# ECOLOGY AND EVOLUTION OF THE SYMPATRIC MASCARENE WHITE-EYES, *ZOSTEROPS BORBONICA* AND *ZOSTEROPS OLIVACEA*

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THE Zosteropidae, or white-eyes, are a small paleotropical group of generalized passerines that have colonized more oceanic islands than any other passerine family (Moreau, 1964). While two species of *Zosterops* rarely coexist in mainland avifaunas, multiple invasions of small islands have resulted in several cases of bona fide sympatry. One such case involves the endemic Mascarene white-eyes, *Z. borbonica* and *Z. olivacea*, which are sympatric on Mauritius and Réunion Islands in the western Indian Ocean. Whereas niche expansion in a reduced competitive environment seems to be frequent in island colonists (Mac Arthur and Wilson, 1967; Keast, 1968), studies of the Mascarene white-eyes, here reported, suggest that the first white-eye to colonize the Mascarene islands became more specialized, rather than more generalized, in the absence of competitors. A second successful colonization by a generalized white-eye and subsequent sustained coexistence of the two species was apparently facilitated by the specialization of the first arrival.

## THE MASCARENE ISLANDS

The two major Mascarene islands, Mauritius and Réunion, lie approximately 400 miles east of Madagascar and are separated from each other by only 90 miles (Figure 1). Mauritius includes 720 square miles compared to Réunion's 1,000 square miles, and reaches a maximum elevation of only 3,041 feet while Réunion rises to 10,069 feet, the highest point in the Indian Ocean. Réunion, the more rugged of the two islands, is composed of two deeply eroded overlapping shield volcanos (Upton and Wadsworth, 1966), one of which (Piton de la Fournaise) is still active. In comparson, Mauritius is a low island with rolling, accessible hills. The location of these islands at the southern edge of the tropics insures a relatively stable climate, which is divided into a warm rainy season lasting from December through April and a cooler dry season from May through October.

Both Mauritius and Réunion were originally covered by evergreen forest composed of a variety of hardwood species, but the presence of many valuable timber species soon promoted the wholesale destruction of these forests by the early colonists. The indigenous forest on Mauritius is now restricted primarily to less than 7,000 acres in the southwestern plateau region (Vaughan and Wiehe, 1937), while considerably more native forest has persisted intact in the rugged interior of Réunion. One is never

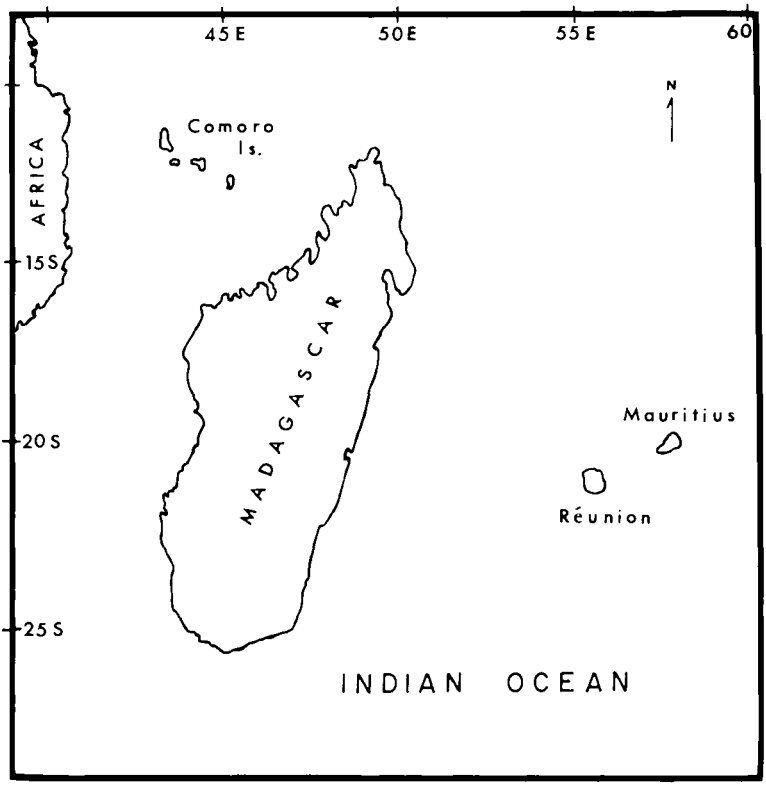


Figure 1. Location of Mauritius and Réunion Islands in the western Indian Ocean.

very far from conspicuous human disturbance and the encroachment of exotic plant species on either island. Open tree savannas once replaced the evergreen forest on the dry western coasts of both islands, but these were completely destroyed by the early 17th century (Rivals, 1952). Réunion's extensive highlands above 1,800 m support a relatively undisturbed heath (*Philippia*) vegetation.

The Mascarene islands are perhaps best known to ornithologists for the wholesale extinction of a bizarre avifauna (see Hachisuka, 1953; Greenway, 1958) that resulted when the islands were colonized. Over 50 per cent of Mauritius' known original avifauna and 40 per cent of Réunion's are now extinct. Recent discussions of the remaining endemic landbirds are available in Rountree et al. (1952), Newton (1958) for Mauritius, Milon (1951) and Berlioz (1946) for Réunion, and Watson et al. (1963) for both islands.

## Field Work

The field data and specimens forming the basis for this report were obtained during expeditions to the Mascarene islands in 1964 and 1967. In 1964 I was on Mauritius from August through October and on Réunion for one week in August and all of November. Robert W. Storer, my field companion in 1964, contributed to the information gathered at that time. In 1967 I spent 9 months on Réunion studying variation in *Zosterops borbonica*, and in the course of this work made frequent observations of both Réunion white-eyes. Finally, some information has been obtained from captive *Zosterops borbonica* and *Zosterops olivacea* (*olivacea*) maintained on Réunion and at The University of Michigan.

Data and specimens were collected at 102 different localities on Réunion, but most of the information discussed in this paper was obtained at six principal study areas. As these are mentioned repeatedly below, each is described briefly:

*Beaufonds* (*Ste. Marie*).—Altitude 200 m, annual rainfall 2,425 mm. Located on the island's north side on the sugar cane estate of Armand and Georges Barau, this study area consists of a private garden with a variety of tropical fruits, flowers, and vegetables, and an adjacent ravine with a flowing stream and dense vegetation, primary *Eugenia jambos* (Myrtaceae). Both white-eyes were most plentiful on the north and east sides of the island in such ravines. Field work at Beaufonds consisted of several visits from August through November.

*Etang Salé les Bains.*—Altitude 60 m, annual rainfall 713 mm. This lowland tract is on the island's hot, dry west side. Work was conducted in the extensive, dry open forests which are under the supervision of the Service des Eaux et Forêts. In addition to *Casuarina* and *Pithecellobium dulce* (Leguminosae) important plants include *Melia azedarac*h (Meliaceae), *Lantana camara* (Verbenaceae), and *Schinus terebinthifolius* (Anacardiaceae). Field work consisted of regular visits from July to November, and the color-banding and release of 41 *borbonica* in July for subsequent observation. *Z. borbonica* was plentiful here, but no *olivacea* was ever seen.

*Tévelave Heights.*—Altitude 1,650 m, annual rainfall 2,000 mm. This highland locality is directly above le Tévelave (altitude 1,000 m) at the Ligne Dominiale on the island's west side and upland from Etang Salé les Bains. The forests here consist primarily of young, regenerated Tamarin-des-hauts (*Acacia heterophylla*) with an understory of heath (*Philippia*) and bracken fern (*Pteridium aquilinum*). Scattered *Hypericum* are also present. Observations and collections were made at this locality in May and from July through November. Both *borbonica* and *olivacea* were common.

*Cilaos, Forêts du Grand Matarum.*—Altitude 1,400 m, annual rainfall 2,666 mm. This tract lies 1 km north of Cilaos at the base of Piton des Neiges. The forest is indigenous "bois de coleur," categorized as "moderately wet forest of middle altitudes" by Rivals (1952); it contains many hardwood species, including *Dombeya* spp., *Nuxia verticillata* (Loganiaceae), *Eugenia cotinifolia* (Myrtaceae), *Hypericum* spp. (Hypericaceae), and some introduced *Cryptomeria* (Taxodiaceae). Epiphytes, mosses, orchids, and lichens cover the branches of the older trees. This was the most important study area for information on the feeding ecology and relationships of the two white-eyes. A total of 53 *borbonica* and 15 *olivacea* were color-banded and released here.

*Forêt du Bébour.*—Altitude 1,400 m, annual rainfall 4,704 mm. This study plot is in one of the wettest forests on the island. The indigenous forest, "high altitude wet forest" of Rivals (1952), includes most of the important species found at Cilaos and many additional ones, the most conspicuous being numerous tree ferns (*Cyathea*).

Other important plants include *Forgesia borbonica* (Saxifragaceae), *Ardisia* (= *Icacorea*) spp. (Myrsinaceae) and introduced *Fuchsia coccinea*. In April and May, 44 *borbonica* and 9 *olivacea* were color-banded and watched regularly. The plot was then not revisited until November and December when additional studies were made for comparison. Both white-eyes were plentiful here, *olivacea* outnumbering *borbonica*.

*Nez de Boeuf (Plaine des Cafres).*—Altitude 2,060 m, annual rainfall 2,000 mm. This high altitude study tract in the ericaceous heath zone overlooks the ravine of the Rivière des Remparts. Interspersed in the extensive heath vegetation, in the hollows and other wind-protected sites, are dense clumps of the endemic *Sophora nitida* (Leguminosae) which, when flowering in August, are an important food source for white-eyes. *Hypericum*, which blooms shortly after the *Sophora* and throughout the summer, is also abundant in this region. White-eyes of both species were numerous. A total of 33 *borbonica* and 6 *olivacea* were trapped and banded here in August, and watched regularly for flower feeding habits and species interactions from August through November.

## THE MASCARENE WHITE-EYES

*Nomenclature.*—For the purpose of this paper, which is a discussion of the ecological relationships of the sympatric Mascarene white-eye species, I use the nomenclature of Moreau (1967) as follows: *Zosterops olivacea olivacea* for "oiseau (zo zo) vert" of Réunion, *Zosterops olivacea chloronothos* for the "oiseau pit-pit" of Mauritius, *Zosterops borbonica borbonica* for the "oiseau blanc" of Réunion, and *Zosterops borbonica mauritiana* for the "oiseau manioc" of Mauritius. The nomenclature of Mayr (1967) is followed for "Indo-Australian" species.

*Distribution and behavior.*—Unlike the other remaining Mascarene endemics, which seem to depend on the remnants of indigenous forest, *Z. borbonica* is an abundant and ubiquitous species on both Mauritius and Réunion. Although it occurs in nearly all kinds of vegetation, it is primarily a species of open and disturbed habitats rather than intact original forest. It is a common bird throughout Mauritius and the lowlands of Réunion where human influence is inescapable, but it is scarce in the relatively undisturbed central forests of Réunion except around the edges of clearings, streambeds, and roadsides.

Like most white-eyes, *borbonica* is a conspicuously social species. On both Mauritius and Réunion it is usually encountered in parties of 6 to 20 individuals that move cohesively and noisily through the forest, feeding, bathing, and resting together. These flocks move in a follow-the-leader style with conspicuous display of the white rump patch in flight. Such flocks are formed throughout the year. In at least some white-eyes, e.g. *Z. lateralis*, flocking is a winter phenomenon only and is replaced by territorial defense by mated pairs during the breeding season (Fleming, 1943).

The green Mascarene white-eye, *Z. olivacea*, is decidedly less common on both islands than is *Z. borbonica*. *Z. o. chloronothos* is now quite rare. It

used to occur regularly in the gardens of Vacoas and Curepipe on Mauritius but now does so only infrequently (Jean Vinson, pers. comm.) and is restricted primarily to the remote forests and scrub of the southwestern plateau. Here it may actually be more common than is generally realized, as it is easily overlooked unless one is familiar with its call note; with a little experience one can usually find several *Z. o. chloronothos* in the course of a day's hiking. In 1964 they were most common near Mt. Cocotte and Plaine Champaigne, where I found up to 10 individuals in a single day.

*Z. o. olivacea* is a much more common bird than is *Z. o. chloronothos*, but it is rarely as abundant as *Z. b. borbonica*. Its distribution from sea level to above 2,300 m altitude excludes only the dry western coastal regions; nevertheless it does occur in the wetter forests above 900 m on this side of the island. *Z. o. olivacea* is also rather uncommon in the lowland forests in the south of Réunion but becomes more numerous on the northern and eastern coasts where it lives primarily in wooded ravines with flowering *Eugenia jambos*. It is most plentiful and outnumbers *Z. borbonica* in the wet highland forests of the interior where introduced *Fuchsia* grows in profusion. Its distribution in the high altitude heath zone follows that of protected pockets of *Sophora* and *Hypericum*. Unlike *borbonica*, *olivacea* does not appear to be an edge species; it rarely wanders into gardens and is often found in heavy forest in the vicinity of certain favored flowers.

*Z. o. olivacea* is an aggressive, asocial white-eye that occurs in isolated pairs throughout the year rather than in small flocks. Rarely are several individuals together without some interaction; in areas with many flowers much of their time is spent in aggressive chasing and chattering, for they are highly territorial throughout the year in relation to flowers.

Estimates of total population size of these species on Réunion, based primarily on rough estimates of population density established by capture-recapture techniques at Cilaos and Etang Salé les Bains, are 556,000 for *Z. b. borbonica* and 154,000 for *Z. o. olivacea*. The *borbonica* figure is probably an underestimate as minimal densities were used purposely in the calculations, whereas the *olivacea* estimate may be somewhat high.

*Z. b. borbonica* and *Z. o. olivacea* both breed during the austral spring in late September through November and December. I found one nest of *olivacea* under construction as early as 10 August, but whether this species normally starts nesting earlier than *borbonica* is not clear. *Z. b. borbonica* is conspicuously social throughout the breeding season, adjacent pairs nesting as close as 50 feet, sometimes in loose semicolonial groups. "Helpers" sometimes feed the young. There is no indication of territoriality or nest area defense in this species, which thus may resemble *Z.*

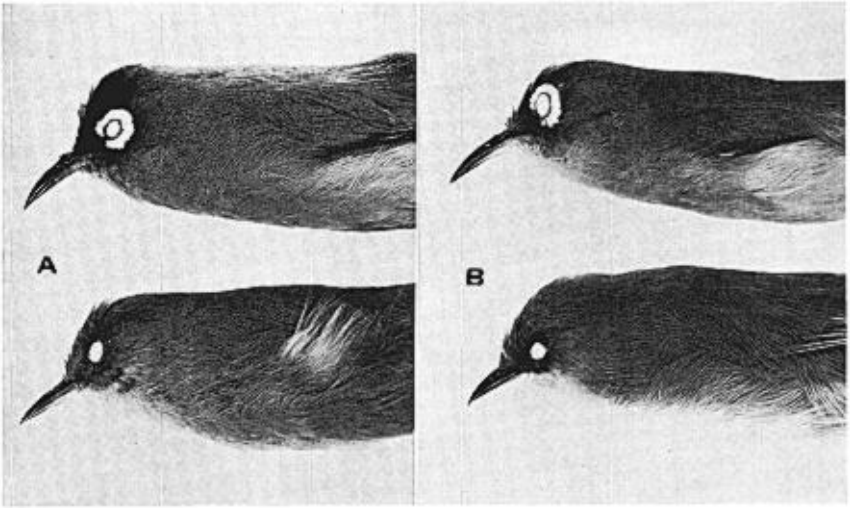


Figure 2. Sympatric pairs of Mascarene white-eyes. A, Réunion: upper, *Z. o. olivacea*; lower, *Z. b. borbonica*. B, Mauritius: upper, *Z. o. chloronothos*; lower, *Z. b. mauritiana*.

*virens* of South Africa (Broekhuysen and Winterbottom, 1968). *Z. o. olivacea*, on the other hand, breeds in isolated pairs close to productive flowering plants and defends the immediate area against all other *olivacea*.

*Z. borbonica* and *Z. o. olivacea* both huddle and engage in mutual preening or "allopreening" as has been noted in other species of white-eyes (Harrison, 1968). This is observed far more frequently in *Z. borbonica* than in *Z. o. olivacea*, in which it is restricted to occasional sessions between (mated?) pairs. In my aviaries when both species were present, *olivacea* usually huddled and preened with conspecific individuals, but interspecific huddling and preening were not uncommon.

*Plumage coloration.*—*Z. borbonica* differs markedly from typical white-eyes in plumage color, for instead of being yellow-green it varies from dull gray to rich brown, and it lacks the conspicuous white eye-ring of most *Zosterops*. Furthermore it has three groups of white feathers, the upper tail coverts, the axillary feathers, and the crural feathers (ankles), which are often effectively displayed in combination against the rest of the plumage. The white rump patch in particular is unusual in Zosteropidae. Color variation in *Z. borbonica* is pronounced and involves the presence or absence of brown pigments (phaeomelanins) as well as variation in the intensities of both gray and brown pigmentation. A detailed analysis will be published elsewhere; suffice it to say here that in color *Z. b. mauritiana*, an all-gray form, is similar to one of the color variants of *Z. b. borbonica*.

Although *Z. olivacea* is grayer than any continental African species and lacks a yellow throat, it conforms to the basic white-eye color pattern in being conspicuously green above with yellow or yellow-green upper and undertail coverts and in having a large, contrasting white eye-ring. In both subspecies the lower back, rump, and upper tail coverts are green. The nape and upper back of *Z. o. olivacea* also contain considerable green and thus differ from the predominately gray upperparts of *Z. o. chloronothos*. The crown of *olivacea* is usually blackish and contrasts with the rest of the upperparts, while in *chloronothos* it is gray and continuous with the coloration of the rest of the head, nape, and back. Only occasionally are there traces of black or tinges of green in this form. Both subspecies have blackish lores. Below the two differ with respect to 1) the intensity of gray on the belly, *chloronothos* being much lighter than *olivacea*; 2) the color of the flanks, which have a strong brownish wash in *chloronothos*; and 3) the presence of green feathers along the midline of the belly of most *olivacea* but of no *chloronothos*.

Both yellow pigmentation and the white eye-ring appear to be rather flexible evolutionary characteristics in the Zosteropidae, for they have been lost repeatedly in insular forms (Moreau, 1957). The white rump of *Zosterops borbonica* is probably a derivative of the pale rump color of many *Zosterops* (Moreau, op. cit.) and the axillary tufts are only slightly more elaborate than those found in some other species, for example *Z. lateralis*.

*Soft part coloration.*—In freshly taken specimens of both *Z. borbonica* and *Z. o. olivacea* the irides are brown, the feet dark gray, and the bill black with a gray base to the lower mandible. *Z. o. chloronothos* differs from *Z. o. olivacea* in having light brown feet and a light brown base of the lower mandible.

*Size.*[1]—*Z. borbonica* is a normal white-eye in size and proportions, though the bill tends to be slightly weaker and more pointed than in typical *Zosterops* (Moreau, 1957). Wing lengths average 55 mm in the lowlands and increase with altitude on Réunion[2] to an average of about 58 mm. The average tail/wing ratio of the species is 0.74. Bill lengths average 13.6 mm. There are no significant mensural differences between *Z. b. borbonica* and *Z. b. mauritiana*.

*Z. o. olivacea* and *Z. o. chloronothos* have unusually long bills, which average 15.6 and 16.8 mm respectively. Their bill/wing ratios are higher than those of any other African white-eyes and are exceeded by only a few species on small Pacific islands (Moreau, 1957). *Z. o. chloronothos* is also unusually short tailed (tail/wing ratio = 0.64), whereas *Z. o. olivacea* is

[1] Summaries of measurements can be found in Moreau (1957) and Storer and Gill (1966).
[2] Detailed analysis of mensural variation in *Z. borbonica* will be published elsewhere.

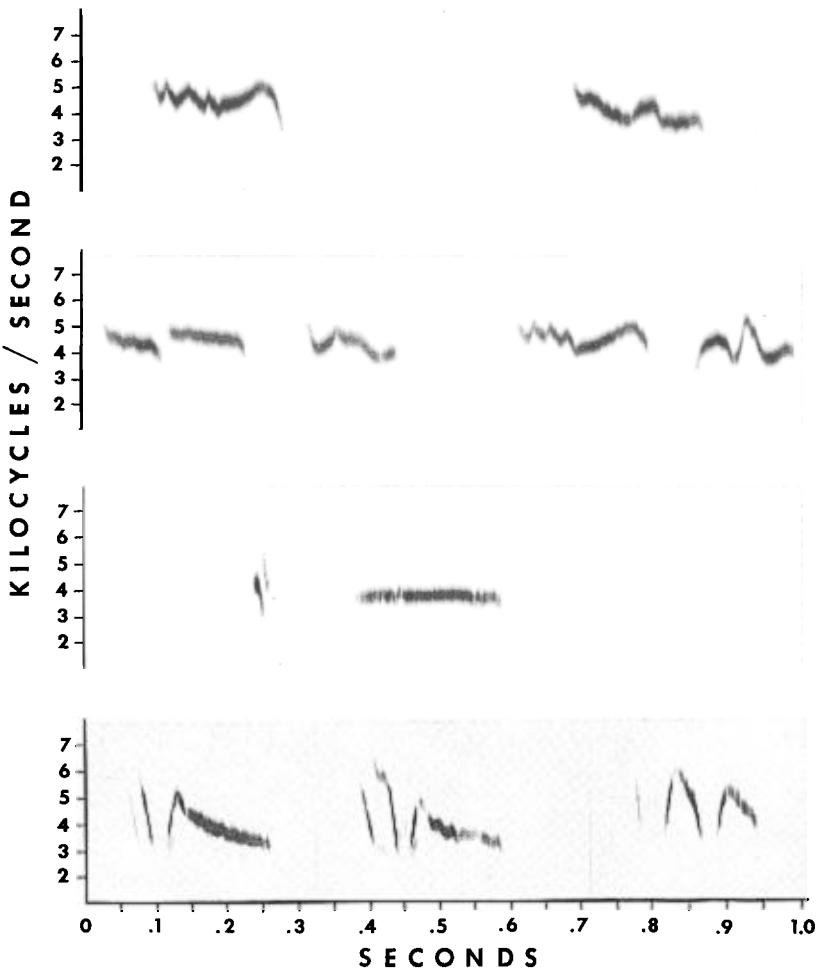


Figure 3. Spectrograms (using wide bandpass filter and normal pattern) of call notes of *Zosterops borbonica*. Top row: two patterns of single-noted "eeee" from feeding *Z. b. borbonica*. Second row: two patterns of double-noted "eeee-eeee" from feeding *Z. b. borbonica*. Third row: "chip eeee" from agitated *Z. b. borbonica*. Bottom row: three patterns of "p-treee" call from feeding *Z. b. mauritiana*.

normal in this respect (tail/wing ratio = 0.71). The two subspecies of *Zosterops olivacea* differ markedly in their measurements, *Z. o. chloronothos* being shorter winged, proportionately much shorter tailed, and slightly longer-billed than *Z. o. olivacea*.

Both races of *Z. olivacea* are, of course, longer-billed than the *Z. borbonica* with which they are sympatric. The bill length ratios of the two

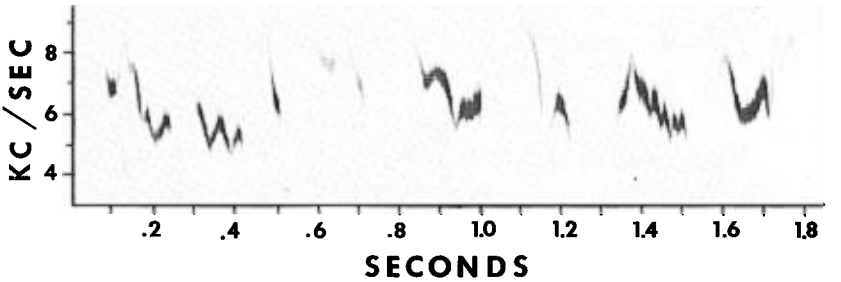


Figure 4. Spectrogram (as above) of portion of evening song of *Z. b. borbonica.*

pairs of sympatric species are 1.2 for *Z. o. chloronothos/Z. b. mauritiana* and 1.1 for *Z. o. olivacea/Z. b. borbonica.* Also *chloronothos* is slightly smaller (wing length 3 mm shorter) than *mauritiana. Z. o. olivacea* is slightly larger than most *Z. b. borbonica* but has a wing length comparable to large *borbonica* of the Réunion highlands.

*Vocalizations.*—The vocalizations of the Mascarene white-eyes differ between species and also between conspecific populations on the different islands. The common feeding and flock call of *Z. b. mauritiana* is a soft, inflected, and slightly warbled "p-tree" or "p-tee" whereas the call *Z. b. borbonica* uses in similar situations is a plaintive "eeee" or double "eeeee-eeee" (Figure 3). When agitated, *borbonica* gives emphatic chips followed by a piercing "eeeeeee," a call that resembles the "p-treee" of *mauritiana* (Figure 3). Chips are occasionally given by *mauritiana*, and individuals of both populations sometimes use rapid series of chips in flight.

In late evening and again for a few minutes just after daybreak during the breeding season on Réunion from late August through December, male *Z. b. borbonica* repeatedly deliver an elaborate loud warbling song (Figure 4) from a tall exposed perch, such as a *Casuarina* tree, heath bush, or even television antenna. Occasionally full song is heard later in the day, and foraging individuals sometimes render short warbled phrases. So conspicuous and locally well-known is the singing on Réunion that it is surprising not to hear it on Mauritius. I never heard this song from *Z. b. mauritiana* despite numerous visits to the forest in late afternoon in September and October, and when asked about the possibility of such a vocalization, Jean-Michel Vinson, an experienced local ornithologist on Mauritius, was also quite certain he had never heard it. Thus it would seem that conspicuous dawn and evening singing is not characteristic of *Z. b. mauritiana,* but is of *Z. b. borbonica.*

*Z. b. borbonica* also has a different muted song, a catbird-like (Mimidae) assemblage of sweet warbled phrases, chip notes, sputters, and squeaks.

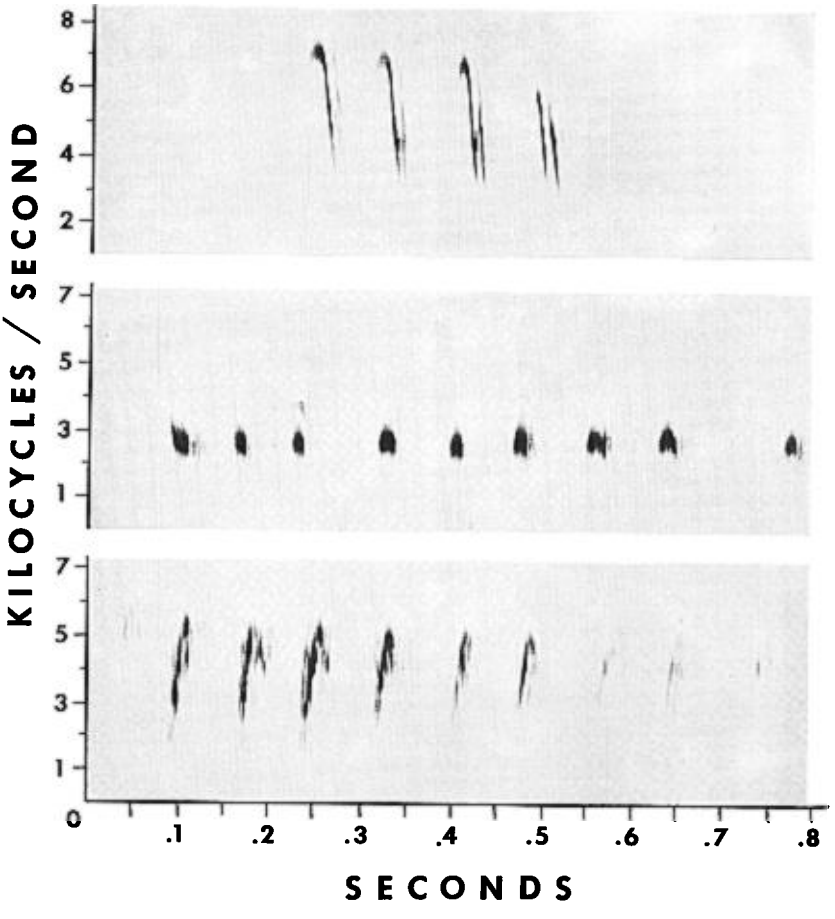


Figure 5. Spectrograms (as above) of call notes of *Zosterops olivacea*. Top row: series of four emphatic "tchip" notes of *Z. o. olivacea*. Middle row: series of "tu" notes from active *Z. o. olivacea*. Bottom row: series of "pit" notes from *Z. o. chloronothos*.

This song is heard frequently at any time of day as the white-eyes come into breeding condition in August and September. Finally as they are preparing to roost, *Z. b. borbonica* give a distinctive extended soft twittering. I could predictably and immediately elicit this vocalization from isolated captive individuals simply by turning off the lights late at night.

The vocalizations of *Z. o. olivacea* and *Z. o. chloronothos* are also distinct, both from each other and from those of the *Z. borbonica* with which they are sympatric. The only call I ever heard from *chloronothos* was an explosive "pit-pit-pit" (Figure 5), the basis of the local creole name

"oiseau pit-pit." Particularly in flight these same notes are often repeated in rapid succession to form a prolonged sputter. Both these calls are similar to the "pit" call note and flight sputter of *Foudia rubra* (Ploceinae), another Mauritian forest endemic. The call usually rendered by active *Z. o. olivacea* is a single "tsip" or a series of "tu-tu-tu" notes (Figure 5). When flying or excited, as well as in aggressive situations, these white-eyes give an emphatic "tchip-tchip-tchip," the components of which are structurally unlike the "pit" notes of *Z. o. chloronothos* (Figure 5). When two or more *Z. o. olivacea* are together, they utter loud, excited bursts of "tu" and "tchip" notes. Finally, *Z. o. olivacea* has a loud, warbled song similar to the muted song of *Z. b. borbonica*, but it is always much louder and usually has "tu" and "tchip" notes interspersed among the warbled phrases, one of which is very similar to the principal phrase of *borbonica*'s evening warbling. This song can be heard throughout the day; there is no burst of singing in the late evening or early morning as in *borbonica*.

The common call note or contact notes many white-eyes use as they forage is a plaintive sparrow-like chirp or cheep, which often differs very little between widely separated species. To my ear the "p-teee" of *Z. b. mauritiana* is very similar to the contact calls of *Z. japonica* in Hawaii and *Z. lateralis* in New Zealand, both of which have been described as "creee" (Fleming, 1943; Peterson, 1961). The contact notes of *Z. virens* and *Z. senegalensis* must also be very similar in that they are close to *Z. lateralis* (Mees, 1969: 332). The only described call notes that might resemble those of *Z. olivacea* (either population) are the staccato "tsip-tsip-tsip" of *Z. japonica simplex* (Mees, 1957: 129) and perhaps the "splutter" of *Z. virens* (Skead and Ranger, 1958).

Many white-eye species are known to have elaborate melodius songs. The "warbling song" of *Z. lateralis* (Fleming, 1943) is similar to the muted breeding song of *Z. borbonica* in context, timing in relation to the breeding season, and composition. The typical daytime songs of *Z. o. olivacea* and of *Z. virens* (Skead and Ranger, 1958), with their rambling and mimicking qualities, also belong to this set of presumably homologous vocalizations. Restricted dawn and/or evening singing has been reported for relatively few species, e.g. *Z. virens* (Skead and Ranger, 1958), *Z. ceylonensis* and *Z. japonica* (Mees, 1957). The "challenge song" of *Z. lateralis* (Fleming, 1943) is probably homologous, but can be heard throughout the day, presumably functioning in territoriality.

Discussion of evolutionary differences in vocalizations must, of course, remain highly speculative without detailed documentation and comparison of many species repertoires. However the vocalizations of *Z. borbonica*, especially its call notes, are similar to those of *virens* and *lateralis*. The components of *Z. b. borbonica*'s vocal repertoire seem to be the same as in

*lateralis*. The vocalizations of *Z. b. borbonica* and *Z. b. mauritiana* have diverged to the extent that their contact calls are different, and *mauritiana* has lost the evening warbling (challenge song). More detailed study of *mauritiana* may reveal other differences. The call notes of *Z. o. olivacea* and *Z. o. chloronothos* are quite different from those of typical white-eyes, and *Z. o. olivacea* lacks a special dawn song (challenge song). More information on *Z. o. chloronothos'* vocalizations is needed before detailed comparison with *Z. o. olivacea* will be meaningful.

*Feeding.*—*Z. borbonica* typically feeds in small flocks of 6 to 20 individuals that, on Mauritius in August and September, often include some of the other endemic forest species such as *Foudia rubra* (Ploceidae), *Coquus* (= *Coracina*) *typicus* (Campephagidae), and occasionally *Z. o. chloronothos*. *Z. borbonica* is always the most numerous "nucleus" species, the others appearing to join the flock but temporarily. On Réunion interspecific mixing is less common, *Tchitrea borbonniensis* (Muscicapidae) being the only regular associate of white-eye flocks. *Z. o. olivacea* rarely joins such flocks and is normally quite independent in its feeding behavior.

*Z. borbonica* usually forages like a warbler for insects, which it captures as they flush, extracts from crevices in the bark, leaf buds, and epiphytes, or gleans from the undersides of leaves and branches. Titmouselike hanging upside down is common, and *Z. b. borbonica* often creeps along tree trunks and branches, both horizontal and vertical, in a manner quite like that of the Black-and-white Warbler (*Parulidae-Mniotilta varia*). Only once have I seen *borbonica* fly-catching, one evening in 1964 when several *Z. b. mauritiana* flew repeatedly from a sapling into a cloud of small midges.

The insect food *borbonica* takes includes flies, beetles, moths, pupae, and eggs. Although these white-eyes are frequently seen taking caterpillars, few stomachs examined contained them. Similarly spiders are taken regularly, but they do not form the bulk of *borbonica*'s arthropod diet. *Z. b. mauritiana* often feeds on *Flatopsis nivea* (Hemiptera, Flattidae), which sometimes occur in large concentrations (J. Vinson, pers. comm.). *Z. b. borbonica* feeds heavily on white flies (Homoptera-Aleyrodidae) that are abundant on the undersides of bracken fern (*Pteridium aquilinum*) fronds in the understory of young tamarin (*Acacia heterophylla*) forests. Birds in captivity consume house flies and *Drosophila* in large quantities.

*Z. borbonica* also eats a variety of fruits, particularly during the winter months when insects are relatively scarce, and is reported to damage fruit in private gardens and commercial orchards in the lowlands. Of the 357 *Z. b. borbonica* stomachs examined between May and August, 44 per cent contained fruit, compared to only 11 per cent of 333 stomachs examined between September and December, the normal breeding season of the

TABLE 1
FLOWERS VISITED BY RÉUNION WHITE-EYES

| Plant species | *Z. b. borbonica* | *Z. o. olivacea* |
|---|---|---|
| *Fuchsia coccinia* (Onagraceae) | X | X |
| *Camellia sinensis* (Theaceae) | | X |
| *Kalanchoe bryophyllum* (Crassulaceae) | X | |
| *Eugenia jambos* (Myrtaceae) | X | X |
| *Melia azedarach* (Meliaceae) | | X |
| *Lantana camara* (Verbenaceae) | X | |
| *Pelargonium capitatum* (Geraniaceae) | | X |
| *Musa* sp. (Musaceae) | | X |
| *Cuphea platycentra* (Lythraceae) | X | |
| *Geniostoma* sp. (Loganiaceae)[1] | | X |
| *Aphloia theaeformis* (Flacourtiaceae)[1] | | X |
| *Forgesia borbonica* (Saxifragaceae)[1] | | X |
| *Dombeya* spp. (Malvaceae)[1] | X | X |
| *Hypericum* spp. (Hypericaceae)[1] | X | X |
| *Sophora nitida* (Leguminosae)[1] | X | X |

[1] Native to Réunion Island.

species. Fruits that *Z. b. borbonica* eats include the berries of *Lantana camara*, *Schinus terebinthifolius*, *Solanum* sp., *Cordyline* sp. (Liliaceae), *Eugenia continifolia*, *Aphloia theaeformis*, papaya (*Carica*), guava (*Psidium*), and raspberries (*Rubus*). Such unusual items as flower stamens, a tiny snail, and heath (*Philippia*) buds were found once or twice in the *Z. b. borbonica* stomachs.

*Z. b. borbonica* regularly visits and extracts nectar from flowers, although the amount of such feeding depends on the locality and time of year. Where certain flowers grow in profusion, as *Kalanchoe bryophyllum* does at Etang Salé les Bains in July, *Eugenia jambos* at Beaufond (Ste. Marie) from September to December, *Fuchsia coccinia* in the Forêt du Bébour from September to April, and *Sophora nitida* at Nez des Boeuf (Plaine des Cafres) in August, flower feeding is common. In the highlands the white-eyes' foreheads often turn yellow with accumulated pollen. Table 1 lists the flower species at which I saw *borbonica* feeding. In the highlands *Sophora* and *Hypericum* are most important. In the wet forests *Dombeya* trees are visited frequently and may be especially important in that, unlike most of the native plants, some *Dombeya* is in flower throughout the year.

An indication of the importance of nectar relative to insect foraging and fruit eating can be obtained from the counts I made of feeding individuals in the Cilaos study area from September to December. These counts were obtained by recording what each white-eye was doing when first noticed as I walked slowly through the area. Flower visits constituted 6.5 per cent (8 of a total of 122 observations). Fruit feeding was observed only 5 per cent of the time (6 observations). Thus flower feeding is about as frequent

as fruit feeding during the breeding season, perhaps more so, but it is much less frequent than insect foraging, which comprised 80.5 per cent of the observations recorded in this period.

To get at the nectar of *Fuchsia* flowers the white-eyes pierce the base of the corolla with their bills. Usually they work on the flowers while dangling on a cluster of three or four blossoms, but they often reach out and pull the desired bloom to a branch with the bill, pin it to the perch with one foot, and then puncture it. Alternatively they simply reach out from a perch with one foot and hold the flower in position. They use similar techniques on the *Kalanchoe* flowers.

The basic elements of *borbonica*'s feeding ecology seem to be the same on Mauritius and Réunion, but perhaps because of the scarcity of flowers in the Mauritian forest, I rarely saw *Z. b. mauritiana* feeding at flowers; once near the beach at Le Morne several visited the red flowers of introduced flame trees (*Erythrina*) in the company of Spotted Weavers (*Ploceus cucullatus*).

Unlike *Z. b. mauritiana*, *Z. o. chloronothos* rarely forages for insects among the leaves and branches of the forest vegetation, but rather restricts its feeding activities to flowers. Single individuals or pairs constantly move about and visit isolated flowers, often covering substantial distances between flowers. This behavior is partly responsible for the apparent scarcity of this species, for they appear suddenly, feed briefly at the few flowers present, and then leave. The paucity of flowers in August and September, even in the vicinity of Mt. Cocotte and the Macabe Forest, the strongholds of this species, may force them to visit isolated productive flowers. Two of the flowering species at which *chloronothos* fed were *Bakerella hoyifolia* and *Trochetia uniflora*. In addition to nectar these white-eyes do take some insects, which I found in several stomachs. Once I saw an individual insert its bill between the overlapping petals of a *Trochetia* flower and spread them apart slightly. The only *chloronothos* I saw feeding at a nonflowering site was a single individual that dangled briefly from a tree fern (*Cyathea*) frond and then flew to a second tree fern where it probed at the base of the crown.

*Z. o. olivacea* also seems closely tied to and dependent upon available flowers. Rarely does one find this white-eye far from some conspicuous flower, and it is truly plentiful only near a profusion of such favorites as *Hypericum*, *Sophora*, and *Fuchsia*. In addition to the usual white-eye favorites, *olivacea* visits a wider variety of flowers than does *borbonica* (Table 1). Nectar is almost certainly the primary attraction, though some insects are also taken. The flower parts themselves are sometimes eaten, as I found stamens in the stomachs of three specimens collected in the

Cirque de Salazie and noticeable amounts of pollen in two other stomachs. Several times I saw *olivacea* hover in front of a flower.

Nearly all *Z. o. olivacea* stomachs examined contained some insect material but I rarely noted this form gleaning the foliage for insects. In 9 months on Réunion I accumulated only 20 sightings of insect foraging by *olivacea*, though such behavior was recorded whenever noted. I never saw *olivacea* foraging in the creeperlike fashion so often used by *borbonica*.

*Z. o. olivacea* is an adept flycatcher. In November, 1964, Storer and I watched several individuals fly-catching from telephone wires along the road near St. Rose. This may be unusual, as I did not see it in 1967, but I did frequently see them fly-catching from tall pine trees. Probably the most frequent mode of fly-catching is in flowering bushes and sap trees (see below) where aerial insects are captured as the white-eyes hop from one branch to another. Insects may be grabbed while the bird is in the air, or often just snapped out of the air without leaving the perch. Bill clicks are audible at close range. Similarly in my aviary *olivacea* caught *Drosophila* by flying out from a perch, whereas *borbonica* usually caught those flies that had landed.

*Z. o. olivacea* never or only very rarely eats fruit. I never saw it do so in the field or found fruit in any stomachs examined. In captivity *olivacea* ignored various fruits that *borbonica* ate readily.

An apparent offshoot of nectar feeding by the Réunion white-eyes is their habit of drinking sap. In early September near Cilaos I found a young *Claoxylon glandulosum* (Euphorbiaceae) that was being used as a source of sap. At many places along the branches, particularly the younger, green ones, the bark had been stripped away from the underlying wood, and sap was oozing from the exposed broken edges. Each stripped area was extensive, often up to 6 inches long, but the sap was flowing only from a relatively small unhealed section. To me this sap tasted rather bitter, but the tree was tended almost constantly by one banded *olivacea*, which moved from one break to another in quick succession and drank the freshly accumulated sap droplets by running its slightly opened bill along the oozing edge and flicking its tongue in and out. This particular white-eye actively defended the tree against all other white-eyes of both species that came near.

That this was not just an unusual case of sap feeding was confirmed the following week near Plaine des Chicots. There I found an old *Claoxylon* (appropriately called "bois d'oiseaux" by the creoles), its branches covered with gaping, bare scars, most of them old and dry, but an *olivacea* was feeding at several running fresh ones. A short time later a *borbonica* came and fed at the same sites. A month later near La Possession I watched several *borbonica* and some butterflies feeding at the exposed edges of

some broken bark on a large *Acacia* that had apparently been damaged in a storm.

The generalized feeding behavior of *borbonica* resembles that of most other white-eyes, which take a variety of food items including insects, fruit, and nectar. White-eye insect-foraging is usually done in flocks and includes warblerlike foliage gleaning, searching of terminal leaf branches, and in some species titmouselike hanging upside down (*Z. virens, Z maderaspatana*) or occasional fly-catching (*Z. pallida*). The regular trunk-creeping behavior of *boronica* does not have common parallel elsewhere in the family, though both *Z. chloris intermedia* and *Z. lateralis* have been noted clinging to the trunks of trees and moving upwards in small jumps (Mees, 1957: 41; 1969: 23). Most *Zosterops* also eat ripe fruits and berries. But nectar is apparently of minor importance in the diet of most white-eyes (Moreau et al., 1969: 42). Apparently most species of white-eyes take nectar only occasionally, and those few that take nectar regularly always do so as a supplement to the fruit and insects that form the major portion of their diet. Thus in feeding habits *borbonica* is similar to or perhaps slightly more generalized than other white-eyes, but *olivacea* emphasizes flower-feeding far more than typical white-eyes and also replaces the usual modes of insect foraging by fly-catching. The aggressive behavior and defense of flowering bushes by *olivacea* is also unusual for a white-eye as is the avoidance of fruit.

*Interspecific feeding relationships.*—Although the activities of *borbonica* and *olivacea* are usually conducted separately, positive associations of the two species do occur. Occasionally *Z. o. chloronothos* is seen with feeding flocks of *Z. b. mauritiana* (Niven, 1965; pers. observ.), but my impression was that the association was always a loose one that was interrupted by *chloronothos'* tendency to fly between widely separated flowers rather than to forage in the continuous fashion of *borbonica*. Similar associations of the two species in the same feeding flock on Réunion were extremely rare, for only once in 9 months did I see *olivacea* (three individuals) with a feeding flock of *borbonica*. Associations of *olivacea* and *borbonica*, however, are frequent in the vicinity of certain flowering plants, especially in groves of flowering *Sophora*, extensive groves of *Fuchsia*, and in ravines with flowering *Eugenia jambos*. Elsewhere, in the absence of such concentrations of flowers, an association between the two species is likely to be brief, occurring only when passing *borbonica* pause to feed at relatively isolated *Hypericum* bushes.

Interspecific aggression is common between the two white-eye species in the vicinity of these flowers, and it is invariably one-sided: *olivacea* is aggressive, *borbonica* is submissive. The interspecific encounters are distinctly less intense than intraspecific ones. Whereas defense is not relaxed

TABLE 2
COMPARISON OF MASCARENE WHITE-EYES TO TYPICAL WHITE-EYES

| Character | Typical white-eyes (*virens*, *lateralis*, *palpebrosa*, etc.) | *Zosterops b. borbonica* | *Zosterops o. olivacea* |
|---|---|---|---|
| Coloration | Carotenoids; eye-ring | No carotenoids; no eye-ring | Reduced carotenoids; eye-ring |
| Proportions | Normal | Normal | Long bill; short tail (*Z. o. chloronothos*) |
| Vocalizations | | | |
| Seasonality | Breeding season only | Breeding season only | All year?? |
| Warbling song | Present | Present (muted) | Present |
| Challenge song | Present: all day (*lateralis*); dawn and evening (*virens*) | Dawn and evening (absent in *Z. b. mauritiana*) | Absent |
| Flocking | Winter only (*lateralis*) all year in other ssp.? | All year | Rarely |
| Territoriality | Breeding-nest area (*lateralis*); absent or sporadic (*virens*) | None | Flowering bushes |
| Food | Insects, fruit, nectar | Normal, though with increased creeping on tree trunks and branches | Flower-feeding; insects by fly-catching |

until nonresident *olivacea* are driven away, intruding *borbonica* are chased briefly and then tolerated if they do not leave. Admittedly *borbonica* often gains some advantage by appearing in small groups, forcing the defending *olivacea* to displace several individuals in succession. Nevertheless persistence by the chased bird seemed to aggravate an intraspecific challenge but resolve an interspecific one. In addition, wing quivering by *borbonica* seemed to ease the interspecific relationship, while at other times the *borbonica* simply left a flowering *Hypericum* when an *olivacea* appeared nearby, suggesting a well-defined dominance relationship. The net result was that the *borbonica* usually succeeded in feeding at some of the flowers defended by an *olivacea*.

Aggression at flowering *Hypericum* and *Sophora* was especially conspicuous and included actual contact of fighting birds at times. While resident *olivacea* dominated other white-eyes of both species, they were occasionally displaced from their own bush by the introduced weaver, *Foudia madagascariensis*.

## DISCUSSION

On both Mauritius and Réunion islands live two white-eyes, one of which is a typically generalized, highly social species and the other an unusually

TABLE 3
SUMMARY OF MASCARENE WHITE-EYE SPECIES CHARACTERISTICS

| Character | *Zosterops olivacea* | | *Zosterops borbonica* | |
|---|---|---|---|---|
| | *olivacea* | *chloronothos* | *borbonica* | *mauritiana* |
| Crown color | Black | Gray | Gray/brown | Gray |
| Back color | Green | Gray | Gray/brown | Gray |
| Belly color | Dark gray with green in center | Light gray; no green | White to gray and brown | White |
| Eye-ring | Present | Present | Absent | Absent |
| Foot color | Dark gray | Light brown | Dark gray | Dark gray |
| Bill color | Black wth gray base | Light brown | Black with gray base | Black with gray base |
| Tail/wing (mean) | 0.71 | 0.64 | 0.74 | 0.74 |
| Bill/wing (mean) | 0.27 | 0.32 | 0.24 | 0.25 |
| Feeding call | "Tsip or tu tu" | "Pit-pit" | "Eeee-eeeee" | "P-tree" |
| Mimic warbling | Loud | ?? | Muted | ?? |
| Challenge song | None | ?? | Dawn and evening | None |
| Flower feeding | Frequent; habitual | Frequent | Occasional | Occasional |
| Insects | Fly-catching | + (method?) | Warbler + creeping | Warbler (+ some fly-catching) |
| Fruit | Never | ?? | Frequently in winter | ?? |
| Flocking | Very rarely | ?? | Habitually | Habitually |

aggressive, specialized flower-feeding species. The generalized species, *borbonica*, is closer to other white-eyes in virtually all aspects of its biology than is the specialized species, *olivacea* (Table 2). *Z. borbonica*'s departures from the "norm" include relatively simple changes in plumage color, an increased emphasis on trunk creeping as a mode of insect foraging, and some modification of the vocal repertoire. It is primarily a species of edge and disturbed habitats. *Z. olivacea*, on the other hand, is primarily a species of the indigenous forests and differs from normal white-eyes in bill and tail proportions, call notes, absence of social and flocking behavior, increased aggressiveness in relation to feeding sites, and a shift to flowers as its primary food source.

The many differences between the two insular populations of each species are summarized in Table 3; the differences between *Z. o. olivacea* and *Z. o. chloronothos* are much greater than those between *Z. b. borbonica* and *Z. b. mauritiana*. The two races of *olivacea* differ in vocalizations, plumage

coloration, overall size, and proportions of the bill and tail, whereas the two races of *borbonica* differ primarily in their vocalizations. Thus, interinsular divergence has been greater in *olivacea* than in *borbonica*.

*Sequence of colonization and evolutionary change.*—In view of the uniformity of continental *Zosterops*, one assumes that the ancestor(s) of both *borbonica* and *olivacea* were typical generalized white-eyes. Several hypothetical sequences of colonization of Mauritius and Réunion by white-eyes and differentiation of the endemic forms exist. As interchange between the two islands has been frequent (Moreau, 1957: 402), a white-eye that colonized one of the islands probably reached the other a short time later, at least in relation to the timing of a second successful colonization of the islands from the mainland.[3] Hence a single invasion of the Mascarene islands or separate invasions of Mauritius and Réunion followed by speciation and exchange of species between islands seem unlikely hypotheses. Consequently I favor a hypothesis of double invasion of the islands, the first arrival giving rise to one of the modern species and the second arrival giving rise to the other.

The question then follows whether the first successful colonist was the ancestor of the specialized *olivacea* or the generalized *borbonica*. *Z. olivacea* has certainly diverged farther from a typical white-eye in habits and morphology, excluding plumage coloration, than has *borbonica* and is a bird of the indigenous forest rather than disturbed habitats. Its populations on Mauritius and Réunion are also more different from each other than the comparable pair of *borbonica* populations, a fact suggesting, though not necessarily indicating, a longer separation. These facts alone suggest that *olivacea* was established on Mauritius and Réunion before the arrival of *borbonica*'s ancestor. Furthermore if *borbonica* colonized the Mascarenes first and retained its preference for edge habitats and generalized feeding habits, then the ancestor of *olivacea*, which was also a generalized white-eye, would have had to shift its ecological preferences, adapt to the indigenous forest, which was for some reason not inhabited by *borbonica*, and perhaps dominate the established *borbonica* in order to colonize the island in the face of congeneric competition.

Rather than occurring immediately after and making possible the second colonization, it seems likely that the major ecological shift gradually followed the first successful colonization, for as Lack (1969: 48) has noted, "any new arrival must compete immediately with the established species and either its existing adaptations enable it to do so successfully straightaway or it is eliminated without time to evolve adjustments." I submit that the ancestor of *olivacea* increased its flower-feeding frequency and

[3] For the purposes of these arguments the actual geographical origin of the colonists is not important.

dependency as it adapted to the Mascarene forests, and that some time later the ancestor of *borbonica* was able to colonize these same islands by virtue of being a generalized white-eye favoring edge and disturbed habitats as was the ancestor of *olivacea*. Subsequent competitive interaction between the two species may then have caused *olivacea* to become an even more specialized flower-feeder, to shift from normal modes of insect foraging to fly-catching, and to give up fruit-eating. The change from social to aggressive, nonsocial behavior in *olivacea* presumably accompanied its increased dependence on flowers. With time *olivacea*'s aggressive defenses of flowers may have affected *borbonica* which, by losing the white eye-ring and carotenoid pigmentation, became less subject to the interspecific aggression evoked by these typical white-eye plumage characteristics.

I suggest, therefore, that the first white-eye to arrive in the Mascarene islands became more specialized, rather than more generalized, in a reduced competitive environment. "Specialized" and "generalized" are admittedly only relative and somewhat ambiguous terms. We do not know to what extent ancestral *olivacea* fed on flowers as opposed to fruit or insects and to what extent it sacrificed fruit and insects for nectar before the arrival of *borbonica*. The initial increase in flower-feeding by *olivacea* was presumably a broadening of its feeding repertoire and an increase in generalization. The subsequent shift to flower-feeding to a point that was essentially irreversible once *borbonica* colonized the island, or even to the point that made possible *borbonica*'s successful arrival and ecological expansion, was certainly a loss of the opportunistic generalization that characterizes continental *Zosterops*.

Selection operates solely as a function of overall reproductive success, and the degree to which a species specializes is determined by the location of peak reproductive success within an array of potential modes of existence, the sum of which corresponds to the species' "fundamental niche" (Hutchinson, 1965: 32). Interspecific competition will determine an optimal "realized niche," which, in the presence of specialists, may emphasize generalized behavior rather than specialized. In the absence of interspecific competition, the direction of such species' evolution may shift towards a more specialized "realized niche," one of which is specialized nectar feeding.

Competition between flower-feeding birds is often intense. Aggressive chasing by feeding sunbirds (Nectariniidae) and honey eaters (Meliphagidae) is a familiar sight in Africa and Australia respectively, and interspecific aggression is common when several species of hummingbirds feed in the same tree (Cody, 1968). Competition and aggression between similar-sized sunbirds and honey eaters has also been described from the Moluccan islands (Ripley, 1959). In New Zealand aggressive Bellbirds (*Anthornis*,

Meliphagidae), often prevent silver-eyes (*Z. lateralis*) from taking nectar at feeding stations and it seems that honey eaters may also limit nectar feeding from flowers at many localities (Falla et al., 1966). Thus in the absence of specialized flower feeders white-eyes may experience a "competitive release" with respect to flower-feeding.

The process of evolutionary change hypothesized above for the Mascarene white-eyes bears a strong resemblance to the "taxon cycles" described by Wilson (1961) and Greenslade (1968) for Melanesian ant and Solomon Island bird faunas respectively. In this "cycle," islands are colonized by species that occupy marginal, disturbed, and coastal habitats in source areas. On the islands these species move into the indigenous forest that lacks the competitive forest species of the mainland. Replacement by new colonists occurs in the lowlands and with time rarity, extinctions, restriction to mountain areas of the interior, and relict distributions result.

Many white-eyes are found primarily in open and disturbed vegetation. Like certain coerebids (Moynihan, 1969) they seem to be "marginal" species, which are opportunistic generalists thriving in disturbed environments and characteristic of island situations, both montane and oceanic. The frequent ecological separation of two or more white-eyes in the same geographical region (Table 4) suggests that this process of specialization and progressive adaptation to indigenous forest in the absence of competitors may be very important in white-eye evolution.

*Sympatry in white-eyes.*—This study was initiated because of the unusual occurrence of sympatry in the genus *Zosterops* despite its broad paleotropical distribution. At first glance there are, excluding the Mascarenes, 22 possible cases of sympatry, but only 7 of these are bona fide, as altitudinal, geographical, or major ecological separations are involved in the others (Table 4). Six of the seven non-Mascarene cases of actual sympatry are on small islands, but unfortunately few details on the habits of these white-eyes are available. On Ponape and Palau in Micronesia, *cinerea*, the more abundant species is known to dominate and chase *conspicillata* (Baker, 1951).

A greater incidence of congeneric sympatry on islands than on continents, such as that in white-eyes, is contrary to the trend found in other groups (Grant, 1968). It seems that white-eyes persist in continental faunas by virtue of being generalized and marginal species. While the coexistence of two such generalists is not possible, specialization is also prevented by the presence of already good specialists in other groups. But, by virtue of their social behavior, preferences for edge habitats, and perhaps other attributes, white-eyes have proved exceptionally good at colonizing islands, where increased specialization by the first arrival, which is made possible by

TABLE 4
SYMPATRY IN THE GENUS *ZOSTEROPS*

| Locality | Species | Ecology | Reference |
|---|---|---|---|
| AFRICA | | | |
| Zululand | a) *virens*<br>b) *senegalensis* | a) evergreen forest<br>b) open vegetation | Moreau, 1957 |
| Kenya and Somalia | a) *abyssinica*<br>b) *senegalensis* | a) dry lowlands<br>b) mountains | Moreau, 1957 |
| Grand Comoro I. | a) *mouroniensis*<br>b) *senegalensis* | a) high alt. heath<br>b) lowland forest | Benson, 1960 |
| Réunion[1] and Mauritius | a) *borbonica*<br>b) *olivacea* | a) insects and fruit<br>b) flowers | Present study |
| AUSTRALASIA | | | |
| Ceylon | a) *ceylonensis*<br>b) *palpebrosa* | a) above 3,000 ft<br>b) below 4,000 ft | Henry, 1955 |
| Malaya and Thailand | a) *everetti*<br>b) *palpebrosa* | a) middle and high elev.<br>b) coastal | Delacour, 1947 |
| Luzon | a) *montana*<br>b) *nigrorum*<br>c) *japonica* | a) high (3,000–8,000 ft)<br>b) low and moderate alt., *SE* Luzon<br>c) lowlands | Delacour and Mayr, 1946 |
| Mindanao | a) *montana*<br>b) *everetti* | a) over 6,000 ft<br>b) 0–5,000 ft | Mees. 1957 |
| Sumatra | a) *montana*<br>b) *atricapilla*<br>c) *palpebrosa* | a) mountain tops<br>b) above 1,000 m<br>c) 200–1,600 m | Mees, 1957 |
| Borneo | a) *atricapilla*<br>b) *everetti*<br>c) *palpebrosa* | a) mountains above 3,000 ft<br>b) N and NW Borneo-submontane<br>c) lowlands (W Born.), mangroves and coast | Smythies, 1960 |
| Java | a) *montana*<br>b) *palpebrosa*<br>c) *flava* | a) mountains<br>b) middle elevation<br>c) coast | Delacour, 1947; Mees, 1969: 314 |
| Celebes | a) *chloris*<br>b) *anomala*<br>c) *consobrinorum*<br>d) *atrifrons* | a) southwestern arm; open cultivated country, 0–1,200 m<br>b) southern arm; deforested hills<br>3) southeastern arm<br>d) northern arm | Mees, 1961 |
| New Guinea[1] | a) *atrifrons*<br>b) *fuscicapilla*<br>c) *novaeguineae* | a) 400–1,200 m, all New Guinea<br>b) 1,200–2,200 m, west New Guinea<br>c) 1,200–2,400 m, east New Guinea | J. Diamond (in litt.) |
| Australia | a) *lutea*<br>b) *lateralis* | a) mangroves<br>b) scrub | Serventy and Whittell, 1951 |

TABLE 4 (CONTINUED)

| Locality | Species | Ecology | Reference |
|---|---|---|---|
| Yunnan[1] | a) *palpebrosa siamensis*<br>b) *japonica simplex* | ?? | Mayr, 1967 |
| PACIFIC ISLANDS | | | |
| Fiji and Tonga[1] | a) *lateralis* | a) open country and light forest 0–850 m | J. Diamond (in litt.) |
| | b) *explorator* | b) light forest and hill forest 200–1,350 m | |
| New Caledonia | a) *xanthochroa*<br>b) *lateralis* | a) forest<br>b) bush and semi-open woodland | Mees, 1969: 138 |
| Lifu[1] (Loyalty Is.) | a) *minuta*<br>b) *inornata*<br>c) *lateralis* | a) all habitats<br>b) forest and scrub<br>c) gardens and forest | Mees, 1969: 141, 123, 97 |
| New Hebrides[1] | a) *flavifrons*<br>b) *lateralis* | a) forest, scrub<br>b) scrub and openings | Mees, 1969: 135, 98; J. Diamond (in litt.) |
| Kulanbangra | a) *murphyi*<br>b) *rendovae* | a) hills<br>b) lowlands | Mayr, 1945 |
| Bougainville | a) *ugiensis*<br>b) *metcalfii* | a) mountains<br>b) lowlands | Mayr, 1945 |
| Ponape[1] and Palau (Caroline Is.) | a) *conspicillata*<br>b) *cinerea* | see text (p. 55) | Baker, 1951 |
| Norfolk I.[1] | a) *tenuirostris* | a) forest and secondary growth | Mees. 1969 |
| | b) *albogularis* | b) forest | |
| | c) *lateralis* | c) secondary growth | |

[1] Actual sympatry involved.

reduced competition, facilitates a second successful invasion and ultimately sustained sympatric coexistence of two species.

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## SUMMARY

As one of the few cases of sympatry in the genus *Zosterops*, the Mascarene white-eyes include a typical generalized species, *borbonica*, and a specialized flower-feeding species, *olivacea*. *Z. borbonica* is a species of edge and disturbed habitats and differs from typical white-eyes in plumage coloration, in frequent trunk creeping as a mode of insect foraging, and in some modification of its vocal repertoire. Its two insular populations, *Z. b. borbonica* on Réunion and *Z. b. mauritiana* on Mauritius, differ primarily in their vocalizations. *Z. olivacea* is a species of the indigenous forests and differs from normal white-eyes in bill and tail proportions, vocalizations, absence of social and flocking behavior, increased aggressiveness in relation to feeding sites, and a shift to flowers as its primary food source. Its two insular populations, *Z. o. olivacea* on Réunion and *Z. o. chloronothos* on Mauritius, differ in vocalizations, plumage coloration, overall size, and proportions of the bill and tail.

It is argued on the basis of comparisons presented in this paper that the ancestor of *olivacea* colonized the Mascarene islands before the ancestor of *borbonica*. In the absence of flower-feeding competitors *olivacea* then adapted to the indigenous forest and increased its dependence on nectar feeding. This increased specialization enabled the ancestor of *borbonica* to colonize the Mascarene islands sometime later. The rarity of sympatric *Zosterops* on continents is explained in terms of competition between two generalists. On islands where "competitive release" encourages specialization, double invasions lead to sympatric coexistence of white-eyes.

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