

Preprint: Pacific Science 75:543-559. Definitive version at <https://bioone.org/journals/pacific-science/volume-75/issue-4>

THE STRUCTURE AND DYNAMICS OF ENDANGERED FOREST BIRD COMMUNITIES IN THE MARIANA ISLANDS

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Abstract. I studied population densities of forest bird communities in the Mariana Islands of Saipan, Aguiguan and Sarigan in order to evaluate hypotheses concerning seasonal shifts in populations, habitat effects on densities, inter-island differences in densities, social group size and underlying reasons for community structuring. With the exception of one species, I found no evidence to support the hypothesis that seasonal shifts occur in populations. Hence, this island system differs in this regard from mainland tropical forests. I also found, contrary to theory, no evidence that the presence of altered habitat permits populations to be greater than they would be in their absence, as disturbed habitat had far lower densities of most species than native forest. Furthermore, I found no support for the hypothesis that social group size differs seasonally as a consequence of differential breeding activity, which is again contrary to findings for mainland tropical forests. A high density of nectar resources on two islands appeared responsible for high population densities of the Micronesian Myzomela on them. Inter-island density comparisons showed strong evidence for there being unfilled niches on Sarigan, thereby making the island a favorable site for species translocations. Examination of the prehistoric composition of Marianas forest bird communities indicated that they once resembled in density structure those of the comparatively pristine Palau Islands. Removing ecologically similar but now absent species from the original Mariana communities likely resulted in reduced competition for resources in ways that increased niche breadth and, thus, populations. The wholesale loss of species in the Marianas has led to communities in which three ecologically versatile species now account for the vast majority of individuals in the community.

The avifauna of the Mariana Islands is among the most endangered on Earth. The southernmost island of Guam has, since the 1980s, lost virtually all of its native birds to the introduced Brown Tree Snake (*Boiga irregularis*), with several of its endemic species extinct (Wiles et al. 2003) and others surviving only in captivity or translocated populations (U.S. Fish and Wildlife Service 2009). Indeed, all other inhabited islands in the chain are at risk of being invaded by these snakes, making the bird communities on them critically imperiled (MAC Working Group 2008).

Despite its endangerment, this avifauna remains

among the most unstudied of any on American soil. Although population surveys are performed routinely (e.g., Amar et al. 2008, Camp et al. 2009, Zarones et al. 2014), few quantitative field investigations into the community ecology, foraging or social behavior of Marianas species have occurred in the past 30 years and even the most basic natural history of many species remains unknown. Only a behavioral study of the Mariana Crow (Faegre et al. 2019) and the notable community studies of Fricke et al. (2017) and Linck et al. (2020) have added significantly to our knowledge since the earliest quantitative ecological investigations of Craig (1989, 1990, 1992a) and Craig and Beal (2002).

From 1990 to 1993, I performed seasonal population surveys of forest birds on the islands of Saipan, Aguiguan and Sarigan. Although I have report-

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FIG. 1. Marpi limestone forest in the vicinity of the Banadero Trail, Saipan.

ed previously on aspects of these surveys (Craig et al. 1993a, 1996), a more comprehensive, statistically defensible investigation that incorporates features of social behavior and synthesizes findings from my earlier studies is now possible due to analytic advances made in quantitative population estimation (Thomas et al. 2010, Research Unit for Population Assessment 2020). Such analyses permit testing of community structuring hypotheses, including that of Engbring et al. (1986) that populations shift seasonally due to differential breeding activity. Breeding seasonality is well documented for tropical forest birds, although patterns among species are complex (Stouffer et al. 2013). However, seasonal population shifts are known for tropical mainland forests (Almazán-Núñez et al. 2018). Moreover, Linck et al. (2020) hypothesized that anthropogenic Marianas habitats permit inflation of the notably enormous population densities beyond that possible if solely native habitats were present. This idea relates to the broader notion that anthropogenic habitats have higher resource abundance for certain species (review in Shochat et al. 2003). Moreover, they provide a pre-snake baseline for evaluating the hypotheses that flock size in social species is directly related to population decline (Craig 1990) and that social group size differs seasonally due to differential breeding activity associated with changes in resource availability. Such seasonal flock alteration is known for mainland tropical forests (Develey and Perez 2000).

Community structuring questions that relate to patterns of population density and what they reveal about the nature of island systems also can be inves-

tigated. All of the Mariana Islands are faunally depauperate, as predicted by island biogeographic theory for such remote islands (MacArthur and Wilson 1967), although their present species complement is at best half of its pre-human complement, with particularly forest floor inhabitants missing (Steadman 1999). Close relatives of many of the extinct Marianas species survive in the far less ecologically disturbed Palau Islands (Engbring 1992), so a comparison of the density structure of these two island groups can reveal something of the community consequences of faunal depletion.

A more complete understanding of the structure and dynamics of this system is also now particularly essential in light of recent efforts to translocate to uninhabited islands species not historically present on them (MAC Working Group 2008). Craig and Beal (2002) cautioned that translocation protocols must consider the potential for negative population effects due to ecological overlap between extant and previously absent species. Particularly small forest passerines have population densities likely at habitat saturation, the species interact aggressively and densities of some species are less on comparable islands where an ecologically similar species is present. Hence, the order of introduction may determine long-term translocation success and success may mean the difference between species survival and extinction.

METHODS

Study areas. Saipan and Aguiguan are predominantly raised coral islands, with Saipan inhab-

ited and Aguiguan uninhabited. Uninhabited Sarigan, in contrast, is the summit of a stratovolcano that last erupted ca. 12,000 years ago, although neighboring Anatahan and a nearby undersea volcano continue to erupt explosively (Brainard 2012). The climate of all islands is characterized by uniform temperatures, a December–early June dry season and a late June–November wet season. The dry season has reduced rainfall, easterly trade winds and reduced flowering and fruiting by most native trees, whereas the wet season is largely windless, has greater rainfall (Young 1989) and has greater flowering and fruiting by native trees (Craig 1996). Typhoons are frequent and exert a strong influence on the structure of natural habitats (Fosberg 1960).

Native forest on Saipan and Aguiguan is largely restricted to steep slopes with limestone-derived soils. Termed limestone forest, it is relatively xerophytic except at the highest elevations of Saipan (300–466 m), where near cloud forest conditions prevail. The forest is typically dense, with a 10–20 m canopy dominated by two widespread Indo-Pacific trees, *Pisonia grandis* and *Cynometra ramiflora*, and an understory of primarily *C. ramiflora* and *Meiogyne cylindrocarpa* (Craig 1992b). Level areas were cultivated for sugarcane (*Saccharum officinarum*) until 1945,

when they were abandoned and grew up to alien thickets of predominantly *Leucaena leucocephala* on Saipan and *Lantana camara* on Aguiguan. However, thickets near native seed sources have since been invaded by native trees (Craig 1994)—a direct consequence of seed dispersal by indigenous birds (Caves et al. 2013).

Native forest on Sarigan is largely restricted to steep, rocky slopes of the northwestern portion of the island, where species composition is similar to that on Saipan and Aguiguan, although deep ravines are often vegetated primarily by the native *Hibiscus tiliaceus*. Copses of native forest also occur at the caldera summit of the island, where they occur within a matrix of swordgrass (*Miscanthus floridus*) savannah. Less steep slopes are vegetated by initially planted coconut palms (*Cocos nucifera*), termed agriforest (Engbring et al. 1986), although these long-abandoned plantations have been invaded particularly by *Hibiscus tiliaceus*. Since my surveys there, feral ungulates have been eliminated from the island, which is allowing native forest to recover (Brainard et al. 2012).

Bird surveys. On Saipan, I performed counts in the predominantly limestone forests of the Marpi region (Fig. 1), which has the most extensive native forest remaining on the island. I surveyed on a semi-abandoned hiking trail, the



FIG. 2. *Leucaena* thickets in the vicinity of Laderan Hakmang, Saipan.



FIG. 3. Limestone forest terraces of Aguiguan.

Banadero Trail, located along the west slope of a steep escarpment known as Suicide Cliff, and on a modern hiking trail along the Laderan Tangke cliffline. I counted at these routes from October, 1990 to July, 1993, which thereby constituted three complete years of quarterly surveys. I also established in March, 1993 two routes along abandoned roads at Laderan Hakmang (Fig. 2), the site of a World War II fighter air field that had grown into a xeric mosaic of *Leucaena* thickets and meadows with scattered introduced and native trees. In addition, I counted along a route at Sabanan Fiiang, a World War II hospital site that had similarly grown to xeric *Leucaena* thickets with scattered introduced and native trees, particularly *Casuarina equisetifolia*. These sites have since been developed. A fourth route traversed a more mesic mosaic of meadows, swordgrass savannah, abandoned coffee plantations, alien thickets and copses of native trees at the highest elevations of the island's central mountain—Takpotchau. Most of this route remains intact, as do the native forest routes.

On Aguiguan (Fig. 3), which possesses more extensive native forest than does Saipan, I performed single surveys in May, 1992 in the predominantly limestone forests on the steep western slope of the island, following Engbring et al.'s (1986) transect routes 2 and 4. On Sarigan, I established a transect on the northwest portion of the island in September, 1990 that ascended from near sea level to the edge of the caldera, with agriforest along

most of its route (Fig. 4). I placed a second route through native forest copses in the caldera (Fig. 5). I made duplicate surveys at the slope transect and a single survey of the caldera transect at Sarigan.

I surveyed using the variable circular plot technique (Reynolds et al. 1980), chosen because of its utility in rough tropical terrain (Scott et al. 1986) and its well-developed theoretical underpinning that accounts for differential detectability of species (Buckland et al. 2001, Thomas et al. 2010). I surveyed 15 points each at the Saipan limestone forest routes, whereas at the more disturbed sites I surveyed 14 and 10 points at Laderan Hakmang and 17 points each at Sabanan Fiiang and Takpotchau. On Aguiguan, each route contained 16 points and on Sarigan the slope route had 20 and the caldera 10 points. At each survey point, I classified the habitat present in a 50 m diameter circle centered on the point as native forest, disturbed habitat or agriforest.

Based on the frequency with which birds provided cues, which I recorded to be almost entirely aural or aural plus visual, I established count periods of eight min/station, as did Engbring et al. (1986) in these same habitats. Similarly to the Hawaiian forest bird survey (Scott et al. 1986), points were 100 m apart, measured with a hip chain, in all forest sites except at Laderan Tangke, where I placed two stations 200 m and 300 m from neighboring stations to avoid disturbed habitat. On disturbed sites, I placed points 150 m apart to improve sampling independence in habitats where birds



FIG. 4. Agriforest at low elevations on Sarigan.

could be detected farther from a point.

At each point, I estimated the distance to each bird detected. To calibrate distance estimates, I placed colored plastic flagging at 10, 15, and 20 m intervals (the maximum distance to which it was easily visible in limestone forest) from selected census points and periodically walked from a point to distantly vocalizing birds to verify distance estimates. Surveys began at sunrise, were conducted under conditions of minimal rain and low wind, albeit higher in the dry season, and took ca. 3.5 hr to complete.

Analysis. I computed population densities with Distance 7.3 software (Thomas et al. 2010, Research Unit for Population Assessment 2020) using the protocols of Buckland et al. (2001) to select detection functions. Based on initial plots of species detection probability vs. detection distances, I grouped similar observations, often into 5–10 categories, with interval cut points placed between favored rounding distances to minimize data “heaping” and to improve robustness of density estimation. I explored the fit of detection data to six models recommended by Buckland et al. (2001): uniform/cosine, uniform/simple polynomial, half normal/cosine, half normal/hermite polynomial, hazard rate/cosine and hazard rate/simple polynomial. As also recommended by Buckland et al. (2001), I explored truncating detection data to eliminate the largest 5–10% of values, which can facilitate model fitting by eliminating outliers.

When doing so improved model fit, I employed this technique. I sought a conventional distance sampling model that yielded a smooth curve with near 100% detection probability at the left shoulder and evaluated fit by visual inspection of plotted data, with Akaike’s Information Criterion and with chi-square goodness of fit tests and computed variance empirically. Because model fitting is most effective for species with >60 distance estimations, whenever exploratory data analysis dictated that doing so was appropriate, I pooled observations in developing detection functions. Doing so was particularly valuable when estimating densities of locally small populations where local detections were insufficient for computing densities. However, I computed separate detection functions for individual habitat types.

Although a number of population surveys are available for the Mariana Islands, many have not considered adequately aspects of social behavior, variance among surveys, potential seasonal shifts in detectability or observer perception in compiling and interpreting results (e.g., Martin et al. 2008). It has long been known that such issues can have substantial impacts on results obtained (Skirvin 1981, Sauer et al 1994, Farmer et al. 2012) and renders evaluation of population trends with data from different observers questionable. Moreover, insufficient familiarity with the subtleties of vocal repertoire can lead to misidentifications and missing individuals and species on counts (Craig and Chan-



FIG. 5. Native forest copses in swordgrass savannah at caldera on Sarigan.

dran 1993).

In this study, I used my six years of field notes on social behavior and observations of banded birds to inform considerations of whether individuals detected or species clusters, i.e., social groups (Thomas et al. 2010), should be the basis of density measurement. For small passerines other than the Micronesian Myzomela (*Myzomela rubrata*), I assumed all individuals encountered at a survey station were part of a cluster, as all were generally detected within 40 m. In the case of the Micronesian Megapode (*Megapodius laparouse*) and Mariana Kingfisher (*Todiramphus albicilla*), in those instances when an individual was present > 70 m from others, I considered it not part of the cluster. Population estimates reported are of individuals/km² as based on cluster size detections and do not distinguish individuals as to sex.

For species found on surveys primarily as singing males, the sexually dimorphic Micronesian Myzomela and, based on observations on color banded (Craig 1992a) individuals, the Saipan Reed Warbler (*Acrocephalus hiwae*), I computed densities for males encountered. Moreover, as I did not observe the Mariana Fruit Dove (*Ptilinopus roseicapilla*) and White-throated Ground Dove (*Pampusana xanthonura*) to occur in social groups, I computed densities for them based on individuals encountered. In both these latter species, males and females vocalize (R. Camp pers. comm), so population estimates do not distinguish sex.

Details of behavioral and banding procedures are in Craig 1989, 1990, 1992a, 1996, 2002, Craig et al. 1993b and Craig and Beal 2002. I also reviewed my 1988 community vocalization recordings to provide additional verification of the types of vocalizations and vocal interactions typically recorded during surveys. As noted for the Mariana Islands by Linck et al. (2020), the reliance in this study on the perceptions of a single observer maximizes inter-island, habitat and seasonal comparability of results. In reporting results, where possible I also fill in knowledge gaps concerning the social organization of individual species.

Because I observed repeatedly at the same two Saipan native forest transects, these observations are repeated measures. So, I employed repeated measures analysis of variance to examine annual and seasonal patterns exhibited by these Saipan surveys. In these and other tests, I checked the fit of data to model assumptions with data plots, frequency histograms, normal Q-Q plots, residual plots, Shapiro-Wilk normality tests, Levene's homogeneity of variance tests and Mauchly's W test. When assumptions were violated, I employed data transformations to normalize data and stabilize variances. When assumptions remained poorly met, I used nonparametric tests.

To study further the structuring of these communities, I examined density in a manner related to computing community evenness but without reducing the community to a single metric—the proportionate contribution of each species to total density.

For species encountered as singing males, the Micronesian Myzomela and Saipan Reed Warbler (*Acrocephalus hiwae*), I doubled computed density values to account for females. Although doing so yields an imperfect measure in that it does not account for juveniles or unmated birds, it improves comparability of this study with others by making estimates that of total population density. For comparison, I plotted densities reported for the similarly depauperate native forest bird communities of the Mariana Island of Rota (Camp et al. 2014) and the island of Hawaii (Scott et al. 1986), the more diverse communities of the island of Grand Bahama (Emlen 1977) and the Palau Islands of Babeldaob and Peleliu (Engbring 1992), and the tropical Atlantic forest of mainland Brazil (Marsden et al. 2001). As I was one of three observers on the Palau surveys, these results are particularly comparable to those of this study. I fitted a curvilinear regression line to each data set, choosing a best fit curve based on maximizing its r^2 value and, as a comparison, computed Pielou community evenness.

Absolute densities in the Palau Islands cannot be compared directly with the results of this study, as the Palau Islands transects covered forested and non-forested habitats, thereby reducing apparent densities of forest inhabitants. Moreover, for Hawaii I computed densities based on the entire potential range of the species, thereby also reducing densities compared to portions of their range where they reached their greatest abundance.

RESULTS

Social characteristics. I encountered the majority of species as social groups during surveys—often small family groups of three to five, although birds also could be encountered as individuals. These included the Micronesian Megapode, Mariana Kingfisher, Rufous Fantail (*Rhipidura rufifrons*), Micronesian Starling (*Aplonis opaca*), Golden White-eye (*Cleptornis marchei*) and particularly the Bridled White-eye (*Zosterops conspillatus*), which exhibited complex social structure involving family groups merging into larger flocks and then dispersing back into smaller groups (Craig 2002). Based on observations of banded individuals, the Rufous Fantail and Golden White-eye defended all-purpose territories, whereas the others occupied home ranges. Moreover, while performing earlier behavioral studies (e.g., Craig and Beal 2002), I repeatedly observed the Mariana Fruit Dove to fly >100 m above the forest canopy, indicating that it occupied a home range rather than an all-purpose territory. Similarly, repeated observations of extended flights of at least 300 m above the forest canopy by the White-throated Ground Dove indicated that it also occupied a home range. The primarily thicket-inhabiting and loudly vocal Saipan Reed Warbler

was all-purpose territorial (Craig 1992a) and detectable from forest transects, although it occasionally entered interior forest as well.

On Saipan, the Micronesian Myzomela occurred primarily as individuals in native forest. However, in the denser populations of Sarigan agri-forest and Aguiguan native forests, I generally found three to four individuals/ point. Most were males defending all-purpose territories, although some were family groups and others appeared to be individuals converging on abundant nectar sources, so population estimates from these islands may be somewhat inflated. For comparison, when in Program Distance I performed experimental computations of Rufous Fantail and Golden White-eye density using individuals vs. clusters as the basis of measurement, using individuals increased density estimates by about a third over that for clusters.

Although I occasionally detected the White Tern (*Gygis alba*) and Mariana Swiftlet (*Aerodramus bartschi*) above the forest canopy on surveys and I observed both to nest in forest, neither used forest habitat and, thus, I did not consider them to be part of the forest community. In addition, although I made three Saipan detections of the feral Red Junglefowl (*Gallus gallus*) during surveys, including finding an active nest, its rarity away from human habitation made a meaningful estimate of forest populations impossible. However, birds I encountered were indistinguishable in appearance and behavior from forest birds that I observed in Indonesia, so they functioned as wild birds. On Sarigan, a single migrant Amur Falcon (*Falco amurensis*) appeared briefly at a native forest copse during surveys, although I did not include it in data analysis as it was not a resident. The introduced Island Collared Dove (*Streptopelia bitorquata*), occurred infrequently at the edge of forest transects but could be detected from them and on occasion entered interior forest, so I report its densities here.

Annual and seasonal comparisons. For duplicated Saipan surveys in native forest, examination of the sum of densities computed for all species provided an index of total community population density. It demonstrated no significant multivariate or univariate within- or between-subject effects among transects, seasons or years (Table 1). Similarly, for species that could be examined parametrically—the Mariana Fruit Dove, Mariana Kingfisher, Bridled White-eye, Golden White-eye, Rufous Fantail and Micronesian Starling—few strong density differences occurred among transects, seasons or years (Table 1). The Bridled White-eye showed a significant multivariate ($F = 9.00$, $df = 2,3$, $P = 0.05$) and within-subject contrast ($F = 22.69$, $df = 1,4$, $P < 0.01$) year x season interaction. Lower 1990–1991 wet season counts were principally responsible for this difference (Table 1). Moreover,

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TABLE 1. Annual and seasonal comparisons of forest bird population densities on Saipan.

	1990—1991		1991—1992		1992—1993	
	Wet season	Dry season	Wet season	Dry season	Wet season	Dry season
<i>n</i>	4	4	4	4	4	4
Total density						
Mean	8630.0	10515.8	11872.5	11280.0	11919.6	10775.1
SD	2127.9	696.5	868.9	2052.2	905.5	1510.0
Micronesian Megapode (birds/km ²)						
Mean	27.6	15.5	15.7	24.8	34.0	30.9
SD	23.6	15.6	15.5	22.5	15.6	12.4
Mariana Fruit Dove (birds/km ²)						
Mean	37.8	46.2	53.6	31.2	32.3	31.2
SD	13.8	11.3	34.2	20.8	24.7	11.5
White-throated Ground Dove (birds/km ²)						
Mean	103.8	74.5	82.4	104.3	89.4	74.5
SD	71.6	57.0	65.5	89.4	100.3	51.6
Philippine Collared-dove (birds/km ²)						
Mean	5.5	5.6	6.8	5.6	10.1	8.9
SD	4.3	8.5	7.7	4.3	17.3	7.3
Mariana Kingfisher (birds/km ²)						
Mean	46.6	35.0	43.1	42.3	38.2	44.4
SD	13.6	6.5	9.5	11.2	5.4	13.5
Rufous Fantail (birds/km ²)						
Mean	1557.4	1538.7	1883.1	1778.7	1776.8	1681.7
SD	579.0	198.4	175.6	175.5	280.0	170.2
Micronesian Myzomela (males/km ²)						
Mean	38.5	166.9	171.5	205.4	141.2	475.0
SD	49.2	87.7	73.2	72.6	87.7	306.3
Bridled White-eye (birds/km ²)						
Mean	4369.1	6515.6	6858.6	6420.2	6852.6	5971.8
SD	1515.5	555.6	383.3	2008.8	798.3	682.6
Golden White-eye (birds/km ²)						
Mean	2073.1	1845.4	2325.5	2322.6	2661.2	2051.8
SD	478.9	403.7	718.6	307.9	337.4	477.2
Saipan Reed-warbler (males/km ²)						
Mean	11.5	9.9	10.0	16.5	13.2	13.2
SD	19.0	11.4	8.5	19.8	16.2	10.8
Micronesian Starling (birds/km ²)						
Mean	358.9	262.5	422.1	328.5	270.5	391.7
SD	127.4	42.9	110.1	63.2	177.2	159.0

the Mariana Kingfisher differed in density between transects ($F = 8.48$, $df = 1,4$, $P = 0.04$), with densities averaging greater at Laderan Tangke. The Mariana Fruit Dove also showed a multivariate ($F = 27.54$, $df = 2,3$, $P = 0.01$) and within-subject contrast ($F = 49.03$, $df = 1,4$, $P < 0.01$) year x transect interaction, with Laderan Tangke populations declining each year whereas Banadero Trail's were more stable. Nonparametric examination of the remaining species also showed little tendency for populations to vary seasonally. Only the Micronesian Myzomela showed a significant trend (Wilcoxon $Z = -2.60$, $n = 12$, $P < 0.01$), with birds far more abundant in the dry season in two of the three years (Table 1).

As with population densities, there was generally little difference in detectability between wet and dry seasons within native forest (Table 2). Despite my failure to find such differences in native forest, mean detection distance increased from native forest to disturbed habitats in all instances. Size of social groups showed limited differences between seasons but more differences among habitats (Table 3). The Bridled White-eye occurred in larger flocks and the Golden White-eye and Rufous Fantail in smaller groups in disturbed habitats. In agriforest, the Micronesian Starling tended to occur in smaller groups, whereas the Micronesian Megapode occurred in larger groups. My nine observations of megapodes in Sarigan native forest had a mean group size of 1.4—similar to that of native forest populations on Saipan, so the difference appeared to be a function of habitat rather than simply Sarigan having a larger total megapode population. Reasons for this habitat relationship are unclear, however, and warrant further study. Only the Mariana Kingfisher did not differ appreciably among habitats.

Although making inter-island comparisons of long-term repeated measure Saipan data with brief duration independent measures from other islands was statistically problematic, examination of computed densities revealed several substantial differences (Table 4). Most notably, total populations on Sarigan were a fraction of those on other islands even when comparing the same habitat and season. Only the Micronesian Myzomela and Micronesian Megapode had much higher population densities on Sarigan, although Micronesian Myzomela densities within Sarigan native forest were still similar to those on Saipan. Aguiguan populations were at the high end of densities found for dry season Saipan native forest, primarily because of high Micronesian Myzomela densities found there, although Golden White-eye and Mariana Fruit Dove densities also averaged greater. Notably, while conducting banding in the heavily flowering and fruiting *Lantana* thickets on Aguiguan, I caught multiple adult male Micronesian Myzomelas at a single loca-

tion, suggesting that territoriality broke down around the dense nectar resource in the thickets.

Similarly, although performing statistical comparisons were also problematic for long-term repeated measures of two native forest transects vs. single independent measures from four disturbed habitat transects on Saipan, substantial differences existed between the two habitats. For most species, densities in native forest were multiple times greater than in disturbed habitat. Total density in disturbed habitat was roughly half that of native forest and only species that were not forest specialists—the Island Collared Dove and Saipan Reed Warbler—had densities greater in disturbed habitat (Table 4).

Community comparisons. Examination of patterns of density among forest bird communities showed much higher densities on all Mariana islands compared with other communities although Hawaiian species at their centers of density (Scott et al. 1986) were comparable in density to Marianas species (Table 5). Moreover, although likely part of a larger continuum, when I considered proportionate contribution to community density, two groups of trends tended to emerge. Pacific islands with depauperate faunas all showed a pattern where the most abundant three species accounted for 83–93% of total density. In contrast, more diverse island communities and particularly mainland tropical communities showed individuals more evenly distributed among species (Fig. 6).

DISCUSSION

Although in previous investigations I uncovered evidence for seasonal changes in breeding activity among some species (Craig 1992a, 1996), this generally did not translate into annual or seasonal population shifts in native forest. The dip in Bridled White-eye densities occurred only in a single season of a single year, so did not appear to be a general trend. The few other species differences noted related to location rather than season. Only the Micronesian Myzomela showed a more consistent, strong dry season increase in density even though I had previously found no evidence for it having a breeding peak at this season. Foraging observations demonstrated that during the dry season, the species fed on nectar particularly from *Erythrina* trees and males even appeared to defend individual trees (Craig and Beal 2002). This large tree species with large flowers, the eighth most important tree in native forests in the 1990s (Craig 1992b), dropped its leaves and flowered heavily during the dry season at a time when other species flowered less. Hence, the population increase may be explained via the establishment of additional dry season territories, as most birds encountered were singing males. However, as noted, non-

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TABLE 2. Seasonal and habitat detection distances (m) of Mariana Island forest bird species.

	Wet season		Dry season		Kruskal-Wallis χ^2
	Agriforest	Native forest	Native forest	Disturbed habitat	
Micronesian Megapode					
Mean	35.3	49.7	54.0		2.8
SD	22.8	38.0	31.4		$P = 0.24$
<i>n</i>	17	36	26		
Mariana Fruit Dove					
Mean		62.4	68.2	156.8	38.8
SD		30.2	33.9	96.0	$P < 0.01$
<i>n</i>		107	167	46	
White-throated Ground Dove					
Mean		27.2	21.6		603.5
SD		17.5	13.7		$P = 0.16$
<i>n</i>		40	37		
Philippine Collared-dove					
Mean		58.5	55.2	89.6	5.1
SD		21.6	33.4	60.2	$P = 0.08$
<i>n</i>		20	29	23	
Mariana Kingfisher					
Mean	44.3	67.2	65.0	89.7	26.2
SD	18.9	25.1	26.9	45.4	$P < 0.01$
<i>n</i>	17	129	145	44	
Rufous Fantail					
Mean		17.9	14.9	25.3	64.4
SD		7.2	5.8	11.5	$P < 0.01$
<i>n</i>		178	213	56	
Micronesian Myzomela					
Mean	20.5	21.9	15.3	28.0	53.2
SD	11.9	10.8	7.3	12.6	$P < 0.01$
<i>n</i>	126	39	147	55	
Bridled White-eye					
Mean		15.4	14.3	24.7	80.1
SD		4.8	5.2	8.6	$P < 0.01$
<i>n</i>		180	212	58	
Golden White-eye					
Mean		14.9	13.6	24.0	38.6
SD		6.3	5.7	10.7	$P < 0.01$
<i>n</i>		167	190	35	
Saipan Reed-warbler					
Mean		44.8	47.5	65.1	5.2
SD		22.0	19.4	40.2	$P = 0.08$
<i>n</i>		21	24	35	
Micronesian Starling					
Mean	21.3	25.7	26.2	52.6	19.8
SD	10.5	16.3	14.5	28.7	$P < 0.01$
<i>n</i>	12	118	122	20	

TABLE 3. Seasonal and habitat comparisons of social group size in Mariana Island bird species.

	Wet season		Dry season		Kruskal-Wallis χ^2
	Agriforest	Native forest	Native forest	Disturbed habitat	
Micronesian Megapode					
Mean	1.8	1.3	1.2		9.1
SD	0.9	0.5	0.4		$P = 0.01$
<i>n</i>	17	36	26		
Mariana Kingfisher					
Mean	1.5	1.5	2.5	1.5	1.0
SD	0.7	0.6	0.9	0.7	$P = 0.81$
<i>n</i>	17	129	213	44	
Rufous Fantail					
Mean		2.7	2.5	2.2	9.5
SD		1.1	0.9	0.8	$P < 0.01$
<i>n</i>		178	332	56	
Bridled White-eye					
Mean		8.2	8.4	10.1	12.8
SD		4.3	4.0	3.7	$P < 0.01$
<i>n</i>		180	212	58	
Golden White-eye					
Mean		2.6	2.4	1.9	13.4
SD		1.0	1.0	0.9	$P < 0.01$
<i>n</i>		167	190	35	
Micronesian Starling					
Mean	1.1	1.4	1.4	1.5	5.4
SD	0.3	0.6	0.6	0.7	$P = 0.15$
<i>n</i>	12	118	122	20	

territorial birds may converge on abundant nectar sources (Craig 1996), which could further drive a seasonal population increase. This relationship is presently threatened by the demise of *Erythrina* due to invasion of the Marianas by an introduced gall wasp (*Quadrastichus erythrinae*; Rubinoff et al. 2010). With the exception of the Micronesian Myzomela, then, there is no evidence to support the hypothesis of seasonal population shifts.

The generally much lower population densities of species in disturbed habitats compared with native forest provides strong evidence that these environments are inferior for most species. This finding does not, therefore, support the hypothesis that the extent of altered habitat permits populations in native forest to be greater than they otherwise would be. Furthermore, this hypothesis is inconsistent with the expectation that the forest bird species co-evolved for millennia with the native forest environment and are best adapted to it. Linck et al. (2020) also expressed skepticism concerning this hypothesis. Only marginal forest inhabitants showed denser population in disturbed habitats and the Micronesian Myzomela, the only forest species appearing to benefit from human activity, showed densities in them comparable to those of dry season native forest. The prevalence of heavily flowering coconut palms in disturbed habitats likely explains much of this species' population size there, as birds

typically occupied these trees in such places.

The lack of a seasonal difference in native forest detectability further strengthens the case for there being little seasonal shift occurring in population densities. Only the Micronesian Myzomela showed a substantial drop in mean detection distance from the wet to dry season, which is likely related to its increased dry season density. In contrast, most species showed a clear increase in detection distance from native forest to disturbed habitat. This increase appears to reflect in part the ability to detect individuals at greater distances in the more stunted, albeit still dense thicket habitats, as well as to the much less dense populations of most species in disturbed habitats. Evidence for shifts in size of social groups also appears related primarily to habitat rather than to seasonal differences. Hence, the hypothesis that social group size differs seasonally as a consequence of differential breeding activity is also not supported.

In the case of the most gregarious of flocking species, the Bridled White-eye, my measures of a mean flock size of about eight provide a baseline against which to compare newer measures. The maximum flock size I observed was at least 50. As populations declined on Guam, flock size appeared to decline steadily (Craig 1990), so measures of mean and maximum flock size could provide an early indicator of the consequences of Brown Tree

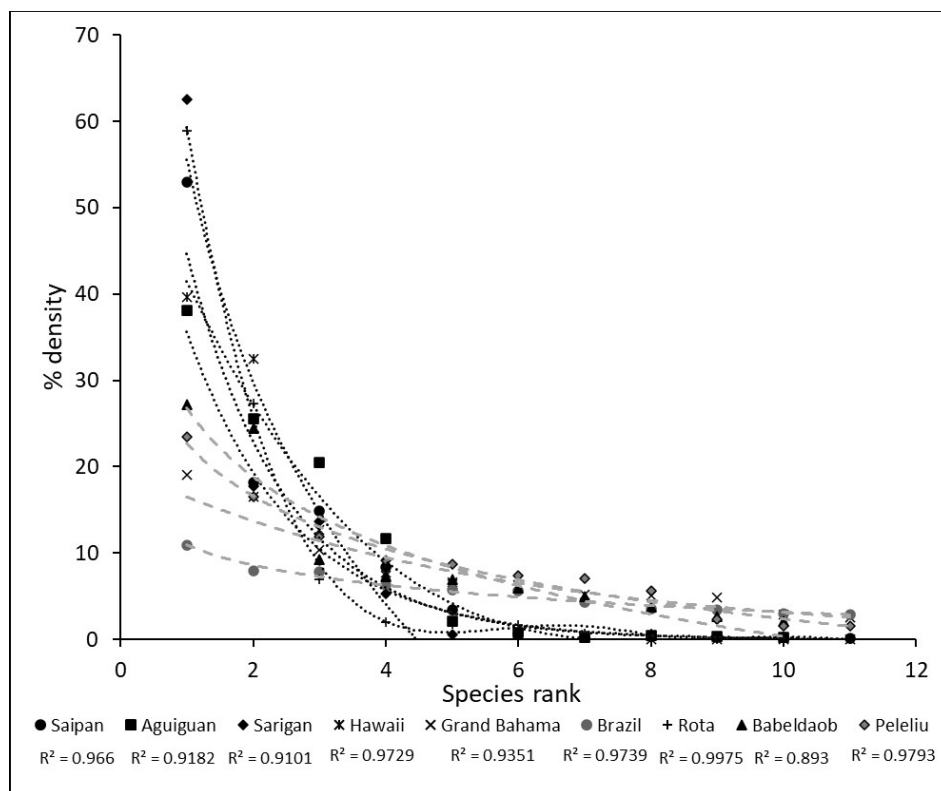


FIG. 6. Percent population density for each community member at eight tropical islands and one tropical mainland site, with fitted curvilinear regression lines. Species counts are truncated on the graph to 11 species.

Snake establishment. For comparison, on the Mariana Island of Rota, where the Rota White-eye (*Z. rotensis*) is rare, in 1990-1992 Craig and Taisacan (1994) typically found two to three birds together and a maximum flock size of 10. Into the 1960s, this species was far more abundant and widespread on this island (Engbring et al 1986, S. Taisacan pers. comm.), and flock size was likely then greater.

Inter-island comparisons of avifaunas showed that the population densities of Saipan and Aguiguan native forests were generally similar. This appeared to be a consequence of their similar bird communities (Craig and Chandran 1993) and native forest habitats (Chandran et al. 1993). Despite this, several species occurred more densely, particularly the Micronesian Myzomela. This latter difference was almost certainly related to an abundant nectar source on Aguiguan, *Lantana*, for this principally nectarivores species (Craig and Beal 2002). Similarly, its density on Sarigan was related to the near canopy monoculture of coconut palms at lower elevations. The high density there occurred because the tree's tubular flowers and heavy flowering provided an abundant nectar source. However, the Micronesian Myzomela did not expand its numbers in native forest beyond that found on Saipan, as the habitat was similar on both islands.

Despite the comparatively higher densities of the Micronesian Myzomela and Micronesian Megapode on Sarigan, the most notable difference encountered among the islands was the dramatically lower total density of birds on Sarigan. This could be because of the presence of feral ungulates on the island, although feral ungulates were also present on Aguiguan, often called Goat Island, where bird populations were high. Moreover, Sarigan's remaining species' densities were generally similar to those found on the other Mariana islands, where Craig (1996) has argued that species' populations are likely at carrying capacity. The low community density even in native forest suggests instead that niches are unfilled and the few extant species are unable to expand niches sufficiently to make use of all available resources. Further behavioral study on individual Sarigan species could help to verify that this is the case.

The evidence of unfilled niches indicates that species translocations to Sarigan are likely to succeed. Indeed, translocation of Bridled and Golden White-eyes to Sarigan has been successful and, notably, the Mariana Fruit Dove has colonized the island on its own (Radley 2012). Support for the presence of unfilled niches will be provided by future population surveys that show an increase in

TABLE 4. Island, seasonal and habitat comparisons of Mariana Island forest bird densities.

	Sarigan		Aguiguan	Saipan		
	Wet season Agriforest	Native forest	Dry season Native forest	Wet season Native forest	Dry season Native forest Disturbed habitat	
<i>n</i>	2	1	2	12	12	4
Total density						
Mean	2917.7	1157.7	13259.3	10807.3	10857	4640.2
SD				2061.7	1418.6	763
Micronesian Megapode (birds/km ²)						
Mean	277.1	299.6	68.9	25.8	23.7	
SD				18.6	17.0	
Mariana Fruit Dove (birds/km ²)						
Mean			127.7	41.2	36.2	11.7
SD				25.0	15.6	5.4
White-throated Ground Dove (birds/km ²)						
Mean		89.4	41.9	91.9	84.4	32.0
SD				73.4	63.3	63.8
Philippine Collared-dove (birds/km ²)						
Mean			23	7.4	6.7	15.2
SD				10.3	6.4	12.7
Mariana Kingfisher (birds/km ²)						
Mean	28.8	10.4	28.6	42.6	40.6	28.1
SD				9.8	10.6	18.2
Rufous Fantail (birds/km ²)						
Mean			1777.4	1739.1	1666.4	638.0
SD				375.9	194.0	122.0
Micronesian Myzomela (males/km ²)						
Mean	2397.9	231.1	1949.8	117.1	282.4	259.5
SD				88.0	222.8	64.2
Bridled White-eye (birds/km ²)						
Mean			5805.9	6026.8	6302.5	3189.2
SD				1529.4	1171.8	706.5
Golden White-eye (birds/km ²)						
Mean			3121.9	2353.3	2073.3	366.0
SD				545.6	417.2	70.5
Saipan Reed-warbler (males/km ²)						
Mean				11.6	13.2	52.5
SD				13.8	13.5	26.1
Micronesian Starling (birds/km ²)						
Mean	213.9	527.2	314.3	350.5	327.6	48.3
SD				143.2	107.3	47.3

total community density. Fortunately, translocation of the Bridled White-eye occurred first, as it has high ecological overlap with but is socially subordinate to the Golden White-eye (Craig 1990, Craig and Beal 2002). An earlier introduction of the Golden White-eye could conceivably have interfered with successful establishment of the Bridled White-eye. The Rufous Fantail, which benefits from white-eyes by following behind them and capturing insects that they flush (Craig 1996), should be a later choice for translocation.

In examining patterns of density within the native forest bird communities of the Mariana Islands, comparison with the Palau Islands is instructive. On the Palau Islands, there are two species of small flocking white-eyes that behave much like the Bridled White-eye as well as a larger species. All are ecologically similar in that they engage in a variety of foliage gleaning and probing behaviors, with the smaller two species even foraging simultaneously in the same tree (pers. obs.). Prehistorically, two small and one larger species of white-eye also appear to have existed on multiple Mariana Islands (Steadman 1999), with the ecologically similar (Craig and Taisacan 1994) extant Rota species considered to be separate from the Bridled White-eye (Slikas et al. 2000). Similarly, there are two species of kingfishers in Palau and, based on the findings of Steadman (1999), two extant species also once likely occurred on multiple Mariana Islands. Moreover, there were once three species of flycatchers in the Mariana Islands as well as four species of doves, a parrot-finch (*Erythrura* new species), a parrot (Psittacidae new species) and three species of rails, much as presently reside in the Palau Islands (Steadman 1999).

On the Mariana Island of Tinian, where I made qualitative and limited quantitative observations, a second species of flycatcher, the Tinian Monarch (*Monarcha takatsukasae*) also occurs, which is socially dominant to the Rufous Fantail. I observed the Rufous Fantail appear to have its foraging space largely reduced to forest understory compared with birds on Saipan (Craig and Beal 2002). Moreover, its population, as computed by Engbring et al. (1986) using the same observers at the same time on both islands, was on Tinian 19% less than on Saipan. Similarly, populations of the Bridled White-eye on Tinian, where the socially dominant Golden White-eye is absent, averaged 24% greater than on Saipan. On Saipan, the Bridled White-eye is largely restricted to foraging in the forest canopy (Craig and Beal 2002), whereas on Tinian it appears less restricted (pers. obs.). Hence, we may expect that the density relationships among Mariana forest species once resembled in evenness those of the Palau Islands because particularly ecologically similar additional species compete for resources in ways that reduce niche breadth and, perhaps, populations.

The wholesale loss of species in the Marianas has, then, led to communities in which three ecologically versatile species (Craig 1990, Craig and Beal 2002) account for the vast majority of individuals in the bird community.

ACKNOWLEDGEMENTS

This research was funded by University of Connecticut Research Foundation grant 1171-000-22-00119-35-156/168 and Pittman-Robertson Federal aid to wildlife, Boy Scouts of America, Carmen Safeway Meitetsu, CNMI Emergency Operations Center, Joeten Enterprises, Mobil Oil Corporation, Pacific Islands Aviation, Payless Supermarket, Radio Com Corporation, Saipan Ice Company, Shell Marianas and Townhouse Corporation. B. Lussier, R. Chandran, H. Sabino, A. Ellis and R. Kaipat assisted with aspects of the field work and A. McPhetres, president of Northern Marianas College, enthusiastically supported this and other studies in the Marianas. R. Camp and D. Pratt provided commentary on the original draft of the ms. Contribution 29 of Bird Conservation Research, Inc.

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TABLE 5. Sorted densities (birds/km²) and Pielou evenness calculations for tropical forest bird species.

	Saipan	Aguiguan	Rota	Sarigan	Hawaii	Babeldaob	Peleliu	Grand Bahama	Brazil
Evenness	0.57	0.64	0.55	0.66	0.54	0.76	0.77	0.85	0.88
Species	5971.8	5805.9	1404.3	1054.4	331.3	416.0	664.0	113.5	164.0
density	2051.8	3899.6	651.4	299.6	271.4	375.0	468.0	98.5	119.0
	1681.7	3121.9	165.7	231.1	106.2	142.0	337.0	61.7	118.0
	950.0	1777.4	46.7	89.4	64.7	111.0	261.0	44.4	94.3
	391.7	314.3	41.7	10.4	53.2	107.0	247.0	39.8	86.0
	74.5	127.7	39.7		4.3	91.0	209.0	37.7	84.3
	44.4	68.9	17.4		3.9	76.0	201.0	31.0	64.0
	31.2	46.0	17.2		0.5	57.0	159.0	30.5	52.3
	30.9	41.9			0.5	41.0	67.0	28.7	50.8
	26.4	28.6			0.1	33.0	45.0	17.0	44.6
	17.9				0.1	31.0	44.0	15.2	43.8
					>0.1	28.0	38.0	14.1	41.9
					>0.1	9.0	32.0	11.5	41.3
					>0.1	6.0	30.0	11.0	40.8
						5.0	14.0	7.6	40.4
						3.0	9.0	4.8	36.9
						1.0	4.0	4.2	35.4
							3.0	2.8	34.3
							2.0	2.0	33.5
							1.0		27.9
									26.5
									23.6
									20.9
									3.4
									2.3
									13.1
									3.1
									9.7
									12.4
									9.7
									11.4
									5.5
									13.0
									15.3
									10.9
									0.7
									4.7
									2.9
									13.4
									9.7
									17.5
									17.0

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