INTRA-ISLAND VARIATION IN THE MASCARENE WHITE-EYE ZOSTEROPS BORBONICA

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Color forms of *Zosterops borbonica* on Reunion Island (top to bottom): gray morph; highland brown-headed brown morph; lowland brown-headed brown morph; gray-headed brown morph.

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INTRODUCTION

Geographic variation reflects the genetic divergence of conspecific populations through natural selection; it thereby serves as primary evidence of the evolutionary process. Although every local population differs from adjacent populations with respect to the frequency of some characteristics, conspicuous phenotypic differentiation on a microgeographic scale is evident primarily in terrestrial and relatively sedentary animal groups. Geographic variation in highly mobile organisms such as birds, however, tends to involve great distances or else conspicuous isolation. The characteristic uniformity of most local bird populations seems to reflect genetic unity that is the combined result of gene flow between adjacent demes and the resistance of coadapted gene pools to fragmentation by disruptive selection (Mayr, 1963:296, 361). Yet, the preciseness of avian adaptation to climatic gradients (James, 1970) and the surprising rapidity of population character divergence in *Passer domesticus* (Johnston and Selander, 1964) continue to emphasize the overriding importance of natural selection as the primary determinant of patterns of geographic variation.

A bird population on a small oceanic island is characteristically homogeneous in color and size. Although inter-island differentiation is common, intra-island variation is exceptional. Until the discovery of four apparent races of a white-eye, *Zosterops borbonica,* on Reunion Island (Storer and Gill, 1966), Jamaica was the smallest island (4,540 square miles) known to have geographically separated bird populations sufficiently distinct to be considered subspecies. Reunion Island is only about 1,000 square miles in area. No other island with an area of less than 10,000 square miles is 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. This study examines the patterns of phenotypic variation in *Zosterops borbonica* on Reunion Island and considers their evolutionary origin and maintenance.

REUNION ISLAND

Reunion Island is one of the Mascarene Islands, a group of three oceanic islands of volcanic origin in the western Indian Ocean. Reunion is situated approximately 500 miles east of Madagascar (Figure 1) at latitude 21° 00′ S and longitude 55° 30′ E, is elliptical in shape, 39 miles long by 29 miles wide, and encompasses about 1,000 square miles. It is both the largest of the three Mascarene Islands and the highest, reaching an elevation of 10,068 feet.

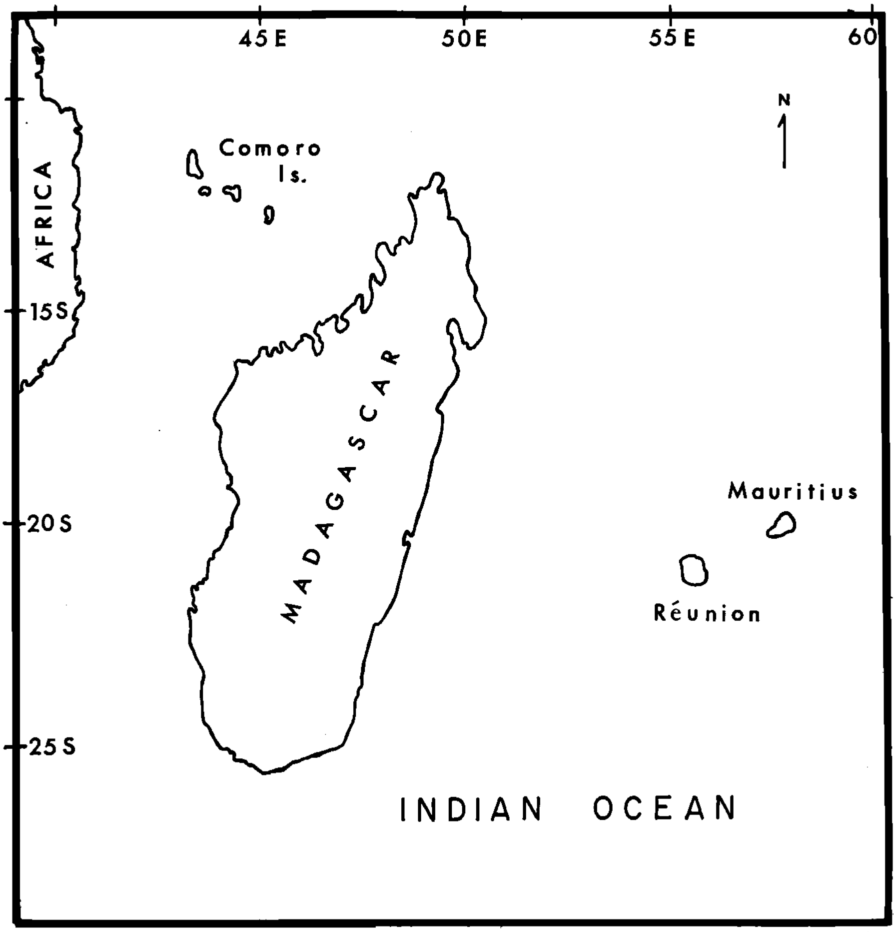

FIGURE 1. Location of the Mascarene islands of Reunion and Mauritius in the western Indian Ocean. The third Mascarene island, Rodriguez, is located 250 miles to the east.

Reunion's faunal relationships are with Madagascar and the other islands in the western Indian Ocean. The island was colonized primarily from Madagascar (Moreau, 1957:399) although, judging from the similarity of their faunas, interchange between Mauritius and Reunion islands must have occurred quite frequently. At least 8 species of birds became extinct shortly after man's arrival on Reunion in 1663. Today the land bird avifauna includes 11 indigenous and 16 introduced species. Discussions of these species are available in Milon (1951), Berlioz (1946), and Watson *et al.* (1963).

Topographically Reunion Island is an extremely rugged island, rising steeply

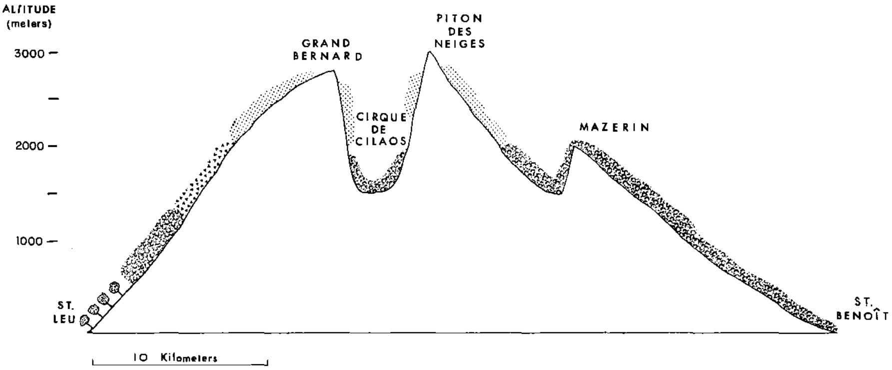

FIGURE 2. Cross-section of Reunion Island. Original vegetation above St. Leu as follows (from sea level): savanna, evergreen forest, tamarin forest, heath.

from the sea with little room for coastal plains (Figures 2 and 3). It is composed of two overlapping shield volcanos (Upton and Wadsworth, 1966:3): Piton de la Fournaise (also called le Volcan; 8,342 feet), an active volcano forming the southeastern third of the island, and Piton des Neiges (10,068 feet), an extinct volcano in the northwest. The latter, as a result of "extreme development of amphitheatre-headed valley erosion" (Upton and Wadsworth, 1966:5), is dissected up to depths of 2,500 meters by deep gorges and three huge basin-like "cirques." The youngest lavas erupted from Piton des Neiges between 100,000 and 350,000 years ago in the late Pleistocene (Chamalaun and McDougall, 1966).

The location of Reunion Island at the southern edge of the tropics ensures a rather stable, mild climate which is divided into a warm rainy season from November to April, and a cool dry season from May to October. Midsummer days average two and one-half hours longer than winter days and five to six degrees centigrade warmer. Average monthly rainfall on the windward side of the island is about 100 cm higher in the wettest month, March, than in the driest month, August. The difference on the island's dry side is about 15–20 cm.

Reunion Island's rugged relief promotes marked local variation in temperature and rainfall (Figure 4). The average rainfall on the west coast, which is in a rain shadow, is less than 100 cm a year, whereas on the eastern windward slopes it reaches 800 cm a year. Temperature decreases about 7°C with each 1,000 meters altitude, or about 2°C per 1,000 feet. Highlands over 2,000 meters are 14° to 16° colder than the coast, where temperatures average about 22°C in the summer.

Rainfall data and temperature records in the form of ten-year summaries for 112 and 30 Reunion localities, respectively, were made available by the

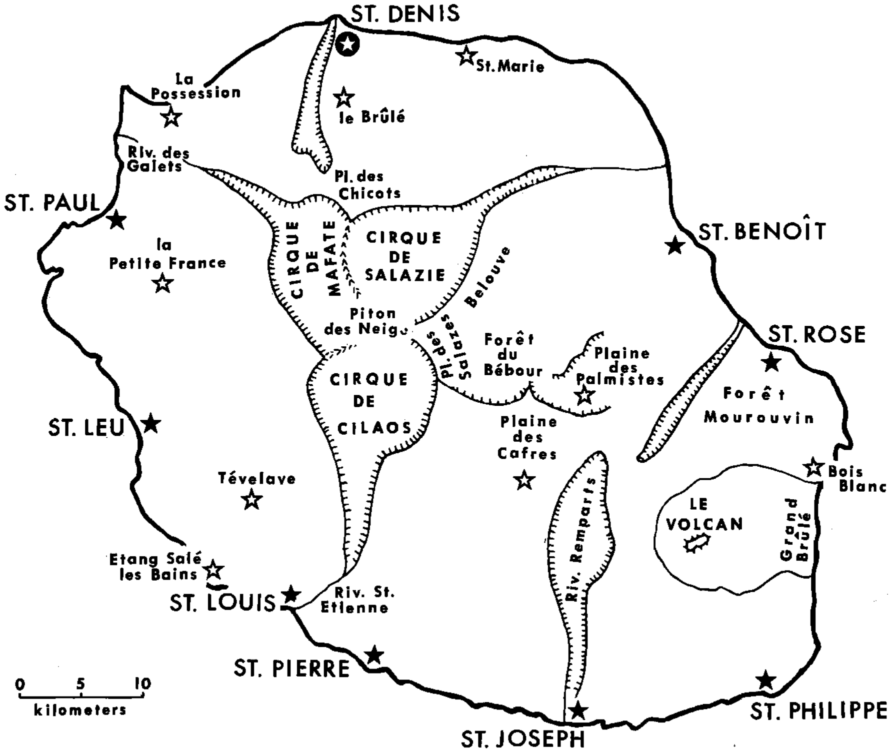

FIGURE 3. Reunion Island localities.

Service Météorologique de la Réunion. For a few additional localities for which records have been kept only a few years, I computed averages from the annual "Bulletins Climatologiques" published by the same service. Many of my collecting localities were sufficiently far from an actual meteorological station that I used rainfall values from isohyetical charts based on the ten-year summaries and calculated temperatures regressed from existing altitudinal correlations. Two temperatures have been used in this study 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 either from existing altitude markers or from a 1:50,000 topographical map published by the Ministère des Travaux Publics et des Transports (Institut Geographique National) of France.

Corresponding to variation in local climates is a diversity of habitats. The indigenous vegetation is described by Rivals (1952) and its distribution on the island before the arrival of man is illustrated in Figures 2 and 5. The

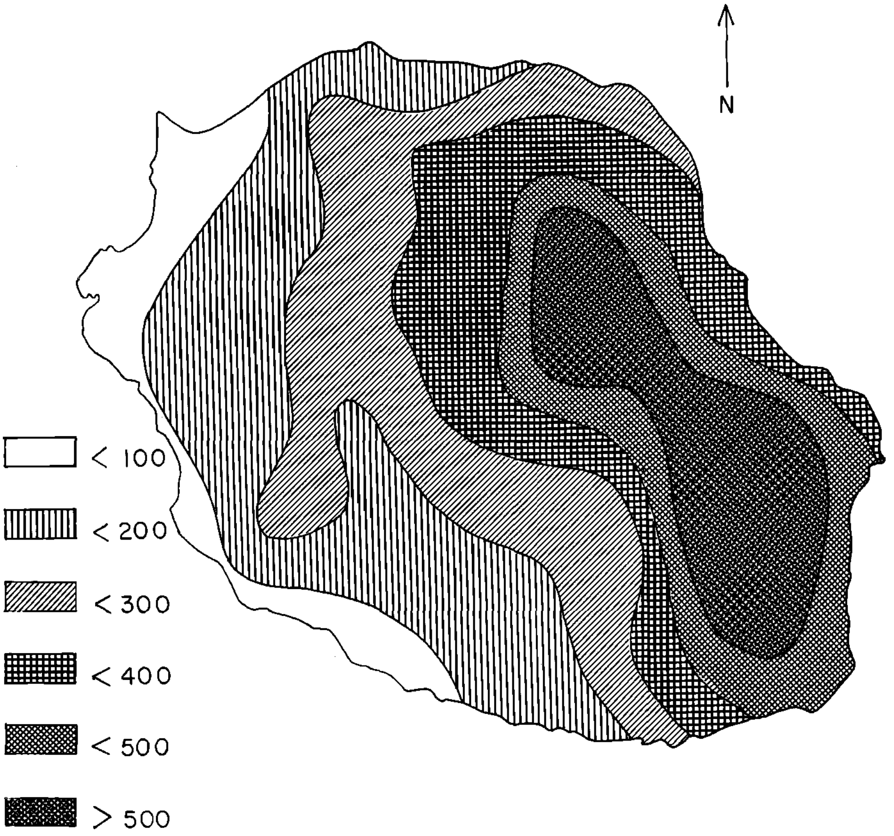

FIGURE 4. Distribution of annual rainfall on Reunion Island. Isohyets are in cm.

vegetation of certain study areas is described in Gill (1971). Originally there was a tree savanna in the arid northwestern lowlands (below 400 meters elevation), while a tamarin (*Acacia heterophylla*) forest rich in epiphytes and ferns occurred in protected localities between 1,200 and 2,000 meters elevation, and high altitude heath was present above 2,000 meters elevation. Most of the island, however, was covered by complex evergreen forest with trees about 10 meters high and rarely exceeding 15 meters. It included many species with irregular distributions, and could be subdivided on the basis of predominant species and prevailing climate.

The indigenous vegetation has been almost completely destroyed below 900 meters elevation on the west side of the island and below 400 meters elevation on the east side; it has been replaced by sugar cane fields, pasturage, and the exotic plants that typically surround human habitations. Scrub vegetation or thickets of various mixtures of heath (*Philippia*), guava (*Psidium*),

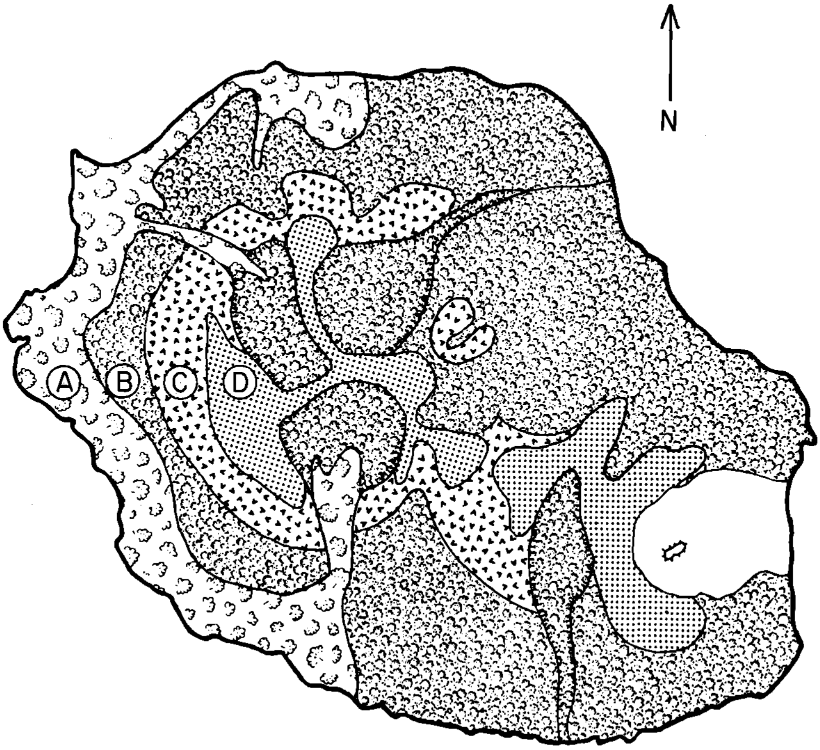

FIGURE 5. Original vegetation of Reunion Island (adapted from Rivals, 1952). Patterns from the west side of island to the center represent the following: A, savanna; B, evergreen forest; C, tamarin forest; D, heath. The clear area around le Volcan represents recently formed lava which usually lacks vegetation.

Lantana, and *Rubus* have replaced the original forests in many cutover areas. Although the proportions of the component species may vary greatly, this vegetation tends to be distinct from other habitats in that it is relatively open with no overhead canopy and is low and dense in over-all structure. Physiognomically it is closest to the low ericaceous vegetation of the high altitudes and often includes some of the same plant species. The lowland ravines contain lush growths of *Eugenia jambos* (Myrtaceae) on the east side of the island and of *Schinus terebenthifolius* (Anacardiaceae) and *Pithecollobium dulce* (Leguminosae) on the dry west side. On the west coast near Etang Salé les Bains a large tract of forest with *Casuarina equisetifolia* (Casuarinaceae), *Pithecollobium dulce, Melia azedarach* (Meliaceae), and *Schinus terebenthifolius* as the dominant plants, replaces the otherwise barren cane fields and goat pasturage of the area. Along the southeastern coast from Ste. Rose to St. Joseph relatively undisturbed forest composed primarily of *Mimusops* spp.

(Sapotaceae) descends to about 200 meters elevation. The recent lava flows and young, poor soils of this area have not encouraged agricultural expansion. The forests of Grand Brûlé on the southern slopes of le Volcan represent a pioneer stage of colonization of the new lava and are composed primarily of *Casuarina* with a fern (*Acrostichum*) understory.

Much of the indigenous vegetation at higher altitudes is still intact although one is never far from some human disturbance or exotic species. Between 900 meters and 1,400 meters elevation on the western slopes of Reunion the cultivation of geranium (*Pelargonium*), for its essential oils, has led to widespread damage to the forest, which was cleared in plots for planting and which provides firewood for the distillation process. In some areas at moderate elevations, e.g., la Petite France (1,100 meters) and Plaine des Cafres (1,200 meters), the introduced white acacia (*Leucaena glauca*) is now predominant. The wet central forests of Bébour are relatively undisturbed although a dense undergrowth of introduced *Fuchsia coccinia* 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 Reunion's original habitats, although some, especially near Plaine des Cafres, has been converted into pasturage.

FIELD STUDIES

Expeditions were made to Reunion Island in November, 1964, and from April to December, 1967. The 1964 field work was a preliminary survey undertaken with Robert W. Storer that resulted in our original cognizance of the problem. Field work in 1967 included intensive sampling throughout the island and studies of the white-eye's habits, through observations of color-banded individuals. I also maintained captive *Z. borbonica* on Reunion Island and at the University of Michigan.

I visited 102 localities on Reunion Island; these are listed by reference number in Appendix I and are shown on an outline map of the island (Figure 6). The locality names and coordinates were taken from the topographical map mentioned earlier.

The few specimens of *Zosterops borbonica* contained in major collections are labelled only "Reunion Island" and consequently had little or no value for the present study of variation within the island's confines. As a result all specimens used in this study were obtained during the two above-mentioned expeditions. The 1964 specimens have been deposited in the U. S. National Museum collections and the rest in the collections of The University of Michigan Museum of Zoology. In all, 759 specimens from 76 different localities were taken. I would remind those persons who may feel some concern about taking specimens of an endemic bird species from a small oceanic island not

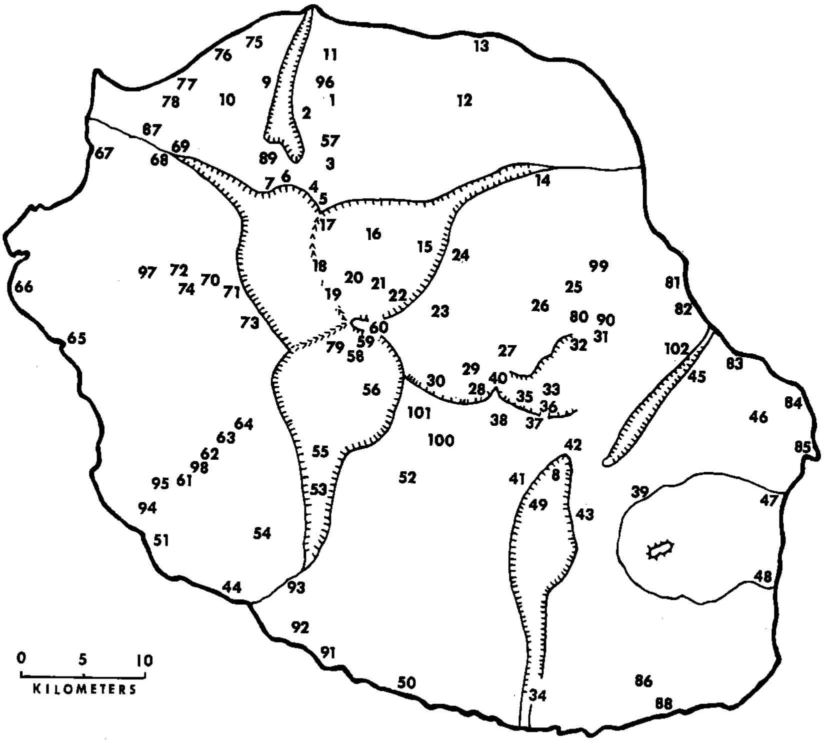

Figure 6. Localities visited on Reunion Island (see Appendix I).

only that *Zosterops borbonica* is abundant on Reunion Island, having undoubtedly benefited from human disturbance rather than suffered, but also that the species continues to flourish despite annual predation by local inhabitants.

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.

BIOLOGY OF *ZOSTEROPS BORBONICA*

Zosterops borbonica is an endemic Mascarene species found only on the two main islands, Mauritius and Reunion. Although 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 Zosteropids. Furthermore, the species has acquired white "anklets," a distinctive white rump patch formed by the white upper tail coverts, and white axillary feathers which are frequently exposed like sunbird pectoral tufts. *Zosterops borbonica* was once included in the genus *Malacirops* with the gray white-eye (*Z. modesta*) of the Seychelles Islands, but Moreau (1957:400) maintained that the few plumage peculiarities distinguishing these species did not merit separate recognition at the generic level. He consequently synonymized *Malacirops* with *Zosterops* (see also Moreau, 1967). To date there is no evidence as to the affinities of *Zosterops borbonica.*

Color variation in Reunion *Zosterops borbonica* was recognized in various early works, but its nature was subsequently the source of much taxonomic confusion and speculation. Pollen and van Dam (1868:74), the first authors to recognize the extent of the color variation, thought it resulted from individual but not sexual differences. Shortly thereafter, Hartlaub (1877:95) restricted the name "*borbonica*" to brown-backed, gray-headed forms and, on the basis of two specimens in the Newton collections now at Cambridge University, described (pp. 97–98) 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 underparts. Gadow (1884:195–196) 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 he 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, respectively. Gadow also suggested that the brown-backed form could represent the winter plumage of the species rather than the adult female. Newton and Newton (1888) criticized these conclusions and supported Hartlaub's earlier recognition of two species.

Patterns of geographic distribution of the various color forms were first described by Storer and Gill (1966), who delineated four subspecies (see frontispiece) from Reunion Island: *Z. b. borbonica,* a gray-headed, brown-backed form of the island's northern lowlands; *Z. b. xerophila,* a dry western lowland form which was entirely brown above and whitish below; *Z. b. alopekion,* a brown-backed, brown-headed form with dark gray and brown underparts from the central forests; and *Z. b. edwardnewtoni,* an all gray form from the highland heath zone. Moreau (1967:333) maintained the conventional pair of subspecies, Z. *b. mauritiana* on Mauritius Island and Z. *b. borbonica* on Reunion Island.

Unlike most remaining endemic Reunion birds, which depend on the remnants of indigenous forest, *Z. borbonica* is common in most habitats, including gardens, evergreen forests, *Casuarina* forest, and highland heath. But despite its seemingly broad habitat tolerances, it is primarily a species of open and disturbed areas rather than intact forests; its present distribution reflects the widespread destruction of original habitats. In tracts of undisturbed interior forests it is decidedly scarce except at the edges of large clearings and along streambeds.

Like most white-eyes, *Z. borbonica* is a social species usually encountered in parties of 6 to 20 individuals. Such flocks are formed throughout the year although there is a tendency for the birds to break up into pairs at the height of the breeding season. I rarely observed intraspecific aggression; it never seems to be associated with territorial or nest site defense. When groups of feeding *Z. borbonica* pass close to active nests they are joined by the nesting birds, not chased, and nests are sometimes built within 50 feet of each other in a loose colonial arrangement.

Throughout the year individual *Zosterops borbonica* frequently huddle closely together in pairs or groups while resting or engaging in mutual preening. Such allopreening has been noted in other species of white-eyes (Harrison, 1965:195; Eddinger, 1967). I have never witnessed any aggression in *Z. borbonica* that was the result of proximity. Rather, a white-eye avoids the huddling actions of another individual simply by leaving. Only rarely does a single resting white-eye refuse an opportunity to huddle, and in the Mascarene forests it is commonplace to see two white-eyes sidle along a branch until they touch each other.

Z. borbonica feeds primarily on insects, but eats a variety of fruits particularly during the winter. Flower feeding is frequent at certain favored flowers. A detailed discussion of *borbonica*'s feeding ecology is available in Gill (1971).

Zosterops borbonica coexists on Reunion Island with *Zosterops olivacea*, which is an aggressive, nonsocial, specialized flower feeder. *Zosterops olivacea* feeds primarily at flowers, catches insects by fly-catching, and rarely eats fruit. It is usually found in pairs, not flocks, and defends selected flowering plants against both *Z. borbonica* and other *Z. olivacea*. *Zosterops olivacea* also is more closely tied to the complex forests of the central highlands where there is a variety of suitable flowers. *Zosterops olivacea* seems to have been the first white-eye to colonize the Mascarene Islands and *Zosterops borbonica* arrived sometime later. The differences between the two species and their probable evolution are discussed in detail elsewhere (Gill, 1971).

Breeding in *Zosterops borbonica* is seasonal as it is in most Mascarene species and occurs during the austral summer. In early August, 1967, I noted a sudden increase in testicular size in these birds; enlargement continued until full size, averaging about 7 × 5 mm, was reached in early October. Preceding this morphological indication of breeding readiness, however, were noticeable changes in behavior. Starting in the last week of July intraspecific chases with repeated displacement were regular in feeding white-eye flocks. Certain apparently subordinate individuals often quivered their wings even when not being chased, and aggressive individuals often prominently displayed their white axillary tufts and rump patch. Pronounced vocal activity including elaborate singing began at about the same time as the intraspecific chasing.

Nesting begins in late September and October and continues through December, perhaps into January and February. In 1967 I noted the first fledged young on 14 October and found both fledged young and evidence of nestlings up to the last day of field work on 21 December. The peak of breeding activity seems to occur in October and November; local residents confirm this observation. While I have no evidence of double broods the presence of many nests with eggs in December, 1948 (Milon, 1951:141), suggests that some pairs may breed more than once a year.

Although the general timing of breeding was the same throughout Reunion Island from September through December, there were some indications of local variability. I found nests with eggs in the second week of September in the wet lowlands at Beaufonds (Ste. Marie). Yet in the highlands at le Tévelave (1,700 m) and Cilaos (900 m) I did not observe active nest building until the first week of October despite regular checks. On the dry west coast there was an abortive nesting attempt at Etang Salé les Bains in mid-September that coincided with an abnormal and temporary burst of growth of the vegetation, but elsewhere on this coast (e.g., St. Paul) nest building was not observed until the end of October. Thus it seems likely that local populations breed in accord with local seasonality, which may stagger the onset of nesting as much as a month between different localities.

Cooperative feeding of the young takes place at least in certain circumstances. The only *Z. 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 brought 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. Isolated family groups occasionally included an extra male that actively fed the young. Similar cases of cooperative feeding 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, 1968:80).

In *Zosterops borbonica* a complete, prebasic molt follows breeding. Of 83 adult *borbonica* specimens taken in December, 13 were molting body feathers. Presumably January through March, the warmest months of the year, are the months when the majority of the population molts, but I have no information for this period. Of the 143 specimens handled in May, 15 were completing their molt with traces of body molt and molting feathers in the crown being evident. All *borbonica* collected or banded at this season were in fresh, unworn plumage. No molt of any kind was evident during June and most of July, but an incomplete (pre-alternate) molt, restricted primarily to the head, was taking place in 45 of the 103 *borbonica* banded in August and September. This molt results in no change of the plumage coloration. I have no information on the extent of the postjuvenal (first prebasic) molt which presumably takes place from January to March at the same time as the adult prebasic molt.

Except for local concentrations of individuals at abundant food sources, populations of *Z. borbonica* appear to be sedentary throughout the year. First there were no major changes in the distribution of white-eyes during my field work from April to December, 1967. Also, individuals color-marked during the winter months at several localities were resighted at these same localities during the nesting season. For example, of the 44 individuals I color-banded at the edge of the Forêt du Bébour on 30 April and 1 May, 4 were observed during brief visits to this locality in September and December. At Plaine des Chicots I color-banded 19 *borbonica* in early May, and resighted 4 of these in the same hollow during two hours of observation in early September. Finally 11 of 37 individuals banded near Cilaos, in late July and early August, were seen again between 16 October and 20 December in the same tract of forest. These observations indicate that while *Zosterops borbonica* may be quite mobile within a particular area, local populations are sedentary.

White-eye predators are few on Reunion Island. No owls or small bird hawks are known from the island and the large native harrier, *Circus aeruginosus*, shows no aptitude for catching small forest birds, but feeds instead on introduced mammals and gallinaceous birds. In the lowlands, nest predation by rats, an introduced snake (*Lycodon aulis*), and an introduced lizard (*Calotes versicolor*) has been reported by local residents. Although the practice is officially discouraged, large numbers of white-eyes are still caught for food by the natives of Reunion Island with bird lime.

COLOR VARIATION IN *ZOSTEROPS BORBONICA*

Specimen Examination

I evaluated color characters visually against a standard gray background in north sky light on bright to cloudy bright days in the morning in Ann Arbor, Michigan. I evaluated each character independently of the others and subdivided it into a series of character states that included as many intermediate categories as I could consistently distinguish (Table 1). I compared each specimen to a reference specimen which represented each character state. I also studied, through microscopic examination, the distribution and intensity of feather pigments.

Basis of the Color Variation

In *Zosterops borbonica*, as in certain other birds, for example, *Junco* (Miller, 1941:179) and *Parus* (Frank, 1938:164), color variation depends

TABLE 1

Index to Color Characters in *Zosterops borbonica*

Character	Character states	Reference specimen[1]
Back color	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
Head color		
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
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
Face	0 – entirely gray	213 577
	1 – ocular gray and postauricular gray continuous and broad with only slight brown	213 569
	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	213 661
Auriculars	0 – pure gray	213 567
	1 – slight brown, especially 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
Underpart color		
Amount of gray	0 – white	213 901
	1 – increasing intensities of gray	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
Amount of brown in breast	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

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[1] University of Michigan Museum of Zoology specimen numbers.

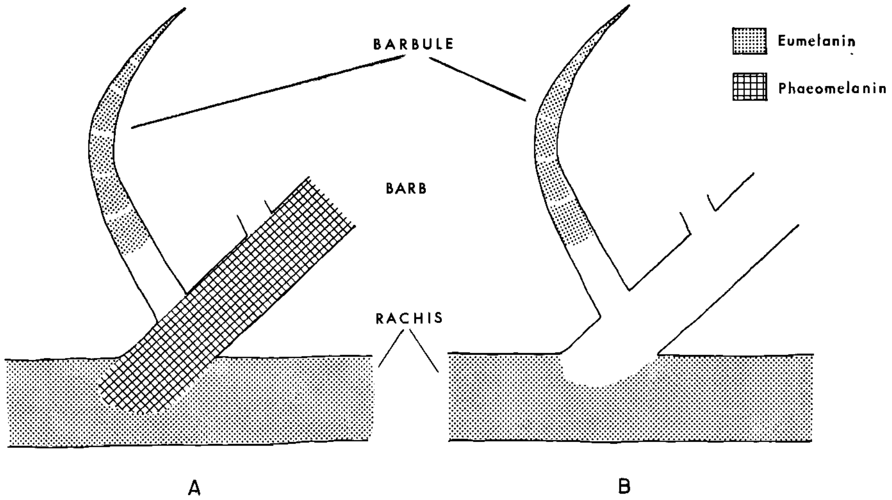

FIGURE 7. Distribution of pigments in a brown (A) and a gray (B) feather of *Zosterops borbonica.*

on the presence and amount of two types of melanins: eumelanins, which are blackish granules, and phaeomelanins, which are reddish or light brown granules. The eumelanins of *Zosterops borbonica* are type B granules (see Moreau, 1957:323) deposited in dense concentrations in the barbules and to a lesser extent the rachis of each feather, but not the barbs (Figure 7). The phaeomelanins correspond to Moreau's type C granules and are deposited in the barbs and rachis but not the barbules. The basic difference between gray and brown in the plumage of *Zosterops borbonica* lies simply in the addition of phaeomelanins to a feather with eumelanin to produce brown.

Several important aspects of the color variation depend on where phaeomelanins are deposited in the plumage. 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 due to sex or age differences once the definitive plumage is attained.

BACK COLORATION

Dimorphism.—I distinguished five categories of back coloration in my specimens of *Zosterops borbonica* from Reunion Island (Table 1). Of the 343 adult specimens from localities with more than one phenotype for back color, 301 (87.7 per cent) are either pure gray-backed (Category 0) or pure brown-backed (Category 4), whereas only 42 specimens (12.3 per cent) are intermediate (Figure 8). Of the 42 intermediate specimens, 30 were classified in Category 1, 5 were put in Category 3, and only 7 (2 per cent) were

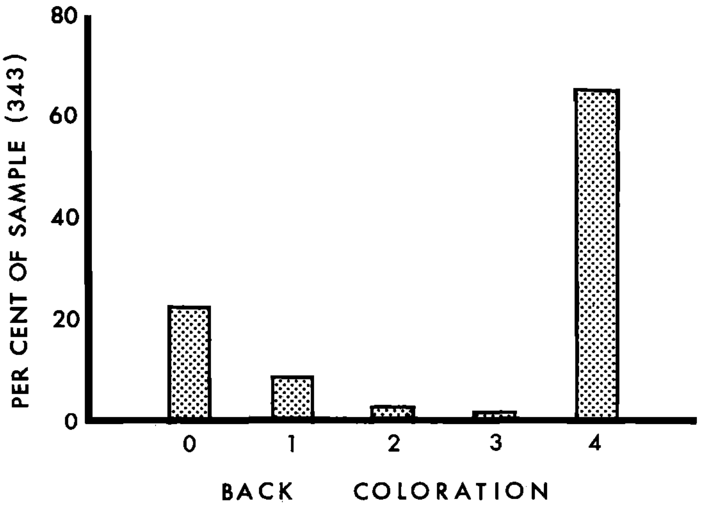

FIGURE 8. Back coloration of 343 adults from localities known to have more than one back color phenotype. Category 0, "pure" gray morphs; Categories 1–3, intermediates; Category 4, "pure" brown morphs (see Table 1).

markedly intermediate, i.e., in Category 2. Thus this character is strongly dimorphic, with only a slight tendency towards intermediacy, and intermediacy usually involves scattered traces of brown pigmentation in otherwise gray-backed individuals. Pure gray-backed individuals tend to have traces of brown elsewhere in the plumage particularly on the flanks, and specimens in intermediate back color categories show corresponding increases in the intensity of brown in these areas. Unless otherwise stated, when I use the terms "gray morphs" and "brown morphs" I am referring to individuals in Categories 0–1 and 3–4, respectively.

Geographic distribution of gray and brown morphs.—The proportion of gray morphs was ascertained for the 83 localities for which 6 or more individuals (specimens and sight records combined) were available.

The 45 localities at which gray morphs or intermediates were recorded comprise a large, continuous region in the center of the island (Figure 9); none are at coastal localities. At only one locality (number 42 at 2,300 meters) did I find only gray morphs; no specimens were taken but all nine birds observed there were assignable to categories 0 or 1. In contrast, many lowland localities have only brown morphs.

I counted the numbers of gray and brown morphs at several localities during the early winter and again at the beginning of breeding season (Table 2). Some variation between counts, due primarily to sampling error, is present

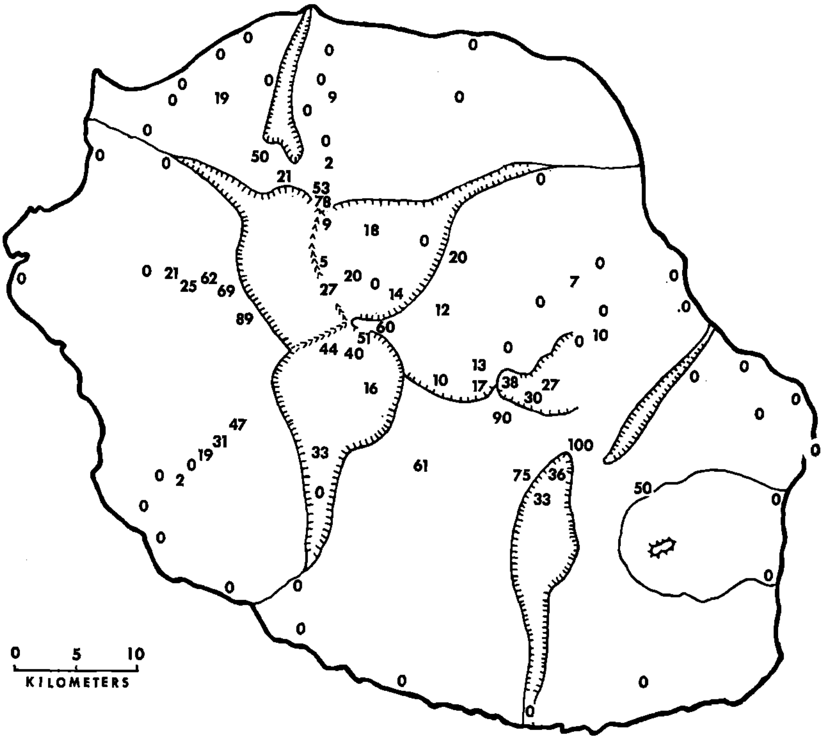

FIGURE 9. The percentage of gray morphs (including Category 1) found at each of 83 major sampling localities where data for six or more individuals were available.

and to be expected in these data, but the consistency of the results for each locality is evidence of seasonal stability of the ratio of the two morphs.

An exception to this general observation was noted at Nez de Boeuf (Plaine des Cafres) at 2,060 meters elevation on the edge of the Ravine de la Rivière des Remparts, where an endemic leguminous tree, *Sophora nitida*, whose flowers seem especially attractive to white-eyes, was abundant. The relative frequency of gray morphs at this locality increased from 30 per cent to about 70 per cent between August and early September, 1967, as the *Sophora* flowers waned (Figure 10). The stabilization of the morph ratio after early September, as well as my observations of white-eyes moving up and down the adjacent cliffs during the day at the height of the *Sophora* flowering, indicate that brown morphs move up temporarily from the adjacent lowlands to feed at these flowers.

Altitude is the most important factor affecting the distribution and relative abundance of gray morphs. A regular altitudinal increase in the percentage of gray morphs occurred along five transects I made from the coast to the highlands in areas of relatively continuous, undissected topography (Figures 11, 12, and 13). On four of the five transects the relative abundance of gray morphs increased continuously with altitude above 1,350 meters. On the fifth transect (St. Benoît to la Plaine des Palmistes—open triangles in Figure 13), the relative abundance of gray morphs increased continuously above 720 meters elevation; the predominance of open scrub, which is physiognomically similar to heath, rather than forest at low altitudes may have been influential because scrub vegetation was present at all non-cirque localities below 1,300 meters elevation where gray morphs were recorded (Table 3). This is evidence of specific habitat preferences by gray morphs. With only one exception (locality 52) high gray morph frequencies (over 60 per cent) were not recorded below 1,600 meters elevation (Table 3).

Topography also affects the proportions of gray morphs. This can be seen in samples from inside the deeply eroded cirques. The data available for the Cilaos and Salazie cirques (Figure 14) show high gray morph frequencies at relatively low elevations and marked fluctuations in the percentage of gray morphs at different altitudes. 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. This great reduction of distances separating extreme altitudes promotes unpredictable mixtures of

TABLE 2

SEASONAL STABILITY OF THE PROPORTIONS OF BROWN AND GRAY MORPHS AT VARIOUS LOCALITIES ON REUNION ISLAND

Locality	Date	Number of gray morphs	Number of brown morphs	Per cent gray	Type of record
4	4–6 May	10	7	58.8	Banded birds
	9 September	10	10	50.0	Sight
5	7 June	24	5	82.7	Sight
	9 September	44	16	73.3	Sight
16	19 April	2	10	16.7	Sight
	20 June	2	10	16.7	Specimens
	3 November	2	8	20.0	Sight
27	12 May	0	21	0	Sight and specimens
	26 November	0	12	0	Sight and specimens
40	28 April–1 May	15	29	34.1	Banded birds
	6 September	10	14	41.6	Sight
58	15 June	33	53	38.4	Sight
	26–29 July	11	17	39.3	Banded birds
	17 October	10	15	40.0	Sight
73	25 May	9	1	90.0	Specimens
	5 November	12	1	92.3	Sight and specimens

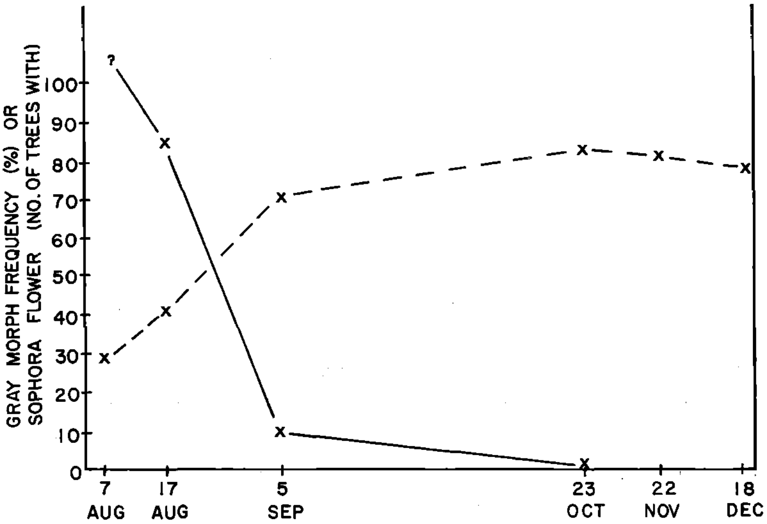

FIGURE 10. Temporal change in the ratio of gray morphs (dashed line) and abundance of *Sophora* flowers (solid line) at Nez de Boeuf. The data are for 1967, except those for November are from 1964.

color forms, because any movement up or down the cliffs by white-eyes would quickly alter the situation existing as a result of altitudinal effects.

Behavioral interactions of gray and brown morphs.—I have analyzed several behavioral features to determine whether brown and gray morphs associate non-randomly. On 9 September on the Plaine des Chicots, when white-eyes were coming into breeding condition but prior to actual nesting, I encountered many isolated foraging pairs (bisexual?) of white-eyes and recorded the morphs involved. At Cilaos I recorded the morphs involved in all intraspecific chases noted early in the breeding season, as well as for established pairs of breeding adults, and pairs of white-eyes engaged in huddling and allopreening. The expected frequencies of various possible associations were calculated from the observed percentages of both morphs present in the two areas. The observed and expected frequencies were then tested for significance by use of a χ^2 test (Table 4). Both the associated pairs of white-eyes at Plaine des Chicots and the mated pairs at Cilaos proved to be random with respect to plumage type. On the other hand huddlings and chases were recorded more frequently between like morphs than was to be expected if the partners had been chosen randomly from the total local population. Interpretation of these results is clearly difficult; however a lack of morph discrimination in relation to mating, as is suggested by the random pairing associations at Cilaos, would result in the maintenance of polymorphism.

Genetics of back coloration.—Juvenal *Zosterops borbonica* have patterns of upperpart coloration similar to those of the adults. Some are entirely gray corresponding to the pure gray morph adults and have similar variations in the presence of brown in other parts of the plumage. Others are brown and equivalent to brown morph adults in both back and head coloration.

Most of my specimens in juvenal plumage were taken with presumed parents near Cilaos where both brown and gray morphs are common, the former predominating about 3:2. I avoided flocks that included several families and instead concentrated on finding isolated family groups. After establishing that the adults present were feeding the young, I collected the

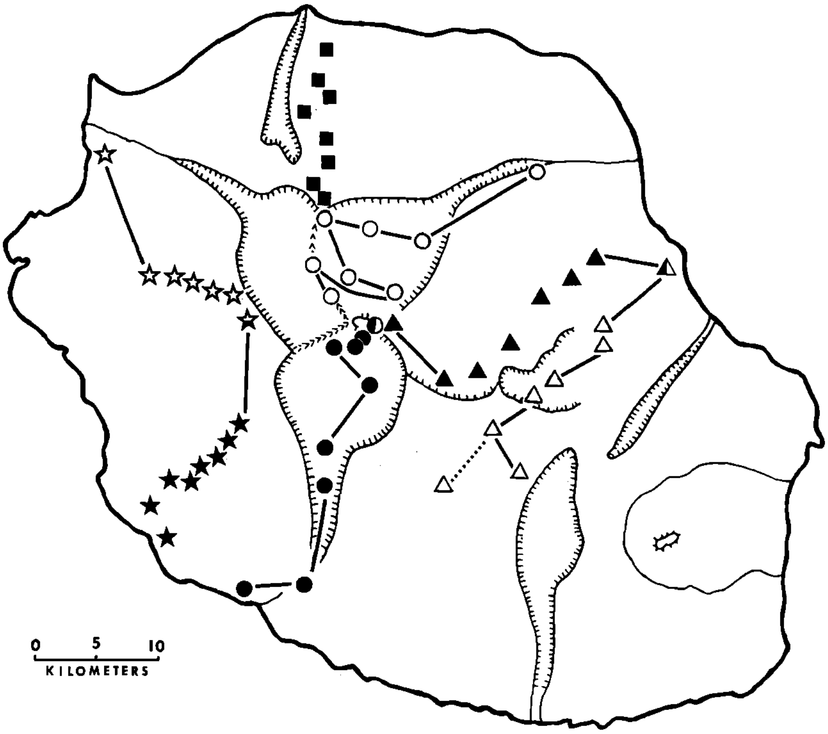

FIGURE 11. Transects made on Reunion Island.

Transects from coastal to highland areas: *Open stars,* St. Paul to Piton des Epinards via le Petite France (Localities 67, 97, 72, 74, 70, 71, 73 in sequence); *Closed stars,* Étang salé les Bains to Piton des Epinards via le Tévelave (Localities 51, 94, 95, 61, 98, 62, 63, 64, 73 in sequence); *Squares,* St. Denis to Plaine des Chicots (Localities 11, 96, 1, 2, 57, 3, 4, 5 in sequence); *Closed triangles,* St. Benoît to Plaine des Salazes via Takamaka and Forêt du Bébour (Localities 81, 99, 25, 26, 27, 29, 30, 60 in sequence); *Open triangles,* St. Benoît to Plaine des Cafres via La Plaine des Palmistes (Localities 81, 90, 31, 33, 35, 52, 38, 41 in sequence).

Transects in deeply eroded cirques: *Open circles,* Cirque de Salazie (Localities 14, 15, 16, 17, 20, 22, 18, 19, 60 in sequence); *Closed circles,* Cirque de Cilaos (Localities 44, 93, 53, 55, 56, 79, 58, 59, 60 in sequence).

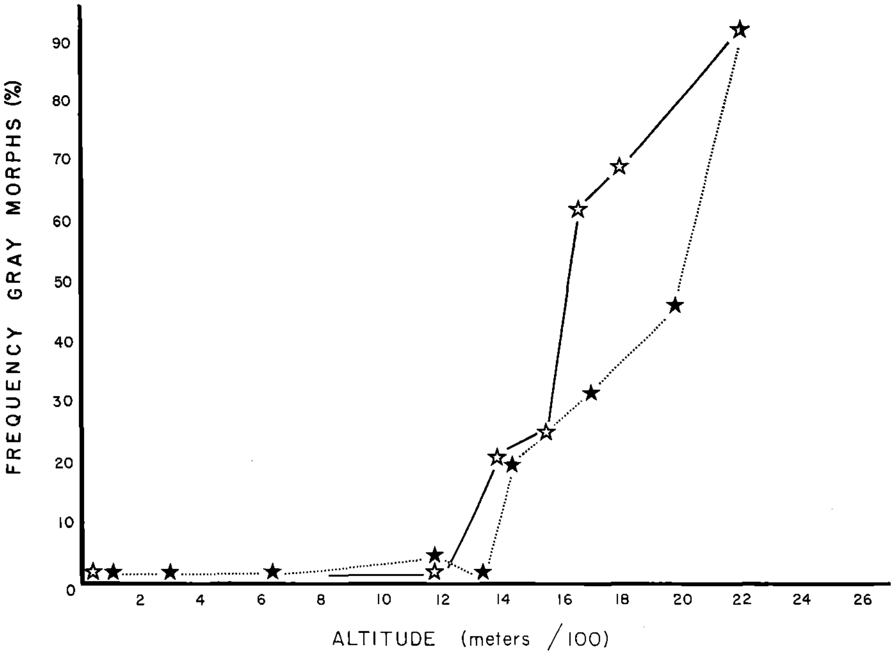

Figure 12. Altitudinal relationships of gray morph frequencies on west slope transects. See Figure 11 for localities and symbols.

entire group or as many as possible. In two such family groups an extra adult male was helping the presumed parents feed the young, but each of these "helpers" was the same in plumage color as the presumed male parent and thus did not affect the color relationships in question. I placed the juvenal specimens in color categories equivalent to those used for adults (Table 1), except I omitted Category 3 because I doubt that it is discernible in this plumage.

The mixed broods collected (Table 5) suggest that the genetic basis of back color may involve a simple pair of alleles with some modifiers. The production of a brown morph young by gray parents and the consistent production of brown young by brown parents suggest that gray is dominant over brown.

In conclusion, the sympatric occurrence of gray and brown morphs at numerous upland localities, the formation of mixed pairs, and the production of mixed broods seem to leave little doubt that the discontinuous variation in back color and associated characters of *Zosterops borbonica* on Reunion Island conforms to a classical situation of genetic polymorphism. This has been defined as "the occurrence together in the same locality 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, 1964:84). The altitudinal variation in the proportions of the two morphs presumably reflects

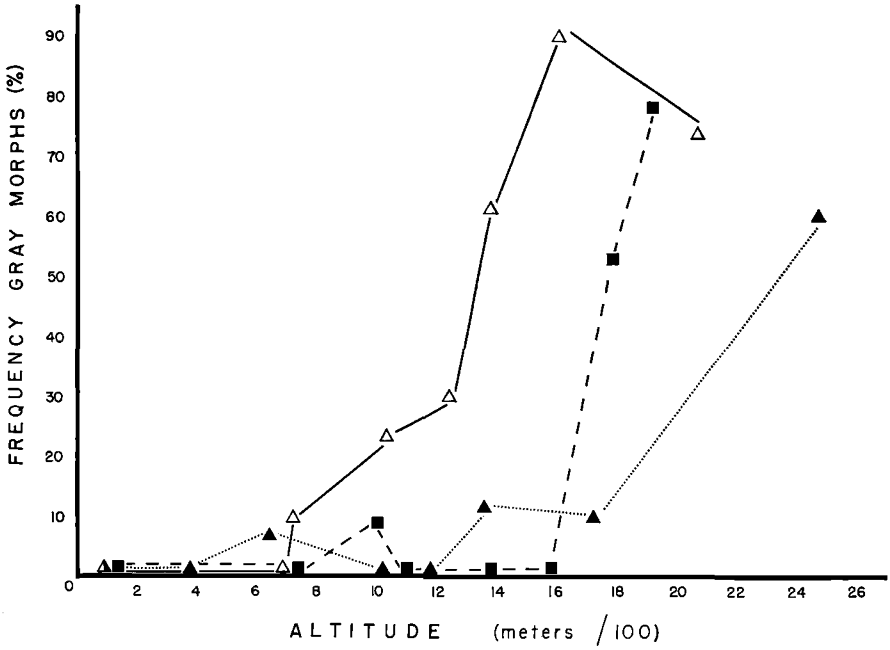

FIGURE 13. Altitudinal relationships of gray morph frequencies on north and east slope transects. See Figure 11 for localities and symbols.

a difference in the selective advantage of one genotype over the other under certain environmental conditions.

HEAD COLORATION IN BROWN MORPHS

All gray morphs have gray heads. The color of the head of brown morphs varies from entirely gray to entirely brown. I have considered four characters for head coloration: crown, nape, face, and auriculars (Figure 15), each of which I subdivided into five character states representing increasing amounts of phaeomelanin pigmentation (Table 1). To obtain a single Head Character Index (HCI) for each specimen, I summed the values of the four character states, thus producing 17 indices ranging from the entirely gray-headed form (HCI = 0) to the entirely brown-headed form (HCI = 16). Over one-half of the 592 brown morph specimens in my collection scored either 0 or 16, and the remaining 45.3 per cent were distributed among the 15 intermediate indices (Figure 16).

Brown pigment appears in the nape before it does elsewhere on the head, and, as it increases in intensity on the nape, is gradually added to the crown. The appearance of brown in the auriculars is closely correlated with its appearance in the crown, but the face is brown only in those specimens with intense

TABLE 3

SYNOPSIS OF GRAY MORPHS LOCALITIES

Locality number[1]	Altitude (meters)	Vegetation	Sample size	Per cent gray morphs[2]
60	2,460	Heath	10	60
39	2,300	Heath	12	50
42	2,300	Heath	9	100
73	2,200	Heath	28	92
41	2,060	Heath	112	75
59	2,000	Heath	35	51
64	1,980	Heath	32	47
19	1,940	Heath	11	27
5	1,910	Heath	89	78
71	1,780	Tamarin	103	62
4	1,780	Tamarin and Heath	47	54
30	1,720	Forest	20	10
63	1,700	Tamarin	67	31
8	1,700	Forest	11	36
70	1,660	Tamarin	24	62
6	1,650	Forest	24	21
38	1,600	Heath	48	90
23	1,590	Forest	8	12
3	1,580	Forest	63	2-GH
74	1,550	Tamarin	40	25
18	1,530	Forest	20	5
62	1,440	Forest	36	19
72	1,400	Acacia and Forest	19	21
58	1,400	Forest	79	40
24	1,400	Forest	10	20
40	1,400	Forest	63	38
52	1,380	Acacia and Heath	13	61
89	1,360	Forest	26	50
28	1,360	Forest	37	16
22	1,350	Forest	42	14
29	1,350	Forest	23	13
35	1,250	Forest and Scrub	10	50
20-C	1,160	Scrub	20	20
17	1,100	Gardens and Scrub	11	9
61	1,080	Forest and Scrub	41	2
33	1,060	Acacia and Scrub	11	27
49	1,060	Scrub	15	33
1	1,000	Scrub	33	9-GH
56-C	1,000	Casuarina	31	16
79	900	Scrub	18	44
10	820	Scrub	16	19-GH
31	720	Scrub	31	10-GH
16-C	680	Scrub	27	18
25	640	Scrub	15	7-GH
55-C	300	Casuarina	27	33

[1] C = Cirque locality.

[2] GH = Locality at which the brown morphs have gray heads.

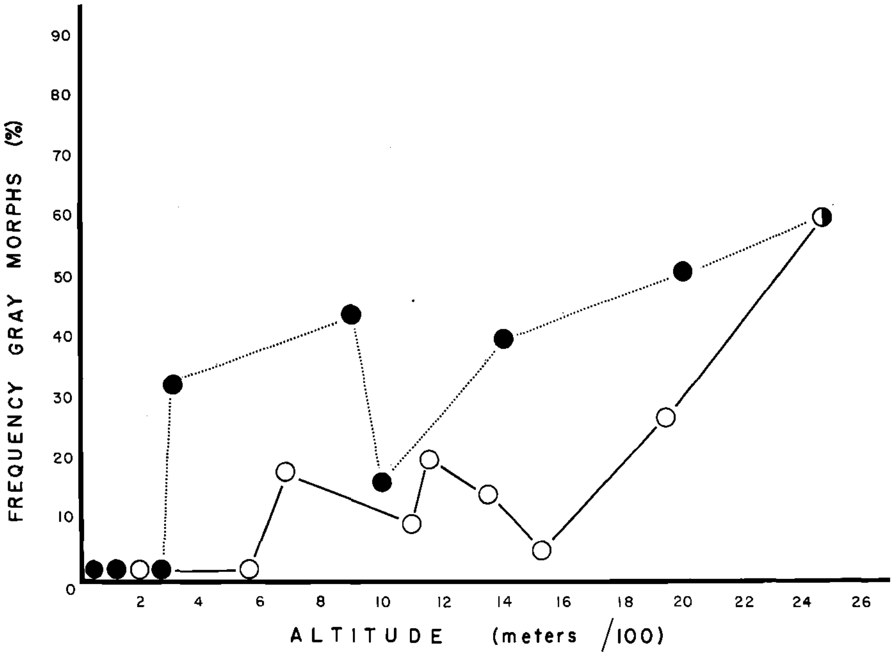

FIGURE 14. Altitudinal relationships of gray morph frequencies on cirque transects. See Figure 11 for localities and symbols.

brown in the crown. This correlation produces three categories of brown morphs that are visually distinct in the field: those with all gray heads (HCI 0–2), those with discernible brown on top of the head (nape and crown) but with gray faces (HCI 3–9), and those with brown heads and faces (HCI 10–16).

I calculated the mean Head Character Index of all adult brown morph specimens from each locality (Figure 17). Mean indices at the brown end of the spectrum (12–16) characterize localities on the west side of the island from the Rivière des Galets to the Rivière St. Etienne, the cirques of Cilaos and (probably) Mafate and the island's central highlands. Indices at the gray end of the spectrum (0–3.4) characterize localities below 1,580 meters elevation on the north and 1,380 meters elevation on the east side of the island. A band of intermediate indices (8–11) about five kilometers wide connects the ranges of the two extreme types on the eastern slope in the interior of the island. This zone of contact 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. On the northwest coast the region of contact is reduced to the rocky bed of the Rivière des Galets, about 500 meters across. Here the mean index changes

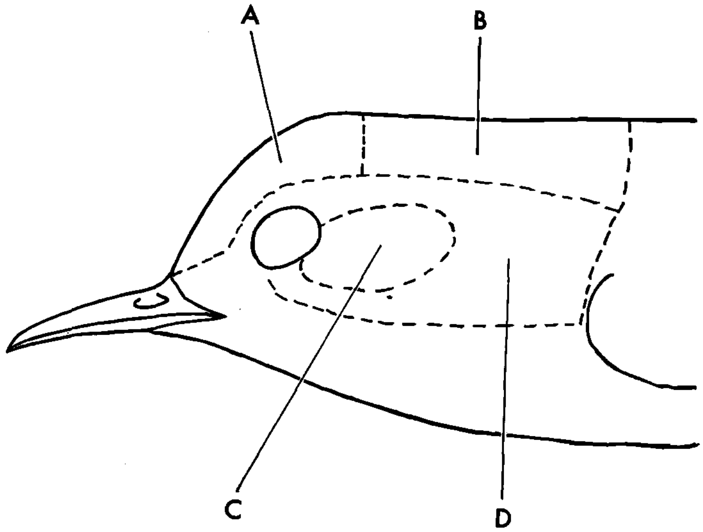

FIGURE 15. Areas of the head used to determine the Head Character Index: A, crown; B, nape; C, auriculars; D, face.

abruptly from 13.6 on the river's south side (locality 68) to 2.9 on the river's north side (locality 87).

Low but intermediate indices (5.0–6.2) also characterize localities on the island's southern coast between the Rivière St. Etienne and Bois Blanc. Paralleling the abrupt change on the northwest coast at the Rivière des Galets is a sharp break in the mean index across the Rivière St. Etienne, from 14.1 on the north side (locality 44) to 5.4 on the south side (locality 93). Head coloration also changes abruptly across a coastal lava flow just south of Bois Blanc. Observations just to the north of locality 47 revealed primarily pure gray-headed birds, while on the south side of the lava flow all white-eyes observed had sufficient brown on the nape to be discerned through field glasses. This brown-naped form is characteristic of all coastal localities between Rivière St. Etienne and Grand Brûlé. Frequent examples of this form also appear in a disjunct pocket at localities 98 and 62 above le Tévelave, resulting in lower mean indices there than at surrounding localities.

Throughout the island the mean index tends to increase with altitude. On the west coast some gray is present in the face of most birds, while, at higher elevations on the slopes faces are completely brown. On the eastern slopes the increase in mean index reflects the change from lowland gray-headed forms to highland brown-headed forms, including some introgression of brown head color characteristics into localities below the zone of contact.

Increased phenotypic variation is evident in the zone of contact (Figure 18) and reflects interbreeding between the brown-headed and gray-headed forms. Nevertheless over 50 per cent of the specimens from localities in this zone are typical extreme forms (HCI 0–1 or 15–16), indicating the operation of isolating mechanisms of some kind.

The most obvious environmental factors correlated with the east-west separation of the gray-headed and brown-headed brown morphs are the differences in rainfall (see Figure 4) and the corresponding differences in vegetation. The coastal range of the brown-headed form between the Rivière des Galets and the Rivière St. Etienne is uniformly arid receiving less than 100 cm of rain a year, whereas the wet southeast coast receives over 400 cm a year. High rainfall characterizes most of the coast occupied by the gray-headed form, except for the northwestern coast, but the climate there clearly is ameliorated by extensive irrigation and garden plantings.

An indication of differences in dehydration tolerances of these color forms was inadvertently obtained when I shipped 20 live *Zosterops borbonica* from Reunion Island to Michigan by airplane. The trip, which lasted 48 hours, tested the white-eyes tolerance of water deprivation because the water drinkers in the shipping box became clogged. Of the 20 birds in the shipment, 6 were gray morphs from le Tévelave, 6 were gray-headed brown morphs from Beaufonds (Ste. Marie), and 8 were brown-headed brown morphs from several

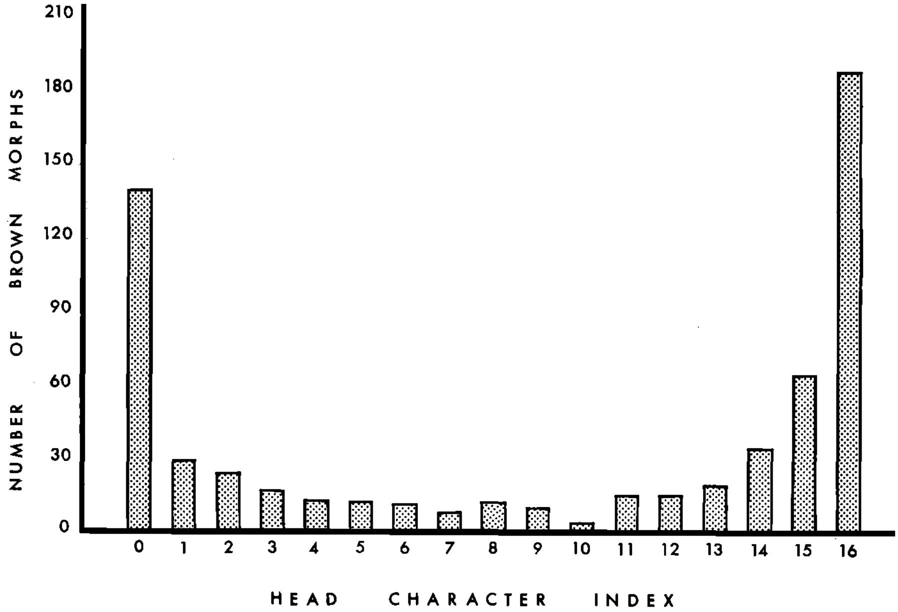

FIGURE 16. Number of brown morph specimens with given Head Character Indices (pure gray head = 0; pure brown head = 16).

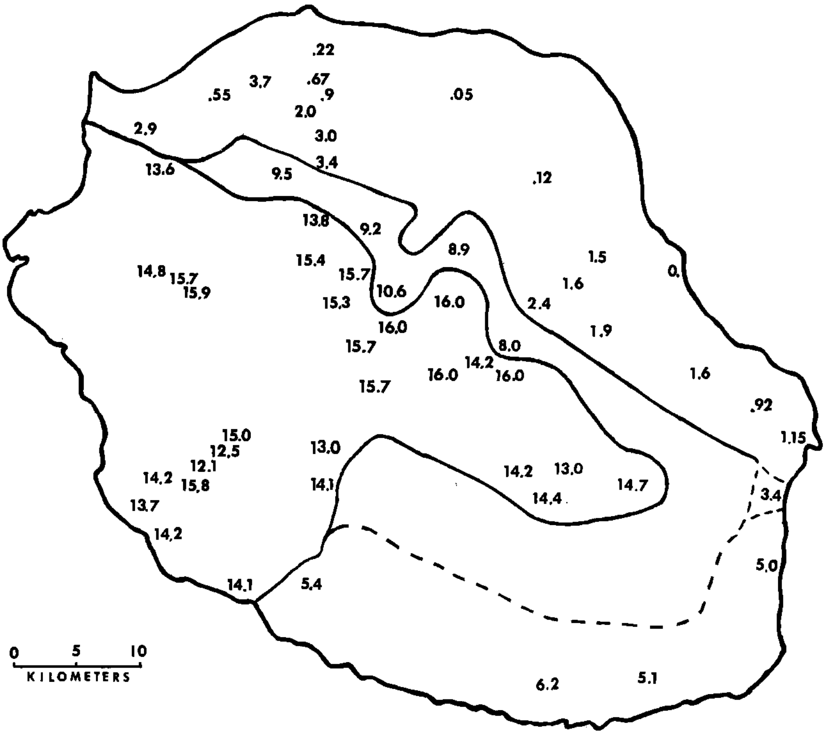

FIGURE 17. Geographic variation in head color of adult brown morph specimens. Figures indicated are mean Head Character Indices for each locality sampled. Lines delineate distributions of brown-headed brown morphs (11.5–16.0), gray-headed brown morphs (0–3.4), a zone of contact of these two (8.0–10.6), and brown-naped brown morphs (5.0–6.2).

locations on the west slopes. Only 2 of each of the first two categories survived the trip, whereas 7 of the 8 brown-headed individuals were alive, though dehydrated, upon arrival at Detroit, Michigan. The probability that such differences in survival would occur by chance alone is less than 1 in 10 (Table 6).

Brown-headed brown morphs range to the highest part of Reunion Island, while brown morphs with gray heads have a more limited altitudinal distribution, usually below 1,380 meters elevation. Thus brown-headed brown morphs replace gray-headed brown morphs at high altitudes as well as in the arid lowlands, and seem to occupy a wider range of climatic extremes. The selective advantage of brown-headed brown morphs appears to be lowered at the wet middle elevations on the west side of the island, e.g., localities 98 and 62 above le Tévelave, where I found small numbers of birds that had brown napes only included in the local populations.

TABLE 4

BEHAVIORAL INTERACTIONS OF GRAY AND BROWN MORPHS OF *Zosterops borbonica*

Association		Within morph			Between morph	χ^2
		Gray × Gray	Brown × Brown	Total		
Prebreeding associations (Plaine des Chicots)	Observed	6	2	8	4	.0003
	Expected			7.3	4.7	
Intraspecific Chasing (Cilaos)	Observed	3	12	15	4	4.19 5.514*
	Expected			10.3	8.7	
Mated pairs (Cilaos)	Observed	3	8	11	4	1.02
	Expected			8.1	6.9	
Huddling pairs (Cilaos)	Observed	6	17	23	3	29.84***
	Expected			14.1	11.9	

* $P < .05$.

*** $P < .001$.

TABLE 5

BACK COLOR OF ADULT *Zosterops borbonica* AND THEIR PRESUMED OFFSPRING

Back color of parents[1]			Number of pairs	Number of offspring of each back color[1]			
♂		♀		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

[1] See Table 1 for definitions of categories.

TABLE 6

DIFFERENTIAL SURVIVAL OF *Zosterops borbonica* COLOR VARIANTS UNDER CONDITIONS OF EXTREME WATER DEPRIVATION

Color variant	Lived	Died	Totals
Gray morphs and gray-headed brown morphs	4	8	12
Brown-headed brown morphs	7	1	8
	$\chi^2 = 3.71$[1]		

[1] $P < .05 = 3.84$; $P < .10 = 2.71$.

It should be apparent at this point that gray morphs occur primarily in the high altitude range of the brown-headed brown morphs. I recorded gray morphs at only five localities (numbers 1, 3, 10, 25, 31) in the range of the gray-headed brown morph, and at these localities they occur at low frequencies ranging from 1.7 to 19 per cent of the local populations. At locality 1 (1,000 meters) I collected a pair of recently fledged siblings, one of which was a gray morph while the other had a gray head and brown back; this observation is evidence that gray morphs and gray-headed brown morphs are compatible color phases.

The replacement of gray-headed white-eyes by brown-naped white-eyes near Bois Blanc takes place in a region of very high rainfall, but does not coincide with any conspicuous climatic change (see Figure 4). This situation may relate to the fact that the lush forests on the slopes of le Volcan are moderately wet forests of low altitudes (Rivals, 1952), which no longer are present elsewhere on the island. Also this is the only part of Reunion Island subjected to volcanic eruptions in recent times, and lava flows may serve to isolate these forms.

In summary (see Figure 19), a brown morph with a gray head is the form of the northern and eastern lowlands of Reunion Island. Its coastal distribution stops abruptly at the Rivière des Galets where it is replaced by a brown morph with a brown head south of the river, and also at the recent lava flows of Grand Brûlé where it is replaced by a brown morph with a brown nape and gray face. Although this brown-naped form occurs in low frequencies at scattered localities in the range of the gray-headed brown morph, the change from the predominance of one to the other across the lava flows at Grand Brûlé is pronounced. The brown-naped form is the only form of *Zosterops borbonica* at lowland localities on the south coast of Reunion Island as far west as the Rivière St. Etienne, where it is replaced by the brown-headed form on the opposite side of the river. The brown-headed form thus occupies the entire arid west coast of Reunion Island between the Rivière St. Etienne and the Rivière des Galets. Both riverbeds are only about 500 meters across and are dry, except for a small stream, during most of the year. Thus the coastal contacts of these forms all involve abrupt changes of phenotypes across conspicuous geographic barriers.

The altitudinal transitions between these same color forms are not as abrupt. The brown-headed form is found at all altitudes on the west side of the island, but is replaced by the gray-headed brown morph below 1,580 meters on the

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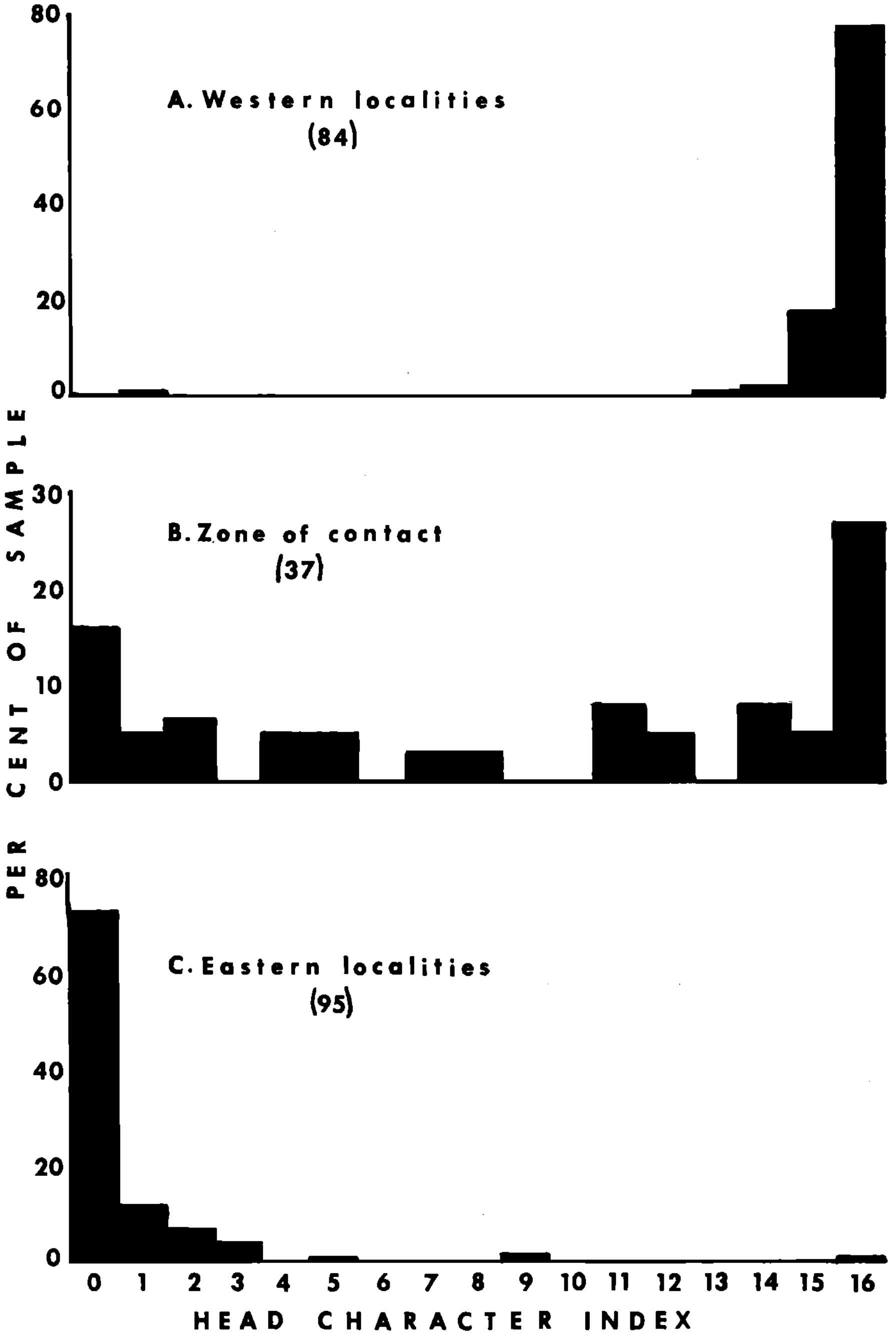
FIGURE 18. Head character variability in zone of contact (Localities 6, 16, 21, 24, 27) compared with adjacent areas (Western localities—18, 19, 20, 58, 56, 60, 30, 23, 29, 40; Eastern localities—12, 14, 25, 26, 99, 31, 81, 45, 46, 85). Sample size in parentheses.


A. Western localities
(84)
B. Zone of contact
(37)
C. Eastern localities
(95)
PER CENT OF SAMPLE
0
20
40
60
80
0
10
20
30
0
20
40
60
80
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
HEAD CHARACTER INDEX

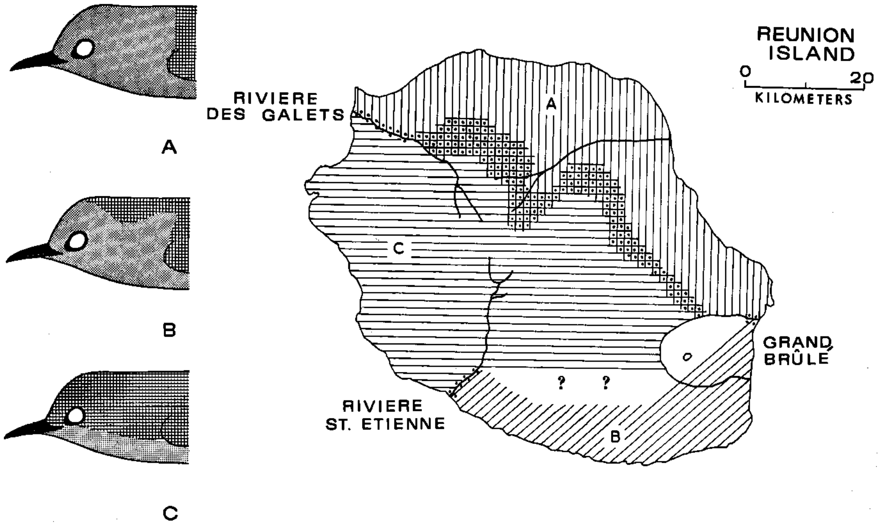


FIGURE 19. Distribution of brown morphs of various head colors. Zones of contact and overlap are indicated by dots within the crosshatching. In the figures of the birds, stipples indicate gray areas and crosshatching indicates brown areas.

north and 1,380 meters on the east sides of Reunion Island. The transition between the two takes place in a hybrid zone about five kilometers wide. Parental phenotypes compose at least 50 per cent of the hybridizing populations, suggesting the operation of some form of partial reproductive isolation. I have little information from the middle elevations on the south side of the island where the brown-naped form must also be replaced by the brown-headed form. Usually only brown morphs with brown heads occur at high altitudes with the gray morph.

UNDERPART COLORATION

Variation in the color of the underparts involves both phaeomelanin and eumelanin deposition. Eumelanins are distributed over the entire plumage of the underparts and vary in concentration to such an extent that the color of the underparts ranges from nearly pure white to lead gray. 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 confined primarily to the flanks and breast and thus are more restricted in the underpart coloration. While all brown morphs have intensely pigmented reddish-brown flanks, the phaeomelanin deposition in the breast plumage varies greatly.

Eumelanins.—To evaluate the eumelanin deposition in the underparts I compared all specimens with a series of nine selected specimens representing graded intensities of melanin deposition from white (Character State 0) to lead

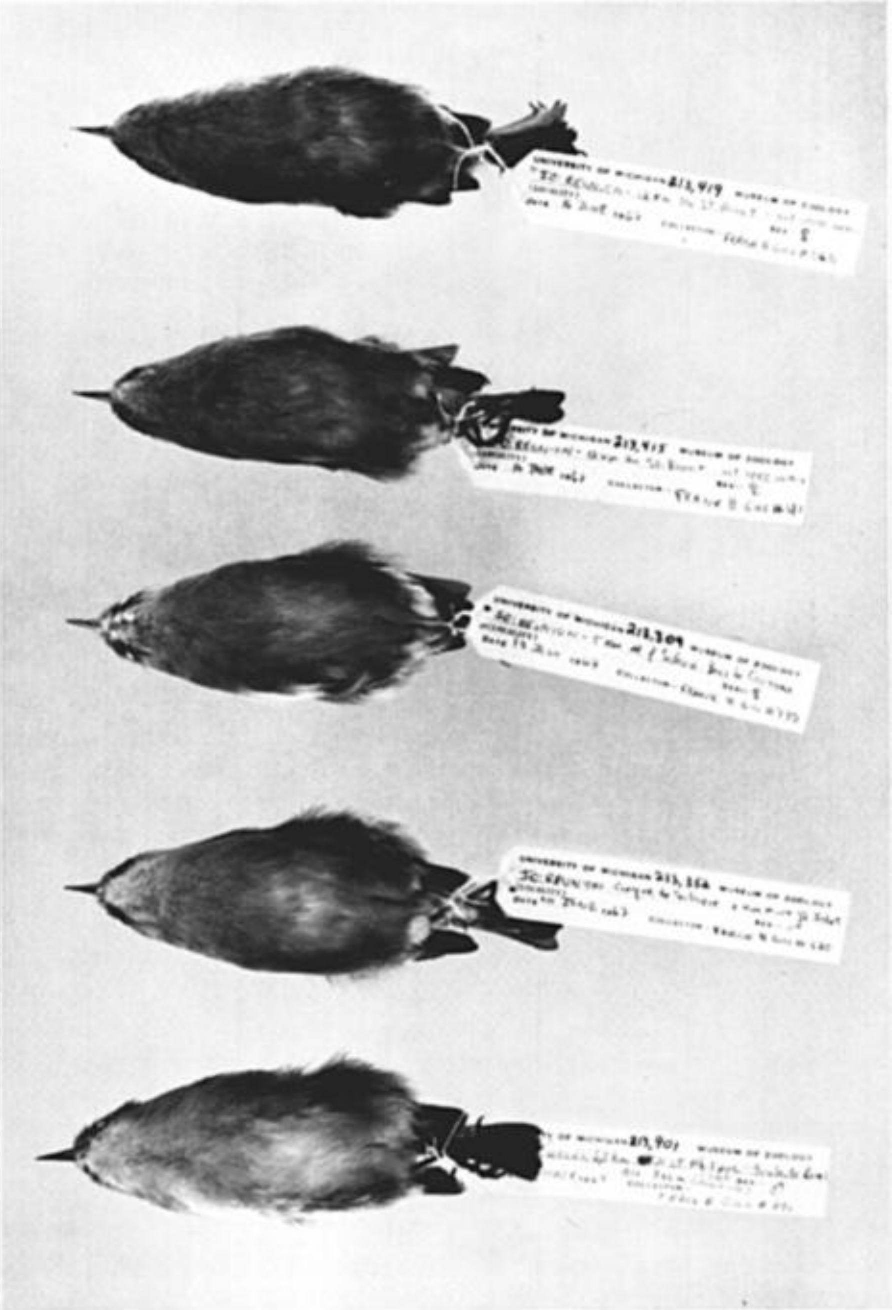


FIGURE 20. Some reference specimens used to represent different degrees of gray color in the underparts. From bottom to top—visual indices 0, 2, 4, 6, 9.

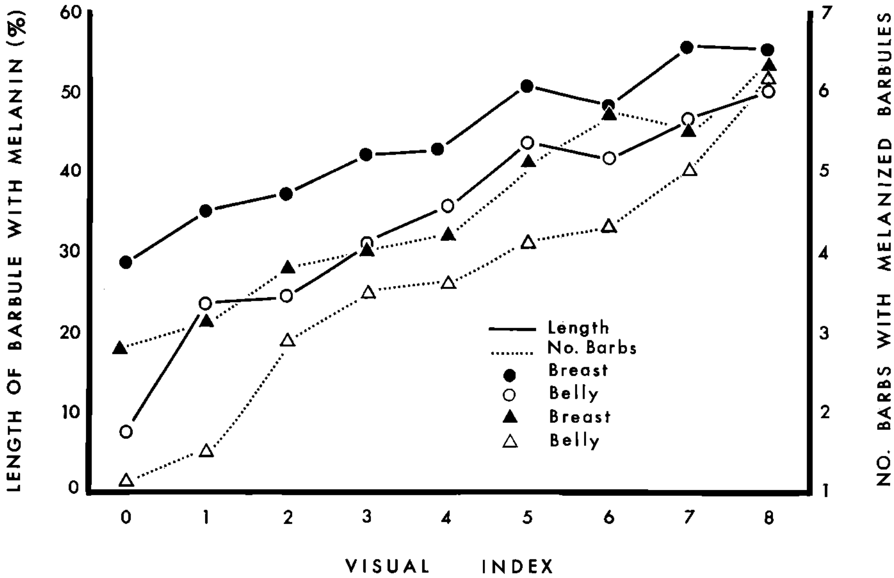


FIGURE 21. Relation of the extent of eumelanization in feather structure as indicated microscopically to the intensity of underpart gray coloration which is grossly visible.

gray (Character State 8) (Figure 20). Although the total aspect of the underparts was included in this single evaluation, I gave slightly greater consideration to the belly coloration than to the breast because of the higher variability of the latter and the disruptive influence of phaeomelanin deposition in some specimens. Following the initial sorting I surveyed each category for homogeneity and reevaluated incongruous specimens. Then I compared all specimens again 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 13.5 per cent of my total sample, and reevaluated them 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 category and a single specimen was two steps from the original. In view of the fine distinctions between categories and the numerous variables affecting such color determinations (see Bowers, 1956), I think this amount of error is acceptable and unlikely to affect significantly the major results which follow.

Differences in gray which can be detected by gross examination of specimens correspond at the microscopic level to differences in the extent of melanization of the barbules (Figure 21). I quantified my microscopic observations in two ways. First, the number of barbs with melanin-bearing barbules at their base, on one side of the rachis, was counted from the tip of the feather inwards. The count was terminated when downy barbules replaced those of contour feather

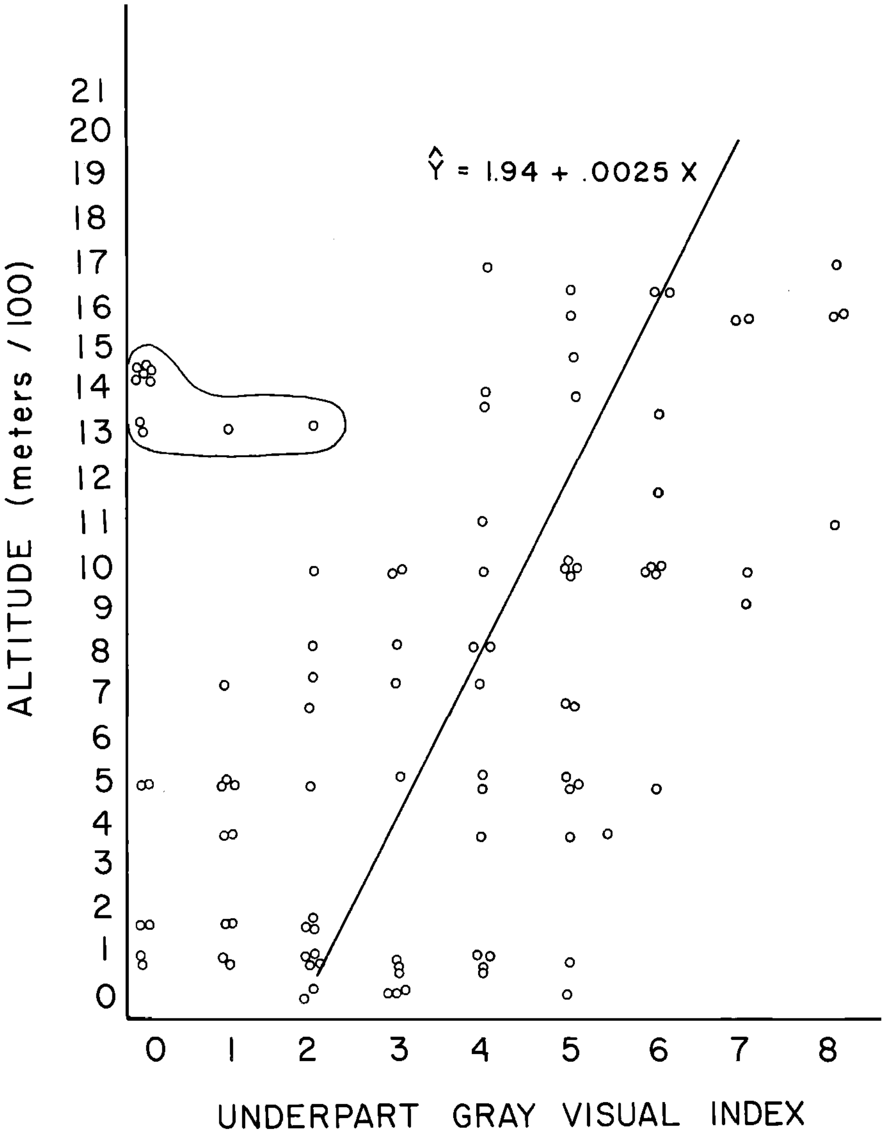


FIGURE 22. Relationship of altitude to intensity of gray coloration in the underparts in "brown-naped" white-eyes (Head Character Indices 1–9). Specimens from localities 98 and 62 are encircled and have not been included in the regression analysis (see text for explanation).

TABLE 7

RELATION OF ENVIRONMENTAL FACTORS TO VARIATION IN UNDERPART GRAY COLORATION IN *Zosterops borbonica*

REGRESSION ANALYSIS

Regression equations	Coefficient of determination	F value	Degrees of freedom
Gray-headed brown morphs (HCI = 0)			
2.66 + .0021*** Alt.	0.386	70.43***	114
2.04 + .0019*** Alt. + .0014** Jan. Rain	0.428	41.63***	111
2.29 + .005** Jan. Rain - .005** Aug. Rain	0.19	13.36**	111
Brown-naped brown morphs (HCI = 1–9)			
1.94 + .0025*** Alt.	0.364	52.64***	92
1.15 + .0024*** Alt. + .0016* Jan. Rain	0.384	28.35***	91
1.77 + .0087*** Jan. Rain - .015*** Aug. Rain	0.280	17.73***	91
Brown-headed brown morphs (HCI = 10–16)			
1.41 + .0022*** Alt.	0.497	258.00***	261
1.38 + .0018*** Alt. + .0021*** Jan. Rain	0.534	154.90***	270
1.95 + .0056*** Jan. Rain - .0016 Aug. Rain	0.315	62.11***	270
Gray morphs			
4.87 + .0007*** Alt.	0.067	6.94*	96
4.53 + .0007** Alt. + .0006 Jan. Rain	0.075	3.88*	95
6.05 - .0012 Jan. Rain + .0051* Aug. Rain	0.048	2.38	95

STANDARD PARTIAL REGRESSION COEFFICIENTS

	Gray-headed brown morphs	Brown-naped brown morphs	Brown-headed brown morphs	Gray morphs
Altitude	0.556	0.591	0.580	0.254
Rainfall (Jan.)	0.238	0.141	0.232	0.089
Altitude/Rainfall (Jan.)	2.33	4.19	2.50	2.85

* $P < .05$.

** $P < .01$.

*** $P < .001$.

structure. Second, I measured the length of the barbule that contained melanin and expressed this as a per cent of the total length of the barbule. This was done by arbitrarily picking a full length posterior barbule near 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 minimized. This procedure was followed for feathers plucked from four or five randomly chosen skins from each visual category and for a minimum of six feathers from each skin, three from the breast and three from the belly. A significant correlation of these criteria with the visual categories is evident (Figure 21).

There is a strong correlation between the intensity of gray in the underparts

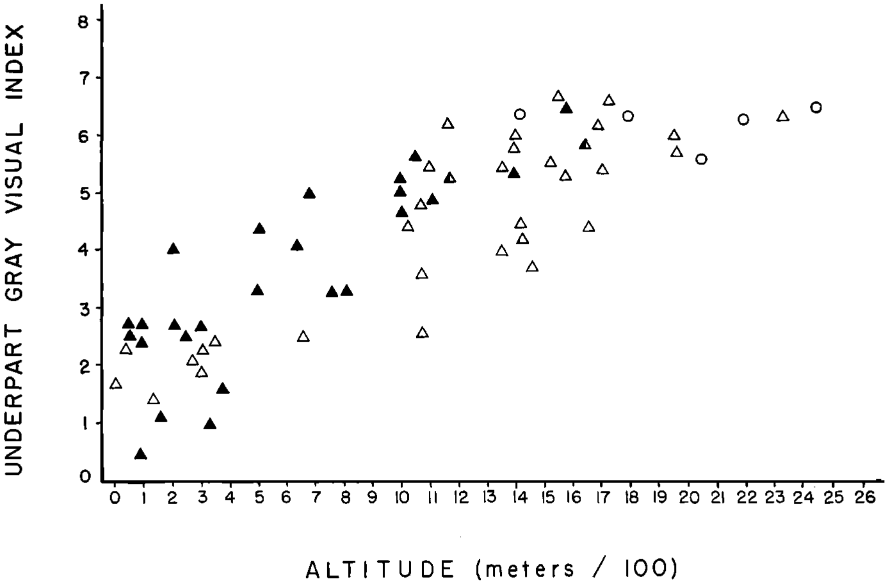


FIGURE 23. Relationship of altitude and the intensity of gray coloration of underparts of birds from various localities. The mean index of the sample is used for each locality. Open triangles indicate brown-headed brown morph localities; closed triangles indicate gray-headed brown morph (including brown nape phenotypes) localities; circles indicate gray morph localities.

and altitude (Figure 22), coastal populations of *Zosterops borbonica* being whitish below while those in the highlands tend to be dark gray. Some of the variation in this relationship is the result of average differences between color forms; for example, white-eyes at western localities average somewhat lighter below than at other localities.

Linear regressions showing the relationship of underpart coloration to altitude and rainfall were computed separately for gray morphs, gray-headed brown morphs (HCI 0), brown-naped individuals (HCI 1–9) and brown-headed individuals (HCI 10–16). (For discussion of statistical procedures, see p. 40). All of these regressions are significant, but only weakly so in gray morphs (Table 7). The three brown forms have nearly identical regression coefficients (slope) but different intercepts. Brown-naped individuals have lighter underparts than gray-headed, while brown-headed individuals are lightest of all. The coefficients of determination are similar for brown-naped and gray-headed individuals, but lower than for brown-headed individuals, in which the regression accounts for nearly one-half of the variance.

At only three localities (55, 62, 98) could I detect a significant difference in the underpart colorations of coexisting color variants (head and back color

TABLE 8

RELATIONSHIP OF PHAEOMELANIN DEPOSITION IN THE BREAST AND THE HEAD CHARACTER INDEX

Head Character Index	Index of brown coloration in breast				
	0	1	2	3	4
11	13[1]	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

[1] Number of specimens.

characters only). 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 at this locality. At localities 98 and 62, which are adjacent, I found many brown-naped white-eyes (HCI 1–9) with white underparts, which were significantly lighter than the rest of the gray-bellied individuals at these two localities. These particular brown-naped specimens also depart from the altitudinal relationship of underpart color that characterizes other brown-naped birds (Figure 23).

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 by itself is significant in all 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. Altitude is at least twice as important as January rainfall in all forms, as indicated by the ratio of the standardized partial regression coefficients (Table 7).

Like other aspects of the variation in *Zosterops borbonica* the basis of the variation in underpart gray coloration appears to be genetic. I kept together in captivity under identical environmental conditions 11 *Zosterops borbonica* including 3 light-bellied lowland forms (Index 3) and 8 highland birds (Indices 6–8). Despite the fact that 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 converged as one would expect if they were determined epigenetically.

Phaeomelanins.—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 8. Phaeomelanins are not evident in the breast coloration of any brown morph specimen with

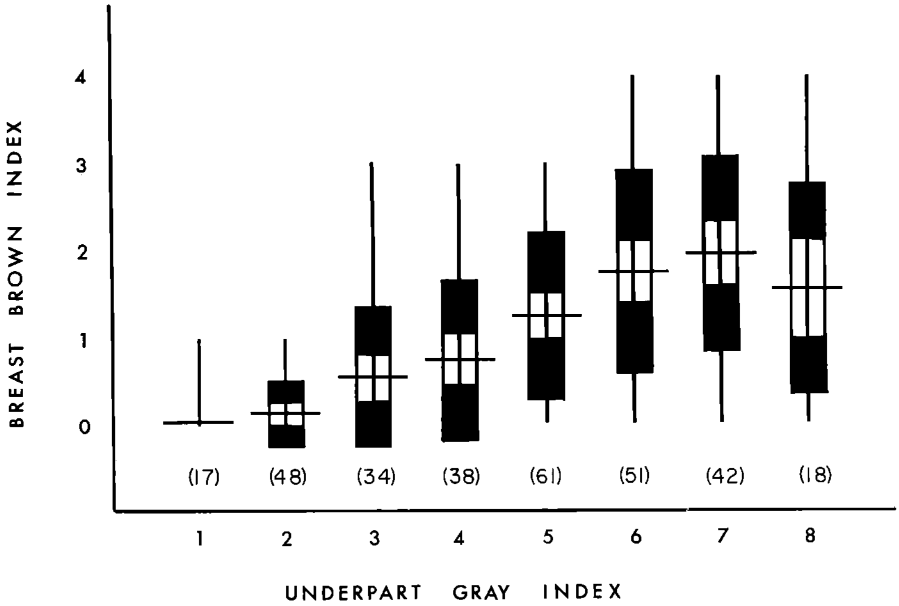


FIGURE 24. Relationship of intensity of brown on the breast and of gray on the underparts in brown morph specimens with Head Character Indices of 11 or more. Vertical line, range; horizontal line, sample mean; black rectangle, one standard deviation of the mean; white rectangle, two standard errors of the mean; sample sizes are given in parentheses.

a Head Character Index of less than 11. Faint brown pigmentation can be discerned in some specimens with Head Character Indices 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, in those with completely brown heads. Strong and extensive rufous color in the breast was present in only a few pure brown-headed specimens.

An increase in the average amount of brown in the breast with increased intensity of gray in the underparts 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.

There is a large continuous region on Reunion Island (Figure 25) in which the mean locality indices for breast coloration are less than 1.0, indicating a predominance of birds with no brown on their breasts although usually a few individuals with some traces of phaeomelanin deposition were present. This region includes the western side of the island below 1,400 meters and a long narrow band that presumably extends up the Rivière des Galets across the cirques of Mafate and Salazie to the Plateau de Belouve (Trou de Fer), Takamaka, and eventually the Rivière de l'Est, Pas de Bellecombe, and the

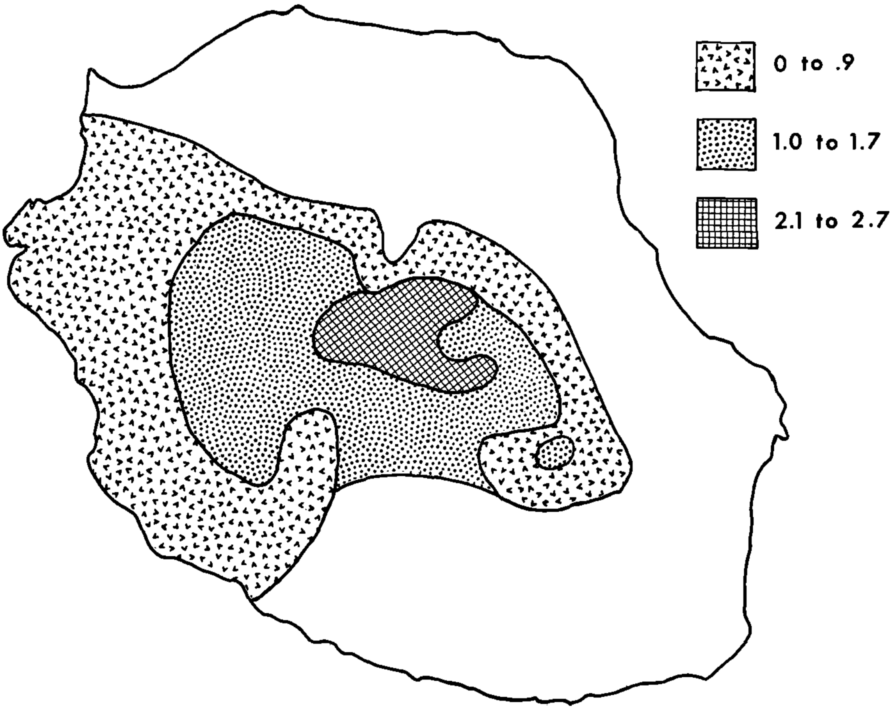


FIGURE 25. Geographic distribution of brown-headed morphs with different amounts of brown in their breast plumage. Figures indicated are mean Breast Brown Indices for each locality sampled.

Rivière des Remparts. The section of this band from the Cirque de Salazie to Takamaka and Rivière de l'Est coincides with the 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 most brown morphs have brown heads as in the case of the western side of the island.

The mean index for amount of brown in the breast increases as one proceeds inland. One finds a greater percentage of brown-headed white-eyes with brown breasts at high elevations (above 1,400 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 Bèbour, Plaine des Marsouins, Plateau de Duverney, and an isolated pocket at the head of the ravine of the Rivière des Remparts.

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 (the type locality of *Z. b. alopekion*

TABLE 9
AVERAGE INDEX OF BROWN IN BREAST COLORATION[1]

Locality	Altitude	Average index
44	0	0.0
51	40	0.2
68	120	0.2
53	270	0.0
55	300	0.3
94	300	0.0
54	340	0.2
95	640	0.1
16	680	0.8
26	1,010	0.5
49	1,060	0.6
61	1,080	0.3
97	1,080	0.3
17	1,100	0.2
27	1,180	1.2
35	1,250	1.7
98	1,330	0.5
22	1,350	0.8
29	1,350	1.1
72	1,400	0.0
58	1,400	2.1
24	1,400	0.9
40	1,400	2.3
62	1,440	1.0
18	1,530	1.5
23	1,570	2.3
70	1,660	1.4
8	1,700	1.7
63	1,700	1.4
30	1,720	2.3
71	1,800	1.0
64	1,980	0.6
41	2,060	0.9
73	2,200	1.5
39	2,300	0.7
60	2,460	2.7

[1] Based on specimens with Head Character Indices of 11 or more.

Storer and Gill) virtually all brown-headed white-eyes 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 (Table 9), but it is distinguished by being one of the wettest highland areas on the island.

MENSURAL VARIATION

SPECIMEN MEASUREMENTS

All specimens of *Zosterops borbonica* were measured by me. Wing length (arc) was measured to the nearest 0.5 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 (1957:326); tarsal length was measured from the back side of the middle of the tibiotarsal-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 throat cotton was removed were recorded to the nearest 0.1 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" should be understood to be the cube

TABLE 10

Correlations of Size Characters of *Zosterops borbonica*[1]

Character pair	Brown morphs		Gray morphs
	HCI 0–7	HCI 10–16	
Wing-tail	0.689***	0.785***	0.708***
	(190)	(235)	(79)
Wing-tarsus	0.202*[2]	0.472***	0.305**
	(194)	(254)	(91)
Wing-bill	0.012	0.288**[2]	–0.040
	(196)	(254)	(86)
Wing-weight	0.174	0.516***	0.213
	(96)	(97)	(42)
Tail-tarsus	0.174	0.372****[2]	0.314**[2]
	(184)	(235)	(82)
Tail-bill	0.005	0.222*[2]	–0.160
	(187)	(234)	(77)
Tail-weight	0.193	0.549***	–0.060
	(96)	(90)	(40)
Bill-tarsus	0.076	0.419***	0.163
	(190)	(255)	(91)
Bill-weight	0.352***	0.422***	0.521***
	(94)	(95)	(41)
Tarsus-weight	0.310**	0.477***	0.312*
	(94)	(94)	(44)

[1] Coefficients are linear product-moment correlation coefficients. Males and females are not considered separately. Sample sizes indicated in parentheses below each coefficient. Significance indicated by asterisks: * $P < 0.5$, ** $P < .01$, *** $P < .001$.

[2] Correlation not significant independent of weight.

root rather than the original 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.

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. Multiple regression analyses using the least squares method 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). Chi-square tests follow the procedures of Bailey (1959). The Mann Whitney U Test (Siegel, 1956) was used for the comparison of sample means. Estimates of sample variances were not calculated for samples of fewer than five

TABLE 11

REGRESSION ANALYSES OF ALTITUDINAL SIZE VARIATION IN *Zosterops borbonica*

Color form and character	Sample size	Intercept	Regression coefficient $(\times 10^{-3})$	Computed F value	Coefficient of determination
Brown Morphs HCI = 0–7					
Wing length	187	54.52	0.76	12.22***	0.062
Tail length[1]	85	4.97	0.27	1.15	0.007
Tarsal length	196	18.21	0.39	19.76***	0.092
Cube root of body weight	79	–0.02	–0.04	2.28	0.135
Brown Morphs HCI = 10–16					
Wing length	230	54.70	1.60	98.04***	0.300
Tail length[1]	229	6.90	0.47	15.64***	0.024
Tarsal length	252	18.23	0.60	84.37***	0.252
Bill length[2]	252	8.27	0.12	3.76	0.012
Cube root of body weight	96	2.75	0.106	14.04***	0.435
Gray Morphs					
Wing length	77	56.33	0.407	1.35	0.017
Tail length[1]	77	6.86	0.390	2.86	0.019
Bill length	90	14.07	–0.246	6.33*	0.066
Cube root of body weight	39	9.21	–2.359	1.340	0.169

[1] With correlated effects of wing length removed.

[2] With correlated effects of tarsal length removed.

specimens. The .05 level of significance is required for acceptance of null hypotheses.

Some caution is clearly necessary in the interpretation of parametric statistical treatment of ordinal data like the color rankings used in this study. The problems inherent in the assumption of a normal distribution do not affect the calculation of regression equations but may negate the significance of those regression coefficients which are close to the minimal level of acceptance.

ANALYSIS

Superimposed upon the patterns of color variation in *Zosterops borbonica* on Reunion Island are differences in size and proportions. First, in order to test the interdependence of size characteristics, I analyzed the correlations between all pairs of measurements separately for the three major color forms (Table 10). Wing length and tail length are strongly correlated in all color forms. Wing length (and thus tail length) is significantly correlated with

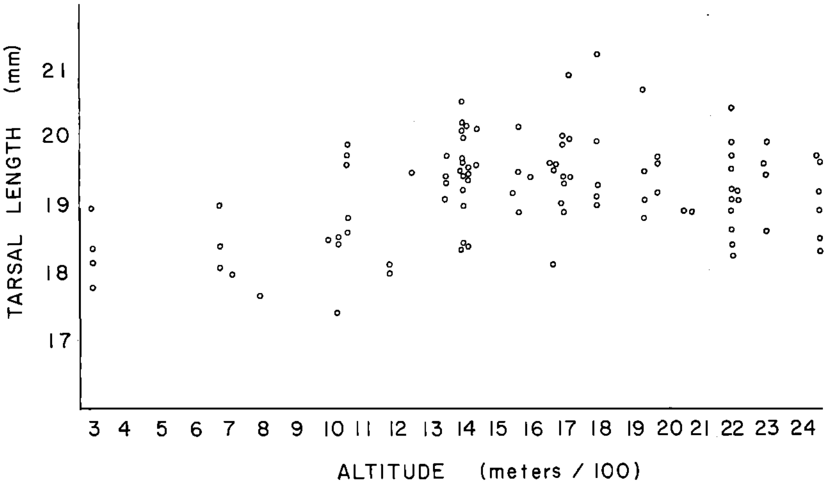


FIGURE 26. The relationship of tarsal length and altitude for gray morphs.

weight only in brown-headed white-eyes (HCI 10–16), while bill and tarsal length are significantly correlated with weight in all color forms. Correlations between other pairs of size characters are affected by mutual correlations with weight. However, the partial correlation coefficients between bill and tarsal lengths in brown-headed white-eyes, and between wing and tarsal lengths in both brown-headed white-eyes and gray morphs are significant independent of weight.

Regressions of size in relation to altitude differ among color forms of *Zosterops borbonica* (Table 11). Wing length increases significantly with altitude in brown morphs at a rate of 0.76 to 1.6 millimeters per 1,000 meters of elevation from an average length of 54.6 millimeters on the coast. Tail length increases significantly with altitude in brown-headed individuals, even after the correlated effects of wing length have been removed. Tarsal length increases significantly with altitude in brown morphs, but the relationship tends to be curvilinear in gray morphs (Figure 26) and therefore has not been analyzed for this form. Bill length increases significantly with altitude in brown-headed individuals, decreases significantly in length in gray morphs (Figure 27), and shows a strongly curvilinear relationship in brown morphs with grayish heads (Figure 28). Weight increases significantly with altitude only in brown-headed individuals.

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, 30, and 31).

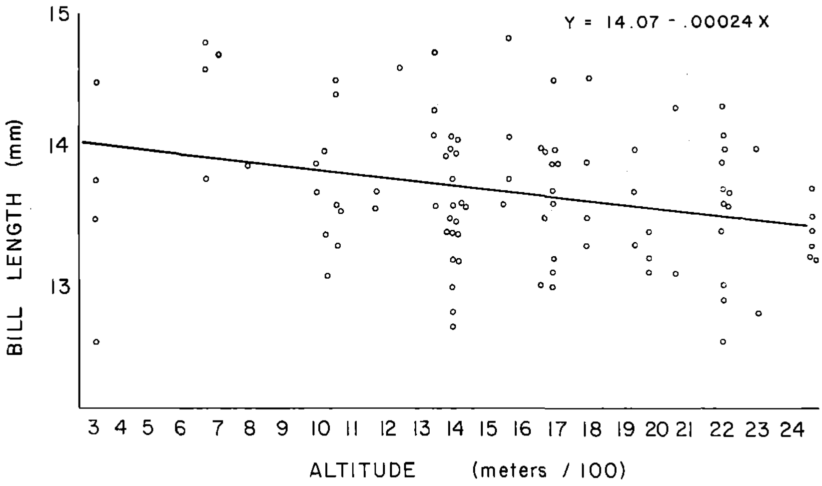


FIGURE 27. The relationship of bill length and altitude for gray morphs.

Localities 11, 12, and 14 have been combined into a single lowland sample of the gray-headed brown morph and localities 44 and 51 were combined into a lowland sample of the brown-headed brown morph. A satisfactory highland sample of the gray-headed brown morph is not available. Brown morphs from highland localities 58, 63, and 30 provide a single sample from the upper limits of abundance of the brown-headed brown morph.

In most populations of *Zosterops borbonica* the sexes differ in both wing length and tail length, males averaging 1.0 to 1.5 millimeters larger than females. There were no sexual differences in tarsal length in any of the populations examined. Sexual differences in bill length characterize only lowland gray-headed brown morphs, in which males average 0.5 millimeters longer than females, and highland gray morphs, in which males average 0.9 millimeters longer than females. Yet, at Cilaos (locality 58), where they are outnumbered by brown morphs, 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 brown-headed brown morphs samples tested.

Lowland gray-headed brown morphs have significantly longer bills than lowland brown-headed brown morphs (Figure 30). The altitudinal correlations of wing length, bill length, and tarsal length in the brown-headed brown morphs result in highland populations averaging significantly larger than lowland populations. Extreme highland individuals have bills the same length as lowland gray-headed brown morphs. Gray morphs at Cilaos have wings and tarsi equivalent in length to the brown morphs with which they are sympatric, but significantly shorter bills, the difference corresponding in

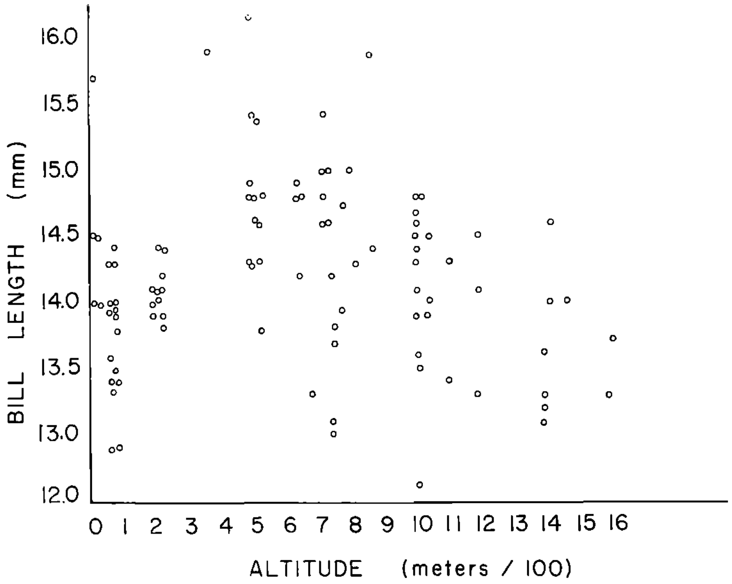


FIGURE 28. The relationship of bill length and altitude for gray-headed brown morphs (HCI 0–7).

magnitude to the sexual dimorphism found in highland gray morph populuations and lowland gray-headed brown morphs. 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.

DISCUSSION

VARIATION IN CONTINENTAL WHITE-EYES

Marked infraspecific variation in white-eyes on the African continent was analyzed by Moreau (1957), and I have used his observations as well as my own examination of museum specimens in comparing *Z. borbonica* with those forms.

The differences in underpart coloration in *Z. borbonica* are easily as great as the color differences characterizing the palest (*senegalensis*) and darkest (*jacksoni*, *reichenowi*) forms of the widespread African species *Zosterops senegalensis*. Color differences between such recognized subspecies as *Zosterops senegalensis stuhlmanni* and *Z. s. jacksoni*, are less pronounced than between extreme variants of *Zosterops borbonica*. The point to be emphasized here, therefore, is that color variation in *Zosterops borbonica* does not simply involve subtle differences but is of a magnitude comparable to or greater than that found in the continental species.

Differences in intensity of carotenoid and particularly melanin deposition, which are the primary source of the color variation in African white-eyes, are often correlated with climatic trends (Moreau, 1957:404). In some forms, *Z. senegalensis demeryi*, for example, melanin deposition is greater in regions with high rainfall even in the absence of parallel changes in altitude or latitude, although most other darkly pigmented forms, *Z. senegalensis stenocricota, Z. senegalensis stuhlmanni*, and *Z. senegalensis reichenowi* are found at high altitudes. Transitions between these forms and bright yellow lowland populations are evident, but the relative effects of rainfall and altitude have not been separated.

The presence of phaeomelanins has an irregular distribution in the Zosteropidae. Only two African white-eyes, *Zosterops pallida* and *Z. mayottensis*, have phaeomelanin pigments in their flank feathers, the usual site of this pigment's deposition in zosteropids, although in *Z. pallida* the extent of phaeomelanin pigmentation in the underparts is reported to vary greatly (Moreau, 1957:380). *Z. modesta* from the Seychelles Islands appears to have minor traces of phaeomelanins throughout its plumage, especially in the underparts (pers. obs.). Several races of the Japanese white-eye, *Z. japonica*, have rufous-washed sides, and in one closely related Chinese species, *Z. erythropleura*, the flanks are actually bright reddish-brown. Several races and insular derivatives of *Z. lateralis*, the widespread Australian species, have rusty flanks. The closest parallel to the brown and gray morphs of *Zosterops borbonica* is found in *Zosterops cinerea* in Micronesia. On the Caroline Islands, *Z. c. cinerea* is an all gray bird very similar to a gray *Z. borbonica* in coloration, but on the Palau Islands, *Z. c. finschii* is a brown bird resembling the brown morph of *Z. borbonica.* However, polymorphic plumage characters are virtually unknown and intense brown plumages are rare in the Zosteropidae.

In African white-eyes wing length increases significantly in relation both to increasing altitude (0.69 mm/1,000 feet of elevation) and decreasing temperature (2.8 mm/10° F) (Moreau, 1957:330). In those birds the relation of tail length to altitude seems to be 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 average tail length becomes proportionately longer relative to increasing average wing length. Bill length increases slightly with decreasing minimum temperature, even after highly correlated effects of wing length (correlation coefficient = 0.83) are removed. Thus white-eyes inhabiting higher or cooler parts of Africa tend to be generally larger than those in the lowlands. No information is available for variation in tarsal 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 is probable that similar

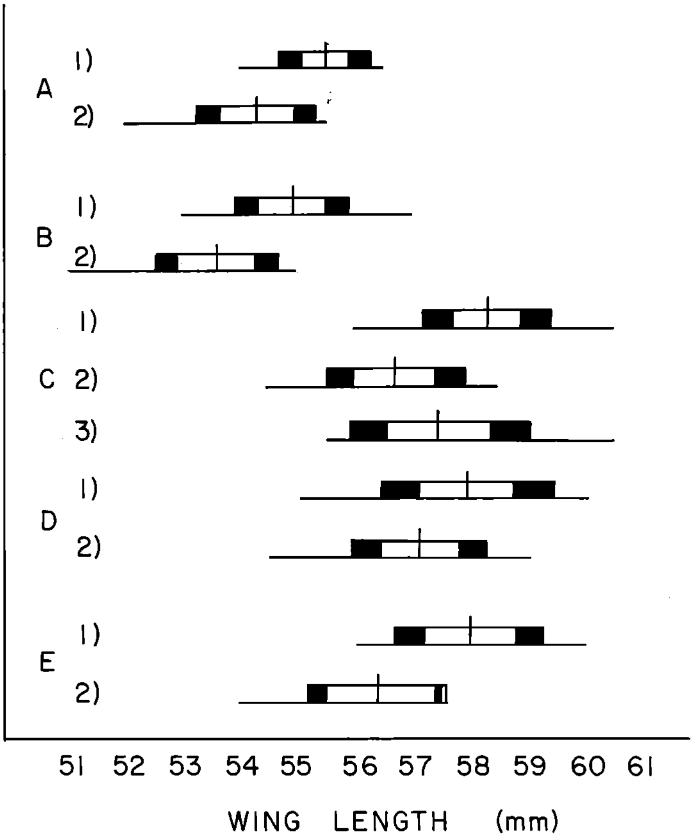


FIGURE 29. Wing length of representative populations of *Zosterops borbonica* on Reunion Island. A. Localities 11, 12, and 14 combined: (1) 15 males, (2) 9 females; B. Localities 44 and 51 combined: (1) 13 males, (2) 10 females; C. Locality 58: (1) 14 brown morph males, (2) 11 brown morph females, (3) 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 of the mean; open rectangles, two standard errors of the mean.)

selective agents are involved. On the other hand, there is no altitudinal correlation of the tail/wing ratio in *Zosterops borbonica*. Indications of such a relationship in Africa (Moreau, 1957:336) are based on ratios of average tail lengths and average wing lengths rather than on averages of the ratios calculated separately for each specimen in the population. The two kinds of ratios are not comparable.

Distances between phenotypically distinct populations of white-eyes 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 (Moreau, 1957:353, 357), although this is poorly documented. Similarly in some areas the altitudinal clines in size are very steep, as, for example, on the edge of the Congo Basin, where populations only 20 and 40 miles apart differ markedly in their measurements (Moreau, 1957:368). Several of the distinctive montane populations in Kenya are separated by geographical and ecological gaps of no more than 25 miles (Moreau, 1957: 363).

In summary, certain aspects of the variation in *Zosterops borbonica*, particularly the ecogeographic clines in size and intensity of melanin depositions, parallel well known patterns of infraspecific variation in continental white-eyes. Other important aspects of *borbonica*'s color variation which relate to the presence or absence of phaeomelanin pigments are unusual, if not unique in the Zosteropidae. Certainly the combination of such discordant, but striking, patterns of geographic variation is not known for any other species

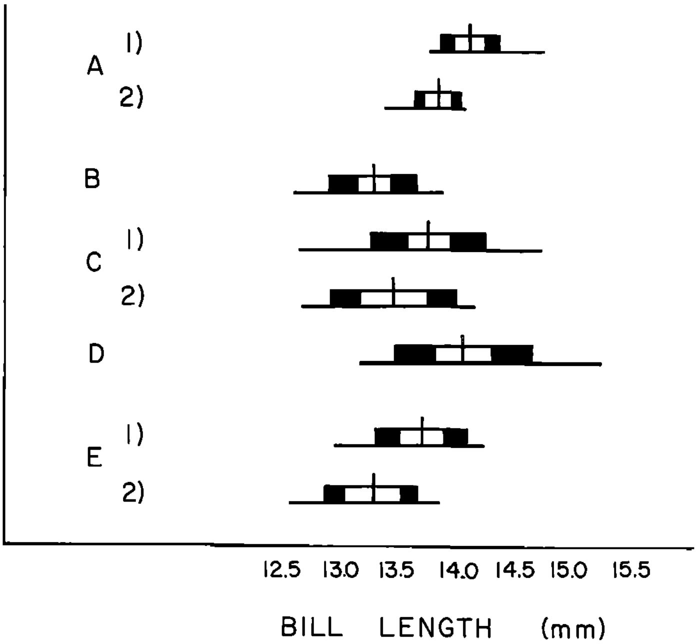


FIGURE 30. Bill lengths of representative populations of *Zosterops borbonica* on Reunion Island. A. Localities 11, 12, 14, and 81 combined: (1) 16 males, (2) 11 females; B. Localities 44 and 51 combined: 28 males and females; C. Locality 58: (1) 26 brown morphs, (2) 13 gray morphs; D. Localities 63 and 30 combined (brown morphs only): 23 males and females; E. Localities 41 and 73 combined (gray morphs only): (1) 17 males, (2) 10 females.

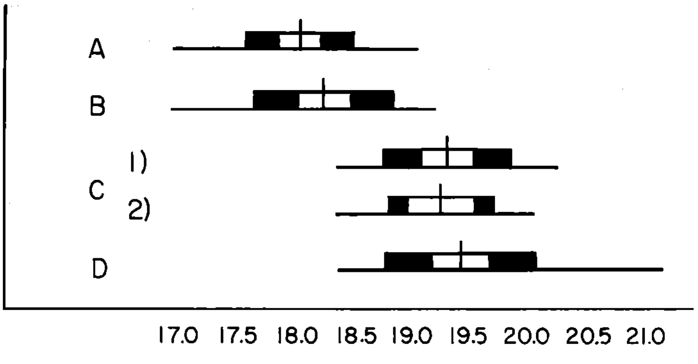


FIGURE 31. Tarsal lengths of representative populations of *Zosterops borbonica* on Reunion Island. A. Localities 11, 12, and 14 combined: 27 males and females; B. Localities 44 and 51 combined: 28 males and females; C. Locality 58: (1) 23 brown morphs, (2) 12 gray morphs; D. Localities 41 and 73 (26 gray morphs only).

of white-eye. The distances involved in clinal aspects of the variation, as well as for the situation as a whole, are less than for any other example of geographic variation in the family.

TAXONOMY OF *Zosterops borbonica*

Variation in size and color of underparts provide no adequate bases for taxonomic distinction of geographically separated populations of *Zosterops borbonica* on Reunion Island. No useful purpose would be served by formal recognition of the ends of the ecogeographic clines in these characters. This applies in particular to *Z. b. alopekion* Storer and Gill, which is simply the dark brown-breasted extreme of underpart color variation in some brown morphs; it is the predominant form at only a few inland localities. In addition, continued recognition of the gray morph, *Z. b. edwardnewtoni*, as restricted by Storer and Gill (1966) and Storer (1968), is clearly inappropriate because it occurs commonly with the brown morph. Various arguments exist for the continued recognition of a brown-headed brown-backed form, *Z. b. xerophila* Storer and Gill (which includes *Z. b. alopekion* Storer and Gill), and a gray-headed brown-backed form, *Z. b. borbonica* (Gmelin). These are geographically distinct semispecies, but arguments for their recognition are weakened by the presence of an inallocatable color phase (the gray morph) common to both populations, and by the presence of "brown-naped" individuals, which although they form a homogeneous coastal population, are also found as variants in the main populations of both "*borbonica*" and "*xerophila.*" In my opinion no combination of existing or additional subspecies will adequately reflect these complex patterns of geographic variation and their probable evolution, and at the same time conform to current standards of taxonomic validity. Consequently, the formal classification of Moreau (1967) should be followed (i.e., all Reunion Island forms should be referred to as *Z. b. borbonica*) and a separate effort be made to understand the variation in *Zosterops borbonica* on Reunion Island.

RELATION OF *Zosterops borbonica mauritiana* TO THE REUNION ISLAND FORMS

Zosterops borbonica mauritiana of Mauritius Island is a gray-backed, monomorphic form of *Zosterops borbonica.* There is no evidence of geographic color variation in this form (Storer and Gill, 1966:7). 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 *Z. b. mauritiana* distinguish it from nearly all gray morph individuals on Reunion Island; only a few extreme pale-bellied gray birds from Reunion Island approach *mauritiana* in appearance. *Z. b. mauritiana* also differs in vocalizations from Reunion Island *borbonica* (Gill, 1971).

EVOLUTIONARY HISTORY OF *Zosterops borbonica*

Here I propose a probable sequence of historical events and evolutionary changes that have led to the present day pattern of variation and distribution of *Zosterops borbonica.* It seems clear to me (Gill, 1971) that the ancestors of *borbonica* colonized the Mascarene Islands after the ancestors of *Z. olivacea*; i.e., *borbonica* was the second successful colonist in this particular case of double invasion of an oceanic island. Also *Z. borbonica* is almost certainly derived from a generalized white-eye that favored edge, disturbed, or relatively open habitats; it has changed little from these ancestral habits.

Before the arrival of man, habitats suitable for *Z. borbonica* were, in my opinion, rather limited on Reunion and existed only in relatively isolated pockets, such as the dry savanna of the west coast and the highland heath zone. Dense evergreen forest once extended to the sea on the wet east coast (Rivals, 1952:64) so that throughout this region *Z. borbonica* was probably restricted to the streamsides and semi-open ravines and perhaps coastal border of the forest, much as it is today. Small numbers of *borbonica* may have penetrated the island's interior along major streambeds, but the species was probably absent from the evergreen forest that covered most of the island. Erosion and landslides must have created some satisfactory edge habitat in the cirques, and in both Cilaos and Mafate this was probably continuous with the savanna that penetrated from the west coast via the ravine slopes

(Rivals, 1952:50). Finally the forests below le Volcan were certainly damaged regularly and rendered suitable by eruptions and new lava flows. Thus several pockets of habitat partially isolated by stretches of uninhabitable evergreen forest were originally available to *Zosterops borbonica* on Reunion Island.

Zosterops borbonica's ancestor was very likely a typical yellow-green white-eye with limited synthesis and deposition of phaeomelanin pigments in the flank feathers. Loss of carotenoids in the plumage and loss of the eye-ring, which may have facilitated coexistence with the aggressive *Z. olivacea* (Gill, 1971:54), may have resulted in a gray white-eye that 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 suggested by the rarity of extensive phaeomelanin pigmentation in Zosteropidae and also by the presence of a monomorphic gray form on Mauritius Island.

Sometime after *Z. borbonica* lost its carotenoids and was established on both Mauritius and Reunion islands, a phaeomelanic morph probably evolved in the Reunion lowlands and, through some selective advantage at low altitudes, it gradually replaced gray morphs throughout the lowlands. Gray morphs thus became restricted to the disjunct highland heath zone where they became increasingly adapted to the cold temperatures and to utilization of the scrub-like vegetation.

I envision the subsequent differentiation within the brown morph as occurring in semi-isolated pockets of suitable lowland habitat: the brown-headed form in the savanna of the island's west side; the gray-headed form in the coastal vegetation and along stream beds on the east side; and the brown-naped form in the disturbed young coastal forests below Piton de la Fournaise, although the last may have arisen through hybridization between the other two forms.

It is impossible to be certain of the extent and nature of the contacts between these populations before the arrival of man on Reunion Island in 1663, although the contacts must have been limited in extent. There is little doubt that human activities, including lumbering 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 have been true throughout the lowlands and especially on the western slopes of the island. In the latter region much of the forest was quickly destroyed, the savanna and highland *Acacia* forests for their valuable timber, and the evergreen forest in connection with the commercial cultivation of geranium. Damage was less extensive in the rugged, largely inaccessible, and very wet forests of the eastern slopes.

As a result the gray-headed brown morphs on the east side of the island were no longer restricted to the rather limited edge habitat along stream beds and ravines; they increased in numbers and expanded toward the savanna on the northeast where they came into contact with the brown-headed brown morphs. Eventually, gray-headed brown morphs advanced westward as far as the Rivière des Galets where the combination of aridity and the river bed proved to be an effective barrier between the two forms. The "brown-naped" form expanded similarly along the southern coast to the Rivière St. Etienne. The original contact of the "brown-naped" population and the population of gray-headed brown morphs was probably very similar to that found today, being restricted by new lava flows south of Bois Blanc.

Brown morphs also expanded their altitudinal range and, particularly on the cleared west slopes, 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 established. The expansion of brown morphs into the highlands also led to the evolution of a series of populations adapted in size and pigmentation to local conditions. The rather rapid evolution of these differences within 250 years is in keeping with recent evidence for rates of racial differentiation in the House Sparrow (*Passer domesticus*) (Johnston and Selander, 1964; Packard, 1967).

CHARACTER VARIATION AND ADAPTATION

The existence of infraspecific gradients of pigmentation and size that are correlated with climate has been recognized since the earliest studies of geographic variation, when it led to the formulation of "ecogeographic rules." More recent studies (James, 1970; Power, 1969; Johnston and Selander, 1964, 1971) have demonstrated the precision and rapidity of such evolutionary adaptation.

The selective advantage of variation in size with relation to temperature differences is presumed to be physiological and related to thermoregulation. This has been disputed (Scholander, 1955), but recent evidence (Brown and Lee, 1969) supports Mayr's intuitive arguments (1956) for the existence of adaptive differences in body size. The relation of relative humidity to thermoregulation and consequently its effects on body size have recently been recognized (James, 1970). The correlation of size in some *Zosterops borbonica* with altitude, as well as in other bird species (Rand, 1936), presumably also reflects thermoregulatory adaptation to temperature and humidity. The meaning of inverse correlations of size with altitude as found in the high altitude gray morph is not known. Finally in addition to being correlated with body size, wing length is subject to a variety of other selective forces including the effects of altitudinal changes in air pressure on flight capability (Hamilton, 1961:185; Moreau, 1957:331).

The evolution of color differences as protection from visual predators is well known. However, differential loss of the color forms of *Z. borbonica* to visual predators does not seem to be significant on Reunion Island, if it occurs at all. Most of the predators on the island, e.g., rats, lizards, snakes, cats, and humans, are restricted in their distribution and are recent arrivals on the island. 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 much of a threat to passerines like *Zosterops borbonica* (see p. 12).

Recent evidence (Lustick, 1969, 1971; Hamilton and Heppner, 1967; Heppner, 1970) indicates that the absorption of solar energy by plumage pigments is important in avian thermoregulation, particularly because of its effects on the insulation value of plumage. Thus increased (melanin) pigmentation and thereby heat absorption may be advantageous in cooler climates. The altitudinal gradients in underpart coloration of *Zosterops borbonica*, which often face the sun on exposed perches early in the morning at high altitudes, might be accounted for in this way. Increased melanin deposition could also help maintain the insulation value of the plumage by reducing feather wear, as well as by assisting in the drying of feathers through the absorption of radiant energy. Although speculative only, this latter hypothesis could help explain the fact that many birds have increased melanin deposition in cold humid climates, i.e., "Gloger's Rule."

At present there are no satisfactory explanations to account for the differences (i.e., brown *vs* gray) in back coloration or head coloration of *Z. borbonica*. Physiological attributes other than plumage color *per se* seem important in determining the geographical distributions of these forms.

Character Divergence in Natural Populations

The principal biological interest in the variation in Reunion Island forms of *Zosterops borbonica* is that such a small geographic area is involved. Such marked microgeographic variation in birds is not only unknown on other oceanic islands, but is also exceptionally rare on larger land masses.

There is no reason to assume that *Z. borbonica* is an unusual or remarkable bird species. Behaviorally it is a typical, social white-eye with generalized feeding habits, and it does not appear to be a uniquely sedentary bird species. Locally it is highly mobile, habitually flying considerable distances over the forests, and it is no way restricted to the ground or dense understory. I have observed banded individuals up to 500 meters from the point at which they were initially captured and banded, and I suspect that they wander freely within several square kilometers of suitable vegetation, perhaps much more.

Generally it seems as if the high dispersal tendencies of birds and the gradual nature of environmental gradients preclude highly localized adaptation.

Furthermore, the importance of geographic isolation, or disruption of the continuity of populations, seems undeniable as a factor promoting evolutionary divergence (Mayr, 1970:296–330). However, the probability and rate of genetic divergence depends also on the magnitude of the selection coefficients in the different environments. The relationship between these two factors must be examined to ascertain the basis of differences or the lack thereof between populations.

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), relative viability (Ford, 1964:50, 62; Sheppard and Cook, 1962; Fisher, 1939), or differential capture by predators (Kettlewell, 1961*a*, 1961*b*), are available for only a few well studied populations of moths, butterflies, snails, and small mammals. The selection coefficients indicated by these studies range from 5 to as high as 90 per cent relative advantage of one genotype over another.

In two studies the selection coefficients required to offset the effects of dispersal in natural cases of clinal variation have been computed; the computed selection coefficients were very low — 0.1 per cent in *Peromyscus polionotus* (Haldane, 1948:284) and .004 per cent in *Amathes glareosa* (Kettlewell and Berry, 1961) — and were well below the actual intensities of selection thought to be operating.

The mathematical relationships between natural selection and dispersal (= gene flow) and the distances over which these two forces interact to produce clinal variation have been treated by Haldane (1948) and Fisher (1950) for simple genetic systems. Haldane's method assumes the following: 1) the species lives in an area which is plane and infinite, i.e., it must be large enough that regions exist where there is *no* polymorphism; 2) the density is equal throughout 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 underlie the polymorphism; and 8) the plane is sharply divided by a straight boundary into two halves.

Assumptions 1 thru 6 are acceptable without major violation for *Zosterops borbonica.* Assumption 5 may not be completely valid, however. The presence of helpers and communal feeding of young in the nest might be taken as indirect evidence of inbreeding, as such behavior would be selectively advantageous to the participating individuals if the parents and helpers were related genetically (Lack, 1968:80). Allochronic differences in the onset of breeding may reduce altitudinal gene flow even further and reinforce the geographic isolation between lowland populations. Finally, any tendency toward differential habitat selection, for which there is some evidence (see p. 17), will also reduce gene flow.

The underlying genetic bases of the polymorphism in this white-eye (Assumption 7) are not clear. However, other similar cases of color polymorphism in birds (Cooke and Cooch, 1968:299; Munro *et al.*, 1968; Hrubant, 1955: 229) appear to be controlled by two alleles with one being dominant and with modifiers being responsible for the intermediate plumage types. The requirement of a sharp boundary (Assumption 8) is violated by our situation. However, Haldane (1948:284) recognizes that in many cases environmental conditions do change gradually and he thinks that in these cases the computed selection coefficient should at least indicate the order of magnitude of selection needed to maintain a cline, i.e., whether selective intensities of the order of 10 or .01 per cent are involved.

The measurements involved in Haldane's formula (1948:283) are the interquartile distance (d), which is the linear distance between the two localities at which the frequencies of one of the phenotypes are 25 and 75 per cent, and the average dispersal distance (m) from hatching site to first breeding site. The intensity of selection in the interquartile region is then considered to be $m^2/2d^2$.

There are no direct measures of dispersal distances for *Zosterops borbonica.* Mean distances of dispersal have, however, been measured for several other bird species. The Song Sparrow (*Melospiza melodia*) disperses about 400 meters (Johnston, 1961). The Wrentit (*Chamaea fasciata*), an inhabitant of dense brush and chaparral, might disperse about 600 to 700 meters (Miller, 1947). The mean dispersal distance of the Great Tit (*Parus major*) is also about 600 meters (Kluijver, 1951:14). I would estimate, therefore, that the mean dispersal distance in *Zosterops borbonica* is about 500 meters. However, the highly social nature of *borbonica's* year-round activities, including the apparent lack of territoriality, must promote the formation of local and perhaps inbred populations. In order to compensate for this, as well as for the earlier stated possible violations of Assumption 5, I have considered that the effective dispersal distance might be as little as 250 meters. 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 much more mobile than some of the other species mentioned above, and would set 1,000 meters as the upper limit to its mean dispersal distance.

Using Haldane's formula, then, I have estimated the interquartile selection coefficients for four of the five clines in the ratio of brown and gray morphs which I sampled on Reunion Island. Separate values were computed assuming mean dispersal distances of 250, 500, and 1,000 meters (Table 12). The resulting selection coefficients range from a low of 0.06 per cent to a maximum of 5.5 per cent.

These calculated selection coefficients are not intended to be actual measures of selection on Reunion Island, but they do provide estimates of the approxi-

TABLE 12

INTENSITY OF SELECTION REQUIRED FOR MAINTENANCE OF CLINES IN THE RATIO OF GRAY AND BROWN MORPHS IN *Zosterops borbonica*

Calculation	Transect[1]			
	A	B	C	D
Locality number with 25 per cent gray morphs	33	6	74	62
Locality number with 75 per cent gray morphs	41	5	71–73	64
Distance (d) between the two localities (in km)	7	4	3	4
Selection coefficient[2]				
With m = 250 meters	.06	.19	.35	.19
With m = 500 meters	.25	.78	1.40	.78
With m = 1,000 meters	1.02	3.10	5.50	3.10

[1] A, St. Benoît to Plaine des Cafres; B, St. Denis to Plaine des Chicots (locality 6 is adjacent to but not actually on this transect); C, Petite France to Piton des Epinards; D, Étang Salé les Bains to Piton des Epinards (see Figure 11).

[2] The selection coefficient (K) $= m^2/2d^2$, where m is the assumed mean dispersal distance and where d is the distance as defined above (after Haldane, 1948). Values indicated are per cent relative advantage of a morph on that part of the cline where it comprises more than half of the population.

mate minimum magnitude of selection that seems to be operating. From them it is apparent that a small selective advantage is sufficient to maintain steep clinal variation in simple morph or allelic frequencies in a mobile small bird.

Studies of natural populations increasingly are revealing demal structures and selection coefficients capable of evolving marked local population differences despite high dispersal rates (Ehrlich and Raven, 1969). There are, of course, lower limits to the size of a geographical area within which a given species can differentiate, but these are well below the actual ranges for most species. Also, genetic markers reveal differences that are much more localized than are the differences in external morphology which classically have been used to describe geographic variation. It is important to recognize, therefore, that gene flow *per se* (i.e., the resulting tendency towards genetic similarity) has probably been overemphasized as a factor preventing the divergence of conspecific populations. Rather, character uniformity over large areas probably reflects a generalized phenotype that adaptively compromises a variety of opposing selective forces. Character uniformity may also reflect a species' inability to evolve locally adapted populations because of genetic homeostasis (see Mayr, 1963:289).

In strong contrast to the clinal situations found in the highland areas on Reunion Island, in the lowlands color forms of *Zosterops borbonica* change abruptly across obvious geographical barriers (river beds and a lava flow).

For example, the coastal ranges of gray-headed and brown-headed brown morphs are separated by the gravel beds of the Rivière des Galets and the Rivière St. Etienne, but the transition between these two forms above 1,400 meters on the east side of Reunion Island is steeply clinal without any apparent barrier. In fact, all altitudinal transitions between color forms are clinal, whereas all coastal contacts involve a barrier. Furthermore, the coastal transitions take place in the absence of conspicuous environmental change. One might conclude, therefore, that the selection coefficients affecting the altitudinal distribution of genotypes are large enough to maintain geographic differences without the restriction of gene flow, whereas the selection coefficients in the lowlands are lower. Geographic transitions between genotypes in the lowlands, therefore, require some restriction of gene flow. A delicate balance between gene flow and opposing selection forces must be involved.

Finally, in analyzing the forces affecting these character divergences, the nature of Reunion Island itself must be considered. Few small islands are as high as Reunion Island or contain comparable ranges of environmental extremes within their confines. Furthermore, a tropical or subtropical location maximizes climatic diversity because a very high island can include both tropical lowlands and alpine mountain tops. Few small tropical islands, but several subtropical islands, including Reunion, Hawaii, Maui, Bali, and Lombok, are that high. Character divergence in birds on these other islands should be looked for. The essential absence of visual predators from Reunion Island may also have been an important factor in the evolution of *Zosterops borbonica,* since release from a need for protective coloration may have increased the evolutionary flexibility of *borbonica*'s plumage coloration. Taken together these considerations suggest that the marked differentiation in *Zosterops borbonica* on Reunion Island resulted from and was made possible by several factors which in themselves are not unusual but which are rarely found in combination in such a small area.

SUMMARY

Zosterops borbonica, a white-eye endemic to the Mascarene Islands in the western Indian Ocean, is characterized by complex patterns of plumage color and size variation within the confines of Reunion Island, a remote volcanic island about 1,000 square miles in area and 3,000 meters high. *Z. borbonica* appears to be the second of the two indigenous white-eyes to colonize this island and has lost the carotenoid pigmentation and white eye-ring characteristic of most of its relatives. However, it is still a typically social white-eye that has a generalized diet and preference for edge and disturbed habitats.

One aspect of the color variation in *Z. borbonica* involves the presence or absence of phaeomelanins in the feather barbs of the back plumage, which produces brown and gray color morphs, respectively. The offspring of mixed matings between morphs were observed; the genetic basis of back color seems to involve a simple pair of alleles with some modifiers. These two color forms are extensively sympatric, but the ratio of the two varies clinally with altitude from 100 per cent brown morph populations occurring in the lowlands to predominately gray morph populations occurring in the highlands. Linear distances between localities at which gray morphs composed 25 per cent and 75 per cent of the population varied from three to seven kilometers. The minimum intensity of selection required to maintain such steep altitudinal clines in the proportions of the two morphs is estimated to be on the order of 1 per cent relative advantage of one morph over the other.

A second aspect of the color variation involves differences in the head color of brown morphs only. Three categories of brown morph head color variants can be distinguished: an all gray-headed form which is characteristic of the wet northern and eastern lowlands below 1,380 meters elevation; an all brown-headed form which is found on the dry western slopes and in the highlands above 1,400 meters elevation; and a brown-naped intermediate which is the form characteristic of the southern coast. Lowland contacts between these different brown morphs are abrupt, coinciding with the Rivière des Galets (gray heads *vs* brown heads), the Rivière St. Etienne (brown heads *vs* brown napes), and recent lava flows near Bois Blanc (brown napes *vs* gray heads). In contrast the altitudinal transition between the gray-headed and brown-headed forms on the eastern slopes of Reunion Island is continuous and steeply clinal over a distance of about five km; samples from this contact zone include a large number of pure brown- or gray-headed forms as well as intermediate phenotypes.

The intensity of eumelanin deposition in the feathers of the underparts varies in relation to altitude in all color forms, the underparts changing from whitish in lowlands to dark gray in the highlands. Extremes of this color variation are more strikingly different than is the case in most mainland subspecies of *Zosterops* which exhibit this variation. The highly significant correlations of this variation with altitude and the absence of significant visual predators on Reunion Island suggest that the differences have physiological value in terms of absorption of radiant energy. In brown-headed brown morphs the intensity and extent of phaeomelanin deposition on the underparts also increases in relation to increasing altitude and rainfall.

Size characteristics vary between color forms and in relation to altitude. Wing length of brown morphs increases about one millimeter per 1,000 meters of elevation. Bill and tarsal lengths also increase with altitude in brown-headed brown morphs. Bill length decreases with altitude in gray morphs. Gray-headed brown morphs have longer bills than lowland brown-headed brown morphs, but about the same length bills as large highland brown morphs. Lowland gray-headed brown morphs and highland gray morphs show sexual dimorphism in bill length.

The following sequence of possible evolutionary events is envisioned as being responsible for the present situation. The brown morph first appeared as a mutant form in the original gray morph populations of Reunion Island. They gradually replaced gray morphs in the lowlands but not the highland heath zone and evolved head color and associated differences while isolated in disjunct pockets of suitable "edge" habitat, e.g., brown-headed brown morphs in the savanna of the arid west coast, gray-headed brown morphs along rivers and stream beds in the east, and brown-naped brown morphs in young forests at the base of the active volcano in the south. It is possible that the brown-naped brown morph arose through hybridization between the other two forms. The present day pattern of geographic distribution of these color forms reflects range expansions and secondary contacts that resulted from human destruction of indigenous forests. Associated altitudinal range expansions have brought brown and gray morphs together and clines have developed reflecting the relative adaptation of the morphs to the lowlands and highlands. The expansions also have led to the development of steep primary clines in the intensity of melanin deposition and size within the past 250 years.

The highly localized differentiation of populations of *Z. borbonica* appears to have been the inevitable result of several factors, e.g., its social and sedentary habits, which, however, are not exceptional or even extreme, its ties to disturbed and edge habitats, the climatic diversity of Reunion Island, and perhaps increased adaptive flexibility resulting from release from some selective agents usually present on continents, such as visual predators. In themselves each of these factors is not very unusual, but they are rarely found in combination within the confines of a small oceanic island.

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APPENDIX I

Summary of Reunion Island Localities[1]

Locality number	Altitude (meters)	Location	Name	Number of specimens
1	1,000	2 km SSE le Brûlé	Val Fleuri	14
2	1,100	3 km SSE le Brûlé	Mamode Camp	9
3	1,580	5.7 km SSE le Brûlé		14
4	1,780	7 km S le Brûlé	Plaine des Chicots (gite)	3
5	1,910	7.7 km S le Brûlé	Plaine des Chicots	6
6	1,650	5.2 km E Dos d'Ane	Plaine d'Affouche	9
7	1,460	3.3 km E Dos d'Ane	Plaine d'Affouche	0
8	1,700	20 km NNE St. Joseph	Rav. Rivière des Remparts	8
9	1,000	8 km SSW St. Denis	Chemin Arnoux	11
10	820	5.3 km ESE la Possession	Piton d'Orange	13
11	90	2 km S St. Denis	Ravine du Butor	10
12	220	3.5 km S Ste. Marie	Beaufonds	17
13	10	2.7 km E Ste. 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	1,100	1 km NE Gd. Islet	Grand Islet	4
18	1,530	3 km SSW Gd. Islet	Col Bemale	11
19	1,940	7 km W Hellbourg	Col de Fourche	11
20	1,160	4 km W Hellbourg	Ravine Farla	10
21	920	2 km W Hellbourg	Rivière du Mat	3
22	1,350	1 km S Hellbourg	Terre Plate	6
23	1,570	2.2 km SW Hellbourg	Plateau de Belouve	10
24	1,400	3.8 km NE Hellbourg	Trou de Fer	10
25	640	9 km SW St. Benoît	Ravine Mathurin	11
26	1,010	12 km SW St. Benoît	Takamaka	11
27	1,180	5 km WNW Pl. des Palmistes (1^{er})	Plateau Duverney	10
28	1,360	7.5 km W Pl. des Palmistes (1^{er})	Forêt du Bébour	0
29	1,350	6.5 km WNW Pl. des Palmistes (1^{er})	Forêt du Bébour	15
30	1,720	9.2 km W Pl. des Palmistes (1^{er})	Plaine des Salazes	10
31	720	4 km NE Pl. des Palmistes (1^{er})	Bras Grand Piton	11
32	860	2.7 km NE Pl. des Palmistes (1^{er})	Piton Camp de Tête	1
33	1,060	1.5 km SSW Pl. des Palmistes (1^{er})	Pl. des Palmistes (2^{eme})	6
34	170	3.5 km NNE St. Joseph	Rivière des Remparts	10
35	1,250	4.2 km SW Pl. des Palmistes		4
36	1,250	4.7 km SW Pl. des Palmistes		
37	1,620	6 km SE Pl. des Palmistes	Rampe de la Grande Montée	0

APPENDIX I (*continued*)

Locality number	Altitude (meters)	Location	Name	Number of specimens
38	1,600	5.5 km le Vingt-Septième	Plaine des Cafres	2
39	2,300	1 km ENE Pas de Bellecombe	Pas de Bellecombe	8
40	1,400	6 km WNW Pl. des Palmistes	Piton de la Plaine des Cafres	7
41	2,060	4.5 km E le Vingt-Septième	Nez de Boeuf	16
42	2,300	7.5 km ENE le Vingt-Septième	Piton de Sable	0
43	2,300	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 Ste. Rose	Forêt Mourouvin	12
46	500	4.2 km S Ste. 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	1,060	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	1,380	3.5 km NNE Plaine des Cafres	Bois Court	0
53	270	8.7 km NNE St. Louis	Petite Serré	7
54	340	5 km N St. Louis	Bras de Patate	4
55	300	6.5 km SSE Cilaos	Le Pavillon	11
56	1,000	2 km SSE Cilaos	Bras de Benjoin	9
57	1,380	4.5 km S le Brûlé		10
58	1,400	1 km N Cilaos	Forêt du Gd. Matarum	37
59	2,000	3 km NNE Cilaos	Petit Matarum	0
60	2,460	4 km NE Cilaos	Cavern Dufour	10
61	1,080	1 km N Tévelave	Forêt Soumise des Bernards (PK 2)	10
62	1,440	2.5 km NNE Tévelave	Forêt Soumise des Bernards (PK 7)	21
63	1,700	4 km NNE Tévelave	Forêt Soumise des Bernards (PK 10+)	29
64	1,980	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 (south side)	10
69	160	7 km SE le Port	Rivière des Galets (north side)	3
70	1,660	11 km ESE St. Paul	Ligne Dominiale	7
71	1,800	11.7 km ESE St. Paul	Camp Dennemont	5
72	1,400	9.5 km ESE St. Paul	(PK 5)	10
73	2,200	14.2 km ESE St. Paul	Piton Maido	14
74	1,550	10.5 km ESE St. Paul	(PK 7)	13
75	20	7 km WSW St. Paul	Ravine Jacques	0

APPENDIX I (*continued*)

Locality number	Altitude (meters)	Location	Name	Number of specimens
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 Ste. Anne	Ste. Anne	0
83	0	Ste. Rose	Monument	0
84	20	5.2 km SE Ste. 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	1,360	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
92	20	4.5 km WNW St. Pierre		0
93	90	4.2 km E St. Louis	Riv. St. Étienne (south 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	1,080	7.6 km ESE St. Paul	La Petite France	10
98	1,330	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	1,740	5 km NNW le Vingt-Septième	Plaine des Cafres	6
101	1,940	7.7 km NNE le Vingt-Septième	Coteau Maigre	10
102	280	5 km E Ste. Rose	Riv. de l'Est	1

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[1] All specimens were taken in 1967, except those for localities 100 and 101, which were taken in 1964.

APPENDIX II

UNDERPART GRAY COLOR VARIATION IN *Zosterops borbonica* ON REUNION ISLAND

Locality number	Altitude (meters)	Sample size	Underpart gray	
			Mean index	Standard deviation
1	1,000	14	4.6	1.50
2	1,100	6	4.8	1.83
3	1,580	11	6.5	1.13
6	1,650	9	5.8	0.45
8	1,700	8	6.2	1.75
9	1,000	11	3.1	1.37
10	820	11	3.3	1.19
11	90	10	2.7	1.25
12	220	13	2.5	0.87
14	200	9	4.0	1.22
16	680	13	3.9	1.44
18	1,530	11	5.5	1.44
19	1,940	10	6.0	1.05
20	1,160	10	6.2	1.31
23	1,570	10	5.3	1.42
24	1,400	10	5.9	1.41
25	640	8	4.1	1.25
26	1,010	11	5.1	1.30
27	1,180	10	5.3	0.67
29	1,350	10	5.5	1.35
30	1,720	9	6.5	0.84
31	720	11	5.0	1.79
33	1,030	6	5.5	1.76
34	170	10	1.1	0.73
39	2,300	6	6.3	1.30
40	1,400	7	6.4	0.78
41	2,060	24	5.6	1.10
44	0	13	1.7	0.87
45	520	12	3.3	1.37
46	500	11	4.4	1.21
47	80	12	2.7	1.37
48	100	11	2.4	1.86
49	1,060	12	4.8	1.75
51	40	17	2.4	0.87
53	270	7	2.1	0.69
55	300	7*	2.3	0.72
56	1,900	7	4.6	0.53
57	1,380	8	5.4	1.06
58	1,400	38	6.0	1.37
60	2,460	10	6.5	1.08
61	1,080	8	2.6	1.30
62	1,440	15**	3.5	1.12
63	1,700	25	5.4	1.34
64	1,980	8	5.7	1.83
68	120	10	1.4	0.71
70	1,660	7	4.4	1.94
72	1,400	9	4.5	1.34
73	2,200	14	6.3	1.24

APPENDIX II (*continued*)

Locality number	Altitude (meters)	Sample size	Underpart gray	
			Mean index	Standard deviation
74	1,550	13	6.7	1.55
85	20	10	2.7	0.95
86	320	6	1.0	0.89
87	70	12	2.6	0.79
93	90	6	0.5	0.55
94	300	9	1.9	0.60
95	640	10	2.5	1.08
96	740	10	3.3	1.25
97	1,080	7	3.6	0.69
98	1,330	6**	4.0	2.11
99	380	7	3.1	2.04

* Gray morphs excluded.

** "Brown-napes" excluded.

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