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MICROHABITAT PARTITIONING AMONG SMALL PASSERINES IN A PACIFIC ISLAND BIRD COMMUNITY

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Abstract.- We report on continuing studies of the small forest passerines of Saipan, Mariana Islands, Micronesia in order to (1) characterize the ecological strategies employed in this threatened but virtually unstudied bird assemblage, and (2) provide a baseline for assessing shifts in foraging and microhabitat use that might follow reestablishment of extirpated populations. Data were gathered on microhabitat selection and foraging behavior, and limited observations are reported on wet-dry season shifts and annual changes in foraging. Two species were primarily canopy species, with one (Bridled White-eye, *Zosterops conspicillatus*) a live-leaf gleaner using smaller perches of taller trees, particularly *Cynometra ramiflora*, and one (Micronesian Honeyeater, *Myzomela rubratra*) a flower prober using larger perches of taller trees. The remaining two occupied the canopy and understory, with one (Rufous Fantail, *Rhipidura rufifrons*) an aerial forager and one (Golden White-eye, *Cleptornis marchei*) a more generalized forager that selected larger perches of a wider variety of smaller trees. Hence, the species ecologically overlap, but are differentiated in use of microhabitat space, including both structural and floristic components, and in manner of foraging. Comparisons of ecological overlap demonstrated that the two white-eye species were the most similar of the four, and that the Rufous Fantail and Micronesian Honeyeater were most dissimilar. Each of the four species also exhibited versatility in their ability to exploit the forest habitat. Such versatility is advantageous in a periodically typhoon-ravaged system, although competitive release could have contributed to this versatility. Prior to reestablishment of prehistorically extinct populations, additional studies should address the degree to which species interactions might influence the outcomes of such efforts.

The historically known avifaunas of tropical Pacific islands have been shown to include only a fraction of the species present at the time of first prehistoric human contact. Prehistoric Hawaiian birds reported by Olson and James (1982) and James and Olson (1991) have more than doubled the known size of the recent Hawaiian avifauna. Elsewhere in the Pacific, Steadman (1999a) has found levels of human-associated extinction paralleling those of Hawaii, even on supposedly pristine Henderson Island (Steadman and Olson 1985). These remnant bird communities yield an incomplete view of original community relationships, but they themselves remain virtually unstudied. Hence, we continue investigations into the quantitative ecology of forest bird communities on the oceanic island of Saipan, Mariana Islands. By studying members of this community, we clarify the ecological strategies that they presently employ, and establish a baseline against which to judge the effects of reestablishing missing species into this community. We also salvage knowledge of the ecology of this community, in the event that all of its species become extinct, as they have on nearby Guam (Savidge 1987, Wiles et al. 1995).

In previous studies of this system, Craig (1989, 1990) made relatively brief observations of the foraging ecology and microhabitat use of the Bridled White-eye (*Zosterops conspicillatus*) and Golden White-eye (*Cleptornis marchei*). Craig (1996) also investigated population densities of Saipan's forest birds, and found that, especially for some of the small forest passerines,

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populations were consistently among the highest ever reported for birds, and may have been at habitat saturation. We report here on the next phase of this investigation: how all species of small forest passerines, the Bridled White-eye, Golden White-eye, Rufous Fantail (*Rhipidura rufifrons*) and Micronesian Honeyeater (*Myzomela rubratra*), exploit the native forest environment. We emphasize observations of the two most ecologically similar species, the Bridled and Golden White-eyes. We report as well on wet-dry season shifts and annual changes in foraging.

STUDY AREAS AND METHODS

We studied the four small forest passerines on Saipan during a wet-dry season cycle in 1990-91. On Saipan, the dry season is typically December-May, and the wet season June-November (Young 1989), a pattern followed during the study period. Events characterizing the dry season include reduced rainfall, establishment of easterly trade winds, and decline in flowering, fruiting, and growth by certain native tree and vine species (although several species flower only at this time). During the wet season, rain increases, particularly in August-September, trade winds break down (Young 1989), and a progression of heavy flowering and fruiting by other native trees and vines occurs (RJC pers. obs.). Typhoons are frequent at this latitude, particularly during the latter half of the year, and exert a strong influence on the structure of forest habitats (Fosberg 1960).

Study area.- Saipan is predominantly a raised coral island 22 km long and 3-10 km wide. We made observations in the Marpi region (15°17'N, 145°47'E) of northern Saipan. Marpi is characterized by steep limestone escarpments vegetated by some of the most extensive native forest remaining on the island. The forest, termed limestone forest, has a canopy dominated by two widespread Indo-Pacific species, *Pisonia grandis* and *Cynometra ramiflora*, and an understory dominated by *C. ramiflora* and the Marianas endemic *Guamia mariannae* (Craig 1992). Such forests are typical of the relatively xerophytic forest communities of the northern Mariana islands of Saipan, Tinian, and Aguiguan (Chandran et al. 1992, Craig 1992, RJC pers. obs.). Surrounding level areas are largely abandoned

agricultural lands (Fosberg 1960) with meadows and thickets dominated by the introduced small tree *Leucaena leucocephala*. Although presently receiving little other than natural (i.e. typhoon) disturbance, the forest has been subjected to centuries of human-related alteration, including cutting, burning, and browsing by feral animals (Fosberg 1960). During World War II, the area was subjected to naval bombardment and was also the site of a major ground campaign. Despite such disturbance and probably because most trees are primarily strand species well adapted to surviving extensive typhoon damage (Fosberg 1960), limestone forest is remarkably resilient and resistant to invasion by exotic species (Craig 1992, 1994).

Foraging observations.- To study methods of habitat exploitation, Craig recorded the position and activity of a bird at the moment of a feeding attempt. The forest had a relatively low canopy (10-15 m) and was on a steep slope, which made canopy and understory vegetation about equally visible. This minimized observational biases related to foraging height. When making observations, Craig wore camouflage clothing, sat on the forest slope, and waited for birds to come within view rather than to search for them and possibly affect their behavior. Foraging individuals were followed for >15 s before observing a feeding attempt, which minimized potential biases associated with initial observations (Hejl et al. 1990). We made observations between 12 Dec. 1990 and 26 Nov. 1991 from 06:30 (first light) to ca 13:00. Observation periods lasted ca 4-6 h. Unlike in temperate forest passerines, during this and previous studies (Craig 1989, 1990) we noted virtually no diurnal pattern in activity levels of these birds, including singing.

Because populations were extremely dense for three of the four species (ca 8-9000 total individuals of the four species in the study area based on density studies of Craig 1996) and because different areas were surveyed during each day's observations, individuals were likely observed only once and, therefore, data were completely independent. During a day's observations, data were recorded from all birds opportunistically observable at one site, and then a new location was chosen for study. Because of the great population densities of the birds studied, a phenomenon difficult to appreciate by observers familiar with temperate bird densities, we could travel as little as 30 m before encountering new individuals, although we more typically traversed ca 60-100 m before again waiting for birds to come into view. The only uncommon forest species (although elsewhere very common on Saipan), the Micronesian Honeyeater, was

encountered at locations hundreds of meters apart; hence, all observations of it were clearly from different individuals.

At the moment of a feeding attempt, we recorded the following: (1) forest zone- top, middle, or lower; (2) tree height; (3) foraging surface- live leaf, dead leaf, branch, trunk, fruit, flower, other (e.g. rolled leaf, bud), or aerial; (4) perch size- <0.25 cm, 0.25-<0.5 cm, 0.5-<1.0 cm, 1.0-<2.0 cm, 2.0-4.0 cm, >4.0 cm; (5) foraging method- glean (removing an item from a surface while perched), probe (thrusting the bill into a crevice, fruit, or flower), hover (removing an item from a surface while hovering), or sally (darting from a perch to capture flying prey), and (6) identity of woody vegetation in which foraging occurred.

To examine tree choice by birds with tree species availability, we compared data on foraging tree choice with existing data on the abundance of trees in the Marpi forest (Craig 1992), which sampled 400 canopy trees to yield importance values (reviewed by Mueller-Dombois and Ellenberg 1974) for each forest tree species. For broad-leaved forests, the importance value is related to a tree species' proportionate contribution to forest foliage (Holmes and Robinson 1981).

Analyses.- We analyzed the 724 observations made on the 4 bird species during this study using univariate chi-square analysis. A one-way analysis of variance was used to investigate the height of trees chosen for foraging by the species, after the assumptions of parametric statistics were determined to be met reasonably. For selection of types of woody vegetation as perches, we limited analysis to the two white-eye species because insufficient data were available for the Micronesian Honeyeater, and the Rufous Fantail foraged primarily aerially. In addition to the nine most common types of woody vegetation (*Cynometra*, *Pisonia*, *Ficus*, *Guamia*, *Premna*, *Intsia*, *Psychotria*, *Melanolepis*, vines) we pooled 17 uncommon woody species (trees and shrubs) into a category called other vegetation (thus eliminating zeros) in chi-square analysis. In addition, we used the 20 tree species with the highest importance values, along with a category for other trees (21 total categories), to make comparisons between use and availability of trees in the manner of Johnson (1980). This method employs ranks of tree availability, and preference is assessed by computing the difference between a tree's abundance rank and the rank of its use. We regressed preference and tree rank using linear and curvilinear models in order to search for a relationship between them.

To evaluate habitat partitioning by the two most comparable and ecologically similar species, the white-eyes, we used logistic regression analysis (PROC LOGISTIC in SAS version 6.08, SAS 1990). This

procedure permits evaluation of each foraging/microhabitat variable in the presence of all other variables, and is a valid analysis given the assumptions and characteristics of the design (Hosmer and Lemeshow 1989). In our initial analysis species was the dependent variable, and (1) forest zone, (2) tree height, (3) foraging surface (4) perch size, (5) foraging method, (6) season, and (7) year were the independent variables. In the presence of other variables, seasonal effects added little to the predictive power of the model, and it was dropped from the final model. The variable year (1988-1989 versus 1990-1991) permitted comparison of the 608 white-eye observations made in this study (1990-91) with the 295 made earlier (1988-1989), so that annual variation in foraging behavior might be assessed for these two species. However, 1988-1989 white-eye data were used in logistic regression analysis only. Year and tree height were entered into the model in their original form. Few observations of activity in the lower forest zone led us to dichotomize this variable into two levels: lower/middle and top. Similarly, perch size was dichotomized into < 0.5 and ≥ 0.5 cm. Parameters within the two remaining independent variables were entered into the regression model as a series of binary variables (foraging surface: flower/other, branch or trunk/other, dead leaf/other, fruit/other, live leaf/other; foraging method: hover/other, probe/other, glean/other). This is a standard dummy variable procedure used in regression analysis (see, for example, Menard 1995, pp. 38-43). Interpretation of the relationship between the species of white-eyes (Bridled White-eye = 0 and Golden White-eye = 1 in analysis) and each regressor variable is based on the sign of the regressor parameter estimates and two-way frequency tables of species with each categorical regressor or, in the case of the continuous variable tree height, on mean ± SD (Hosmer and Lemeshow 1989). For example, a negative sign indicates that as the level of the independent variable increases, the probability of its association with the Bridled White-eye decreases.

To provide a measure of ecological similarity, we computed an index based on those foraging parameters that were comparable among all four species: forest zone, foraging surface, and foraging method. Other parameters were comparable only between certain species and, therefore, these similarity comparisons are conservative. In a manner related to Schoener's (1970) index, we calculated similarity (S) as:

$$S = (\sum |p_{xi} - p_{yi}|) / n,$$

where p_x and p_y are the percents of resource use of species x and y in category i , and n is the number of compared categories (12 in this instance). In this

method, S values range from 0 (highest similarity) to 100 (lowest similarity). Because values are computed from only three directly comparable measures, they may be considered conservative similarity measures.

RESULTS

Community comparisons.- The four community members diverged significantly in use of forest zones ($\chi^2_3 = 86.8$, $P < 0.001$), and formed two subsets in zone use. The Micronesian Honeyeater ($n = 20$) and Bridled White-eye ($n = 337$) were relatively specialized in canopy foraging, whereas the Golden White-eye ($n = 243$) and Rufous Fantail ($n = 95$) commonly used both canopy and mid/lower-forest strata (Fig. 1)

The four species also differed significantly in the size of trees chosen for foraging ($F_{3,698} = 12.1$, $P < 0.0001$), and again diverged into two subsets. Duncan's test showed that the Bridled White-eye ($\bar{x} = 34.5 \pm 7.9$, $n = 367$) chose significantly taller trees (i.e. more canopy trees) than the Golden White-eye ($\bar{x} = 30.7 \pm 8.4$, $n = 265$) or Rufous Fantail ($\bar{x} = 31.1 \pm 9.0$, $n = 55$) (canopy and understory trees). Moreover, although based on few observations, the Micronesian Honeyeater on average chose the tallest trees of the four species ($\bar{x} = 35.0 \pm 7.6$, $n = 15$). Hence, in all cases the choice of forest zone was reflected in the choice of tree sizes.

Such fundamental differences existed between the species in use of foraging surfaces that zero observations in several categories prevented chi-square analysis of the data. Bridled ($n = 335$) and Golden ($n = 240$) white-eyes foraged mostly from live leaves, whereas the Rufous Fantail ($n = 95$) foraged about equally from leaves and aerially, and the Micronesian Honeyeater ($n = 21$) foraged almost entirely from flowers (Fig. 2).

The species differed significantly in use of foraging perches ($\chi^2_2 = 96.6$, $P < 0.01$). The Micronesian Honeyeater ($n = 20$) chose perches

that were on average larger than those used by white-eyes (Fig. 3). The Rufous Fantail rarely foraged from perches, so was excluded from statistical analysis.

As with foraging surfaces, foraging methods were so substantially different between the species that zero observations in several categories prevented chi-square analysis. The Rufous Fantail ($n = 95$) specialized in sallying and hovering, whereas the Micronesian Honeyeater ($n = 18$) concentrated on probing. Bridled ($n = 333$) and Golden ($n = 246$) white-eyes were primarily gleaners (Fig. 4).

Although we discovered no seasonal foraging differences sufficient to yield statistical significance, we noted several subtle seasonal shifts in foraging which more extensive sampling would likely prove real. Most notably, use of certain forest tree species appeared related to flowering and fruiting phenology; e.g. increased use of *Premna obtusifolia* by the white-eye species in the wet season, when the tree species flowered and fruited heavily. Moreover, Micronesian Honeyeaters foraging in native forest in the dry season typically were found at *Erythrina variegata*, which flowered only during this season. Our observations suggested that heavily flowering *Erythrina* may even have been defended by Micronesian Honeyeaters during the dry season.

Ecological similarity between the four species, as measured by the three comparable parameters of forest zone, foraging surface, and foraging method showed that, as previously asserted (Craig 1990, 1996), the two white-eyes were by far the most similar species. In contrast, the Micronesian Honeyeater and Rufous Fantail were the most dissimilar species (Table 1).

White-eye comparisons.- Logistic regression analysis (forward selection method) yielded a model that fit well (residual chi square = 0.11, $df = 1$, $P = 0.74$).

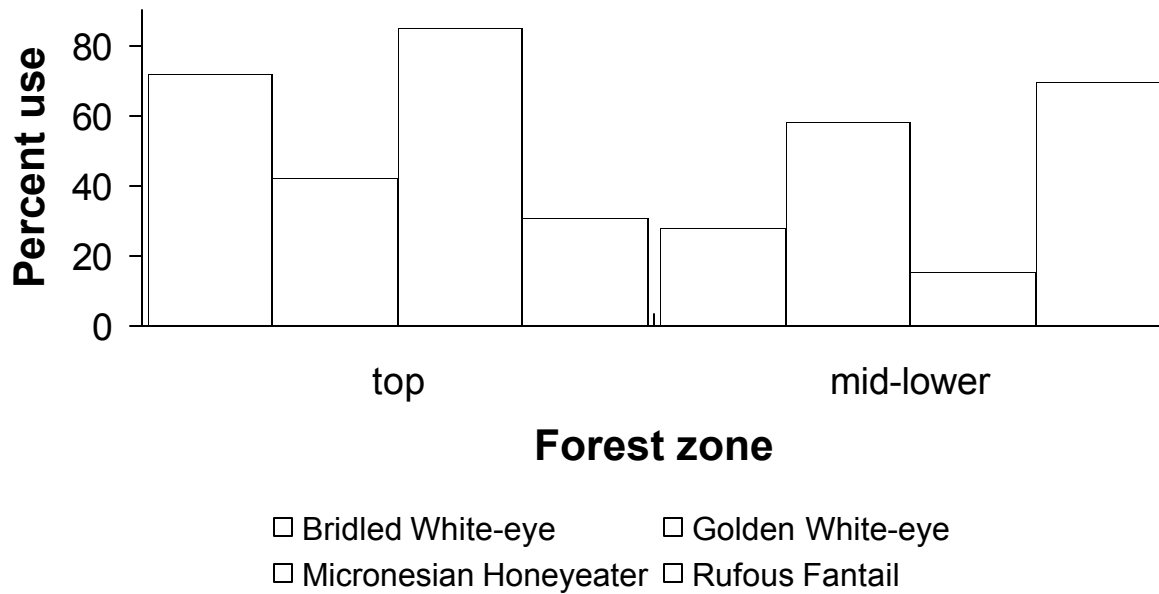


FIG. 1. Four small forest passerines on Saipan differ significantly in percent 1990-1991 use of forest zones.

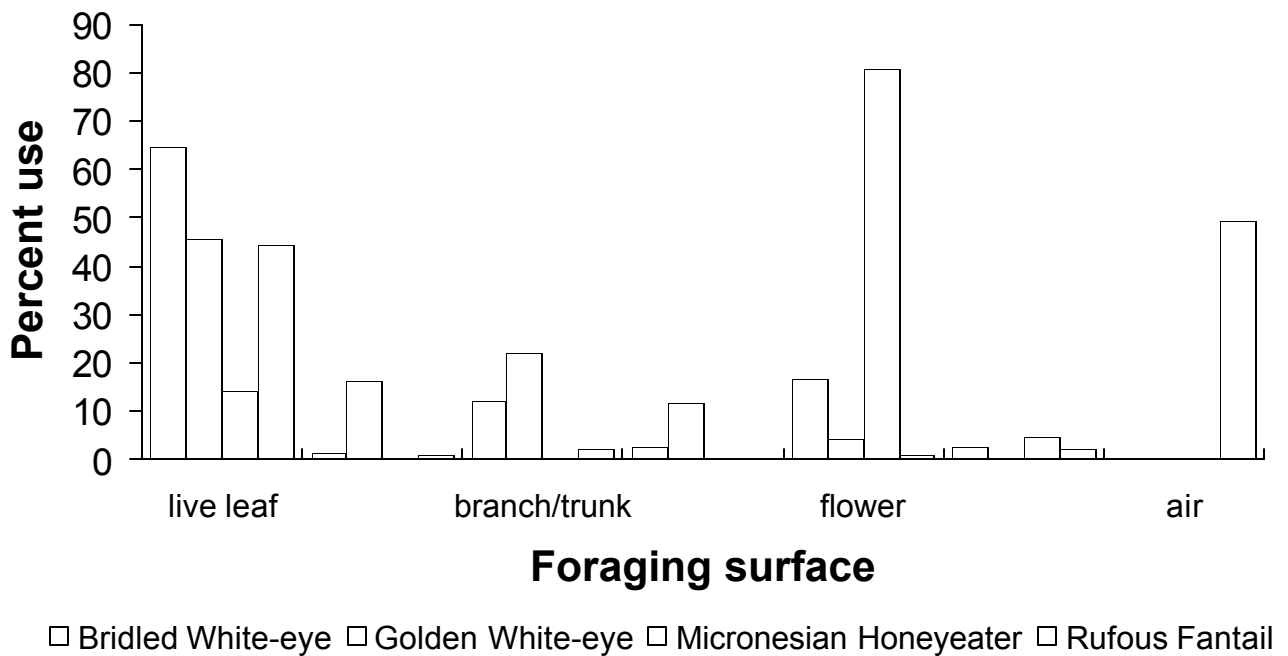


FIG. 2. Four small forest passerines on Saipan fundamentally differ in 1990-1991 percent use foraging surfaces.

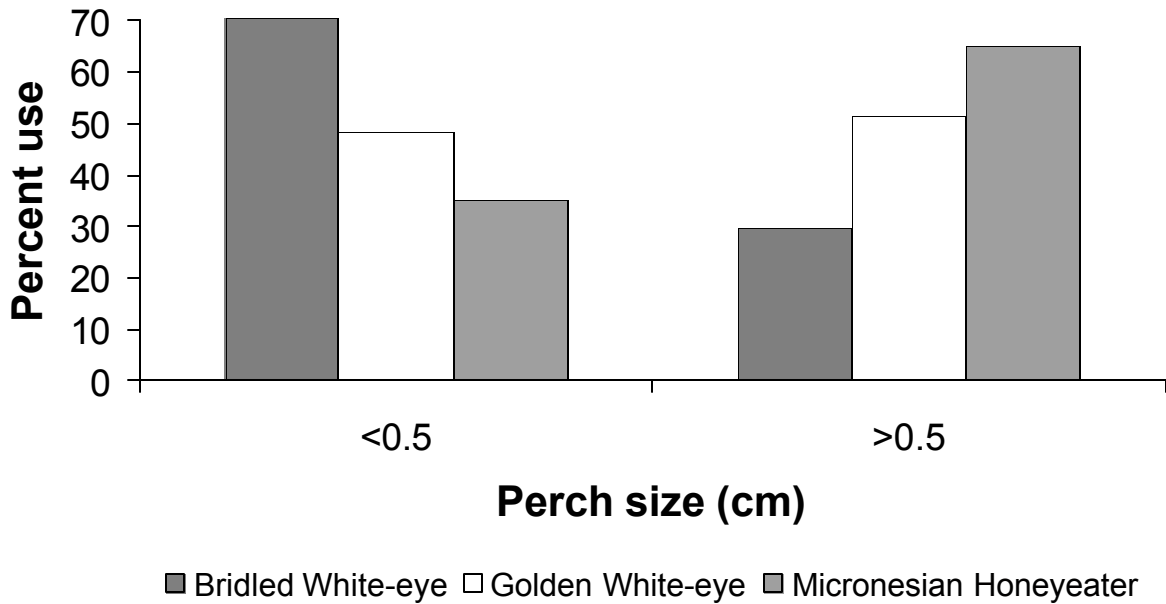


FIG. 3. Three small forest passerines on Saipan differ significantly in 1990-1991 percent use of foraging perches.

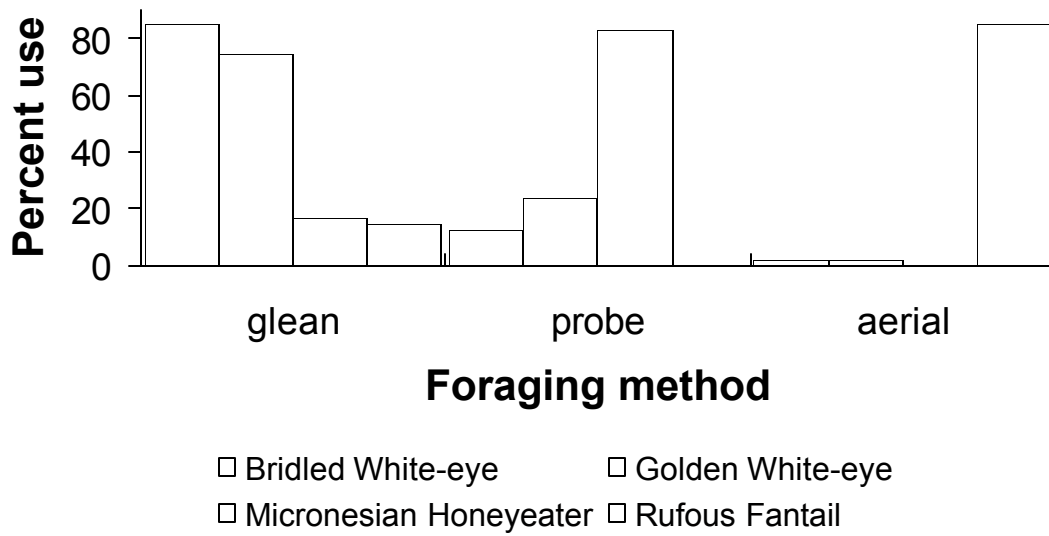


FIG. 4. Four small forest passerines on Saipan fundamentally differ in 1990-1991 percent use of foraging methods.

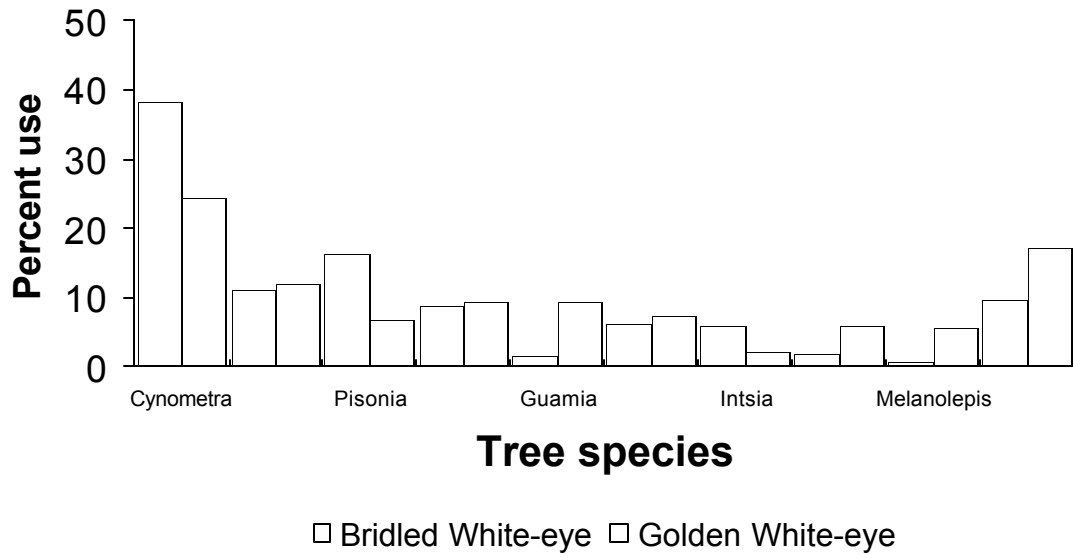


FIG. 5. Two species of white-eyes on Saipan differ significantly in 1990-1991 percent use of woody vegetation.

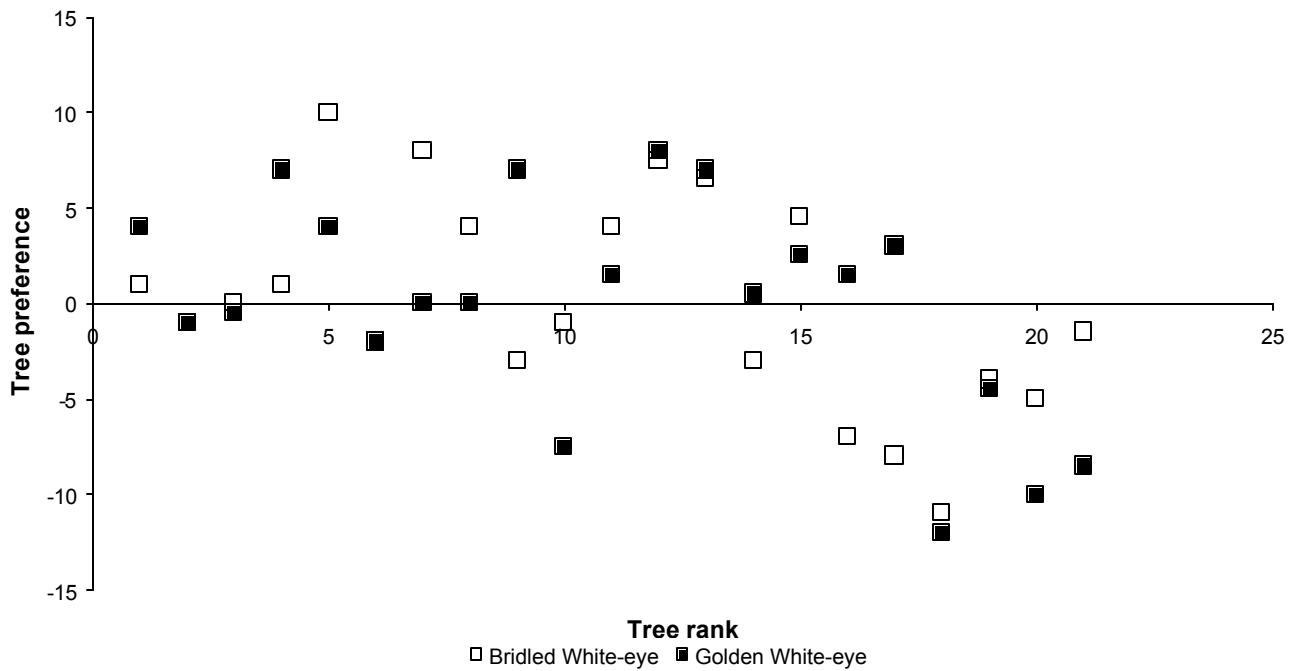


FIG. 6. Saipan tree availability versus 1990-1991 white-eye preference as foraging sites shows a significant inverse relationship. Trees with the lowest ranks have the highest importance values. Preference values < 0 indicate use greater than availability; values > 0 indicate use less than availability.

TABLE 1. Schoener's ecological similarity index for four species of forest passerines on Saipan, 1990-1991.

	Golden White-eye	Rufous Fantail	Micronesian Honeyeater
Bridled White-eye	12.5	29.1	25.0
Micronesian Honeyeater	30.7	37.0	
Rufous Fantail	24.4		

TABLE 2. Logistic regression model demonstrates that white-eye species on Saipan, 1988-1991, differ significantly in foraging. $n = 405$ (Bridled White-eye), 378 (Golden White-eye).

Variable	Parameter Estimate	Wald χ^2	P Value
Intercept	0.0798	0.0020	0.9640
Forest zone	1.2624	45.5509	0.0001
Perch size	-1.0840	34.0574	0.0001
Glean/other	-2.2260	24.7453	0.0001
Year	1.2950	41.2734	0.0001
Tree height	0.0621	30.1911	0.0001
Fruit	1.6755	12.8984	0.0003
Flower	-2.4238	26.4654	0.0001
Live leaf	-0.6879	8.1648	0.0043

TABLE 3. Differences in 1988-1989 versus 1990-1991 percent foraging by Bridled and Golden white-eyes on Saipan (sample sizes in parentheses).

Variable	Bridled White-eye		Golden White-eye	
	1988-1989	1990-1991	1988-1989	1990-1991
Forest zone:				
Top	72.0(103)	72.1(243)	53.3(80)	42.0(102)
Mid-lower	28.0(40)	28.0(94)	46.7(70)	58.0(141)
Foraging surface:				
Live leaf	2.6(114)	66.1(216)	58.5(86)	45.8(110)
Dead leaf	1.4(2)	1.5(5)	7.5(11)	26.3(39)
Branch/trunk	8.0(11)	12.5(41)	15.0(22)	22.1(53)
Fruit	1.4(2)	2.8(9)	7.5(11)	11.7(28)
Flower	6.5(9)	17.1(56)	11.6(17)	4.2(10)
Perch size:				
< 0.5 cm	57.8(37)	70.3(223)	40.0(54)	48.5(115)
≥ 0.5 cm	42.2(27)	29.7(94)	60.0(81)	51.5(122)
Foraging methods:				
Glean	89.7(130)	85.6(285)	74.7(112)	74.4(183)
Probe	6.2(9)	12.6(42)	24.0(36)	24.0(59)
Sally/hover	4.1(6)	1.8(6)	1.3(2)	1.6(4)

The overall predictive power of this model at $P = 0.50$ was 73.4%. Its ability to predict the identity of species from foraging/microhabitat data is also high, with 75.6% of Bridled White-eyes and 71.2% of Golden White-eyes classified correctly. Use of classification tables to assess predictive ability is supported by Menard (1995) and Hosmer and Lemeshow (1989). This predictive ability along with the stability of asymptotic measures of fit (Akaike information criterion, Schwartz criterion, -2 log likelihood, score statistic) assured us that our sample size was adequate at levels of the regressor variables to render a reliable analysis.

The two white-eye species diverged significantly in use of forest zones, with the Bridled specializing in canopy foraging and the Golden using canopy and mid-forest strata. The Bridled White-eye chose to forage in taller trees, i.e. more canopy trees, and specialized more on live leaf and flower foraging surfaces, but ate less fruit than the Golden White-eye. Moreover, the Bridled White-eye selected smaller perches and gleaned more but used other foraging methods less than the Golden White-eye, which in both cases was more of a generalist (Table 2).

Use of woody vegetation types as foraging perches differed significantly between the white-eye species ($\chi^2_9 = 66.5, P < 0.001$), although the tree most frequently used by both species was *Cynometra ramiflora*. Overall, the Bridled White-eye ($n = 333$) specialized more on *C. ramiflora*, whereas the Golden White-eye ($n = 234$) was more generalized in use of vegetation (Fig. 5).

White-eye use of tree species showed a weak but statistically significant relationship to tree availability (Golden White-eye: $r^2 = 0.22, df = 19, P < 0.05$, Bridled White-eye: $r^2 = 0.21, df = 19, P < 0.05$). Both species showed a negative relationship between preference and availability,

with more abundant woody species such as *Pisonia grandis*, *Intsia bijuga*, and *Premna obtusifolia* used less (preference > 0) and less abundant species such as *Psychotria mariana*, *Aidia cochinchinensis*, and *Maytenus thompsonii* (See Craig 1992) used more (preference < 0) than their availability (Fig. 6). However, the second most common forest tree, *Cynometra ramiflora*, showed use by both Bridled and Golden white-eyes to be slightly greater than availability (use - availability ranks = -1 in for both white-eye species).

Foraging between years also differed significantly (Table 3). Principal differences noted were that the Bridled White-eye foraged less from live leaves, more from other foraging surfaces, and more from smaller perches in 1990-91 compared to 1988-1989. The Golden White-eye foraged less in the canopy, less from live leaves and flowers, and more from dead leaves in 1990-1991 compared to 1988-1989.

DISCUSSION

The present assemblage of four small forest passerines on Saipan is composed of two species that are primarily canopy inhabitants, with one (Bridled White-eye) a live-leaf gleaner using smaller perches of taller trees, particularly *Cynometra ramiflora*, and one (Micronesian Honeyeater) a flower prober using larger perches of taller trees. The remaining two species occupy the canopy and understory, with one an aerial forager (Rufous Fantail) and one a more generalized forager which selects larger perches of a wider variety of smaller trees (Golden White-eye). Hence, the species are differentiated in use of microhabitat space, including both structural and floristic components, and in manner of foraging.

Among these species, the most generalized was the Golden White-eye, which used most

foraging strategies investigated. The Bridled White-eye, although specializing more on particular aspects of foraging, also exhibited the capability of using most other foraging strategies. Even the more narrowly specialized Micronesian Honeyeater and Rufous Fantail demonstrated the capacity to use all forest strata and to depart from their typical foraging methods by foliage gleaning. Species capable of using such a variety of foraging behaviors may be reasonably described as versatile foragers, although such a term is indeed a relative one. Versatility certainly is advantageous in this system where particular resources often may be absent for weeks because of nearly annual damage of natural habitats by typhoons. Population collapses, as have been reported in Caribbean forest birds after storms (Rivera-Milán 1995, Wauer and Wunderle 1992), are likely to be moderated in species where foraging and microhabitat versatility permits use of alternate resources when preferred ones become unavailable. However, versatility in foraging also could be related to competitive release, either because these species colonized a faunally depauperate island or because competitors have been eliminated through more recent extinctions.

Although our observations of white-eye foraging and microhabitat use were similar to findings from previous years (Craig 1989, 1990), significant differences between years likely reflects annual shifts in food availability. During our five years of observations on Saipan, we found that typhoons greatly altered the character of forest for weeks. On nearby Rota, a particularly severe typhoon in 1993 caused wholesale habitat changes from which it took years to recover. Moreover, individual wet and dry seasons vary in their intensity, which we observed to influence flowering, fruiting and likely insect abundance.

Observations from other bird communities of tropical Pacific islands offer additional insights into our findings. On the island of Hawaii, Scott et. al (1986) described surviving small passerines of the

native forest assemblage as also including nectarivores, insectivores, flycatchers, and a woodpecker-like species. When habitat variables associated with their distributions were studied, Mountainspring and Scott (1985) found that native species showed few negative relationships (indicating little interspecific competition) despite ecological similarity between some of them. They attributed this finding to resource superabundance. In contrast, in the Galapagos Islands, Grant (1986) reported that food limitation occurred seasonally, and that during such times ecologically similar species of Darwin's Finches diverged in diets in ways suggesting that interspecific competition occurred.

Recent paleontological evidence from the nearby Mariana Islands of Rota, Tinian and Aguiguan indicates that the forests of Saipan once were inhabited by such additional small passerines as a parrot-finch (*Erythrura* sp.), a *Myiagra* flycatcher, a *Monarcha* flycatcher, and a giant white-eye (*Rukia* sp.), as well as several medium-sized species (Steadman 1992, 1999b). Based on qualitative knowledge of the ecology of living or recently extinct Micronesian species in these genera (Baker 1951, Jenkins 1983, Engbring 1988, RJC pers. obs.), such missing community members as these seem likely to have shown, with the exception of the granivorous parrot-finches, substantial ecological overlap with the extant species.

Because extirpated bird populations in the Mariana Islands are targeted for reestablishment (Pacific Island Recovery Team, U.S. Fish and Wildlife Service, pers. comm.), the potential for negative population effects due to ecological overlaps between extant and extirpated species should be considered. Previous observations have shown that the small forest passerines have extremely high population densities likely at saturation densities (Craig 1996), that the species interact aggressively, particularly the ecologically similar white-eyes (Craig 1990, 1996, this study),

and that densities of the Rufous Fantail and Bridled White-eye are less on comparable islands where an ecologically similar species is present (Engbring et al. 1986). These observations suggest that interspecific competition could be an important organizing principle in this community. A rigorous assessment of this potential should be part of any reestablishment program.

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