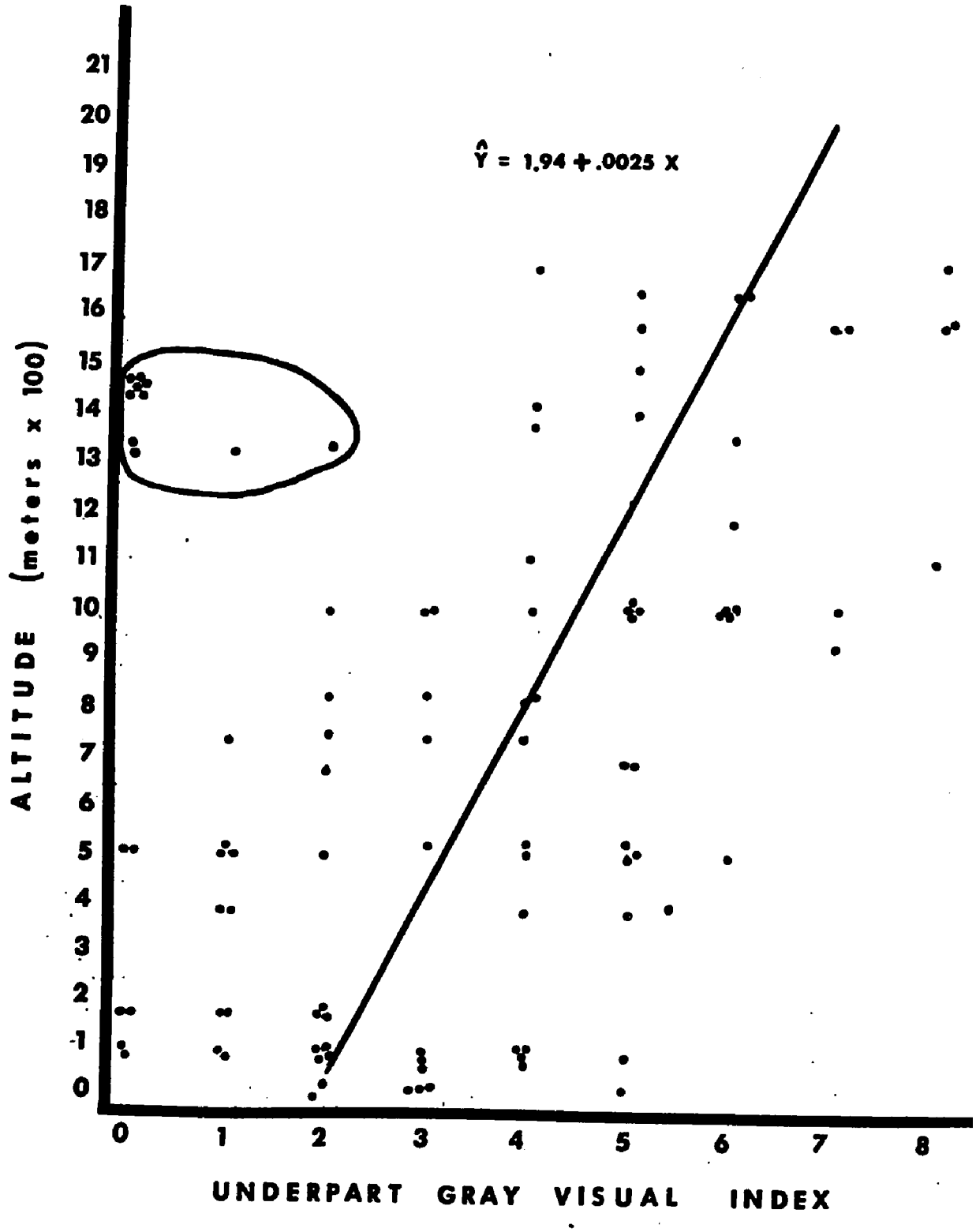

$\hat{Y}$ = 1.94 + .0025 X
ALTITUDE (meters x 100)
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
0
1
2
3
4
5
6
7
8
UNDERPART GRAY VISUAL INDEX

FIGURE 23

Altitudinal Correlations of Intensity
of Underpart Gray Coloration

III. Xerophila (Head Character Indices 11 - 16)

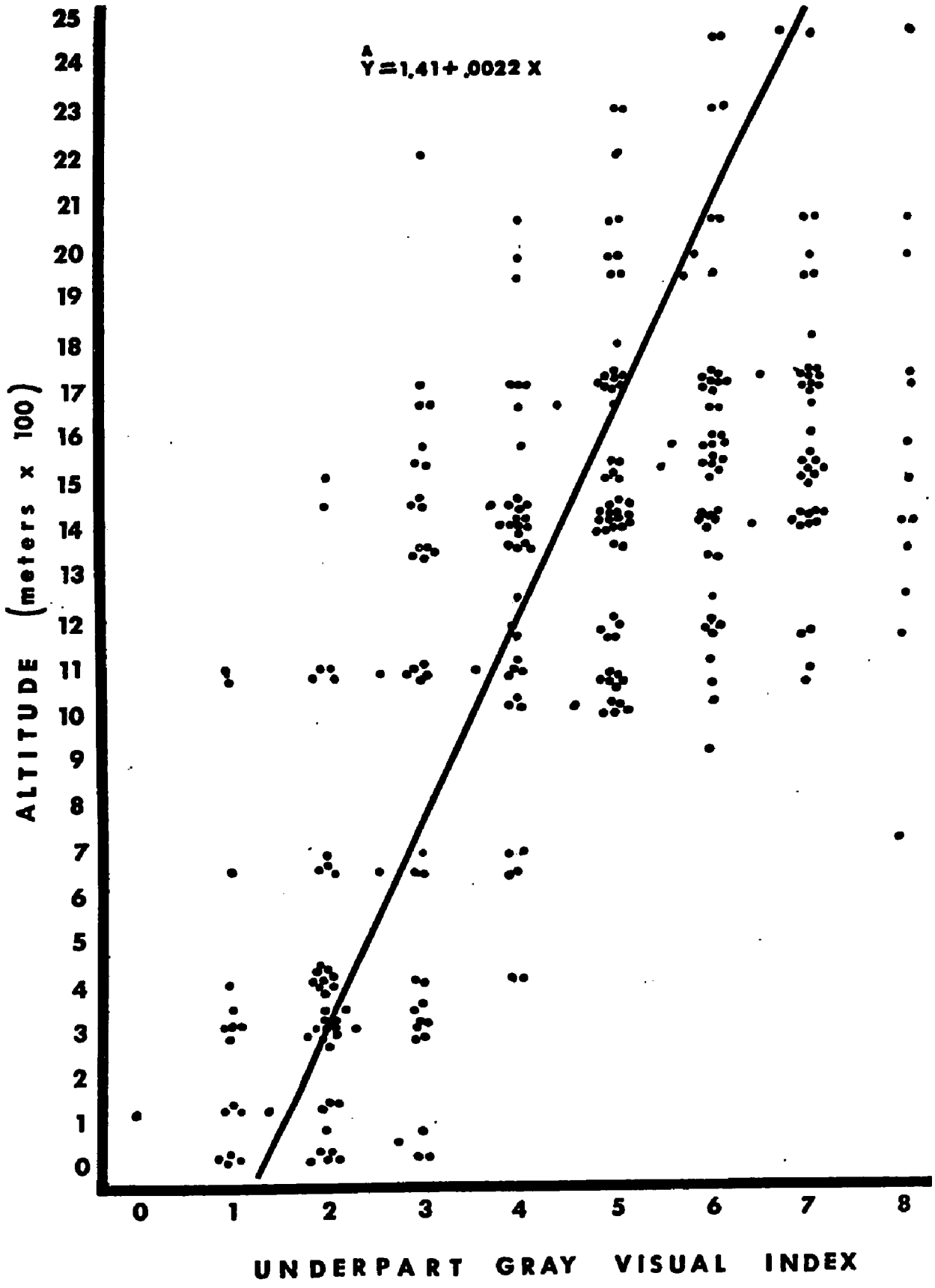
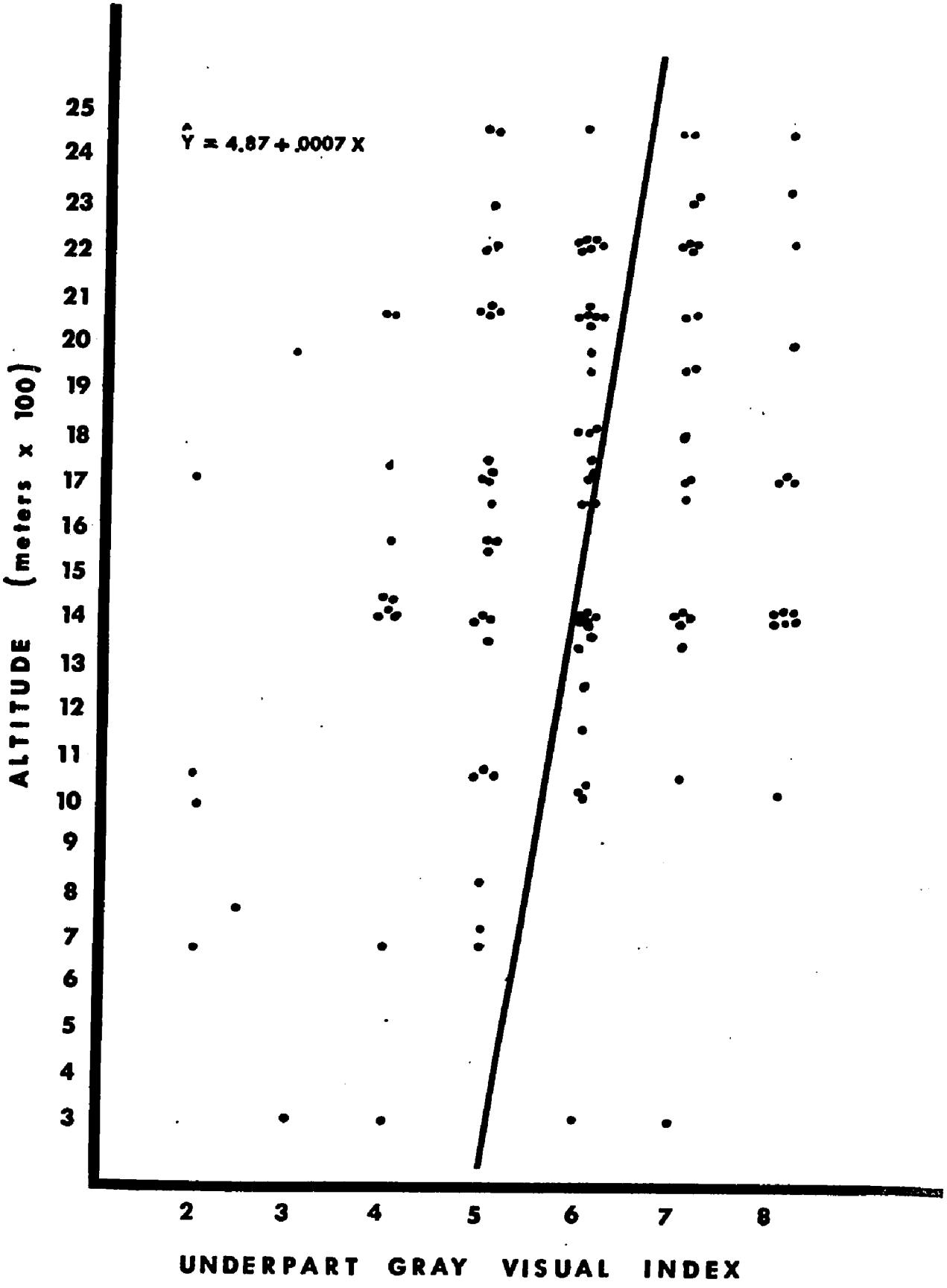

$\hat{Y} = 1.41 + .0022\,X$
ALTITUDE (meters x 100)
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
0
1
2
3
4
5
6
7
8
UNDERPART GRAY VISUAL INDEX

FIGURE 23

Altitudinal Correlations of Intensity of Underpart Gray Coloration

IV. Gray Morphs


$\hat{Y} = 4.87 + .0007\,X$
ALTITUDE (meters x 100)
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
3
4
5
6
7
8
UNDERPART GRAY VISUAL INDEX

Environmental Correlates

There is a conspicuous correlation of the intensity of gray in the underparts and altitude (Figure 22), coastal populations of Zosterops borbonica being whitish below while those in the highlands tend to be dark gray. A maximum average intensity is reached at about 1400 meters elevation. Some of the lateral spread in this relationship is the result of average differences between color forms; for example, white-eyes (xerophila) at west side localities average somewhat lighter below than those at other localities.

The altitudinal correlation is significant in each of the major color forms (Figure 23). "Pure" borbonica and "brown-naped" borbonica show the same degree of correlation (correlation coefficients = 0.621 and 0.603 respectively), while the coefficient for xerophila is slightly, but not significantly higher (0.705). The white-bellied borbonica at Localities 98 and 62 stand apart from all other "brown-naped" borbonica (Figure 23 II) and consequently have been omitted from the correlation and regression analyses of these data. The correlation in gray morphs is weak (0.260) and significant at the .01 level only.

The linear regressions of underpart gray on altitude are significant in each of the color forms, but only weakly so in gray morphs (Table 11). The three brown-morph types have nearly identical regression coefficients

(slopes) but different intercepts. "Brown-naped" borbonica are lighter than "pure" borbonica while xerophila are lightest of all. The coefficients of determination in "pure" borbonica and "brown-naped" borbonica are similar, but lower than in xerophila, in which the regression accounts for nearly one-half of the variance. In gray morphs the regression has an intercept very close to that of xerophila, but with a different concentration of points.

The addition of rainfall as an independent variable increases the coefficient of determination by several per cent in all of the forms, and the regression coefficient of this variable is significant in all of the cases. When regressed by themselves against underpart gray intensity, January and August rainfalls account for less of the variance than the above combination and do not constitute a significant regression in gray morphs. Thus rainfall is of some significance, but it is always of secondary importance relative to altitude. In "pure" borbonica and in xerophila altitude is at least twice as important as rainfall, and in brown-naped borbonica it is four times as important. The two variables are of about the same importance in gray morphs.

Relative humidity data are not available for the majority of the meteorological stations on Réunion, and hence a detailed analysis of its relation to the color variation in Zosterops borbonica is not possible at this time.

TABLE 11. Regression Analyses of Relation of Environmental Factors to Variation in Underpart Gray Coloration in *Zosterops borbonica*

a) REGRESSION EQUATIONS	Coefficient of Determination	F Value	Degrees Freedom
A. "pure" *borbonica*			
1) 2.66 + .0021*** Alt.	0.386	70.43***	114
2) 2.04 + .0019*** Alt. + .0014** Jan Rain	0.428	41.63***	111
3) 2.29 + .005** Jan Rain - .005** Aug Rain	0.19	13.36**	111
B. "brown-naped" *borbonica*			
1) 1.94 + .0025*** Alt.	0.364	52.64***	92
2) 1.15 + .0024*** Alt. + .0016* Jan Rain	0.384	28.35***	91
3) 1.77 + .0087*** Jan Rain - .015*** Aug Rain	0.280	17.73***	91
C. *xerophila*			
1) 1.41 + .0022*** Alt.	0.497	258.0***	261
2) 1.38 + .0018*** Alt. + .0021*** Jan Rain	0.534	154.9***	270
3) 1.95 + .0056*** Jan Rain - .0016 Aug Rain	0.315	62.11***	270

TABLE 11 cont.

a) REGRESSION EQUATIONS	Coefficient of Determination	F Value	Degrees Freedom
D. gray morphs			
1) 4.87 + .0007*** Alt.	0.067	6.94*	96
2) 4.53 + .0007** Alt. + .0006 Jan Rain	0.075	3.88*	95
3) 6.05 - .0012 Jan Rain + .0051* Aug Rain	0.048	2.38	95

b) STANDARD PARTIAL REGRESSION COEFFICIENTS

	"pure" borbonica	"brown-naped" borbonica	xerophila	gray morphs
Altitude	0.556	0.591	0.580	0.251
Rainfall	0.238	0.141	0.232	0.089
Ratio	2.33	4.19	2.50	2.85

* P = .05
** P = .01
*** P = .001

Like other aspects of the variation in Zosterops borbonica the basis of the variation in underpart gray coloration appears to be genetic. I have been keeping together in captivity under identical environmental conditions eleven Zosterops borbonica including three white-bellied lowland forms (Index 3) and eight highland birds (Indices 6-8). Despite the fact these birds have molted their body plumage twice while in the same cage, the differences have been maintained, i.e. their underpart colorations have not increased in uniformity as one would expect of epigenetic determination. Consequently in the remaining discussion I have assumed an underlying genetic basis of all aspects of the color variation in Zosterops borbonica.

Phaeomelanins

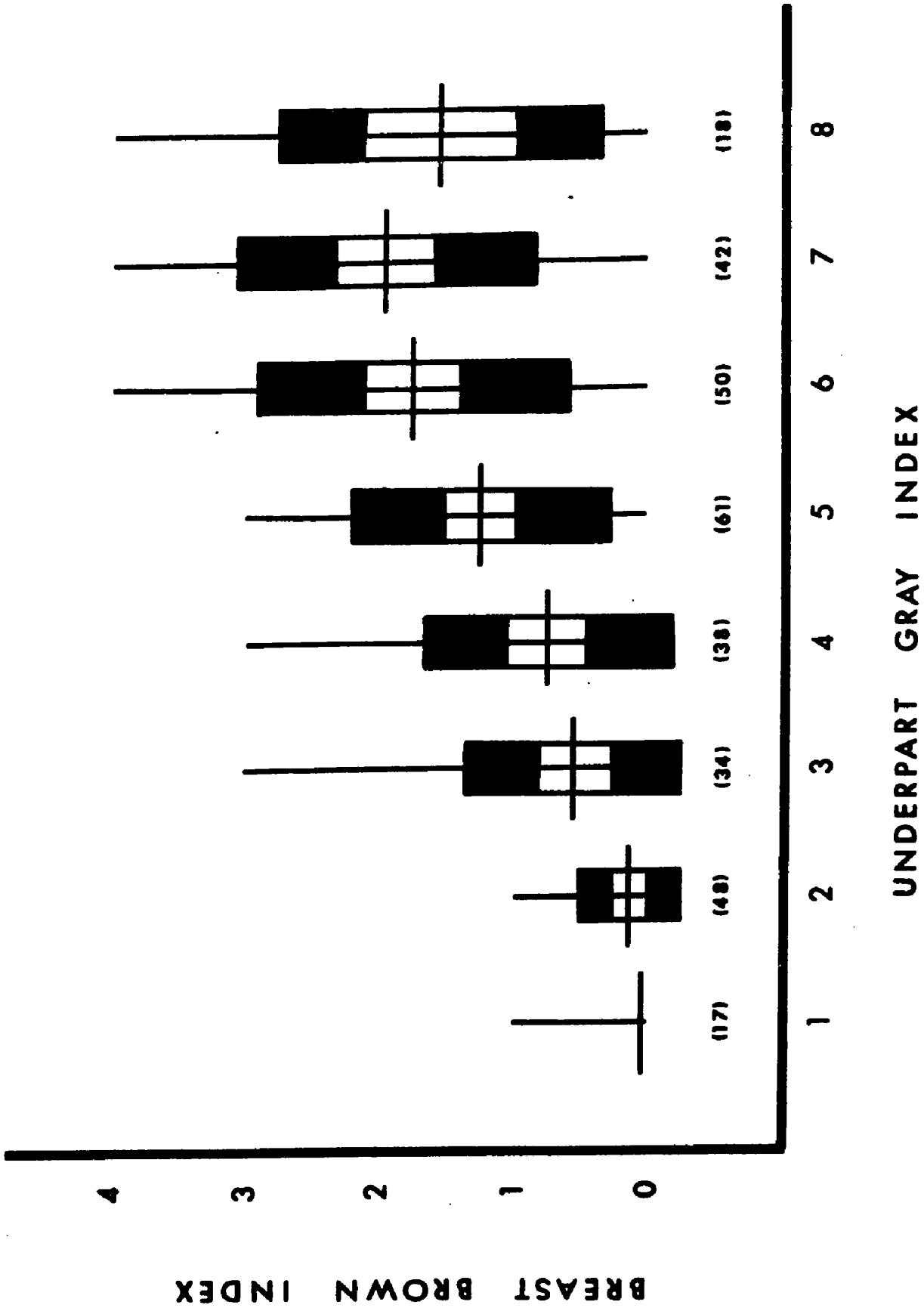
Phaeomelanins are present in the breast coloration of some xerophila but are not to be found in any borbonica, or, indeed, a brown morph specimen with a Head Character Index of less than 11. Its occasional presence in some gray morph intermediates has already been discussed (page 55).

The amount of phaeomelanin deposition in the breast plumage was evaluated in terms of five categories of increasing intensity and distribution (Table 1). Correlations between these categories and the Head Character Indices in brown morphs can be seen in Table 12. Faint brown pigmentation can be discerned in some specimens with Head Character Indices

FIGURE 24

Relation of Breast Brown Index to Underpart Gray Index in Brown Morph Specimens with Head Character Indices of 11 or More

Vertical Line:	range
Horizontal Line:	sample mean
Black Rectangle:	1 standard deviation of mean
White Rectangle:	2 standard errors of mean


BREAST BROWN INDEX
0
1
2
3
4
UNDERPART GRAY INDEX
1
2
3
4
5
6
7
8
(17)
(48)
(34)
(38)
(61)
(50)
(42)
(18)

of 11 to 14, but intense phaeomelanin deposition on the breast occurs only in brown morph specimens with indices of 15 and 16 or, in other words, those with completely brown heads. Strong and extensive breast rufous was present in only a few pure brown-headed specimens.

An increase in the average amount of brown with increased gray is apparent in all brown morph specimens with HCI's of 11 or more (Figure 24). The decrease from Category 7 to Category 8 is not statistically significant. Independence of the genetic control of phaeomelanin and eumelanin deposition in the underparts is indicated by a partial albino specimen (FBG 698) which has a strong band of rufous across the breast but pure white underparts otherwise.

There is a large continuous region on Réunion (Figure 25) in which the mean locality indices are less than 1.0, indicating a predominance of birds with no brown on their breasts but usually a few individuals with some traces of phaeomelanin deposition. This region includes the western side of the island below 1400 meters and a long narrow band that presumably extends up the Rivière des Galets across the cirques of Mafatte and Salazie to the Plateau de Belouve (Trou de Fer), Takamaka and eventually the Rivière de l'Est, Pas de Bellecombe and the Rivière des Remparts. The section of this band from the Cirque de Salazie to Takamaka and Rivière de l'Est coincides with the

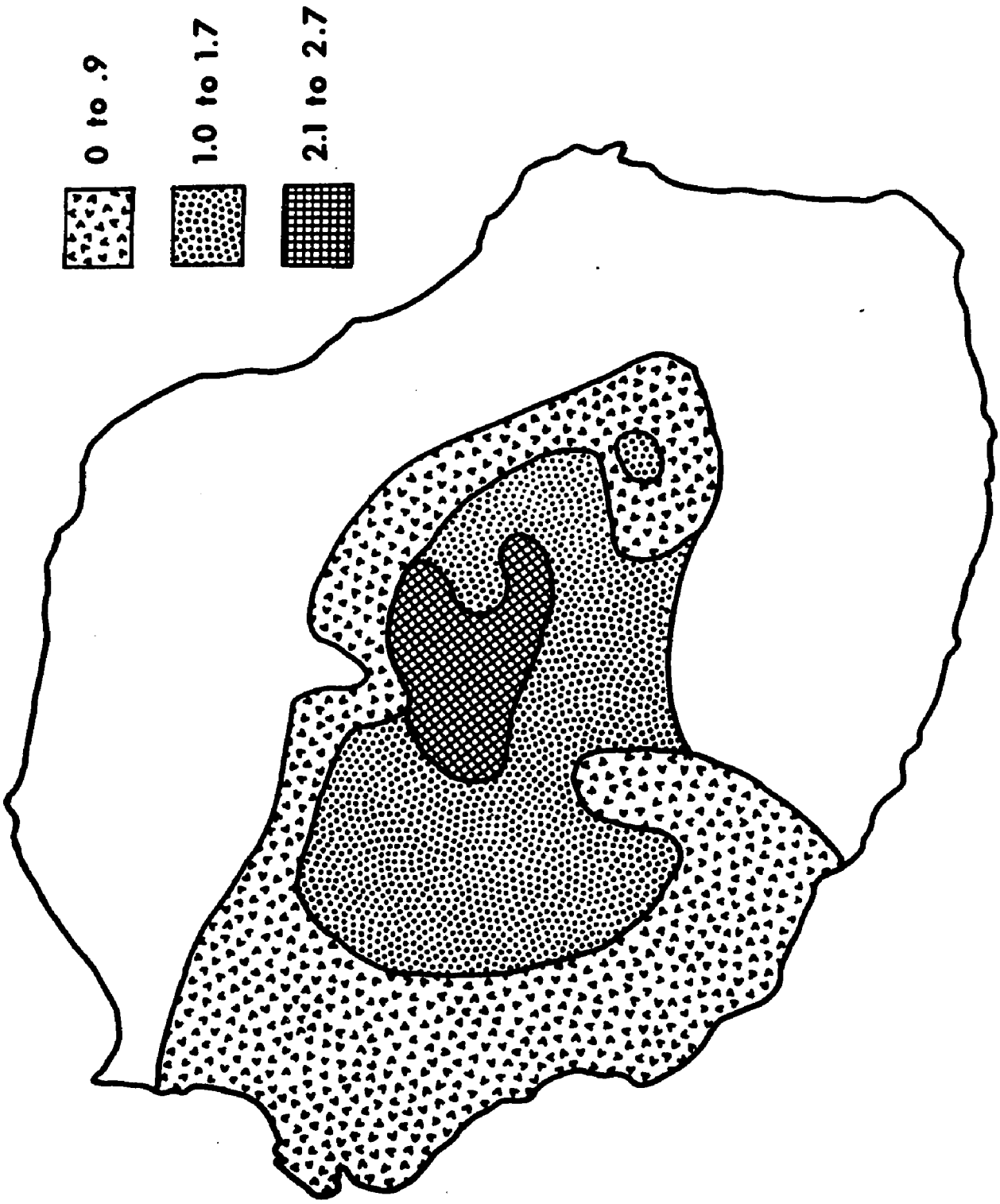
TABLE 12. Relation of Breast Brown to Head Character Index

HEAD CHARACTER INDEX	BREAST BROWN INDEX				
	0	1	2	3	4
11	13[a]	1	0	0	0
12	13	0	0	0	0
13	18	2	0	0	0
14	27	4	0	0	0
15	27	18	8	4	0
16	42	53	50	31	7

[a]Number of specimens

FIGURE 25

Distribution of Intensity of Breast Brown in *xerophila* in Terms of Average Locality Indices


0 to .9
1.0 to 1.7
2.1 to 2.7

zone of contact described earlier on the basis of Head Character Indices. Pas de Bellecombe, the Rivière des Remparts and Nez de Boeuf, however, are localities at which xerophila is the predominant brown morph, as is the case over most of the western side of the island.

The mean index of breast brown increases as one proceeds inland from this circumscribing belt of gray-breasted xerophila. At high elevations (above 1400 meters) on the western slopes including the Brûlé de St. Paul and Brûlé de St. Leu, the major portions of the Cirques of Mafate and Cilaos, and the higher western slopes of the Cirque de Salazie, as well as the Forêt du Bébour, Plaine des Marsouins, Plateau de Duverney, and an isolated pocket at the head of the ravine of the Rivière des Remparts, one finds a greater percentage of xerophila with brown breasts. In this region mean locality indices range from 1.0 to 1.75.

Finally in a rather restricted region in the very center of the island including the upper slopes of the Forêt du Bébour, Plaine des Salazes, Coteau Maigre, Coteau Kerveguen, and Cilaos forests virtually all xerophila have some brown on their breasts, and often this melanin deposition is intense and extensive. This area is not higher than other parts of the island which are characterized by lower indices, but it is distinguished by being the wettest highland area on the island.

That altitude is not the overriding correlate of

increased phaeomelanin deposition in xerophila's breast plumage, as it seems to be for eumelanin deposition in the underparts of this form, is clear from the occurrence of maximum variability and intensities between 1400 and 1700 meters elevation rather than at the highest elevations sampled (Table 13). Additional factors, presumably related either directly or indirectly to the high rainfall in the center of the island are involved.

TABLE 13. Mean Breast Brown Indices at Xerophila Localities (Based on Specimens with Head Character Indices of 11 or more)

Locality	Altitude	Mean Index	Loc.	Alt.	Index
44	0	0.0	29	1350	1.1
51	40	0.2	72	1400	0.0
68	120	0.2	58	1400	2.1
53	270	0.0	24	1400	0.9
55	300	0.3	40	1400	2.3
94	300	0.0	62	1440	1.0
54	340	0.2	18	1530	1.5
95	640	0.1	23	1570	2.3
16	680	0.8	70	1660	1.4
26	1010	0.5	8	1700	1.7
49	1060	0.6	63	1700	1.4
61	1080	0.3	30	1720	2.3
97	1080	0.3	71	1800	1.0
17	1100	0.2	64	1980	0.6
27	1180	1.2	41	2060	0.9
35	1250	1.7	73	2200	1.5
98	1330	0.5	39	2300	0.7
22	1350	0.8	60	2460	2.7

SUMMARY OF THE COLOR VARIATION

Color variation in Zosterops borbonica on Réunion Island includes several distinct aspects. There is, first of all, a color polymorphism with respect to the presence or absence of intense phaeomelanin deposition in the feathers of the back and flanks. Intermediates of several recognizable types exist but are greatly outnumbered by the extreme color forms. The morphs are extensively sympatric in proportions which vary clinally with altitude from pure brown morph populations in the lowlands to predominately gray morph populations in the highlands. There is some indication of a preference for heath or open scrub by gray morphs, but otherwise no differences are apparent in ecology of the two morphs where they are sympatric. Gray morphs closely match in color the grays of heath and Sophora trees whereas brown morphs contrast with these same backgrounds.

Several types of brown morphs can be distinguished, including a brown-headed form (xerophila) and a gray-headed form (borbonica). These predominate in different parts of the island, xerophila occupying the dry western lowlands and all altitudes above 1400 meters elevation, while borbonica occupies a restricted region in the wet lowlands

on the northern and eastern sides of the island. While most of the specimens collected are assignable to one or the other of the two extremes, there is a wide range of intermediates which includes a distinctive brown-naped form that exhibits some independence in its distribution, i.e. inasmuch as it is the predominant form along the southern coast and occurs in an isolated pocket in the range of xerophila as well as in minor proportions throughout the range of borbonica.

Contact between these different brown morphs is abrupt with a sharp break in the character indices and little evidence of geographic intergradation. In the lowlands the breaks coincide with two major river beds, those of the Rivière des Galets and the Rivière St. Étienne, and a recent lava flow near Bois Blanc. A variety of color forms coexist at localities in the interior of the island in the zone of contact between borbonica and xerophila, which averages about five kilometers in width.

The intensity of eumelanin deposition in the feathers of the underparts varies in relation to altitude in all color forms, becoming dark gray below at altitudes over 1400 meters in contrast to white-bellied lowland populations. The correlations are strong in the various brown morphs but relatively weak in gray morphs, which are found primarily over 1300 meters elevation. Temperature seems to be particularly important in relation to

this variation. The intensity of phaeomelanin deposition also varies in the underparts of xerophila; upland populations, particularly those in the wet central forests, have a strong band of rufous across the breast.

RELATION OF ZOSTEROPS BORBONICA MAURITIANA TO THE RÉUNION COLOR FORMS

Zosterops borbonica mauritiana of Mauritius Island is a gray-backed monomorphic form of Zosterops borbonica. We have no evidence of geographic color variation in this form (Storer and Gill, 1966). In plumage color it is basically a gray morph, lacking phaeomelanins except for a slight and variable brown wash on the flanks and occasional traces of brown on the back. However, the white underparts of mauritiana distinguish it from nearly all gray-morph individuals on Réunion as only a few extreme pale-bellied gray birds from Réunion approach mauritiana in appearance. Zosterops borbonica mauritiana also differs in vocalizations from Réunion borbonica, all populations of which have similar repertoires.

SIZE VARIATION

Superimposed upon the color variation in Réunion Zosterops borbonica are demonstrable differences in size and proportions in relation to altitude as well as between color forms. First, in order to test the interdependence of mensural characters, I have computed linear product-moment correlation coefficients for all pairs of measurements separately for each of the three main color forms. Those coefficients significantly different from 0 are listed in Table 14 and because in some cases a significant correlation between two characters may be due to a common correlation with a third character, the partial correlation coefficients have also been tested for significance.

In borbonica significant correlations exist between wing length and tail length, between bill length and weight, and between tarsus length and weight. Wing length and weight are not significantly correlated in this color form.

In xerophila significant positive correlations exist between wing length and tail length and between the lengths of all appendages and weight. The correlations between wing length and bill length, between tail length and tarsus length, and between tail length and bill lengths are not significant when partialled on weight. However,

TABLE 14. Linear Product-Moment Correlations of Mensural Characters in Zosterops borbonica

Character Pair	"pure" borbonica (102)	xerophila (230)	gray morphs (78)
Wing/Tail	.687***	.787***	.694***
Wing/Tarsus	.202*(a)	.472***(b)	.305**(b)
Wing/Bill		.288**(a)	
Wing/Weight		.516***	
Tail/Tarsus		.371***(a)	.313**(a)
Tail/Bill		.222*(a)	
Tail/Weight		.589***(c)	
Bill/Tarsus		.410***(b)	
Bill/Weight	.352***	.422***	.521***
Tarsus/Weight	.310***	.477***	.322**

(a) Correlation not significant when partialled on weight

(b) Correlation significant when partialled on weight

(c) Correlation significant when partialled on wing length

* P = .05
** P = .01
*** P = .001

TABLE 15. Altitudinal Correlations of Size[1]

(sample sizes included in parentheses)

Character	"pure" borbonica	"brown-naped" borbonica	xerophila	gray morphs
Wing	.106	.350***	.547***	.132
	(102)	(86)	(231)	(78)
Tail	-.013	.325***	.562***	.229*
	(102)	(86)	(230)	(78)
Bill	curvilinear		.305***	-.256*
			(253)	(92)
Tarsus	.377***	.245*	.501***	curvilinear
	(106)	(91)	(253)	
Weight	-.043		.363***	-.267*
	(97)		(87)	(44)

[1]Figures are linear product-moment correlation coefficients

* p = .05

** p = .01

*** p = .001

TABLE 16. Regression Analyses of Altitudinal Size Variation

	Intercept	Altitudinal Regression Coefficient	Other Regression Coefficients	Coefficient of Determination	F Value	Degrees of Freedom
A. "pure" *borbonica*						
a) Wing	54.6	+.00031		.011	1.14	1/100
b) Tail	8.75	-.00021	.58 (wing)	.412	34.70***	2/99
c) Tarsus	18.08	+.00049		.142	17.28***	1/104
B. "brown-naped" *borbonica*						
a) Wing	54.5	+.0011***		.123	11.74***	1/84
b) Tail	4.97	+.00026	.64 (wing)	.506	42.55***	2/83
c) Tarsus	18.34	+.00031		.060	5.67	1/89
C. *xerophila*						
a) Wing	54.7	+.0016***		.300	98.04***	1/229
b) Tail	6.9	+.00047	.61 (wing)	.643	205.00***	2/227
c) Bill	8.3	+.00012	.28 (tarsus)	.186	28.61***	2/250
d) Tarsus	18.2	+.0006***		.251	84.37***	1/251
D. gray morphs						
a) Wing	56.3	+.00041		.017	1.36	1/76
b) Tail	6.86	+.00039	.61 (wing)	.501	37.62***	2/75
c) Bill	14.07	-.00024		.066	6.33	1/90

***p = .001

the correlations between bill and tarsus lengths and between wing and tarsus lengths are still significant when the correlated effects of weight have been removed.

In gray morphs wing length and tail length are strongly correlated as are tarsus and bill lengths, respectively, with weight. Tail and tarsus lengths are not significantly correlated when partialled on weight but, as in xerophila, wing and tarsus lengths are.

Within the ranges of variation present in the three color forms, wing length proves to be a valid indicator of body size (weight) only in xerophila, whereas in all three forms both bill and tarsus lengths are weakly, but significantly correlated with weight.

Altitudinal correlations of size are present in Zosterops borbonica, but they differ between the color forms. Wing length is significantly correlated with altitude in xerophila and in "brown-naped" borbonica but not in "pure" borbonica or in gray morphs (Table 15). An increase of 1.1 to 1.6 millimeters in wing length per 1000 meters of elevation takes place in the former two forms, lowland populations of which have wings averaging 54.5 millimeters in length. Tail length is significantly correlated with altitude in xerophila, gray morphs, and "brown-naped" borbonica but not in "pure" borbonica. When partialled on wing length, the relationship is not significant in "brown-naped" borbonica, but still is in

both xerophila and gray morphs. There is no significant change of the tail/wing ratio with altitude in any form.

Tarsus length is positively correlated with altitude in all forms, quite strongly in xerophila (correlation coefficient = 0.501), but the relationship in gray morphs includes some curvilinear elements (Figure 26). In xerophila tarsus length increases 0.59 millimeters per 1000 meters elevation. Bill length also increases with altitude in xerophila (correlation coefficient = 0.305), but decreases in length in gray morphs (correlation coefficient = -0.256). This relationship is still significant in xerophila after the correlated effects of tarsus length have been removed. The relationship is strongly curvilinear in both "pure" and "brown-naped" borbonica (Figure 28), in which maximum length is reached between 500 and 800 meters elevation. Like bill length, weight increases with altitude in xerophila but decreases in gray morphs. In borbonica there is no significant correlation.

The specimens from selected localities whose means are not significantly different and which are consistent with respect to both altitude and color type have been combined to provide samples large enough to permit comparison of the different color forms with respect to size (Figures 29 and 30). Localities 11, 12, and 14 have been combined into a single lowland borbonica sample and Localities 44 and 51 were combined into a lowland xerophila

FIGURE 26

Altitudinal Correlation of Tarsus Length in Gray Morphs

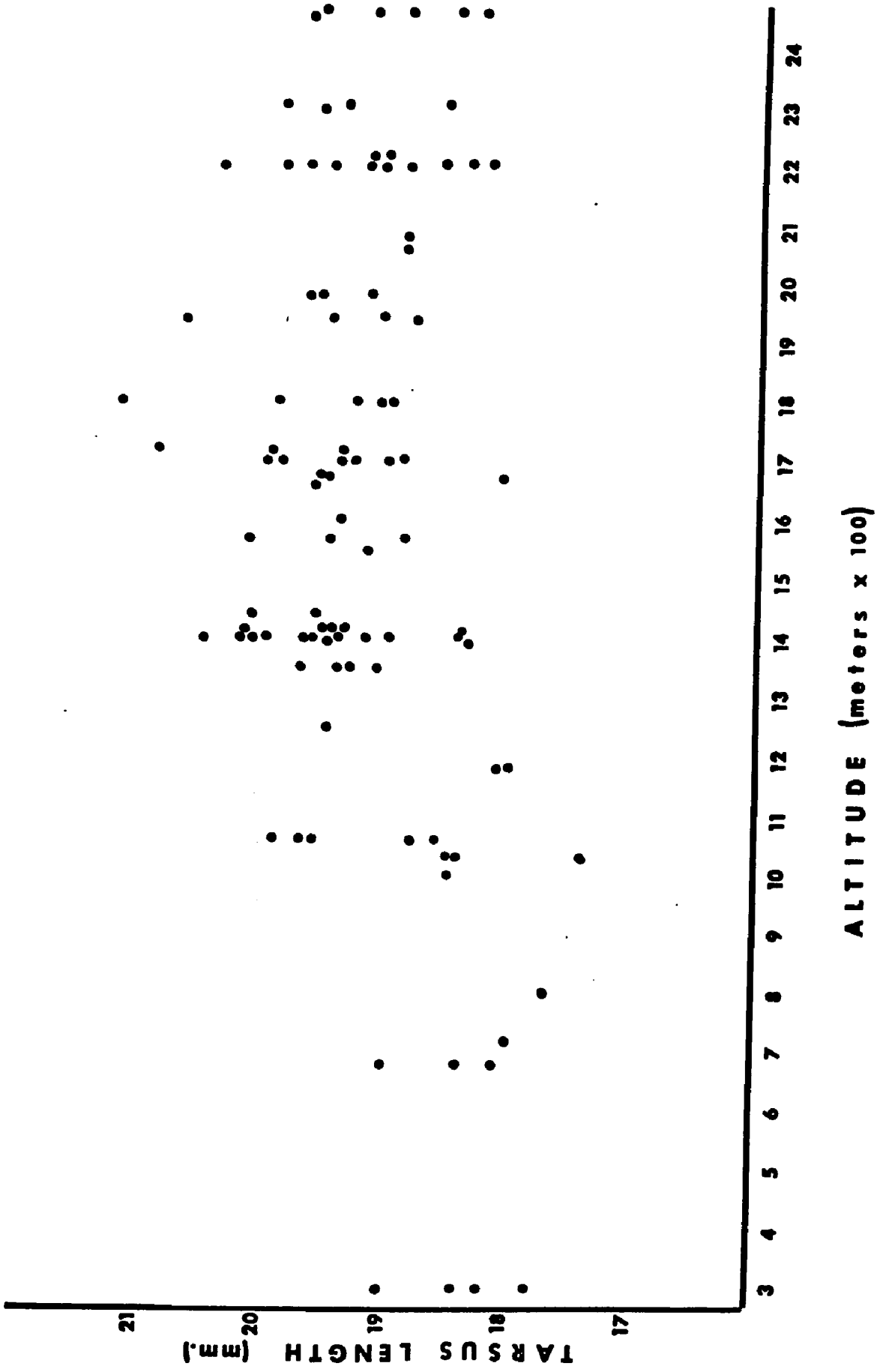

ALTITUDE (meters x 100)
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
TARSUS LENGTH (mm.)
17
18
19
20
21

FIGURE 27

Altitudinal Correlation of Bill Length in Gray Morphs

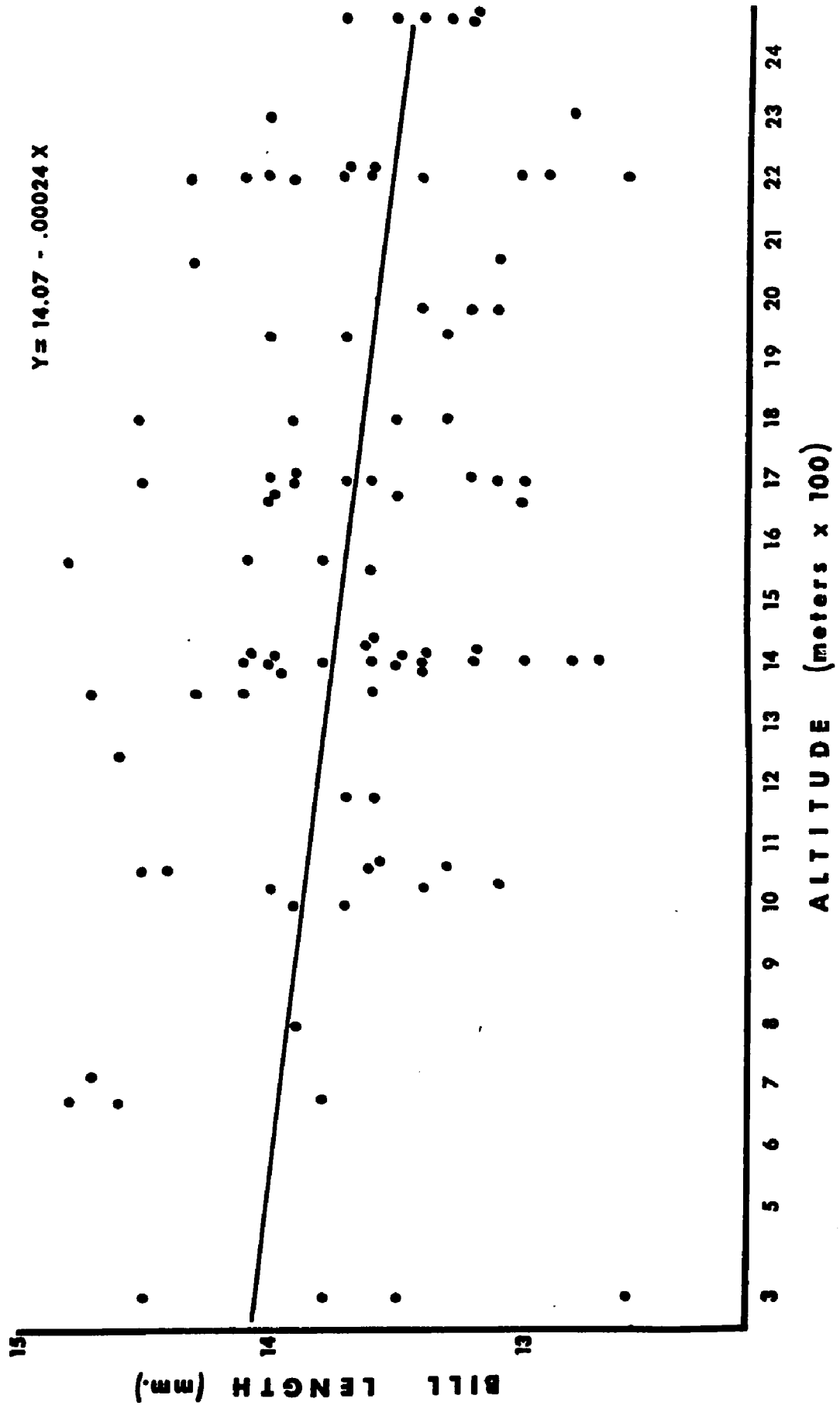

Y= 14.07 - .00024 X
BILL LENGTH (mm.)
15
14
13
ALTITUDE (meters x 100)
3
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24

FIGURE 28

Altitudinal Correlation of Bill Length in borbonica

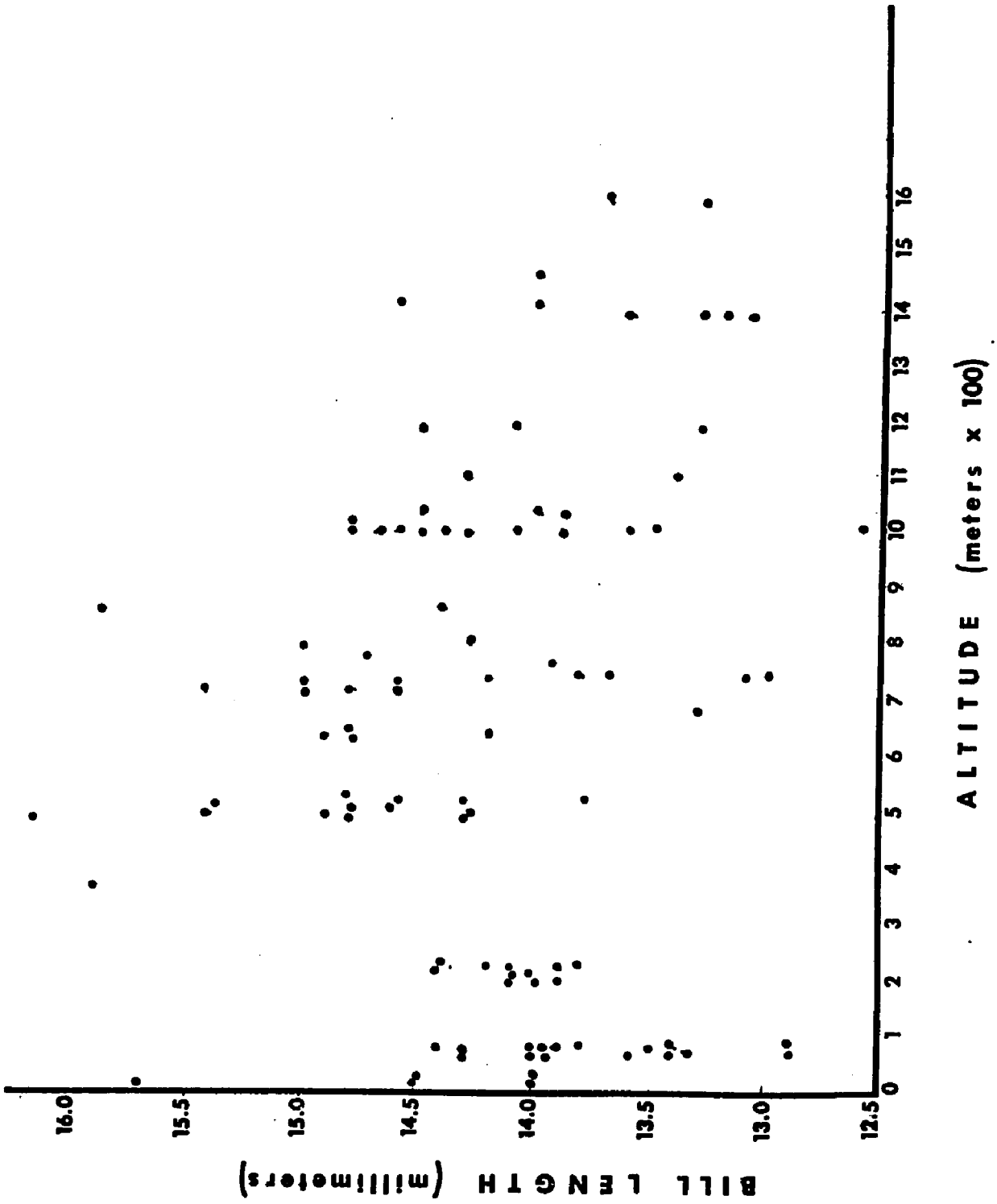

BILL LENGTH (millimeters)
16.0
15.5
15.0
14.5
14.0
13.5
13.0
12.5
ALTITUDE (meters x 100)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

FIGURE 29

Comparison of Wing Lengths of Representative Populations of *Zosterops borbonica* on Réunion

A. Localities 11, 12 and 14 combined:
1) 15 males, 2) 9 females

B. Localities 44 and 51 combined:
1) 13 males, 2) 10 females

C. Locality 58: 1) 14 brown morph males, 2) 11 brown morph females, 3) 12 gray morph males and females

D. Localities 63 and 30 combined (browns only):
1) 13 males, 2) 12 females

E. Localities 41 and 73 combined (grays only):
1) 11 males, 2) 9 females

(Horizontal Line: range; Vertical Line: Sample mean; Black Rectangles: one standard deviation from the mean; Open Rectangles: two standard errors of the mean)

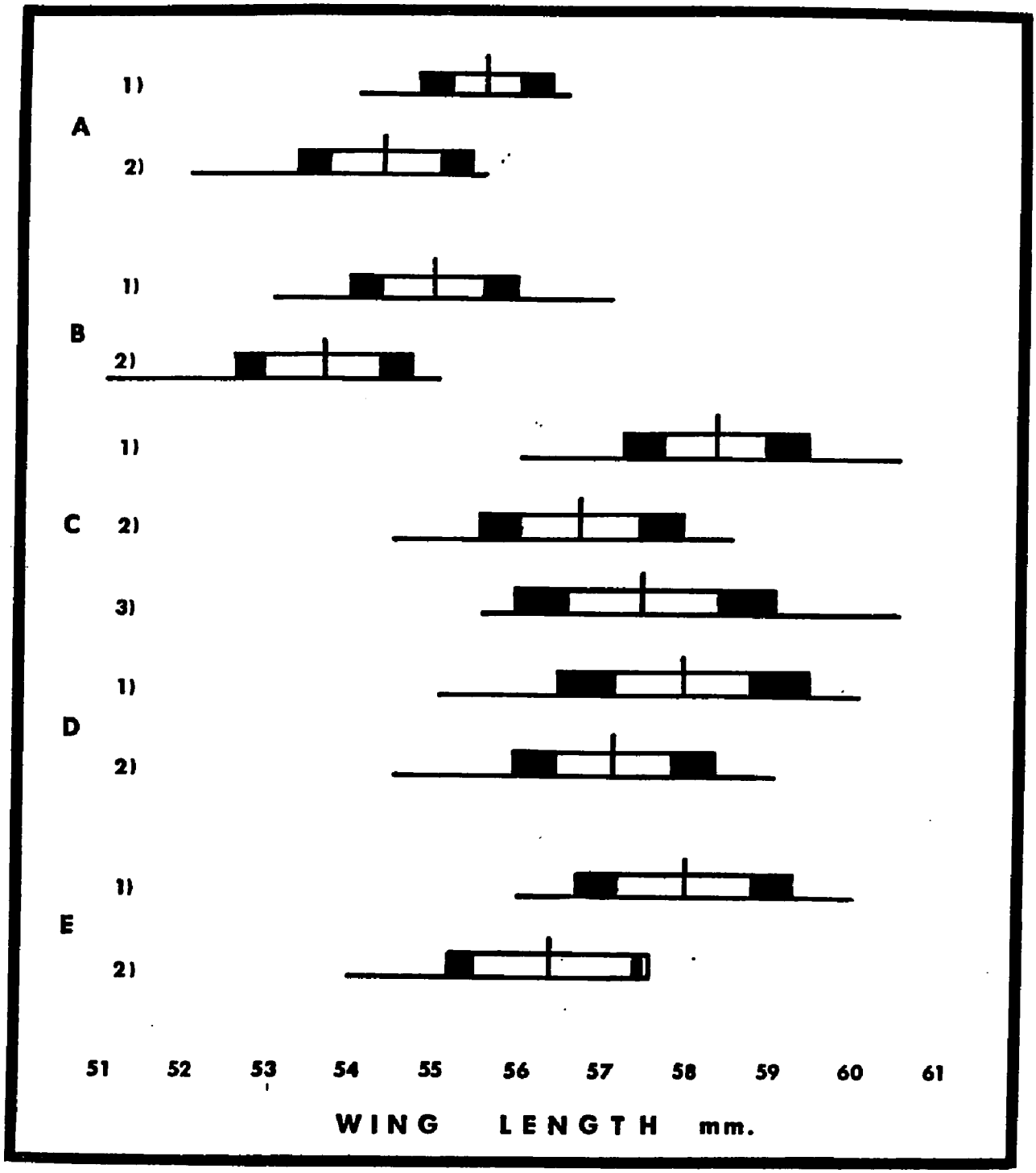

A
1)
2)
B
1)
2)
C
1)
2)
3)
D
1)
2)
E
1)
2)
51
52
53
54
55
56
57
58
59
60
61
WING LENGTH mm.

FIGURE 30

Upper: Bill Lengths of Representative Populations of Zosterops borbonica on Réunion

A. Localities 11, 12, 14, and 81 combined: 1) 16 males, 2) 11 females

B. Localities 44 and 51 combined: 28 males and females

C. Locality 58: 1) 26 brown morphs, 2) 13 gray morphs

D. Localities 63 and 30 (brown morphs only): 23 males and females

E. Localities 41 and 73 (gray morphs only): 1) 17 males, 2) 10 females

Lower: Tarsus Lengths of Representative Populations of Zosterops borbonica on Réunion

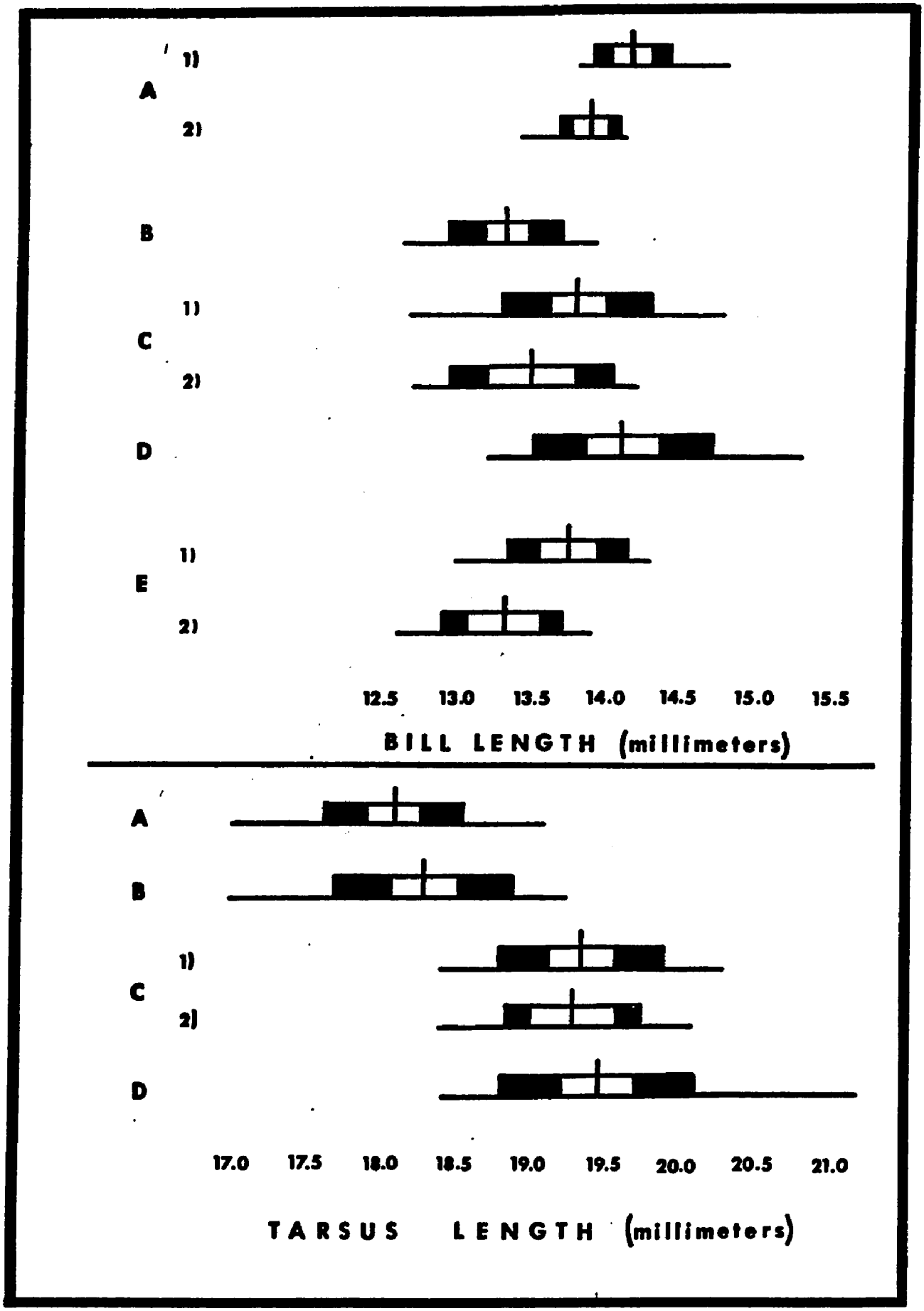
A. Localities 11, 12 and 14 combined: 27 males and females

B. Localities 44 and 51 combined: 28 males and females

C. Locality 58: 1) 23 brown morphs, 2) 12 gray morphs

D. Localities 41 and 73 (26 gray morphs only)

(Horizontal Line: range; Vertical Line: sample mean; Black Rectangles: one standard deviation of the mean; Open Rectangles: two standard errors of the mean)


A
1)
2)
B
C
1)
2)
D
E
1)
2)
12.5
13.0
13.5
14.0
14.5
15.0
15.5
BILL LENGTH (millimeters)
A
B
C
1)
2)
D
17.0
17.5
18.0
18.5
19.0
19.5
20.0
20.5
21.0
TARSUS LENGTH (millimeters)

sample. A satisfactory highland sample of borbonica is not available. Brown morphs have been analyzed separately from gray morphs in the Cilaos population, an upland xerophila locality and for Localities 63 and 30, which in combination provide a single sample from the upper limits of xerophila abundance.

In most populations of Zosterops borbonica the sexes differ in both wing length and tail length, males averaging 1 to 1.5 millimeters larger than females. There were no sexual differences in tarsus length in any of the populations examined. Sexual differences in bill length characterize only lowland borbonica, in which males average .5 millimeters longer than females, and highland gray morphs, in which males average .9 millimeters longer than females. Yet, at Cilaos, where they are outnumbered by xerophila, male and female gray morphs are not different in bill or wing length. There were no sexual differences in bill length in any of the xerophila populations tested.

Lowland borbonica have significantly longer bills than lowland xerophila (Figure 30). The altitudinal correlations of wing length, bill length, and tarsus length in xerophila result in highland populations of this form averaging significantly larger than lowland populations. Extreme highland xerophila have bills the same length as lowland borbonica. Gray morphs have wings and tarsi

equivalent in length to the brown morphs at Cilaos, with which they are sympatric, but significantly shorter bills, the differences corresponding in magnitude to the sexual dimorphism found in highland gray morph populations and lowland borbonica. All gray morph populations are shorter-billed than lowland borbonica. There is no significant intra-insular variation in the tail/wing ratio, which averages very close to 0.74 in all populations of all color forms.

VARIATION IN CONTINENTAL WHITE-EYES

Marked infraspecific variation characterizes white-eyes on the African continent, and the differences in the intensity of carotenoid and particularly melanin deposition which are a primary source of the color variation are often correlated with climatic trends (Moreau, 1957). In accordance with Gloger's Rule, melanin deposition is increased in regions with high rainfall even in the absence of parallel changes in altitude or latitude. For example, Zosterops senegalensis is typically bright yellow across most of northern Africa except in the wet western corner, including Sierra Leone, Liberia, and the Ivory Coast, where the local birds (demeryi) have increased melanins but not carotenoids. Similarly, Zosterops abyssinica flavilateralis shifts from a light yellow form in Kenya and Abyssinia to a very green one in the moist lowlands of Tanganyika, and the most richly pigmented Zosterops senegalensis in southern tropical Africa are those in the very wet mountains at the north end of Lake Nyasa.

Most montane white-eye populations in Africa are more melanic than the surrounding lowland populations. In some regions such as the Abyssinian highlands and Kenyan mountains, a replacement of one species of Zosterops by

another at high elevations (in the evergreen vegetation) appears to be involved, but elsewhere distinct transitions from bright yellow lowland populations to dark green highland ones can be seen, e.g. on the western slopes of the Abyssinian highlands, in the mountains at the head of the Gulf of Guinea (Zosterops senegalensis stenocricota), in the Imatong mountains on the Sudan border, in the high country northwest of Lake Victoria (Zosterops senegalensis stuhlmanni), and in the mountains northwest of Lake Tanganyika (Zosterops senegalensis reichenowi). In Nyasaland there is a complete gradation of very yellow to very green Zosterops senegalensis, the latter occurring primarily at high altitudes in evergreen forest as opposed to the lower, drier country, but a direct transition from one form to the other with increasing altitude on any particular mountainside has not yet been demonstrated. In most of these cases rainfall is positively correlated to some degree with altitude, but unfortunately the relative effects of the two variables have not been separated.

The differences in melanin deposition between white-bellied and gray-bellied Zosterops borbonica is easily as great as between the palest (senegalensis) and darkest (jacksoni, reichenowi) forms of Zosterops senegalensis. Color differences between such recognized subspecies as Zosterops senegalensis stuhlmanni and Z.s. jacksoni are less pronounced than between extreme underpart color variants of Zosterops

borbonica. The point is to be emphasized, therefore, that intra-insular color variation in Zosterops borbonica does not simply involve subtle differences but is of a magnitude comparable to that found in the continental species.

The presence of phaeomelanins has an irregular distribution in the Zosteropidae. Only two African forms, Zosterops pallidus and Zosterops semiflava ssp. have phaeomelanin pigments in their flank feathers, the usual site of this pigment's deposition, though in Zosterops pallidus the extent of phaeomelanin pigmentation in the underparts is reported to vary greatly (Moreau, 1957:380). Zosterops modesta appears to have minor traces of phaeomelanins throughout its plumage, especially in the underparts. Elsewhere, a variety of races of Zosterops japonica have rufous-washed sides, and in one closely-related species, Zosterops erythropleura, the flanks are actually bright reddish brown. Several races and insular derivatives of Zosterops lateralis, the widespread Australian species, have rusty flanks. The closest parallel to the differences between brown and gray morphs of Zosterops borbonica is found in Zosterops cinerea in Micronesia. On Ponape and Kusae islands, Zosterops cinerea is an all gray bird very similar to a gray Zosterops borbonica in coloration, but in the Palau Islands, Zosterops cinerea finschi is a brown bird resembling the brown morph (xerophila) of Zosterops borbonica.

Except for the coloration of the belly which may be either gray or yellow, polymorphic plumage characters are unknown in the Zosteropidae other than Z. borbonica. In South Africa (Transvaal, Zululand etc.) gray-bellied and green-bellied white-eyes (Zosterops virens) do coexist and interbreed (Skead and Ranger, 1958). Elsewhere, however, local populations are either gray-bellied or green-bellied.

In African white-eyes, wing length increases significantly in relation both to increasing altitude (0.69 millimeters per 1000 feet elevation) and decreasing temperature (2.8 millimeters per 10 degrees Fahrenheit). The relation of tail length to altitude seems a function of its high correlation with wing length (correlation coefficient = 0.93) but the tail/wing ratio also increases with altitude, i.e. the tail becomes proportionately longer relative to increasing wing length. Bill length increases slightly with decreasing minimum temperature, even after highly correlated effects (correlation coefficient = 0.83) of wing length are removed. Thus white-eyes inhabiting higher and/or cooler parts of Africa tend to be generally larger than those in the lowlands. No information is available for variation in tarsus length or weight in African white-eyes.

The altitudinal relationship of wing length in Zosterops borbonica is virtually the same as in the African

species and it seems that similar selective agents must be responsible. On the other hand, there is no altitudinal correlation of the tail/wing ratio in Zosterops borbonica. Positive indications of such a relationship in Africa may actually be an artifact of the usage of ratios based on mean tail lengths and mean wing lengths rather than a mean ratio calculated separately for each specimen.

Distances between extreme variants in Africa are usually on the order of hundreds of miles, but in certain cases, as, for example, between Zosterops senegalensis demeryi and Z. s. senegalensis, it appears that the belt of transition is very narrow, perhaps only a few miles wide, although this is poorly documented. Similarly in some areas the altitudinal size clines are very steep, as, for example, on the edge of the Congo Basin, where populations only twenty and forty miles apart differ markedly in their measurements. Several of the distinctive montane populations in Kenya are separated by geographical and ecological gaps of no more than twenty miles.

DISCUSSION

Evolutionary History of Zosterops borbonica

Zosterops borbonica is apparently derived from a typical white-eye that colonized Mauritius and Réunion from Madagascar after Zosterops olivacea and that was able to do so by virtue of being a generalized white-eye adapted primarily to edge, disturbed or relatively open habitats. Zosterops olivacea on the other hand had already become adapted to the indigenous forest and had developed a sunbird-like dependence on flowers and nectar feeding (Gill, MS). Before the arrival of man, suitable "edge" habitat for Zosterops borbonica was rather limited on Réunion and existed only in relatively isolated pockets. The dry tree savanna of the west coast and the highland heath zone were probably both suitable for Zosterops borbonica. Dense evergreen forest once extended to the sea on the wet east coast, and it seems that throughout this region Zosterops borbonica must have been primarily a bird of the streamsides and semi-open ravines much as it is today. The coastal border of the forest should also have been suitable, but I suspect that borbonica was once absent from the evergreen forest that covered most of the island. It may have penetrated the forest

along major streambeds but not in great numbers. Constant erosion and landslides must have created some satisfactory habitat in the cirques, and in both Cilaos and Mafatte this was probably continuous with the tree savanna that penetrated from the west coast via the ravine slopes (Rivals, 1952). Finally the forest below Le Volcan were certainly damaged regularly and rendered suitable by eruptions and new lava flows. Thus several disjunct pockets of habitat isolated by stretches of uninhabitable evergreen forest were originally available to Zosterops borbonica on Réunion.

Zosterops borbonica's ancestor was probably a typical yellow-green white-eye which had a limited capacity for the synthesis of phaeomelanin pigments that were deposited in the flank feathers. The loss of carotenoids (as well as the eye-ring) resulted in a gray white-eye, which very likely resembled the present day Z. b. mauritiana in predominant coloration, including the brownish wash on the flanks. That the original form of Zosterops borbonica was more like a modern day gray morph than a brown morph is supported by the rarity of extensive phaeomelanin pigmentation in the Zosteropidae, and also by the presence of a monomorphic gray form on Mauritius.

Sometime after Zosterops borbonica lost the carotenoid deposition (and was established on both Mauritius

and Réunion) a phaeomelanic morph evolved in the Réunion lowlands, and through some selective advantage at low altitudes gradually replaced gray morphs throughout the lowlands. Gray morphs thus became restricted to the highland heath zone where they became increasingly adapted to the cold temperatures and utilization of the scrub-like vegetation. There seems to be no satisfactory alternative to the sympatric appearance of brown morphs in a gray morph population and subsequent replacement of the latter by the former. The ancestral brown morph probably resembled the all-brown, modern xerophila rather than the gray-headed borbonica, since xerophila inhabits a wide range of environmental extremes as must have been characteristic of the species in order for it to have been widely distributed on the island in the first place. Also a general distribution of phaeomelanins seems a simpler acquisition than the sharply-demarcated pattern of gray-headed borbonica.

I envision the subsequent differentiation between brown morphs as occurring in isolated pockets of suitable lowland habitat, xerophila in the arid tree savanna of the island's west side, borbonica in the coastal vegetation and along stream beds on the west side, and "brown-naped" borbonica in the disturbed young coastal forests below Piton de la Fournaise, perhaps arising through hybridization between xerophila and borbonica types.

It is difficult to be certain of the extent and

nature of the contacts between these populations before the arrival of man on Réunion in 1663, but they must have been quite limited. There is little doubt, however, that human activities, including lumbering for valuable wood and burning of the forests from the seventeenth to nineteenth centuries greatly changed the aspect of the island's vegetation and opened much of the previously uninhabitable forest to Zosterops borbonica. This would certainly have been true throughout the lowlands and on the western slopes of the island. In the latter region much of the forest was quickly destroyed, the tree savanna and highland Acacia for their valuable timber, and the evergreen forest in connection with the commercial cultivation of geranium. Damage was less extensive in the rugged, inaccessible and very wet forests of the eastern slopes.

Zosterops borbonica borbonica, in particular, must have greatly benefitted from these changes since it was no longer restricted to the rather limited edge habitat along stream beds and ravines and undoubtedly increased in numbers, expanded towards the tree savanna on the northeast and established contact with xerophila. After the tree savanna was destroyed between St. Denis and Le Port, borbonica probably replaced xerophila in this region and advanced as far as the Rivière des Galets, where the combination of aridity and a broad river bed proved to be an effective barrier between the two forms. "Brown-naped"

borbonica expanded along the southern coast and met xerophila at the Rivière St. Étienne. The contact of "brown-naped" borbonica and "pure" borbonica was probably very similar to that found today, being restricted by new lava flows south of Bois Blanc.

Both brown morphs also expanded their altitudinal range and particularly on the west slopes (xerophila) met the gray morphs which were beginning to occupy lower elevations than was previously possible. Inasmuch as gray morphs were adapted to high altitudes and brown morphs low altitudes, a cline in the proportions of the two was quickly established. The expansion of brown morphs into the highlands also led to the evolution of a series of populations adapted to local climatic conditions. Thus, the increase in melanin deposition in the underparts appears to be a primary intergradation, rather than a secondary cline resulting from the contact of expanding isolated pockets of Zosterops borbonica. The rather rapid evolution of these differences, i.e. within three hundred years, is in keeping with recent evidence for rates of racial differentiation in the House Sparrow (Passer domesticus) (Johnston and Selander, 1964; Packard, 1967). However, the morph ratio clines and contacts between brown morph variants are probably secondary and were established upon contact of previously isolated populations.

Intensity of Selection

Regardless of the actual sequence of events responsible for the differentiation and establishment of contact between the color variants, it is of interest to consider the selective forces which must be maintaining the present day geographic separations and steep clines between extremes. Direct measures of selection coefficients in natural populations based on temporal fluctuations in the proportions of genotypes (Clarke and Murray, 1962; Gershenson, 1945; Merrell and Rodell, 1968), their relative viability (Ford, 1964; Sheppard and Cook, 1962; Fisher, 1939), or differential capture by predators (Kettlewell, 1961 a,b) are available for a few well-studied moth and butterfly, snail, or small mammal populations. These coefficients are on the order of five to as high as ninety per cent relative advantage of one genotype over another. But the continued maintenance of geographic differences in a series of continuous local populations is actually a function of two opposing forces: natural selection, which favors different genotypes in different areas; and dispersal or gene flow, which promotes genetic homogeneity of adjacent populations. The mathematical relationships between these two forces and the distances over which they interact have been treated by Haldane (1948) and Fisher (1950). The two selection coefficients computed by the former method have

proven very low, e.g. 0.1 per cent in Peromyscus polionotus (Haldane, op. cit.) and .004 per cent in Amathes glareosa (Kettlewell and Berry, 1961), and are, in fact, well below the actual intensities believed to be operating.

Haldane's method is applicable to the clines in the ratios of brown and gray morphs in that it assumes the following: 1) the species lives in an area which is plane and infinite, i.e. it must be so large that regions exist where there is no polymorphism; 2) the density is equal through the area; 3) the animals disperse at random; 4) they have one annual generation; 5) mating is at random between the different types; 6) the population is in equilibrium; 7) an autosomal dominant and its allelomorph underly the polymorphism; and 8) the plane is sharply divided by a straight boundary into two halves. Assumptions 1 through 6 are acceptable without major violation for Zosterops borbonica. Admittedly the underlying genetic basis of the polymorphisms (Assumption 7) is not clear (see page 63) but other similar cases of color polymorphism in birds (Cooke and Cooch, 1968; Munro et al, 1968, Hrubant, 1955) appear to have simple diallelic bases with dominance that is affected by modifiers responsible for the intermediate plumage types. The requirement of a sharp boundary is violated by our situation, but Haldane (op. cit.) recognizes that in many cases conditions do

change gradually and believes that a comparison of the interquartile and migration ranges should (still) give the order of magnitude of selection needed to maintain the cline; that is it should be possible to say whether a given cline suggests selective intensities of the order of 10 or .01 per cent.

The essential measurements are 1) the interquartile distance (d) which is the linear distance between the localities at which the frequencies of one of the phenotypes are 25 and 75 per cent, and 2) the average dispersal distances (m) from hatching site to first breeding site. The intensity of selection in the interquartile region is then about $m^2/2d^2$, where m is the average dispersal distance and d is the interquartile distance.

In the absence of direct measures of dispersal distances for Zosterops borbonica, we can try to estimate the approximate limits of this figure. Zosterops borbonica is not a uniquely sedentary bird species with average dispersal distances much lower than are known for other birds. It is highly mobile, habitually flying considerable distances over the forests, and is in no way restricted to the ground or dense understory. I have observed banded birds up to 500 meters from the point at which they were initially captured and banded and suspect that they wander freely within any particular square kilometer of suitable vegetation, perhaps much more.

Mean distances of dispersal (from birth place to breeding place) have been measured for only a few bird species. In the Song Sparrow (Melospiza melodia) it appears to be about 400 meters (Johnston, 1961). The Wrentit (Chamaea fasciata), an inhabitant of dense brush and chaparral, disperses somewhat farther, about 600 to 700 meters (Erickson, 1938), and the mean dispersal distance of the Great Tit (Parus major) is also about 600 meters (Kluijver, 1951). I would estimate, therefore, that the mean dispersal distance in Zosterops borbonica is on the order of 500 meters. The absence of territoriality or restriction of gene flow by other factors (see below) could conceivably reduce it to 250 meters, but this seems like an absolute and probably exaggerated minimum possibility for a highly mobile bird. At the other extreme, I doubt that Zosterops borbonica is any more mobile than some of these other species and would set one kilometer as the upper limit to its mean dispersal distance.

Using Haldane's formula I have calculated the interquartile selection coefficients for four of the five morph ratio clines sampled on Réunion. Separate values were computed for mean dispersal distances of 250 meters, 500 meters and 1000 meters respectively (Table 17). These range from as low as 0.06 per cent to a maximum of 5.5 per cent, indicating the selection need not be very intense to maintain this aspect of the geographic color variation

TABLE 17. Calculation of the Intensity of Selection Required for Maintenance of Morph-Ratio Clines in *Zosterops borbonica* (after Haldane, 1948)

	Transect	A Locality with 25% Gray Morphs	B Locality with 75% Gray Morphs	Distance (d) between A + B (in Km)	Selection Coef. (K) = $m^2/2\ d^2$ (in per cent)
I.	St. Benoît to Plaine des Cafres	33	41	7	a)[1] .064 b)[2] .25 c)[3] 1.02
III.	St. Denis to Plaine des Chicots	6	5	4	a) .19 b) .781 c) 3.1
IV.	Petite France to Piton des Epinards	74	71+	3	a) .35 b) 1.4 c) 5.5
V.	Étang Salé les Bains to Piton des Epinards	62	64	4	a) .19 b) .781 c) 3.1

[1] Mean dispersal distance assumed to be 250 meters

[2] Mean dispersal distance assumed to be 500 meters

[3] Mean dispersal distance assumed to be 1000 meters

in Zosterops borbonica. It is apparent that a small selective advantage is sufficient to maintain clinal variation in simple morph or allelic frequencies in a mobile small bird.

Several factors reduce the effective dispersal distance (with respect to gene flow) between adjacent populations of Zosterops borbonica. First there is the highly social nature of borbonica's year-round activities, including the apparent lack of territoriality, which must promote the formation of local and perhaps inbred populations. The presence of helpers and communal feeding of young in the nest might also be taken as indirect evidence of inbreeding, as such behavior would be selectively advantageous to the participating individuals if the young were related genetically. Allochronic differences in the onset of breeding may also be important in reducing altitudinal gene flow as well as reinforcing the geographic isolation between lowland borbonica and xerophila. The combined effect of these factors would be to decrease the intensity of selection required to maintain the geographic differences.

Nature of the Selective Forces

Although the intensities of selection maintaining the variation in Zosterops borbonica are not especially high there is no denying their ultimate evolutionary

significance and potency. It will be of interest therefore to try to determine even approximately the nature of the selective forces to which Zosterops borbonica is exposed.

The existence of infraspecific gradients of pigmentation and size which are strongly correlated with climatological variation has been recognized since the earliest studies of geographic variation and soon resulted in the formulation of "ecogeographic rules." Among the more important of these are "Gloger's Rule," which relates the intensity of melanin pigmentation to increased humidity, and "Bergmann's Rule," which states that body size tends to increase in the cooler parts of a species' range. Both of these rules extend to patterns of altitudinal variation in birds, highland populations tending to be larger and darker than lowland populations of the same species (Rand, 1936).

The selective advantage of size variations which conform to Bergmann's Rule is presumed to be physiological and related to the problems of thermo-regulation in warm-blooded animals, though this has been disputed (Scholander, 1955; Mayr, 1956). Increased sophistication of physiological studies of thermoregulation will most likely support Mayr's (op. cit.) arguments for the existence of slight, but evolutionarily significant effects of differences in body size. Considering the steepness of the size clines in

white-eyes on both Réunion and Africa, it would seem that the selection coefficients may be even higher than supposed.

While wing length may be an indicator of body size, it is also subject to a variety of other selective forces, including the possible effects of altitudinal changes in air pressure on flight capability (Hamilton, 1961; Moreau, 1957). In Zosterops borbonica wing length is significantly correlated with body weight in one of the color forms (xerophila) but not in others with more limited altitudinal ranges. However, tarsus and bill lengths are significantly correlated with weight in all forms. Altitudinal correlations of weight (and bill length) are positive in xerophila but negative in gray morphs. It may be that body size is influenced at high altitudes in the relatively barren heath zone by problems of adequate nourishment as suggested by Kendeigh (1969).

Protection from visual predators has been emphasized as providing the selective forces responsible for the evolution of ecogeographic color gradients (Bowers, 1960). The advantages of such camouflage are obvious and certainly cannot be ignored. But on Réunion differential loss of the color forms to visual predators does not seem to be important if it occurs at all. Most of the available predators, e.g. rats, lizards, snakes, cats, and humans, are either restricted in their distribution or do not

exert a selective bias within the range of color variation. The one widespread predator against which some protective coloration would seem to be advantageous is the harrier, Circus aeruginosus, but this hawk does not pose a widespread and general threat to Zosterops borbonica (see page 32) as would be necessary for the selective maintenance of the color variation. This forces our attention to physiological explanations, which are the best alternatives to predation. Recent evidence (Lustick, 1969) indicates that differences in pigmentation are important in relation to thermoregulation in birds, functioning primarily through effects on the insulation value of plumage. In addition to a direct warming of the outer layer, the absorption of radiant energy by pigment granules could conceivably assist the drying of feathers and thereby improve their insulative value, particularly in cold, humid environments. Although it is speculative only, this hypothesis could explain trends in melanin deposition that conform to Gloger's Rule. This is not intended to deny the importance of substrate matching and predator concealment, which in many situations probably overrides the physiological advantages of color differences (Norris, 1965). Yet caution against the hasty use of "predation" as the obvious, and therefore only explanation of ecogeographic color change is clearly necessary.

In the high, wet forests at Cilaos on Réunion

white-eyes regularly perched on exposed branches, facing the sun when it first reached them and vigorously preened themselves. Such behavior very likely permits the differences in melanin deposition in the underparts to function in a thermoregulatory sense.

Several possibilities exist as to the nature of the adaptive differences between gray and brown morphs. The striking similarity of the color of gray morphs to the high altitude vegetation (heath and Sophora) cannot be disregarded lightly, and one is tempted to invoke the visual predators which have already been discounted. If the color differences are directly adaptive I can conceive of only two possibilities. Either differences in the absorption of radiant energy exist though no data is currently available, or reduced conspicuousness may be important in borbonica's interspecific relationships with aggressive Zosterops olivacea, since competition seems particularly intense at flowering Sophora and Hypericum in the highlands (Gill, MS). However, gray and brown morphs may prove to differ primarily with respect to some unrelated aspect of physiological adaptation to high and low altitudes respectively.

Finally, as already noted (page 104) the primary differences between xerophila and borbonica seem to be physiological, though probably not directly related to the differences in their coloration.

Lack of Variation in Zosterops olivacea

Unlike Zosterops borbonica, Zosterops olivacea does not vary strikingly but rather is morphologically uniform throughout the island. The fact that one species of white-eye varies on the island does not necessarily prescribe intra-insular variation in its sympatric congener. Differences in the behavior and requirements of the two species may supply at least a partial explanation for the disparity. First, Zosterops olivacea is primarily a bird of the indigenous forest, which unlike the edge habitats was continuously distributed over the island. Hence, there has been no opportunity to establish ecologically-isolated and eventually differentiated populations. Second, Zosterops olivacea is primarily a bird of moderate and high elevations. It is not a particularly common bird anywhere in the lowlands and is completely absent from the arid west coast. It probably never inhabited the original dry tree savanna. Thus Zosterops olivacea has a more limited distribution on the island and faces a narrower range of physiological extremes than does Zosterops borbonica. In addition, it is an aggressive species which is territorial in relation to its food supply and consequently must be forced to disperse far greater distances than is the social borbonica. Olivacea's dependence on a fluctuating supply of suitable flowers must also increase is vagility. The

combined effect of these factors is to increase greatly the size of a panmictic population of Zosterops olivacea and to make intra-insular differentiation unlikely.

Intra-insular Variability

Variation in Zosterops borbonica on Réunion Island is no more extensive or complex than is found in other groups elsewhere in the world, except that the amount of variation is unique for the small size of the island. Climatic correlations of size and the intensity of melanin deposition, geographically separated subspecies, and clines in morph ratios are all well-known aspects of geographic variation in birds on continents (Mayr, 1963). Also, the intensity of selection maintaining the geographic variation is not particularly high compared to what is known to be possible in natural populations. Zosterops borbonica is not a bird of unique habits or especially sedentary and the selective forces involved are widely applicable. All of this suggests that Réunion Island itself is distinctive.

Genetic differentiation in the face of a fixed amount of dispersal is made possible by either increasing the distances involved or by increasing the intensity of the selection gradient. On continents substantial distances are frequent correlates of environmental gradients, while on islands, by definition, the distances

cannot be very great. On the other hand, the range of climatic extremes on an island, which reflects the intensity of the selection gradient is variable and can be considered roughly in terms of the island's vertical relief in relation to its latitude. A very high, mountainous island on the equator will span from a tropical climate at its base to alpine conditions at its summit. With increased latitude the minimum elevation required for alpine conditions decreases, but also one gradually loses the tropical and subtropical lowlands. Thus, the best situation for maximum zonal diversity would be a combination of high mountains and low latitude. However, few small tropical islands are high enough to satisfy these requirements and the next best a position at subtropical latitudes making possible both high (alpine) altitudes and subtropical lowlands. Réunion is one of the few small islands that meets these conditions (Figure 31).

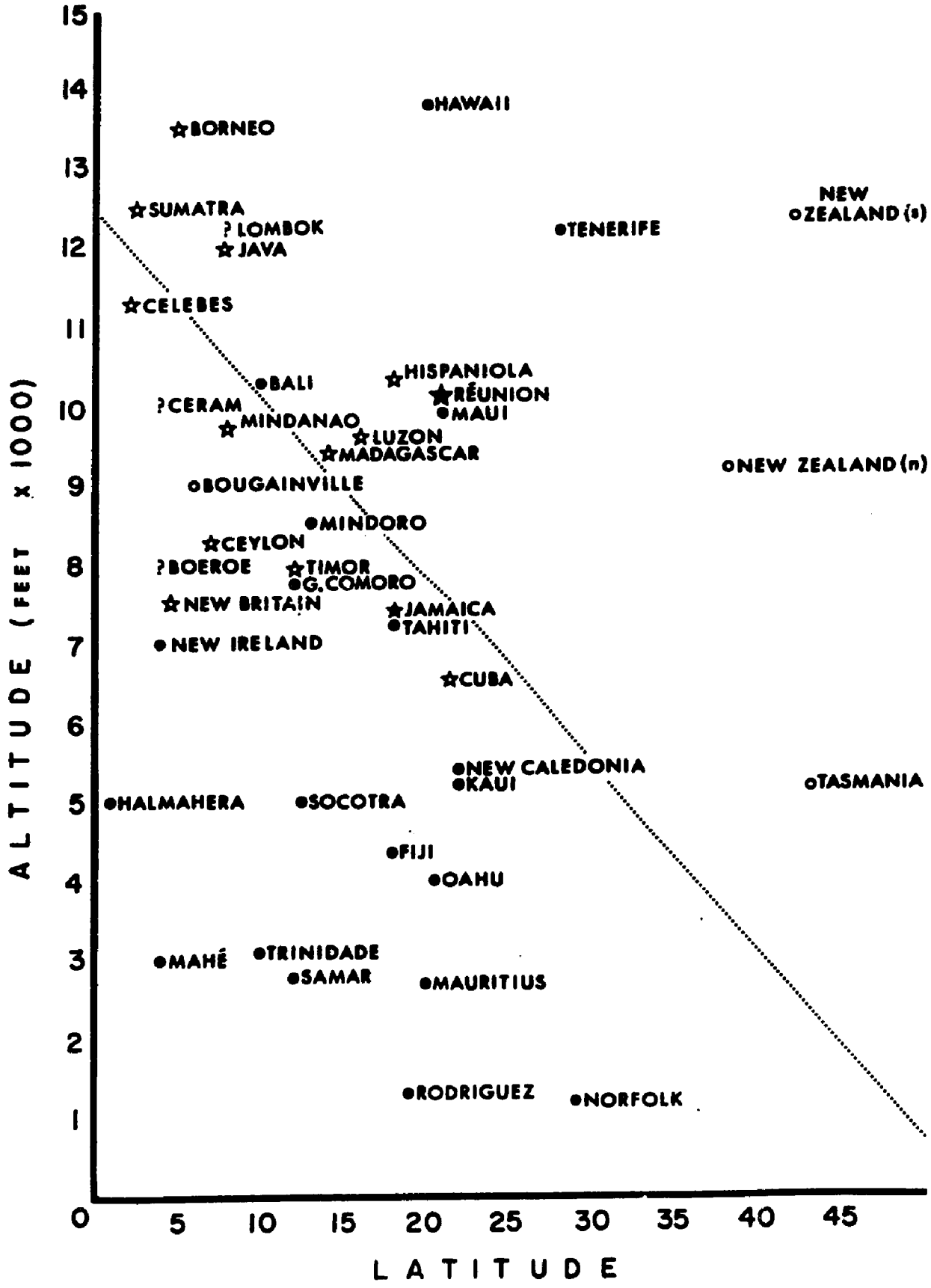
No intra-insular subspeciation is known from the islands of Hawaii or Maui, both of which seem sufficiently diverse by these criteria, but the endemic birds of these islands are known to have undertaken regular altitudinal migrations (Warner, 1968) which might have precluded microgeographic differentiation. Bali and Lombok are two other small islands with high mountains. Again, I know of no cases of subspeciation on these islands but that

FIGURE 31

Relation of the Maximum Altitude of Major Islands

to Their Latitude and Intra-insular Subspeciation

(Open dots = islands more than 10,000 square miles in area with no polytypic species; closed dots = islands less than 10,000 square miles in area with no polytypic species; open stars = islands more than 10,000 square miles in area with a polytypic bird species; closed stars = islands less than 10,000 square miles with a polytypic bird species. Dotted line indicates approximate altitude required for alpine conditions)


ALTITUDE (FEET x 1000)
LATITUDE
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
5
10
15
20
25
30
35
40
45
HAWAII
BORNEO
SUMATRA
LOMBOK
JAVA
TENERIFE
NEW ZEALAND (s)
CELEBES
BALI
HISPANIOLA
RÉUNION
CERAM
MINDANAO
MAUI
LUZON
MADAGASCAR
NEW ZEALAND (n)
BOUGAINVILLE
MINDORO
CEYLON
BOEROE
TIMOR
G. COMORO
NEW BRITAIN
JAMAICA
TAHITI
NEW IRELAND
CUBA
NEW CALEDONIA
KAUI
TASMANIA
HALMAHERA
SOCOTRA
FIJI
OAHU
MAHÉ
TRINIDADE
SAMAR
MAURITIUS
RODRIGUEZ
NORFOLK

may be due to the inadequate state of our knowledge of these avifaunas. Jamaica, on the other hand, is not a particularly high island, but the northeastern side is very wet in comparison to the rest of the island and this difference is apparently sufficient for the maintenance of microgeographic differentiation. It may turn out that on other islands a strong rain shadow effect will compensate for high elevations in establishing a strong selective gradient, though in most cases rain shadows are actually the results of high altitudes.

In conclusion, the rarity of intra-insular subspeciation in birds is not so much a problem of island size in relation to dispersal and the restriction of gene flow as it is the relation of island size and latitudinal position to climatic diversity. The involvement of a bird species with certain habits and dispersal characteristics is important but not unusually restrictive. For example, the intra-insular differentiation in Zosterops borbonica has certainly been enhanced by its restriction to edge habitats and its social behavior, but many other species have similar attributes. Steep character clines are relatively scarce on continents primarily because climatological gradients tend to involve substantial distances, not because of genetic swamping.

What is perhaps most puzzling, considering the apparent ease of interdemal differentiation, are those

monotypic species with widespread continental distributions, because any tendency towards philopatry will subdivide a widely-distributed species into smaller demes between which differentiation is highly probable. In such species there must be intense stabilizing selection and a high premium on genetic homeostasis throughout the range to offset the natural tendency towards adaptation to local conditions. Such questions have received preliminary consideration (Miller, 1956; Johnson, 1966) and it seems that similar studies of the differences between highly polytypic forms and their monotypic relatives will be a productive direction for future research. Furthermore, the absence of geographic variation will probably prove just as important and interesting as its occurrence.

Propriety of Subspecific Nomenclature

The tiny geographic area within which Zosterops borbonica varies and the fact that it is an oceanic island should impose no restriction or elicit any reservation as to the valid application of the subspecies concept, i.e. the bases for nomenclatural decisions should be exactly the same as for cases of infraspecific variation on continents or between islands, namely the existence of taxonomically distinguishable, geographically-defined populations (Mayr, et al, 1953). The primary objective of this study is an understanding of the nature and evolution of

the variation in Zosterops borbonica, not a critical appraisal of the appropriate taxonomy. Nevertheless, certain problems inherent in the application of meaningful nomenclature must be pointed out.

Four subspecific names have been applied to the Réunion situation (Storer and Gill, 1966), e.g. Zosterops borbonica borbonica to the gray-headed brown morph of the wet lowlands, Z. b. xerophila to the brown-headed brown morph of the dry lowlands, Z. b. alopekion to the rufous-breasted, brown-headed brown morph of the central high and Z. b. edwardnewtoni to the all gray morph. As defined solely in terms of head coloration (on page 96), borbonica and xerophila behave as good subspecies with definable ranges in which one or the other clearly predominates. However, retention of alopekion and edwardnewtoni is not as easily justified on taxonomic grounds. Alopekion, which is simply the dark, brown-breasted (Breast Brown Index 2 or higher) extreme of continuous variation in xerophila's underpart coloration, is the predominant brown morph at several inland localities, but these comprise only a small fraction of the island's area. Although gray morphs evolved in isolation from brown morphs, compose more than 75 per cent of four different populations, and are easily distinguished, they now overlap so extensively with brown morphs that a satisfactory subspecific range cannot be defined. While retention of four subspecific names would

certainly facilitate discussion of the evolutionary relationships of the color forms, the validity of the taxonomy would certainly be questionable. On the other hand, reduction of the nomenclature to two valid, operational subspecies obscures the complexity and evolutionary history of the variation. Thus, the operational requirements of subspecific nomenclature conflict with its evolutionary implications and ultimate value. Such problems of the application of the subspecies concept are hardly new (cf Mayr, 1963:348), but they do illustrate the continuing need for careful evaluation of the role of this concept in evolutionary biology.

SUMMARY

1. This study concerns the nature and evolution of geographic variation in color and size of an endemic white-eye, Zosterops borbonica, on Réunion Island in the western Indian Ocean.
2. Color variation includes a polymorphism for the presence or absence of phaeomelanin pigmentation in the feather barbs, distinct geographic groupings of head color variants of the phaeomelanic morph, and ecogeographic gradients in the intensity of melanin deposition in the underparts.
3. Brown and gray color morphs are extensively sympatric in proportions which vary clinally with altitude from pure brown-morph populations in the lowlands to predominately gray-morph populations in the highlands.
4. Brown morphs in the dry western lowlands and at all altitudes above 1400 meters have brown heads (Z. b. xerophila while a gray-headed, brown-backed form (Z. b. borbonica) predominates in the wet northern and eastern lowlands below 1380 meters elevation. A brown-naped intermediate is the only form inhabiting coastal localities between St. Pierre and Grand Brûlé.

5. Contact between the different brown morphs is abrupt with little evidence of geographic intergradation. In the lowlands the breaks coincide with two major river beds, the Rivière des Galets and the Rivière St. Étienne, and a recent lava flow near Bois Blanc. A variety of color forms coexist at localities in the interior of the island in the zone of contact which averages about five kilometers in width.
6. The intensity of eumelanin deposition in the feathers of the underparts varies in relation to altitude in all color forms, the underparts changing from white in the lowlands to dark gray in the highlands.
7. Size characteristics vary both in relation to altitude and between color forms.
8. Ecogeographic gradients of size and melanin deposition similar to those described for Zosterops borbonica and of comparable extent but involving substantially greater distances are known to occur in many continental birds, including other white-eyes.
9. Isolation of populations of Zosterops borbonica in pockets of suitable "edge" habitat available on Réunion before the arrival of man permitted the differentiation of three important color forms which subsequently established secondary contact as a result of expansion made possible by human destruction of indigenous vegetation.

10. Associated altitudinal expansions have led to the differentiation of steep primary clines in size and the intensity of melanin deposition in the underparts within the past 250 years.
11. The intensity of selection currently maintaining the steep altitudinal clines in the proportions of the two color morphs is estimated to be on the order of one per cent.
12. The absence of significant visual predators on Réunion as well as recent experimental evidence from the literature suggests that the differences in underpart melanin deposition have physiological value in terms of the absorption of radiant solar energy. Selective forces maintaining other geographic aspects of the color variation also appear to be physiological in nature.
13. Explanations for the absence of similar intra-insular variation in birds on other oceanic islands seem to lie in the extremes of climatic diversity that are required rather than the effects of interdemal gene flow.
14. The application of suitable subspecific terminology to this case of geographic variation is hindered by a conflict between what is taxonomically operational and what is evolutionarily meaningful.

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APPENDIX I. Summary of Réunion Localities

Locality Number	Altitude (meters)	Location	Name	No. of Specimens
1	1000	2 km SSE Le Brûlé	Val Fleuri	14
2	1100	3 km SSE Le Brûlé	Mamode Camp	9
3	1580	5.7 km SSE Le Brûlé		10
4	1780	7 km S Le Brûlé	Plaine des Chicots (gite)	3
5	1910	7.7 km S Le Brûlé	Plaine des Chicots	6
6	1650	5.2 km E Dos d'Ane	Plaine d'Affouche	9
7	1460	3.3 km E Dos d'Ane	Plaine d'Affouche	0
8	1700	20 km NNE St. Joseph	Rav. Rivière des Remparts	8
9	1000	8 km SSW St. Denis	Chemin Arnoux	10
10	820	5.3 km ESE La Possession	Piton d'Orange	6
11	90	2 km S St. Denis	Ravine du Butor	10
12	220	3.5 km S St. Marie	Beaufonds	6
13	10	2.7 km E St. Marie	Ravine Chevres	0
14	200	5.2 km NE Salazie	Bras de Caverne	9
15	560	1.5 km SSE Salazie	Salazie	0
16	680	2 km ESE Gd. Islet	Rivière Fleurs Jaunes	13
17	1100	1 km NE Gd. Islet	Grand Islet	4
18	1530	3 km SSW Gd. Islet	Col Be Male	11
19	1940	7 km W Hellbourg	Col de Fourche	11

APPENDIX I cont.

Locality Number	Altitude (meters)	Location	Name	No. of Specimens
20	1160	4 km W Hellbourg	Ravine Farla	10
21	920	2 km W Hellbourg	Rivière du Mat	3
22	1350	1 km S Hellbourg	Terre Plate	6
23	1570	2.2 km SW Hellbourg	Plateau de Belouve	10
24	1400	3.8 km NE Hellbourg	Trou de Fer	10
25	640	9 km SW St. Benoît	Ravine Mathurin	11
26	1010	12 km SW St. Benoît	Takamaka	11
27	1180	5 km WNW Pl. des Palmistes (1er)	Plateau Duverney	10
28	1360	7.5 km W Pl. des Palmistes (1er)	Forêt du Bébour	0
29	1350	6.5 km WNW Pl. des Palmistes (1er)	Forêt du Bébour	15
30	1720	9.2 km W Pl. des Palmistes (1er)	Plaine des Salazes	10
31	720	4 km NE Pl. des Palmistes (1er)	Bras Grand Piton	11
32	860	2.7 km NE Pl. des Palmistes (1er)	Piton Camp de Tête	1
33	1060	1.5 km SSW Pl. des Palmistes (1er)	Pl. des Palmistes (2eme)	6
34	170	3.5 km NNE St. Joseph	Rivière des Remparts	10
35	1250	4.2 km SW Pl. des Palmistes	)	4
36		4.7 km SW Pl. des Palmistes	)	

APPENDIX I cont.

Locality Number	Altitude (meters)	Location	Name	No. of Specimens
37	1620	6 km SE Pl. des Palmistes	Rampe de la Grande Montée	0
38	1600	5.5 km N Le Vingt Septième	Plaine des Cafres	2
39	2300	1 km ENE Pas de Bellecombe	Pas de Belle-combe	8
40	1400	6 km WNW Pl. des Palmistes	Piton de la Plaine des Cafres	7
41	2060	4.5 km E Le Vingt Septième	Nez de Boeuf	16
42	2300	7.5 km ENE Le Vingt Septième	Piton de Sable	0
43	2300	8 km SSE Le Vingt Septième	Plaine des Remparts	0
44	0	2.5 km WSW St. Louis	Étang du Gol	13
45	520	5 km WSW St. Rose	Forêt Mourouvin	12
46	500	4.2 km S St. Rose	Forêt Mourouvin	11
47	60	3 km SSW Bois Blanc	Grand Brûlé	12
48	100	10.2 km SSW Bois Blanc	Grand Brûlé	11
49	1060	17 km N St. Joseph	Rivière des Remparts	12
50	20	3 km ESE St. Pierre	Ravine des Cafres	0
51	40	1 km NE L'Étang Salé les Bains	Forêt Dominale	11
52	1380	3.5 km NNE Plaine des Cafres	Bois court	0
53	270	8.7 km NNE St. Louis	Petite Serré	7

APPENDIX I cont.

Locality Number	Altitude (meters)	Location	Name	No. of Specimens
54	340	5 km N St. Louis	Bras de Patate	4
55	300	6.5 km SSE Cilaos	Le Pavillon	11
56	1000	2 km SSE Cilaos	Bras de Benjoin	9
57	1380	4.5 km S Le Brûlé		10
58	1400	1 km N Cilaos	Forêt du Gd. Matarum	37
59	2000	3 km NNE Cilaos	Petit Matarum	0
60	2460	4 km NE Cilaos	Cavern Dufour	10
61	1080	1 km N Tévelave	Forêt Soumise des Bernards (PK 2)	10
62	1440	2.5 km NNE Tévelave	Forêt Soumise des Bernards (PK 7)	21
63	1700	4 km NNE Tévelave	Forêt Soumise des Bernards (PK 10+)	29
64	1980	5.7 km NNE Tévelave	Ravine des Avirons	8
65	180	3 km WSW Trois Bassins	Ravine Chauve Souris	3
66	10	2.5 km S St. Gilles		0
67	0	2.5 km NNE St. Paul	Étang St. Paul	0
68	120	5.5 km SE Le Port	Rivière des Galets (so. side)	10
69	160	7 km SE Le Port	Rivière des Galets (no. side)	3
70	1660	11 km ESE St. Paul	Ligne Dominiale	5
71	1800	11.7 km ESE St. Paul	Camp Dennemont	5
72	1400	9.5 km ESE St. Paul	(PK 5)	5

APPENDIX I cont.

Locality Number	Altitude (meters)	Location	Name	No. of Specimens
73	2200	14.2 km ESE St. Paul	Piton Maido	14
74	1550	10.5 km ESE St. Paul	(PK 7)	13
75	20	7 km WSW St. Paul	Ravine Jacques	0
76	20	8 km WSW St. Denis	Rav. de Grande Chaloupe	0
77	20	1 km NE La Possession	Camp Magloire	0
78	40	1 km SSE La Possession	Grande Ravine	0
79	900	1.7 km W Cilaos	Cilaos (Bras Rouge)	0
80	500	9.5 km SW St. Benoît	Grand Étang	0
81	30	3 km SSE St. Benoît	Ravine Sèche	11
82	10	.5 km SSE St. Anne	St. Anne	0
83	0	St. Rose	Monument	0
84	20	5.2 km SE St. Rose	Piton Ste. Rose	0
85	20	2 km NNE Bois Blanc	Pointe Cascades	10
86	500	6.5 km W St. Philippe	Brûlé du Baril	6
87	70	4 km SE Le Port	Jardin Boyer	16
88	10	2.5 km SE St. Philippe	Mare Longue	0
89	1360	4.6 km NE Dos d'Ane	Plaine d'Affouche	0
90	680	4.7 km NE Pl. des Palmistes (1er)	Morne de l'Étang	0
91	10	1.7 km W St. Pierre	St. Pierre (Oratorio)	0

APPENDIX I cont.

Locality Number	Altitude (meters)	Location	Name	No. of Specimens
92	20	4.5 km WNW St. Pierre		0
93	90	4.2 km E St. Louis	Riv. St. Étienne (so. side)	11
94	300	1.5 km NW Les Avirons	Ravine des Avirons	11
95	640	1.7 km W Tévelave	Ravine des Avirons	10
96	740	1 km SE Le Brûlé	Ravine Butor (Le Brûlé)	10
97	1080	7.6 km ESE St. Paul	La Petite France	10
98	1330	1.8 km NNE Tévelave	Forêt Soumise des Bernards (PK 5.5)	10
99	380	6.6 km SW St. Benoît	Chemin de la Grand Fond	11
100 (1964)	1740	5 km NNW Le Vingt-Septième	Plaine des Cafres	6
101 (1964)	1940	7.7 km NNE Le Vingt-Septième	Coteau Maigre	10
102	280	5 km E St. Rose	Riv. de l'Est	1