FORAGING BEHAVIOR AND MICROHABITAT USE OF TWO SPECIES OF WHITE-EYES (ZOSTEROPIDAE) ON SAIPAN, MICRONESIA

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ABSTRACT.—I studied Golden (*Cleptornis marchei*) and Bridled (*Zosterops conspicillatus*) white-eyes on Saipan in the Mariana Islands, Micronesia. I collected comparative data on social behavior and use of tree zones, foraging surfaces, foraging methods, perch sizes, and tree species in native limestone forest and tangantangan (*Leucaena leucoephala*) thickets. Unlike the flocking Bridled White-eyes, Golden White-eyes were territorial, but the species were aggressive interspecifically. Bridled and Golden white-eyes were similar in their use of limestone forest and tangantangan thickets as foraging habitats. Compared with Bridled White-eyes, however, Golden White-eyes were more generalized foragers (i.e. less specialized on the top outer forest strata, on live leaves as foraging substrates, and on gleaning as a foraging tactic). Golden White-eyes also preferred to forage among dead leaves, on branches, and on fruit, and they foraged by probing. Similarities by both species in their use of limestone forest and tangantangan thickets indicate that they did not alter their foraging strategies greatly to use the different habitats. This flexibility in habitat choice may explain in part why these species have persisted in the face of periodic typhoon damage and extensive human-caused habitat change. Despite the differences in foraging ecology between the species, interspecific aggression indicated that they competed for resources. In temperate communities, species can be ecologically very similar but rarely compete; in this tropical island community, species with only general ecological similarities may still compete for resources.
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BIRDS on oceanic islands have provided important opportunities to study such ecological and evolutionary phenomena as speciation (Mayr 1963), dispersal (MacArthur and Wilson 1967, Thornton et al. 1988), competitive exclusion (Diamond 1975), and adaptive radiation (Grant 1986). Small, isolated islands are also well suited for studies of mechanisms of bird community organization (because the communities are generally very simple) and for detailed investigations of relationships among species. Such detailed autecological study provides the greatest likelihood of understanding community patterns (Conner and Simberloff 1979). Toward this goal, I extend earlier studies on the foraging ecology, microhabitat use, and social behavior of the Bridled White-eye (*Zosterops conspicillatus*) of Saipan, Mariana Islands (Craig 1989), to the taxonomically enigmatic, ecologically unknown Golden White-eye (*Cleptornis marchei*). I compared data on the ecologically similar white-eyes to determine their level of ecological distinctness and to assess how the level of distinctness relates to their social interactions.

The Golden White-eye is the sole member of a genus endemic to the Mariana Islands of Saipan and Aguijan (Fig. 1). It occurs abundantly in all wooded habitats on Saipan, with 1982 populations estimated at 55,522 or ca. 25% that of the Bridled White-eye (Engbring et al. 1986). Population density is similar on Saipan (532 birds/km^2) and Aguijan (573 birds/km^2) (Engbring et al. 1986). Other small passerines in the forests of Saipan include the Rufous Fantail (*Rhipidura rufifrons*) and Micronesian Honeyeater (*Myzomela rubrata*).

Earlier qualitative accounts of the ecology and distribution of Golden White-eyes are conflicting. Stott (1947) reported them difficult to find and restricted to dense forest. In a year-long study Marshall (1949) found them numerous in the forest understory, which suggests that Stott's (1947) report was based on insufficient observations. Marshall (1949) also believed the species did not sing, but Engbring et al. (1986) reported a well-developed song. Marshall (1949) reported that Golden White-eyes fed on invertebrates, fruits, and seeds, and traveled in small flocks of 3 or 4, although sometimes they occurred in groups of up to 12.

STUDY AREAS AND METHODS

I studied birds on Saipan in January and February of 1988 and 1989 (total 532 h). Saipan is 22 km long, 3–10 km wide, and covers 120 km^2. My principal study area was the Marpi Cliffs region at the north end of the island, although I also observed at Mt. Tapotchau, Talufofo, Kagman Peninsula, and Naftan Peninsula (Fig. 1). Birds occur in native limestone forest, which covers 5% of Saipan, and in tangantangan (*Leucaena leucocephala*) thickets, which cover 28% of the island. Limestone forest is largely limited to steep slopes and cliffs, whereas tangantangan thickets occupy flat lowlands and plateaus. These two habitats were described by Craig (1989). Briefly, limestone forest generally has a canopy height of <15 m due to the effects of frequent typhoons, understory vegetation is dense, and most tree species are characterized by spindly growth form and narrow crowns. The introduced tangantangan, seeded aerially after World War II to prevent erosion, occupies land formerly cultivated for sugarcane (Engbring et al. 1986). It grows in dense near-monocultures, usually 6–10 m high.

I studied social behavior, foraging behavior, and microhabitat use of white-eyes at all hours between dawn and dusk (ca. 0645–1830) by recording activities of birds encountered while I traversed areas of habitat. Observations were divided into those made in limestone forest and those in tangantangan thickets. Preliminary observations on Golden White-eyes were made in 1988, and detailed observations comparable to those made on Bridled White-eyes (Craig 1989) were made in 1989. To gather data on foraging and microhabitat use, I generally followed the same procedures used to study Bridled White-eyes outlined below (Craig 1989). I limited observation to the forest interior and avoided the forest edge. Golden White-eyes used the forest edge, but were more typically present in the forest interior. Forest edge and interior observations on Bridled White-eyes did not significantly differ in any instance, and I pooled edge and interior data when comparing them with data on Golden White-eyes.

I divided the habitat in limestone forest into top, middle, and lower zones. The tangantangan thickets were divided into top and lower zones. Outer and inner horizontal zones were also recognized in both habitats. The spindly form of most trees yielded an inner zone of only the trunk and major limbs, and an outer zone of the branched, foliated portion. The foraging surfaces included live leaf, dead leaf, rolled leaf (lepidopteran cocoon), bud, flower, fruit, branch, and trunk. I recorded the following foraging movements: removing prey from a surface while perched (*glean*); thrusting the bill into a crevice, fruit, or flower (*probe*); removing prey from a surface while hovering (*hover*); and capturing flying prey by darting from a perch (*sally*). In Chi-square analyses to compare data from the species and from limestone forest vs. tangantangan thickets, I replaced zero observations in categories with 0.1 (Koehn pers. comm.). This changed Chi-square values only slightly, but the values obtained reflect more precisely the relationships between the species, which probably use each foraging microhabitat, surface, and method at least occasionally. I categorized foraging perch sizes as <0.25 cm, 0.25 to <0.5 cm, 0.5 to <1.0 cm, 1.0 to <2.0 cm, 2.0 to <4.0 cm, and >4.0 cm. Mean values of these size classes were used to analyze the data with a general linear model ANOVA (Freund and Littell 1981). For branches >4.0 cm, I used my field estimates of perch size. I periodically checked my visual estimates of branch diameter by measuring branches with dial calipers. In 1989 I also recorded choice of woody plant species. Data on body mass were gathered from mist-netted birds.

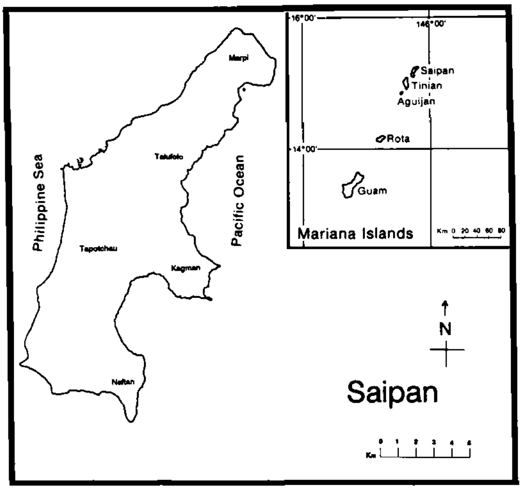

Fig. 1. Principal study areas on Saipan, and the geographic relationship of Saipan to the neighboring Mariana Islands, Micronesia.

Once I found foraging birds in each habitat, I used binoculars to follow them until a feeding attempt was made. Data on the forest zone, foraging surface, foraging movement, perch size, and plant species choice were recorded at the moment of the feeding attempt. To ensure that my sample was representative, I did not knowingly gather >5 observations on one individual. In practice, following an individual through the dense foliage for more than one feeding attempt was difficult. Small passerines were abundant and widespread, and new areas of habitat were sampled each day. Most foraging obser-

TABLE 1. Use (by percentage) of tree zones by white-eyes; sample size in parentheses.

	Top		Middle		Lower	
Habitat/Species	Outer	Inner	Outer	Inner	Outer	Inner
Limestone forest						
Bridled White-eye	68.5 (98)	3.5 (5)	22.4 (32)	3.5 (5)	2.1 (3)	0
Golden White-eye	47.3 (71)	6.0 (9)	32.6 (49)	8.0 (12)	6.0 (9)	0
Tangantangan thicket						
Bridled White-eye	74.0 (154)	7.7 (16)			15.9 (33)	2.4 (5)
Golden White-eye	54.9 (56)	19.6 (20)			16.6 (17)	8.8 (9)

vations were made on different individuals, which minimized nonindependence in the data (Beal and Khamis 1990).

Because observations for this study were made during only one season, the data must be considered in light of this limitation. However, year-round observers (P. Glass and J. Reichel pers. comm.) do not report observing foraging shifts in these small passerines.

RESULTS

Social and foraging behavior.—Golden White-eyes foraged in groups of 2-6 ($\bar{x} \pm$ SD = 3.0 ± 0.9, n = 28). These were family groups, as verified by food begging of juveniles, adult preening and feeding of juveniles, and plumage differences between adults and juveniles. Birds in juvenal plumage were duller than adults, with areas of brownish-yellow on the back and side of the head and brownish-yellow streaks on the breast. A larger group of 8 birds appeared to be two aggressively interacting family groups. Golden White-eyes were territorial, and countersinging between neighboring pairs occurred throughout the day.

Of the four small passerines that inhabited the forests of Saipan, Golden and Bridled white-eyes were the only species to show regular interspecific aggression (n = 9 observations). Golden White-eyes supplanted Bridled White-eyes from perches, chased them, and flew through flocks of foraging Bridled White-eyes, which dispersed them. However, I also observed the two species forage within 2 m. I never saw the smaller Bridled White-eye ($\bar{x}$ = 7.9 ± 0.5 g, n = 9, sexes combined) chase the larger Golden White-eye ($\bar{x}$ = 20.2 ± 1.1 g, n = 4, sexes combined). Rufous Fantails (n = 2) and Micronesian Honeyeaters (n = 1) also chased Bridled White-eyes, and in one instance a Golden White-eye appeared to chase a Rufous Fantail. In contrast to this aggression, Golden White-eyes were sought out by Rufous Fantails to assist in their foraging. Rufous Fantails followed 1-2 m behind foraging Golden White-eyes, hawking insects that Golden White-eyes disturbed from leaves.

Like Bridled White-eyes, Golden White-eyes were versatile foragers (n = 252 observations, mostly on different individuals). They fed on foliage invertebrates, flying insects, nectar, fruits, and flowers. They were more sluggish and moved more deliberately through the foliage than Bridled White-eyes, but they were agile and hung upside down on perches while they searched the undersides of branches and leaves. They also stretched upward from perches to inspect leaves, sometimes standing on leaf clusters. They flew or hopped between perches. Another foraging behavior was to move along branches or slender, leaning tree trunks, and to periodically search the undersides for prey. Foraging occurred in all situations from the ground to treetops.

Foraging ecology.—Golden White-eyes foraged predominantly in the top outer portion of trees, although the proportion was significantly less than for Bridled White-eyes (Table 1) in limestone forest (χ^2 = 14.7, df = 4, $P < 0.01$) and tangantangan thickets (χ^2 = 18.3, df = 3, $P < 0.001$). In both habitats Golden White-eyes foraged mostly among leaves (Table 2). There was a significant difference in choice of foraging substrates in the two habitats (χ^2 = 20.3, df = 6, $P < 0.01$). Fruit and dead leaves were used more, and live leaves and flowers used less in tangantangan thickets than in limestone forest. Use of substrates by Golden White-eyes differed significantly from that of Bridled White-eyes for both limestone forest (χ^2 = 24.5, df = 7, $P < 0.001$) and tangantangan thickets (χ^2 = 54.7, df = 5, $P < 0.001$). Golden White-eyes foraged

TABLE 2. Use (as percentage) of foraging surfaces by white-eyes; sample size in parentheses.

Habitat/Species	Leaf Live	Leaf Dead	Leaf Rolled	Bud	Flower	Fruit	Branch	Trunk
Limestone forest								
Bridled White-eye	80.9 (114)	1.4 (2)	0.7 (1)	1.4 (2)	6.3 (9)	1.4 (2)	6.3 (9)	1.4 (2)
Golden White-eye	57.7 (86)	7.4 (11)	1.3 (2)	0	11.4 (17)	7.4 (11)	12.8 (19)	2.0 (3)
Tangantangan thicket								
Bridled White-eye	82.6 (109)	1.5 (2)	0	0	8.3 (11)	1.5 (2)	3.8 (5)	2.3 (3)
Golden White-eye	50.5 (50)	16.2 (16)	0	0	0	14.1 (14)	16.2 (16)	3.0 (3)

for less time in live leaves and longer on most other surfaces in both habitats than did Bridled White-eyes (Table 2). Both Bridled and Golden white-eyes employed foliage gleaning principally in both limestone forest and tangantangan thickets (Table 3). Golden White-eyes did not differ significantly in their use of methods in the two habitats ($\chi^2 = 1.0$, df = 3, $P > 0.05$), but they differed significantly from Bridled White-eyes in foraging methods in limestone forest ($\chi^2 = 20.2$, df = 3, $P < 0.001$) and tangantangan thickets ($\chi^2 = 23.9$, df = 2, $P < 0.001$). Probing was a more important method for Golden White-eyes than for Bridled White-eyes.

The species differed significantly in their selection of perch size ($F = 16.1$, df = 1, 344, $P < 0.0001$) (Table 4). Furthermore, there was a significant interaction between species and habitats in selection of perch sizes (Type 1 $F = 21.1$, $P < 0.0001$). In limestone forest, Bridled White-eyes chose perches ($\bar{x} \pm \mathrm{SD} = 1.1 \pm 2.1$ cm, $n = 64$) about the same as Golden White-eyes ($\bar{x} = 0.9 \pm 1.1$ cm, $n = 135$) whereas in tangantangan thickets Bridled White-eye used smaller perches ($\bar{x} = 0.5 \pm 0.5$ cm, $n = 167$) than Golden White-eyes ($\bar{x} = 1.6 \pm 2.0$ cm, $n = 91$).

In limestone forest, Golden White-eyes foraged most frequently in *Cynometra ramifolia* ($n = 142$), although I also observed them foraging in most other common native forest trees. Percent use of plants (number of observations in parentheses) in limestone forest was as follows: 33.0% (47) *Cynometra*, 13.3% (19) vines, 10.5% (15) *Erythrina*, 7.7% (11) each *Pisonia*, *Ficus*, 5.6% (8) *Leucaena*, 4.9% (7) *Guamia*, 3.5% (5) *Melanolepsis*, 2.8% (4) *Aglaia*, 2.1% (3) *Premna*, 1.4% (2) each *Maytenus*, *Randia* (2), 0.7% (1) each *Papaya*, *Artocarpus*, *Phyllanthus*, *Pandanus*, *Barringtonia*, *Hibiscus*, *Ochrosia*, *Intsia*. In tangantangan thickets, 74.0% of foraging occurred in *Leucaena* (100), which was overwhelmingly predominant in the thicket canopy and understory. I did not obtain similar data for Bridled White-eyes.

DISCUSSION

Golden and Bridled white-eyes foraged similarly in limestone forest compared with tangantangan thickets. These similarities imply that foraging strategies were not greatly altered in order to use the different habitats. The differences in foraging that existed (such as the frequency with which Golden White-eyes used flowers) reflect the relative absence of large flowers in tangantangan thickets. Tangantangan, the overwhelmingly dominant plant species in thickets, has flowers too small for avian nectivory. Increased fruit consumption in tangantangan thickets was related to the presence of the introduced, weedy *Papaya* scattered through the thickets. In 8 of 14 observations of frugivory, birds ate papayas. This flexibility in habitat choice may explain in part the persistance of these species in the face of periodic typhoon damage and extensive human-caused habitat change.

TABLE 3. Use (as percentage) of foraging methods by white-eyes; sample size in parentheses.

Habitat/ Species	Glean	Probe	Hover	Sally
Limestone forest				
Bridled White-eye	89.0 (130)	6.2 (9)	4.1 (6)	0.7 (1)
Golden White-eye	74.7 (112)	24.0 (36)	1.3 (2)	0
Tangantangan thicket				
Bridled White-eye	94.2 (196)	4.3 (9)	1.4 (3)	0
Golden White-eye	75.5 (77)	21.6 (22)	2.9 (3)	0

TABLE 4. Use (as percentage) of perch sizes by white-eyes; sample size in parentheses.

Habitat	Perch size (cm)					
	<0.25	0.25 to <0.5	0.5 to <1.0	1.0 to <2.0	2.0 to <4.0	>4.0
Limestone forest						
Bridled White-eye	20.3 (13)	37.5 (24)	23.4 (15)	9.4 (6)	4.7 (3)	4.7 (3)
Golden White-eye	4.4 (6)	35.6 (48)	40.7 (55)	11.1 (15)	6.7 (9)	1.5 (2)
Tangantangan thicket						
Bridled White-eye	24.6 (41)	47.9 (80)	23.4 (39)	3.0 (5)	0.6 (1)	0.6 (1)
Golden White-eye	4.4 (4)	16.5 (15)	40.7 (37)	20.9 (19)	9.9 (9)	7.7 (7)

In tangantangan thickets but not limestone forest, the larger Golden White-eye selected larger perches than the Bridled White-eye. Such disparity may be due to differential perch-size distribution in the two habitats. In tangantangan thickets, outer branches of the upper canopy, where Bridled White-eyes foraged preferentially, were typically very slender. The interior thickets, where Golden White-eyes foraged, were composed primarily of heavier branches. In limestone forest, outer branches were not as slender as in tangantangan thickets, nor were lower strata characterized by substantially heavier branches. This would also explain why Golden White-eyes chose larger perches in tangantangan thickets compared with limestone forest. Data on relative availability of perch sizes in these respective habitats are necessary to assess this hypothesis. I hypothesized previously (Craig 1989) that differential use of perches by Bridled White-eyes occurred because a greater range of perch sizes existed in limestone forest. However, in light of the wide range of perches used by Golden White-eyes in tangantangan thickets, this hypothesis seems less plausible than one in which differential perch selection between habitats is a function of perch availability.

I was unable to collect data on tree species use by Bridled White-eyes, and cannot compare the use of tree species by the two species; but, certain patterns of tree use by Golden White-eyes are apparent. *Cynometra ramifolia*, the tree most commonly used, was the most common forest tree in the study areas. *Cynometra* is a small tree with leaves ca. 6–8 cm. Other common species of similar stature and leaf size (like *Guamia mariannae*) were rarely used. By default, I conclude that *Cynometra* was preferred for foraging. Large-leaved species like *Pisonia grandis* may be underrepresented in my sample of tree species selected, because observation was more difficult. Large-leaved trees contributed only a relatively small proportion of the forest canopy in much of the limestone forest.

Golden White-eyes were more generalized foragers, less specialized in use of tree zones, foraging surfaces, and foraging methods than Bridled White-eyes. Furthermore, Golden White-eyes frequently foraged on dead leaves, fruit, and branches, and probed. Bridled White-eyes, in contrast, strongly preferred live foliage gleaning from the forest canopy, which indicates that the species had different foraging specialties. The divergent body masses also imply that the two white-eyes differ in selection of prey sizes (Hespenheide 1973). Although they were the only small forest birds on Saipan in the same foraging guild (foliage gleaners), the two white-eye species were distinctly different in their foraging behavior and in their social organization. The Golden White-eye is territorial, whereas the Bridled White-eye is a nonterritorial, flocking species (Craig 1989). Even though different in foraging and social behavior, the species were interspecifically aggressive, and I therefore believe they competed for resources.

In temperate communities, species can be ecologically very similar but rarely compete (Rotenberry 1980, Craig 1984); in this tropical community, species having only general ecological similarities may still compete for resources. In temperate systems, environments can be variable (Wiens 1977) and food superabundant during particular seasons, which makes resource availability difficult to track for breeding populations (Rabenold 1979). In contrast, on Saipan, conditions may exist that lead to resource limitation. Conditions that might lead to resource limitation (such as population saturation for the available food supply) must be investigated to detect the causes of the observed aggression that occurs between the white-eye species. If such conditions prove pervasive on tropical Pacific islands, then this region may be fundamentally different from continental temperate regions in the principal organizing parameters of its bird communities.

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