

## SEASONAL POPULATION SURVEYS AND NATURAL HISTORY OF A MICRONESIAN BIRD COMMUNITY

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ABSTRACT.—I replicated quarterly population surveys of landbirds on Saipan, Mariana Islands at two environmental scales: habitat specific and island-wide. I determined population densities and the degree of seasonal fluctuation in counts to compare densities in native vs disturbed habitat and to observe whether populations exhibited characteristics of those at either saturation or below saturation densities. I also gathered new data on the natural history of largely unknown species. For seven of the nine forest birds examined, inter-seasonal census variation was greater than intra-seasonal variation, suggesting that most of the species undergo seasonal shifts in population or breeding status (the latter case was indicated for four forest species). The principal difference uncovered between the two census scales was that the Micronesian Honeyeater (*Myzomela rubrata*) was relatively uncommon in native forest but regular on island-wide counts. Otherwise, forest species showed numerous similarities in count trends at both scales. However, habitat-specific data showed that for many species, counts and computed densities were greater in native forest than in disturbed habitat. Independent density assessment (based on a new procedure) for the Bridled White-eye (*Zosterops conspicillatus*) was of the same order of magnitude as that obtained through censusing. The densities reported here, particularly for the Rufous Fantail (*Rhipidura rufifrons*), Bridled White-eye, and Golden White-eye (*Cleptornis marchei*), are among the highest ever reported for birds (>1900/km<sup>2</sup>) and are almost certainly at habitat saturation. Interspecific competition is expected in such a case, and interspecific aggression was prevalent, particularly among ecologically similar species. Received 27 April 1995, accepted 1 Dec. 1995.

Land birds of the Mariana Islands, Micronesia have received limited, mostly qualitative study (e.g., Marshall 1949, Baker 1951, Pratt et al. 1987, Reichel and Glass 1991), and the quantitative ecology of most species remains unknown. Jenkins (1983) reviewed aspects of the natural history of the now mostly extinct (Savidge 1987) avifauna of the southernmost island of Guam, and Engbring et al. (1986) reported population estimates, based on one survey, for Rota, Aguiguan, Tinian, and Saipan. Quantitative scrutiny has been given only to the Nightingale Reed-Warbler (*Acrocephalus luscinia*) (Craig 1992a) and Bridled White-eye (*Zosterops conspicillatus*) and Golden White-eye (*Cleptornis marchei*) (Craig 1989, 1990).

The island of Saipan presently has the most diverse, albeit meager, assemblage of land birds in the Marianas. It consists of three medium-sized predators, the Yellow Bittern (*Ixobrychus sinensis*), Collared Kingfisher (*Halcyon chloris*) and Nightingale Reed-warbler; two herbivores,

the Mariana Fruit-Dove (*Ptilinopus roseicapilla*) and White-throated Ground Dove (*Gallicolumba xanthonura*); four omnivores, the Micronesian Megapode (*Megapodius laperouse*), Micronesian Starling (*Aplonis opaca*), Golden White-eye, and Bridled White-eye, a nectarivore, the Micronesian Honeyeater (*Myzomela rubrata*); and two small insectivores, the Island Swiftlet (*Aerodramus vanikorensis*) and Rufous Fantail (*Rhipidura rufifrons*). Most of these species, or at least their local subspecies, are endemic to the Marianas or Micronesia. Prehistorically, perhaps twice as many species were present (Steadman 1992). Two other species, the Javanese Turtle Dove (*Streptopelia bitorquata*) and Eurasian Tree Sparrow (*Passer montanus*), are present but not native.

This study reports replicated, quarterly population surveys I made of these species on Saipan. They were made at two environmental scales, habitat specific and island-wide, to determine population densities and the degree of fluctuation in populations or breeding activity. Because all species are nonmigratory, I hypothesized that populations might build to the maximum density sustainable by available resources and that little fluctuation in densities generally occurs. I also gathered new natural history data on many species.

#### STUDY AREAS AND METHODS

*Habitats.*—The island of Saipan is predominantly a raised coral island 22 km long and 3–10 km wide. It has a climate with uniform temperatures but seasonal rainfall. Typically, and during this study, the dry season is December–June and the wet season is July–November. Reduced rainfall, establishment of easterly trade winds (Young 1989), and decline in flowering, fruiting, and growth by certain native tree and vine species characterize the dry season. During the wet season rain increases, particularly August–September, trade winds break down (Young 1989), and beginning in the late dry season, many native trees and vines flower and fruit. Typhoons are frequent during the latter half of the year and exert a strong influence on the structure of natural habitats (Fosberg 1960).

Much of Saipan likely was once forested, particularly on limestone soils (Fosberg 1960). Such limestone forest is relatively xerophytic except at the highest elevations (ca 300–466 m), where near cloud forest conditions prevail. This forest is typically dense, with a canopy dominated by two widespread Indo-Pacific trees, *Pisonia grandis* and *Cynometra ramiflora*, and understory of mostly *C. ramiflora* and the Mariana endemic *Guamia mariannae* (Craig 1992b). Other natural habitats, including ravine forest, swordgrass (*Miscanthus floridus*) savannah (both occurring on exposures of volcanic soil), mangrove swamp, freshwater swamp, reed (*Phragmites karka*) marsh, strand forest, and coastal scrub are also present. Combined, native habitats presently cover roughly 30% of the island.

The remainder of Saipan's natural habitats have developed on disturbed sites. Level areas are largely abandoned agricultural lands (Fosberg 1960) vegetated by elephant grass (*Penisetum purpureum*) meadows, and tangantangan (*Leucaena leucocephala*) thickets. Secondary forests of introduced species, particularly sosuge (*Acacia confusa*), white monkeypod (*Albizia lebeck*), and flametree (*Delonix regia*) are also common, as are areas of "agriforest" (Engbring et al. 1986) where trees such as coconut (*Cocos nucifera*) and mango (*Mangifera indica*) are frequent.

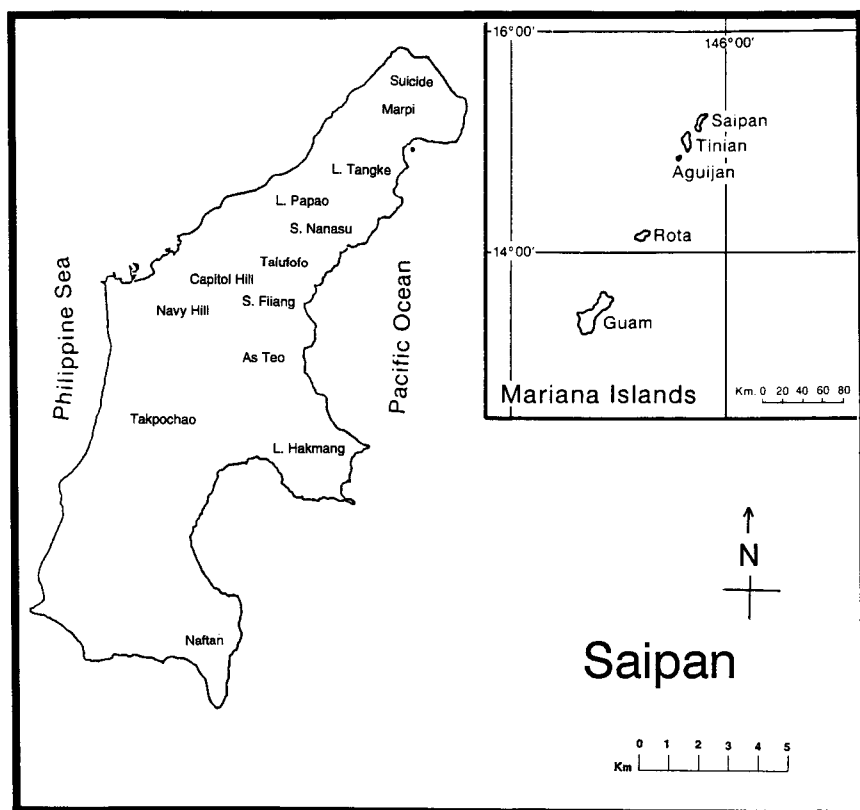


FIG. 1. The island of Saipan, Mariana Islands, with names of principal locations mentioned in this study.

*Bird censuses.*—I performed two types of bird censuses: variable circular plot (Reynolds et al. 1980) surveys and U.S. Fish and Wildlife Service breeding bird surveys. The former were conducted in limestone forests of the Marpi region of northern Saipan (Fig. 1). I censused two separate locations. The first was an old Japanese hiking trail, the Banadero Trail, located along the west slope of a steep escarpment known as Suicide Cliff. The second was a modern hiking trail along the Laderan Tangke cliffline. Marpi is characterized by steep limestone escarpments with the most extensive native forest remaining on the island. The breeding bird survey traversed the island from north to south and covered a variety of habitats.

I used the variable circular plot (VCP) technique, chosen because of its utility in rough tropical terrain (Scott et al. 1986), to survey 15 points each at the two census routes (30 total points). Based on the frequency with which birds provided cues, I established count periods of 8 min/station. Points were 100 m apart except at Laderan Tangke, where one set of stations was placed 200 m apart and another 300 m apart to avoid disturbed habitat. At each point, I recorded all birds seen or heard and estimated the distance of each bird from

TABLE 1  
DETECTION DISTANCES (M) USED FOR COMPUTING POPULATION ESTIMATES OF BIRDS IN  
DISTURBED HABITATS, LIMESTONE FOREST, AND IN THE 1982 SURVEY (ENGBRING ET AL.  
1986)

Species	Disturbed habitats		Limestone forest		1982
	Distance	N	Distance	N	Distance
Micronesian Megapode	0	0	80	32	105
White-throated Ground Dove	— <sup>a</sup>	—	20	51	80
Mariana Fruit Dove	70	20	50	155	159
Collared Kingfisher	70	56	50	283	193
Rufous Fantail	20	127	10	706	58
Nightingale Reed-warbler	50	34	0	0	87
Micronesian Starling	40	30	15	220	66
Micronesian Honeyeater	25	54	15	52	58
Bridled White-eye	15	590	10	2291	33
Golden White-eye	20	70	10	615	42

<sup>a</sup> Because an insufficient sample was available, the distance estimate for limestone forest was used in computations.

the point. Censuses began at sunrise and were conducted under conditions of minimal rain and low wind (although wind averaged higher in the dry season). Practice censuses were conducted in October 1990, and censuses were made at quarterly intervals thereafter in January, April, July, and October, 1991–1992. Replicate data were, therefore, available for each year and for the wet and dry seasons. I also made five replicate censuses each at the two routes from late April to mid-May 1993 in order to assess within-season variation in counts.

Although I attempted to calibrate distance estimates by placing plastic flagging at 10, 15, and 20 m intervals (the maximum distance easily visible in limestone forest) from selected census points and by walking from the point to distantly vocalizing birds during practice censuses, distances were difficult to estimate (Table 1). Indeed, correctly estimating the distance to the roughly 15 birds/census point, under varying conditions of topography, vegetation density, and orientation of the bird to the point, even for an observer with 20 years of censusing experience, seemed an unrealistic expectation. Hence, population densities derived from such estimates are of limited accuracy. I report computed densities and make independent assessments of their utility but use direct counts for many analyses and recommend that future studies compare counts rather than densities when possible.

In addition to these regularly performed surveys, I employed the VCP procedure at three disturbed sites to provide data comparable with those for native forest. Using the same procedures outlined above (except that points were 150 m apart to improve sampling independence in habitats in which birds could be detected farther), I censused 25 points at Laderan Hakmang (Kagman), 17 points at Sabanan Fiiang, and 17 points at Mt. Takpochao (Tapotchau) in March 1993. Laderan Hakmang, the site of a former World War II fighter field complex, is presently a xeric mosaic of meadows, tangantangan thickets, and scattered introduced and native tree species. Sabanan Fiiang, formerly a World War II hospital site, is similarly xeric and largely overgrown by tangantangan and scattered introduced and native trees, particularly ironwood (*Casuarina equisetifolia*). The Mt. Takpochao area, at least in

part a pre-war coffee (*Coffea arabica*) plantation (ca 300 m elevation), is a mesic mosaic of meadows, swordgrass savannah, thickets, and copses of native forest.

The breeding bird survey involved censusing for 3 min at each of 50 roadside stops placed 0.8 km (0.5 mi) apart. Counts began 15 min before sunrise on days with low wind and little rain, and all birds seen or heard to 0.4 km away were recorded. Because the quality of back roads on Saipan is poor, the entire survey took ca. 4.5–5 h to complete. Moreover, the limited availability of back roads necessitated breaking the route into two segments (after station 23) in order to traverse the entire island. Surveys also were conducted quarterly in 1991–1992.

*Additional observations.*—to investigate additional aspects of avian populations and social systems, I mist netted and color banded small passerines in the Marpi native forest and at Capitol Hill. This second site facilitated study of the Micronesian Honeyeater which was uncommon in limestone forest but common in suburban settings.

Intensive banding of Bridled White-eyes at Capitol Hill provided an assessment of population densities independent of those obtained through bird censuses. I banded white-eyes intermittently from February 1992 to June 1993, and in February and May 1993, I recorded the proportion of banded vs unbanded birds present within a 50 m radius of the banding site. To determine population distribution, in May 1993 I also assessed the proportions of banded vs unbanded birds at 50 m intervals to 300 m from the banding site.

I made incidental observations on all Saipan land birds throughout my investigations. I paid particular attention to occurrences of interspecific aggression, and I assessed intraspecific aggression by playing back recorded songs to selected species. Data on breeding, foraging, and microhabitat use also were gathered. From 1988 to 1993, I made additional observations on the nearby Mariana Islands of Tinian (4 d), Rota (69 d), and Aguiguan (6 d).

*Analysis.*—I used the procedure described by Scott et al. (1988) and followed by Engbring et al. (1986) to compute population densities.

For two loudly vocal and wide ranging species, the Mariana Fruit Dove and Collared Kingfisher, VCP census points 100 m apart were inadequate to ensure that observations from each point were independent. For these species, I computed population densities based on 16 alternate census points (at least 200 m apart). Micronesian Megapodes also were detectable at long distances, but because they were sedentary and rare, I was able to distinguish the locations of all individuals encountered.

To obtain independent population estimates for the Bridled White-eye, I employed the Jolly-Seber procedure (Tanner 1978) to analyze capture-recapture data from banding operations. In addition, I used the Lincoln-Peterson index (Tanner 1978) to evaluate populations based on the relative proportions of banded and unbanded birds observed directly around (to 50 m) the banding site (the region assumed to include intersections of home ranges of all birds banded). An assumption of the Jolly-Seber procedure, random sampling of banded and unbanded members of the population, may not have been met because previously captured birds might become net shy. Moreover, the Lincoln-Peterson index requires that no recruitment occur during the study period, an assumption not met during the extended study period. Hence, population estimates based on both methods, particularly the latter, are likely inflated.

To compute population densities,  $P$ , from the above indices, I employed data gathered on the dispersion of marked birds from the banding site. I developed a relation using the number of birds with home ranges intersecting the banding site ( $N$ ) as generated from the two methods above, the area ( $A$ ) of each of  $i$  zones radiating from the banding site at 50 m intervals, the multiple ( $a_i$ ) of the basal zone (0–50 m from the banding site) area ( $A_i$ ) of each  $A_i$  and the proportion of birds banded in each of these areas ( $p_i$ ):  $P = N / \sum_i (a_i p_i)$ .  $P$  was converted to birds/ha by dividing it by the area of the basal zone, 7853 m<sup>2</sup>.

TABLE 2  
COMPARATIVE COUNTS OF BIRDS (BIRDS/10 STATIONS) FOR 1991–1992 (LIMESTONE FOREST),  
THE 1993 SURVEY OF DISTURBED SITES, AND THE 1982 SURVEY (ENGBRING ET AL. 1986)

Species	Limestone forest		Disturbed sites	1982 survey
	1991	1992		
Micronesian Megapode	1.0	1.3	—	0.2
Yellow Bittern	—	—	0.2	0.6
White-throated Ground Dove	1.7	2.1 (2.8) <sup>a</sup>	0.7	0.6
Mariana Fruit Dove	5.9 (5.6) <sup>b</sup>	5.9 (6.8) <sup>a</sup> (7.0) <sup>b</sup>	3.6	20.0
Collared Kingfisher	10.6 (12.5) <sup>b</sup>	10.3 (12.3) <sup>b</sup>	10.0	13.6
Rufous Fantail	25.3	28.4	23.0	45.0
Nightingale Reed-warbler	—	—	6.1	11.8
Micronesian Starling	8.5	7.5	5.4	4.7
Micronesian Honeyeater	2.0	2.3	9.8	22.6
Bridled White-eye	87.3	88.7	107.1	77.0
Golden White-eye	22.1	23.9	12.5	30.4

<sup>a</sup> April counts of species with seasonal shifts in calling frequency.

<sup>b</sup> Based on 16 stations spaced 200 m apart.

#### SPECIES ACCOUNTS

*Micronesian Megapode*.—Believed to have become extinct on Saipan after the early 1930s, it was rediscovered in 1978 by Pratt et al. (1987). This present population, estimated at 25–50 by Glass and Aldan (1987) is suspected to be descended from birds brought to Saipan from more northern Mariana islands by island inhabitants (Engbring et al. 1986). During this study, I estimated 14 birds to be present in native forests (and occasionally in adjacent tangantangan thickets) of the Marpi region. In 1989 I also heard a bird farther south at Laderan Papao, although I found none there in later years. Despite intensive surveys, I located none at Naftan Point, the southernmost point on Saipan, where Glass and Aldan (1987) previously reported individuals. Hence, populations are likely declining. Both direct counts (Table 2) and density estimates (Table 3) for limestone forest were greater than those recorded in 1982 by Engbring et al. (1986), but the present VCP transects overlapped the only remaining range of the species on Saipan, whereas Engbring et al. (1986) surveyed all habitats throughout the island.

No firm evidence of breeding by this endangered species is known from Saipan. However, in 1991 I located the possible remains (soil and rotting vegetation) of an old nest mound in the Marpi forest, similar in dimensions to those which I have observed in interior forests of the Palau Islands (where a different subspecies occurs). Glass and Aldan (1987)

TABLE 3  
COMPARATIVE 1991–1992 DENSITY ESTIMATES (BIRDS/KM<sup>2</sup>) FOR BIRDS OF LIMESTONE FOREST, THE 1993 SURVEY OF DISTURBED SITES, AND THE 1982 SURVEY (ENGBRING ET AL. 1986)

Species	Limestone forest		Disturbed sites	1982 survey
	1991	1992		
Micronesian Megapode	2	3	—	1
White-throated Ground Dove	58	72	24	2
Mariana Fruit Dove	27 (26) <sup>a</sup>	27 (32)	11	25
Collared Kingfisher	43 (51)	42 (50)	26	11
Rufous Fantail	2160	2423	647	456
Micronesian Starling	403	356	48	32
Micronesian Honeyeater	123	138	205	203
Bridled White-eye	5904	5994	3992	2221
Golden White-eye	1935	2095	390	532

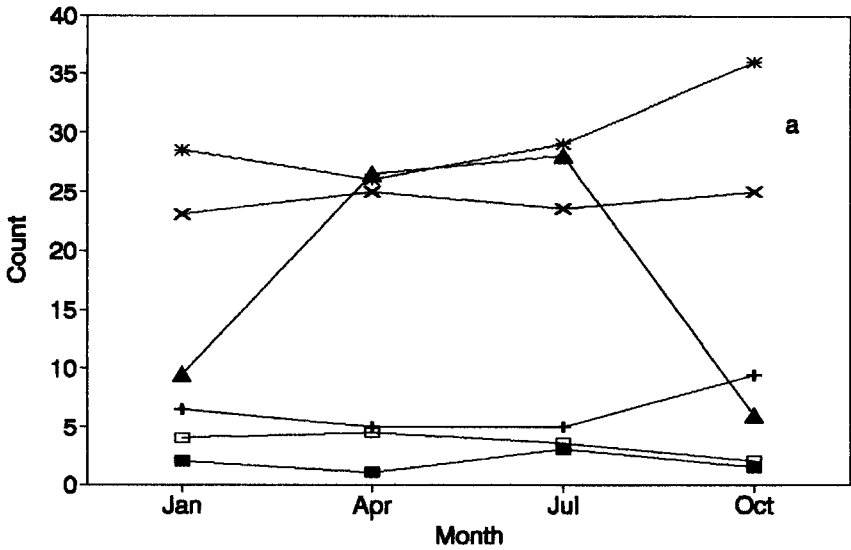
<sup>a</sup> Numbers in parentheses are population estimates based on 16 stations 200 m apart.

suspected a peak in calling (and breeding activity) in January, but in 1991 both limestone forest and island-wide surveys showed a calling peak in July (Figs. 2A, 3A), the month in which I saw two birds engaging in apparent courtship chases (the birds otherwise foraged together and showed no evidence of aggression). This pattern was not repeated in 1992, although replicate counts performed in April 1993 (Table 4) suggested that census variation between seasons was greater than that within a season. Individuals or pairs were sedentary, responded vigorously to playback, and appeared to defend all-purpose territories. Birds could be found in the same areas even between years, although during the study period they invaded new locations on two occasions, thus providing evidence for either territory relocation or reproduction.

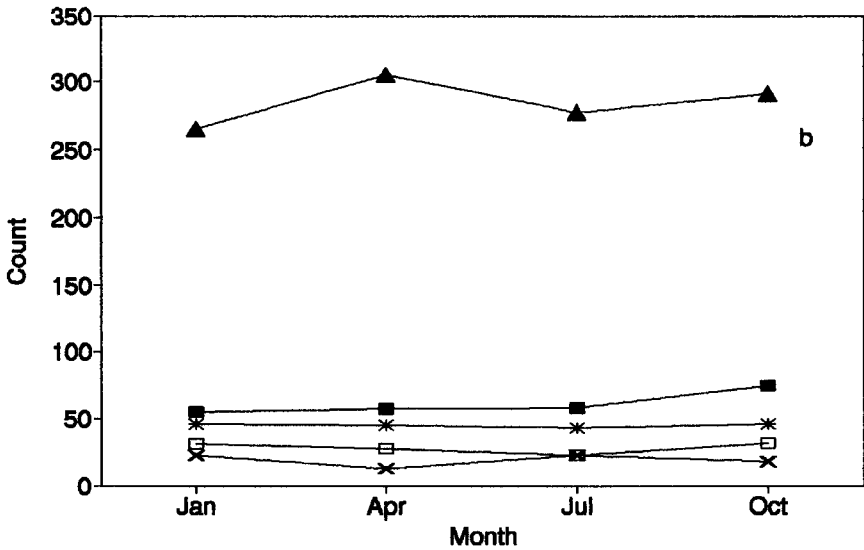
Baker (1951) reported that the Micronesian Megapode is omnivorous, although field observations on foraging are virtually nonexistent. I recorded feeding only once, when I observed an individual capture an insect. Foraging birds generally scratched leaf litter with the feet and, at least occasionally, scratched alternately with one foot and then the other.

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FIG. 2. Mean 1991–1992 population trends of land birds for island-wide counts. (A) MIME—Micronesian Megapode, WTGD—White-throated Ground Dove, MFDO—Mariana Fruit Dove, COKI—Collared Kingfisher, MIHO—Micronesian Honeyeater, YEBI—Yellow Bittern; (B) RUFA—Rufous Fantail, MIST—Micronesian Starling, BWEY—Bridled White-eye, GWEY—Golden White-eye, NRWA—Nightingale Reed-warbler.



■ MIME    □ WTGD    ▲ MFDO  
 \* COKI    × MIHO    + YEBI



■ RUFA    □ MIST    ▲ BWEY  
 \* GWEY    × NRWA



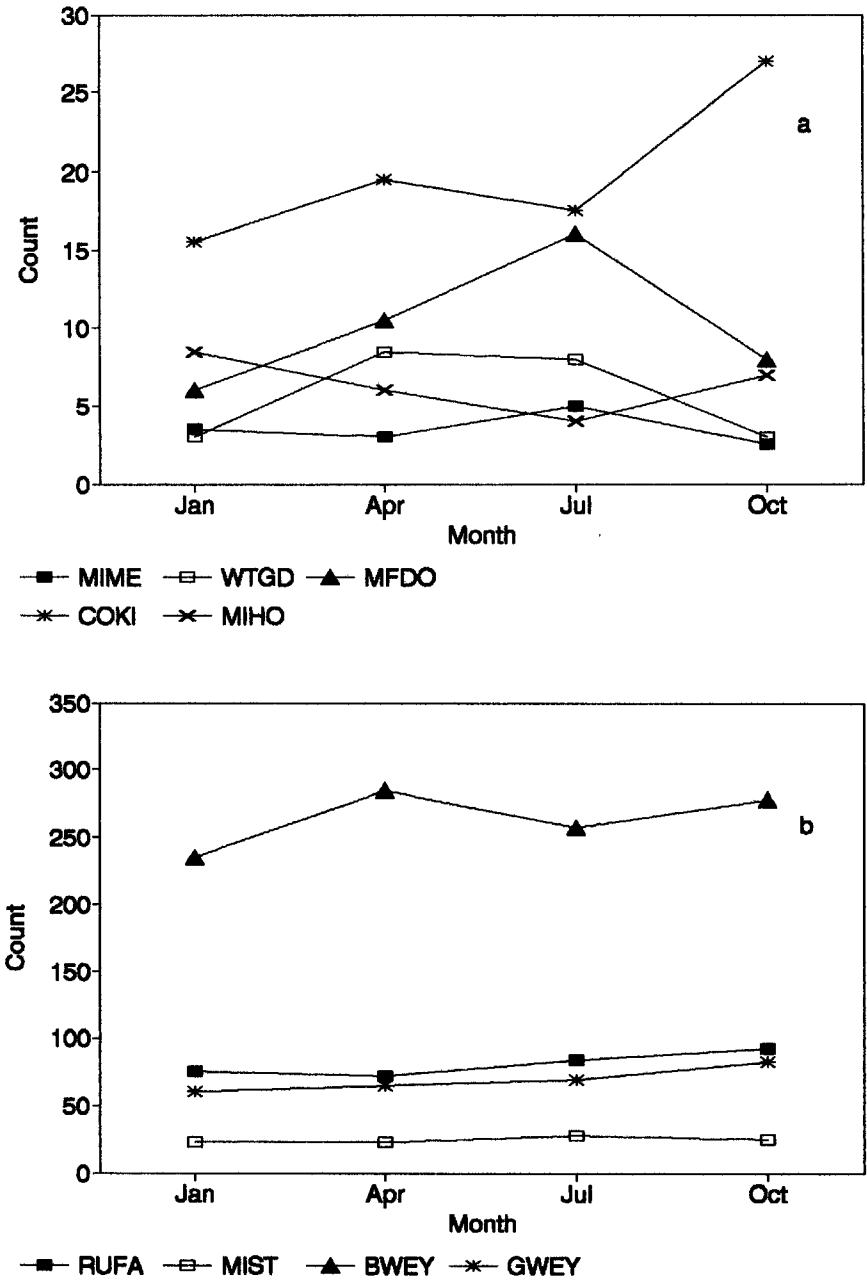


FIG. 3. Mean 1991-1992 population trends of land birds for limestone forest counts. See Fig. 2 for legend abbreviations.

TABLE 4  
 COEFFICIENTS OF VARIATION FOR 1991–1992 LIMESTONE FOREST AND ISLAND-WIDE SURVEYS,  
 AND FOR 1993 REPLICATED (5 TIMES) VCP SURVEYS

Species	Limestone forest		Island-wide survey
	1991–1992	1993	1991–1992
Micronesian Megapode	43.2	27.2	82.8
Yellow Bittern	—	—	33.9
White-throated Ground Dove	57.0	64.4	52.9
Mariana Fruit Dove	50.3	35.2	62.7
Collared Kingfisher	15.1	22.9	15.0
Rufous Fantail	13.4	8.5	14.4
Nightingale Reed-warbler	—	—	29.9
Micronesian Starling	19.0	9.8	22.6
Micronesian Honeyeater	32.4	17.6	11.6
Bridled White-eye	13.4	4.3	18.5
Golden White-eye	18.5	5.0	12.9

Gut contents from two individuals collected on islands north of Saipan contained spiders, insects, seeds, and plant fragments (Stinson 1993a).

*Yellow Bittern*.—This species is typically categorized as a water bird (e.g. Engbring et al. 1986), and it indeed foraged in ponds, marshes, tidal flats, and shorelines. However, the Yellow Bittern also inhabited upland habitat mosaics in which grasslands were an important part. It was absent from the forests of the VCP transects (Table 2) but occurred uncommonly on the island-wide survey and showed weak October peaks each year (Fig. 2A). Direct counts were low at disturbed sites compared to those reported by Engbring et al. (1986) (Table 2), but my sample size was too limited for a valid comparison to be made or for population densities to be computed.

I recorded nesting in February (eggs) in a patch of elephant grass surrounded by tangantangan. Birds were seen in pairs and were observed flying hundreds of meters, thus suggesting that no all purpose territory existed. Observations of foraging were limited to two captures of lizards in upland habitat.

*White-throated Ground Dove*.—Although fairly common (but reported as rare by Jenkins and Aguon 1981), based on the frequency with which flying birds were seen, the species was otherwise visually inconspicuous and called infrequently. Such characteristics resulted in its being poorly censused. However, birds were usually encountered at close range (Table 1) and, therefore, densities computed (Table 3) were high relative to fruit doves.

Despite under-representation on censuses, three of four annual counts made at the two environmental scales peaked in April–July (Figs. 2A, 3A). Such a trend likely indicated an increase in breeding activity during those months (most census detections were of vocalizing birds). Indeed, Stinson (1993b) reported that all 14 nests in the Division of Fish and Wildlife (DFW) files were found between April and September. However, Jenkins (1983) provided evidence that the extinct Guam population could breed year round.

The cyclic nature of counts led to high coefficients of variation for census data compared to Saipan passerines, although even variation within a season was high (Table 4). Based on direct counts, the species appeared more frequent in native forest than in disturbed habitats and more frequent than found by Engbring et al. (1986) (Table 2). Computed densities followed similar trends (Table 3).

The White-throated Ground Dove on Saipan, Rota, and Aguiguan used a range of forest strata (Table 5), including the ground ( $N = 60$ ). These observations contrast with those of Marshall (1949), Baker (1951), Jenkins (1983), and Engbring et al. (1986) who considered the species to be largely or entirely arboreal. On Saipan, it occurred in native forest, secondary forest, agriforest, tangantangan thickets, and habitat mosaics that included fields. In such habitats, it flew for at least 300 m above the canopy, suggesting that it did not defend all purpose territories.

Foraging observations included feeding on the ground on seeds and probing leaf litter (4), feeding on fruits of the native trees *Melanolepsis multiglandulosa* (1) and *Premna obtusifolia* (2), and inspecting papaya (*Carica papaya*) fruits (1). Marshall (1949), Jenkins (1983), and Villagomez (1987) list additional fruits eaten. Many members of the genus are forest understory herbivores (Beehler et al. 1986), but the White-throated Ground Dove appears to be more of a microhabitat generalist.

*Mariana Fruit Dove*.—All counts showed evidence of a population peak in April–July, although the trend was most pronounced in island-wide data (Figs. 2A, 3A). Data from 1983–84 and 1987 roadside call counts on Saipan (Villagomez 1987) showed a similar trend. As with the White-throated Ground Dove, these peaks appeared to represent increases in breeding activity rather than population cycles. Most census detections were of calling birds, and fruiting peaks by certain common native tree and vine species (e.g., *Ficus* spp., *Premna obtusifolia*, *Jasminum marianum*; unpubl. data) corresponded with these high counts. Wet season increases in breeding are known for New Guinea Fruit Doves (Frith et al. 1974). I recorded breeding in February (carrying nesting material), May (egg), and July (nestling), and Stinson (1993b) reported that 35 of 38 nests in DFW files were found between April and September.

TABLE 5  
PERCENT USE OF FOREST ZONES BY NATIVE MARIANA ISLAND DOVES

Species	Forest zone			
	Top	Middle	Lower	Ground
White-throated Ground Dove	45.0 (27) <sup>a</sup>	20.0 (12) <sup>a</sup>	5.0 (3) <sup>a</sup>	30.0 (18) <sup>a</sup>
Mariana Fruit Dove	76.6 (49) <sup>a</sup>	21.9 (14) <sup>a</sup>	1.6 (1) <sup>a</sup>	0

<sup>a</sup> N.

Direct counts showed that the Mariana Fruit Dove was more common in limestone forest than in disturbed habitat, but uncommon compared to that reported by Engbring et al. (1986) (Table 2). However, because I encountered fruit doves at closer range than Engbring et al. (1986) (Table 1), density estimates for limestone forest were similar to those from 1982 (Table 3). Like the White-throated Ground Dove, the cyclic nature of counts produced high variation in seasonal census results. Variation was comparatively low within a season, although still higher than for passerines (Table 4).

The Mariana Fruit Dove appeared to focus activities (N = 64) in upper and mid-forest strata (Table 5). Otherwise, it occupied a range of habitats similar to that of the White-throated Ground Dove. Also, like the preceding species, it flew >100 m (often in pairs) above the canopy, suggesting that it did not defend all-purpose territories. I saw individuals feeding on fruits of the native *Ficus* spp. (9) and *Premna obtusifolia* (2) trees, the vine *Jasminum marianum* (1), and the introduced *Muntingia calabura* (1). Jenkins (1983) and Villagomez (1987) list additional fruits eaten by the Mariana Fruit Dove. Like many members of the genus (Beehler et al. 1986), this species is a canopy frugivore.

*Collared Kingfisher*.—Both limestone forest and island-wide surveys showed that three of four annual counts peaked in October (Figs. 2A, 3A). Seasonal variation in censuses was similar to that obtained for passerines, but lower than that for doves. Variation within was greater than that between seasons (Table 4), which illustrated the difficulty in censusing a species that regularly flew >300 m above the forest canopy. Densities computed (Table 3) are likely exaggerated because of the likelihood of overcount from flight calls made during these long flights. The Collared Kingfisher was encountered with similar frequency on limestone forest and disturbed habitat counts (Table 2), although because it was observed at greater distances in disturbed habitat (Table 1), its computed density was comparatively low. Engbring et al. (1986) found birds with similar frequency to that of this study (Table 2) but with lower computed density

(Table 3) because detection distances were lower in the present study (Table 1).

I detected breeding in January (recently fledged nest), May (nest), and June (nestlings, incubating). The Collared Kingfisher was present in every habitat, including shorelines, wetlands, savannah, disturbed sites, and limestone forest. In forest, I usually observed it flying above the canopy, at the forest edge, or perched in the top of canopy trees. However, it also entered the forest interior, where I mist netted individuals twice. It often occurred in pairs or groups of three to four birds, which probably were family groups.

I observed 15 feeding attempts by the Collared Kingfisher. Prey items included a millipede, grasshopper, unidentified insect, lizards (four confirmed, three apparent), Micronesian Honeyeater, Golden White-eye (attempt), and Bridled White-eye (capture, attempt, apparent capture). Marshall (1949) had previously listed insects, spiders, crabs, lizards, and mice as prey, and he also described frequent but unsuccessful attacks on Bridled White-eyes. Engbring et al. (1986) reported an instance of predation on a Rufous Fantail. The Collared Kingfisher is the only extant native predator on birds in the Marianas.

The importance of this species as a bird predator is reflected in observations of mobbing, scolding, and alarm calls directed against it by other species, including the Bridled White-eye (6), Golden White-eye (1), Rufous Fantail (1), and Micronesian Honeyeater (1). I also saw a Collared Kingfisher chase a Yellow Bittern (1) and fight with a Black Drongo (*Dicrurus macrocercus*) on Rota.

*Island Swiftlet*.—Because of its crepuscular nature, this species was poorly censused by the techniques employed, and census data are not reported. However, incidental dawn/dusk observations and data from the island-wide census demonstrated that, unlike most species, it was found unevenly about the island. Its distribution appeared correlated with the occurrence of suitable nest caves. Hence, it was common in mountainous areas around Takpochao, Capitol Hill, Navy Hill, As Teo, eastern Marpi, Laderan Hakmang, and Sabanan Nanasu but largely absent from western Marpi and flat lowlands throughout the island. I gathered no breeding or behavioral data on the Island Swiftlet.

*Rufous Fantail*.—Annual counts consistently peaked in October (Figs. 2B, 3B). Seasonal variation in counts was lower than that for doves, but variation within a season was still lower (Table 4), suggesting that populations or breeding status changed seasonally. The species was found with similar frequency in limestone forest and disturbed habitats (Table 2), although because birds were detected at greater distances in disturbed habitat (Table 1), computed densities there (Table 3) were relatively low.

Engbring et al. (1986) recorded the Rufous Fantail more frequently than did this study (Table 2), but their computed densities were far lower (Table 3) than in limestone forest, because my detection distances in forest were lower (Table 1).

Breeding was recorded for January (nest construction, eggs, fledglings, juveniles), February (eggs, juveniles), March (nest), April (nestlings), October (nest construction, eggs), and November (nestlings). Jenkins (1983) reported breeding in January–April, June, and November on Guam, and Marshall (1949) believed, based on gonad condition of specimens, that breeding occurred year round. Birds occurred commonly in a variety of wooded and thicket habitats, including beach strand and suburban habitats, but they were largely absent from swordgrass savannah.

Frequently observed food begging in small flocks of three to four birds indicated that these were family groups. Color banding further showed that groups remained at a single location. At such locations, males engaged in song duels with neighbors and responded aggressively to taped playback of songs. Hence, individuals appeared to defend all purpose territories.

Observations of interspecific aggression were restricted to one instance each of supplanting a Bridled White-eye at a perch and chasing a foraging Golden White-eye from near a fantail nest. More frequently, I saw birds following Golden (10) and Bridled white-eyes (10) to capture insects flushed by the foraging activities of these species.

*Nightingale Reed-warbler.*—I regularly recorded birds only on island-wide and disturbed site counts (Table 2). Birds detected on limestone forest surveys were almost all calling from outside the forest. Island-wide counts showed no clear seasonal trend (Fig. 2B). Previous studies at Marpi demonstrated a drop in territorial activity in the wet season by up to 24% (Craig 1992a). Indeed, my only breeding record was for February (fledgling). My inability to detect a similar island-wide trend by this loudly vocal species likely meant that the census data were inherently variable, although the local trend I found might not have been general.

In five years of observing on Saipan, I located Nightingale Reed-warblers in interior forest on only three occasions. These birds did not appear to be territory holders, because on subsequent visits to the same site they were absent. At the disturbed census sites (surveyed in March), I found individuals with lower frequency (Table 2) and density (Table 3) than did the more comprehensive Engbring et al. (1986) survey (made in May), although the species was generally widespread and common on the island. It occurred in all thicket-meadow mosaics, forest edge, reed marshes, and forest openings, but it was absent from beach strand and swordgrass savannah.

Because Nightingale Reed-warblers usually are concealed in thick vegetation, I recorded foraging rarely despite intensive study. Observations included eating insects (3), gleaning invertebrate from leaves (3) and a dead leaf (1), and probing a dead stub (1). Marshall (1949) reported insects, spiders, snails, and lizards as prey. Although the species was intraspecifically aggressive and defended all-purpose territories (Craig 1992a), I saw no interaction between it and other species.

*Micronesian Starling*.—This species showed little clear seasonal trend in censuses (Figs. 2B, 3B). Although seasonal variation in counts was low compared to doves, within-season variation was even lower (Table 4), suggesting a seasonal shift in populations or breeding status. Compared to limestone forest, it was encountered less frequently (Table 2) and observed to greater distances (Table 1) in disturbed habitats. Hence, computed densities (Table 3) were lower in disturbed habitats. It also was found more commonly in limestone forest than by Engbring et al. (1986) (Table 2).

Micronesian Starlings were usually seen in pairs, family groups (based on observations of adults attending food begging juveniles, mist netted juveniles with an aggressive adult nearby) or juvenile flocks (all birds in juvenal plumage). Larger flocks (5–11, not 50 as reported by Marshall 1949), made up mostly of birds in juvenal plumage were likely the product of several nestings by a single adult pair. As Jenkins (1983) reported for Guam, I observed single pairs nesting at the same location nearly year round. Banding showed that birds maintain a home range. The species used virtually all habitats from beach strand to interior forest and sword-grass savannah.

Jenkins (1983) listed a variety of fruits and seeds taken by the Micronesian Starling, and Marshall (1949) described it as omnivorous. I observed birds feeding on fruits of *Ficus* spp. (4), papaya (*Carica papaya*) (3), camachile (*Pithecellobium dulce*) (1) and an insect (1). Reichel and Glass (1990) reported that it preys on seabird eggs.

*Micronesian Honeyeater*.—No clear seasonal trend emerged in census data at either environmental scale (Figs. 2A, 3A). In limestone forest, between season variation was high compared to other passerines and to within-season variation (Table 4), suggesting that seasonal shifts occurred in populations or breeding status. Jenkins (1983) reported breeding on Guam year round, although he was uncertain if breeding peaks occurred. I recorded breeding in February (nest building) and May (courtship). It was uncommon in limestone forest compared to disturbed habitats, as well as to other passerines (Tables 2, 3). Engbring et al. (1986) found that the frequency (Table 2) and computed density of the Micronesian

Honeyeater was higher than I found for birds in limestone forest (Table 3).

The Micronesian Honeyeater was aggressively territorial against conspecifics, chased individuals and dispersed flocks of Golden White-eyes (4), and chased Rufous Fantails (2). I also saw a Micronesian Starling supplant a Micronesian Honeyeater at a perch.

At Capitol Hill, a color banded male had a territory of ca 0.7 ha. Two additional banded territorial males were observed to within 150 m from the banding site. However, repeated mist netting at one site yielded regular capture of unbanded birds (mostly females or juveniles, based on plumage and measurements) which indicated the existence of a population of non-territorial birds. These floaters or nomadic birds may account for the seasonal variation in census data, because they may opportunistically follow ephemeral nectar sources as do certain of the Hawaiian Honeycreepers (Scott et al. 1986).

The species occupied a variety of habitats, including beach strand, mangroves, upland forest, suburban areas, and disturbed habitats. It was largely absent from swordgrass savannah, but particularly common in the vicinity of coconut (*Cocos nucifera*) groves where it fed on nectar. Foraging is discussed in detail by Craig and Beal (ms), and Table 6 lists 11 nectar sources that I recorded.

*Bridled White-eye*.—No clear pattern emerged in counts at either environmental scale, although January counts averaged lowest, probably because higher winds at this season reduced the detectability of this canopy species (Figs. 2B, 3B). Like most passerines, variation in counts was relatively low, and variation between seasons was greater than within a season (Table 4). Although even more individuals were encountered in disturbed habitats than in limestone forest (Table 2), birds detected were at greater distances so that population densities (Table 3) were lower in disturbed habitat. I recorded more Bridled White-eyes (Table 2), and densities computed were far greater than reported by Engbring et al. (1986) (Table 3), because I detected birds at closer range (Table 1).

Banded birds declined in frequency of occurrence,  $p$ , from the banding site to 300 m in an empirically fitted quadratic relationship ( $r^2 = 0.99$ ):

$$p = 1.47x^2 - 1.21x + 53.82,$$

where  $x$  has values from one for the basal zone (0–50 m from the banding site) to six for the outermost zone (251–300 m). Based on this relationship, I solved Equation (3) for my Lincoln-Peterson (8754 bird/km<sup>2</sup>) and Jolly-Seber (7770 birds/km<sup>2</sup>) population estimates, which yielded densities of the same order of magnitude as those obtained through VCP censusing (Table 3).



TABLE 6  
PLANT SPECIES FED UPON BY THREE SMALL FOREST PASSERINES

Plant species	Bridled White-eye				Golden White-eye				Micronesian Honeyeater			
	se <sup>a</sup>	fr	fl	ne	se	fr	fl	ne	se	fr	fl	ne
Vines:												
<i>Momordica charantia</i>	x	x			x	x						
<i>Mikania scandens</i>	?		x									
<i>Passiflora foetida</i>		x										
<i>Operculina ventricosa</i>				x								
<i>Jasminum marianum</i>		x	x									
Trees:												
<i>Pisonia grandis</i>			x	x				x				
<i>Cynometra ramiflora</i>			x	x								x
<i>Premna obtusifolia</i>		x	?	x		x						
<i>Ficus</i> spp.		x				x						
<i>Melanolepis multiglandulosa</i>		x	?			x						
<i>Erythrina variegata</i>				x			x	x				x
<i>Psychotria mariana</i>				x		x		x				x
<i>Morinda citrifolia</i>				x				x				
<i>Artocarpus</i> spp.		x				x						
<i>Aidia cochinchinensis</i>							x	x				x
<i>Pipturus argenteus</i>		x										
<i>Bikkia mariannensis</i>												x
<i>Hibiscus tiliaceus</i>				x								x
<i>Delonix regia</i>												x
<i>Lantana camara</i>		x				x	x					x
<i>Albizia lebbbeck</i>				x								x
<i>Carica papaya</i>		x				x						
<i>Leucaena leucocephala</i>			x									
<i>Cocos nucifera</i>												x
<i>Muntingia calabura</i>		x				x						
Herbs:												
<i>Bidens pilosa</i>		x										

<sup>a</sup> se = seed, fr = fruit, fl = flower, ne = nectar.

The Bridled White-eye was found in all habitats from beach strand to disturbed habitats, suburban areas, and forest. It was less common in swordgrass savannah. I recorded breeding in January (carrying nesting material), February (nestlings, carrying nesting material), August (eggs, carrying nesting material), and October (carrying food). Moreover, I observed food begging by juveniles year-round. Jenkins (1983) also reported that the Guam Bridled White-eye bred year-round. Although it is not territorial, banding demonstrated that birds remain in a home range, and

individuals could be attracted to playback of various flocking calls. Other than scolding Collared Kingfishers, interspecific social interactions involved only an observation of a Bridled White-eye following a foraging Rufous Fantail. No interspecific aggression initiated by Bridled White-eyes was noted. I recorded feeding on seeds, nectar, flowers, and fruit of 22 plant species (Table 6) in addition to invertebrates.

*Golden White-eye*.—No clear pattern emerged in counts at either environmental scale (Figs. 2B, 3B). Although as with other passerines, seasonal variation in censuses was relatively low, intraseasonal variation was still lower (Table 4). The Golden White-eye was decidedly more common in limestone forest than in disturbed habitats (Table 2, 3), although slightly less frequently encountered than by Engbring et al. (1986). Nevertheless, computed densities were greater in this study (Table 3) because I encountered birds at closer range (Table 1).

I recorded breeding in January (gathering nesting material, eggs, fledglings), February (eggs), March (eggs), May (recently fledged nest), June (eggs), July (copulation, carrying nesting material, eggs, nestlings), August (nest construction), and October (eggs). Moreover, I heard song and observed food begging year-round, except during the protracted dry season of 1993, when I heard no singing during June despite my almost daily presence in the field. This latter observation may help to explain Marshall's (1949) failure to detect any song in this species. Other than limited observations reported by Stinson and Stinson (1994), little other data on breeding exist.

Aggression involved chases and dispersing flocks of Bridled White-eyes (20) and Rufous Fantails (2). Golden White-eyes were territorial. Banded males defended territory boundaries against other males and responded, although not vigorously, to playback of recorded songs. Family groups of 3–4 (as demonstrated by food begging of juvenal plumaged birds) were typical. The Golden White-eye occurred in all wooded habitats, including strand forest and suburban areas, although it was generally absent from swordgrass savannah. Foraging is discussed by Craig and Beal (ms); I observed feeding upon invertebrates and the nectar, flowers, and fruit of 13 plant species (Table 6).

#### DISCUSSION

For seven of the nine forest bird species examined, census variation in limestone forest between seasons was greater than that within a season. The remaining two species possessed behavioral characteristics which made them particularly difficult to census. Hence, most or all forest species likely undergo seasonal shifts in either populations or conspicuousness (i.e., increased vocalizations related to breeding). In the case of

doves, strong shifts in vocalizing related to breeding activity are indicated. Many tropical forest passerines increase breeding activity during the wet season (Beehler et al. 1986), but only two species showed consistent peak counts at this time. These, the Collared Kingfisher and Rufous Fantail, are also the only Mariana Island forest species with widespread Indo-Pacific distributions. Other species showed divergence in seasonal counts between years, suggesting that no regular pattern in counts existed. Combined with evidence for year-round breeding for such species as the Micronesian Starling, Micronesian Honeyeater, Bridled White-eye, and Golden White-eye, seasonal variation in counts may, therefore, be caused by actual population shifts or differing peak breeding times related to resource availability. Storms, the vagaries of seasonal patterns, and attendant alteration in food supplies may drive such population or breeding shifts.

For many forest species, peak counts (7 of 9) and computed densities (8 of 9) were greater in native forest than in disturbed habitat. Therefore, native limestone forest, with its comparatively high diversity of tree species, its cooler, wetter microclimate, and variety of food sources, is likely to be superior habitat for most forest species. Only the Micronesian Honeyeater was noticeably more common outside native forest. Presumably, nectar is insufficiently abundant or consistently available to support high densities of this species in limestone forest. However, on nearby Aguiguan, which has forests similar to those on Saipan (Chandran et al. 1992), the Micronesian Honeyeater was common in native forest (Craig et al. 1992). Extensive stands of the introduced *Lantana camara*, are found adjacent to forest on Aguiguan but not Saipan. This shrub flowers year-round and is frequently visited by Micronesian Honeyeaters (Craig et al. 1992).

Censusing at two environmental scales uncovered few clear differences in seasonal trends. The principal difference uncovered was that the Micronesian Honeyeater was relatively uncommon in limestone forest but regular on island-wide counts. Otherwise, forest species showed numerous similarities in counts at both scales, thereby suggesting that a wide range of habitat was suitable for most.

Results of the Engbring et al. (1986) population survey of Saipan birds showed direct counts of roughly the same order of magnitude as those reported in this study. Major differences in counts probably result from this study's survey of primarily native forest, as opposed to all habitats in the 1982 survey. However, the much higher numbers of Mariana Fruit Doves and Rufous Fantails found by Engbring et al. (1986) are not easily accounted for and may indicate population declines in these species. Re-

cent surveys on Aguiguan also detected declines in counts of Mariana Fruit Doves compared to 1982 (Craig et al. 1992).

Although direct counts exhibited similarities, densities reported here are generally well above those computed by Engbring et al. (1986). Most of this difference may be attributed to the shorter distances at which I detected species. Recomputation of densities for my counts using the Engbring et al. (1986) distance estimates indeed yielded similar densities to those they obtained. Shorter detection distances were a consequence of my surveying only in dense, interior forest, whereas Engbring et al. (1986) censused in all habitats. Despite the large difference in results, I believe my density estimates are realistic. Independent density computations for the Bridled White-eye were of the same order of magnitude as those obtained through censusing. Moreover, Craig et al. (1992) pointed out that densities determined for such small passerines as the Golden White-eye translated to encountering one family group of four directly on the transect line once roughly every 100 m. Such a frequency is consistent with field experience for these species.

The densities reported here, particularly for the Rufous Fantail, Bridled White-eye, and Golden White-eye are among the highest ever reported for birds and are similar to those obtained for the most abundant of the Hawaiian Honeycreepers (Drepanidinae) (Scott et al. 1986). Indeed, personal observations of the Common Amakihi (*Hemignathus virens*) and Apapane (*Himatione sanguinea*) in the heart of their present range on Hawaii indicated that densities of Marianas small passerines were similar to those of these Hawaiian species. In temperate forests, in contrast, the density of the Ovenbird (*Seiurus aurocapillus*), the most abundant breeding species in two typical northeastern forest tracts, averaged 149.5–116.8 birds/km<sup>2</sup> (Magee 1989–1993a, 1989–1993b). These densities are about 1/15 that of the similarly territorial Golden White-eye and 1/44 that of the flocking Bridled White-eye. That such immense densities occur suggests that at least some forest birds in the Marianas exist at the maximum densities allowed by resources available in the habitat.

I cannot definitively attribute census variation to population fluctuations, because differences in breeding activity can also produce census variation. Further study is required to demonstrate that populations are at carrying capacity. However, existing at saturation densities is a characteristic of avian communities that is predicted to elicit interspecific competition, particularly between ecologically similar species (MacArthur 1972, Wiens 1977). Interspecific competition is most obviously manifested through aggression, and indeed the most ecologically similar of the small passerines, the two species of white-eyes (Craig 1989, Craig and Beal, unpubl. data) are those for which I observed the most aggression.

The larger Golden White-eye was clearly socially dominant over the Bridled White-eye, and much of the aggression observed involved chases of foraging Bridled White-eyes. Such behavior suggested that the contested resource was food. Based on observations on the four small passerines, the order of social dominance appeared to be Micronesian Honeyeater, Golden White-eye, Rufous Fantail, and Bridled White-eye. In contrast with temperate systems in which bird species can overlap widely in ecological space with little aggression because populations are rarely at saturation densities (Wiens 1977, Craig 1987), this study found aggression prevalent between species that were only generally similar in their ecology (Craig 1989, Craig and Beal, unpubl. data). The existence of populations at the carrying capacity of the habitat most likely accounts for this difference.

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