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DISTRIBUTION, RELATIVE ABUNDANCE, AND HABITAT RELATIONSHIPS OF LANDBIRDS IN THE VAVA`U GROUP, KINGDOM OF TONGA[1]

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Abstract. We assessed the distribution, relative abundance, and habitat preferences of the 12 indigenous, resident species of landbirds that survive in the Vava`u Group, Kingdom of Tonga. We surveyed 16 islands, 10 of which are previously unmentioned in ornithological literature. The islands vary in land area (0.02–96 km$^2$), habitat composition, elevation (20–215 m), and distance (0–10.1 km) from the largest island of `Uta Vava`u. We conducted point counts along transects on 14 of the islands, and placed each count location into one of five habitat categories. Of the 11 species of landbirds that are widespread and at least locally common, 7 (Purple-capped Fruit-Dove *Ptilinopus porphyraceus,* Pacific Pigeon *Ducula pacifica,* Common Barn-Owl *Tyto alba,* White-rumped Swiftlet *Collocalia spodiopygia,* Collared Kingfisher *Halcyon chloris,* Polynesian Triller *Lalage maculosa,* Polynesian Starling *Aplonis tabuensis*) certainly or probably occur on each of the 16 islands. One species (West Polynesian Ground-Dove *Gallicolumba stairii*) is extremely rare (one small population on one island). Three species that we did not record (Many-colored Fruit-Dove *Ptilinopus perousii,* Blue-crowned Lorikeet *Vini australis,* Fiji Shrikebill *Clytorhynchus vitiensis*) probably have been extirpated from Vava`u. The species richness and relative abundance of landbirds on islands in Vava`u are affected more by deforestation and other human activities than by island area, elevation, or isolation.

Key words: endangered species, forest birds, island biogeography, Tonga.

INTRODUCTION

The Kingdom of Tonga is part of the West Polynesian avifaunal region that also comprises Niue, Samoa, Wallis and Futuna, Fiji, and Rotuma (Watling 1982). The extant, indigenous landbirds of Tonga represent 17 genera (none endemic) and 18 species (two endemic). Individual Tongan islands > 10 km^2 sustain 10–13 species of landbirds today, whereas such islands each supported at least 27 species of landbirds when humans arrived about 3,000 years ago (Steadman 1993, 1995, 1998).

Based primarily upon transect surveys, we assess the distribution, relative abundance, and habitat relationships of native landbirds in the Vava`u Group, Kingdom of Tonga. The only other published transect surveys of Tongan birds are those conducted by Steadman (1998) in the Ha`apai Group in 1995 and 1996. Elsewhere in West Polynesia, transect surveys of landbirds have been conducted in American Samoa (Amerson et al. 1982, Engbring and Ramsey 1989, Freifeld 1998) and Western Samoa (Bellingham and Davis 1988, Lovegrove et al. 1992, Park et al. 1992). Another survey in Western Samoa by Evans et al. (1992) was based on sightings only and thus is less useful than sight/sound surveys in quantifying relative abundance. Mist-net surveys have been done on the Tongan island of Late by Rinke (1991), although capture data from mist-nets may not be a reliable indicator of the relative abundance of birds (Remsen and Good 1996). Surveys such as ours provide a first look at the incidence and abundance of landbirds in various habitats. Using similar methods on a regular basis and ideally throughout the year, these surveys are an efficient way to monitor bird populations among habitats that differ in degree of human disturbance.

Ornithological exploration of Vava`u by non-Tongans began with four pencil drawings of

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birds from the expedition of Alejandro Malaspina in 1793 (Sotos Serrano 1982), currently under study by S. L. Olson. E. H. Layard visited `Uta Vava`u in the early 1870s and collected specimens now in the British Museum (Natural History) (Layard 1876). C. H. Townsend collected birds on `Uta Vava`u on 4–5 December 1899 (Townsend and Wetmore 1919). The Whitney South Seas Expedition (WSSE) visited Vava`u in August 1925, yielding the first records of birds from several islands other than `Uta Vava`u. No comprehensive list of species and islands was ever published based on the WSSE data.

Studies of birds in Vava`u since 1925 have been based primarily on sight/sound records. The birds of Vava`u are treated in a general manner in regional books such as duPont (1976), Watling (1982), and Pratt et al. (1987). In spite of accounts of selected species on certain islands (Gill 1988, 1990, Rinke et al. 1992), meaningful lists of species (sensu Remsen 1994) were not available before our work for any individual island in Vava`u, nor had the relative abundances of any species been estimated. Ten of the 16 islands we visited have not been reported previously in the ornithological literature.

METHODS

STUDY AREA

The Vava`u Group is the northernmost of three main clusters of islands in the Kingdom of Tonga (Fig. 1), which is located east of Fiji and southwest of Samoa. The volcanic islands of Late and Fonualei lie to the west and north and are separated from Vava`u by deep water. Vava`u consists of 58 raised limestone islands on a single submarine platform sloping gently to the south, so that most emergent land is on the north side of the platform (Fig. 2). Lowered sea levels during the late Pleistocene glacial interval probably united all or nearly all of these islands into one island > 300 km^2 in land area. By far the largest island in Vava`u is `Uta Vava`u (Table 1). Eleven other islands in Vava`u have land areas > 1 km^2, five of which we surveyed for birds.

The only long-term climate and weather data for Vava`u are from `Uta Vava`u (Thompson 1986), where the mean daily minimum and maximum temperatures range from 23.5°C and 30.2°C, respectively, in February to 20.0°C and 26.6°C, respectively, in August. Sixty-seven percent of the 2,312 mm mean annual rainfall occurs from November through April. The wettest months are March (364 mm, range 126–799) and January (285 mm, range 50–1,009), and the driest are June (105 mm, range 9–393) and August (116 mm, range 12–273). Vava`u lies near the northern limit of the South Pacific trade wind zone, with northeast to southeast winds prevailing about 60–70% of the time, regardless of season.

The human population of Vava`u was about 16,000 in 1993 (Christopher 1994). Archeological sites on `Eua and in the Ha`apai Group of Tonga indicate continuous human occupation for the past 2,800–3,000 years (Burley 1994, Dickinson et al. 1994, Burley et al. 1995). One consequence of this human occupation is the loss of most indigenous species of birds (Steadman 1993, 1995, 1997a). A similar situation is likely to have taken place in Vava`u, although no archeological excavations have taken place there (Davidson 1971).

Volcanic eruptions of Late and Fonualei during the Holocene (last 10,000 years) covered the islands of Vava`u with tephra deposits that have weathered into rich soils suitable for cultivation of food plants. The vegetation on most islands today is thus a mosaic of mature forests (typically covering only the steep land between the limestone terraces), successional or disturbed forests, and active (open) or abandoned (wooded) agricultural plantations. In the absence of human influence, mature forests would be the dominant vegetation on each island we surveyed.

HABITAT CATEGORIES

We divided the terrestrial habitats of Vava`u into five categories: village, open plantation, wooded plantation/early successional forest, submature/disturbed mature forest, and mature forest (Table 2).

1. Village refers to any human habitation site. These areas are devoid or nearly so of native trees or shrubs except coconuts (*Cocos nucifera*) but have scattered non-native trees. There is no regeneration of native vegetation. An irregular grid of dirt roads and paths lies among the houses and other buildings. Non-native vertebrates including dogs, pigs, rats, and chickens are abundant.

2. Open Plantation refers to active agricultural

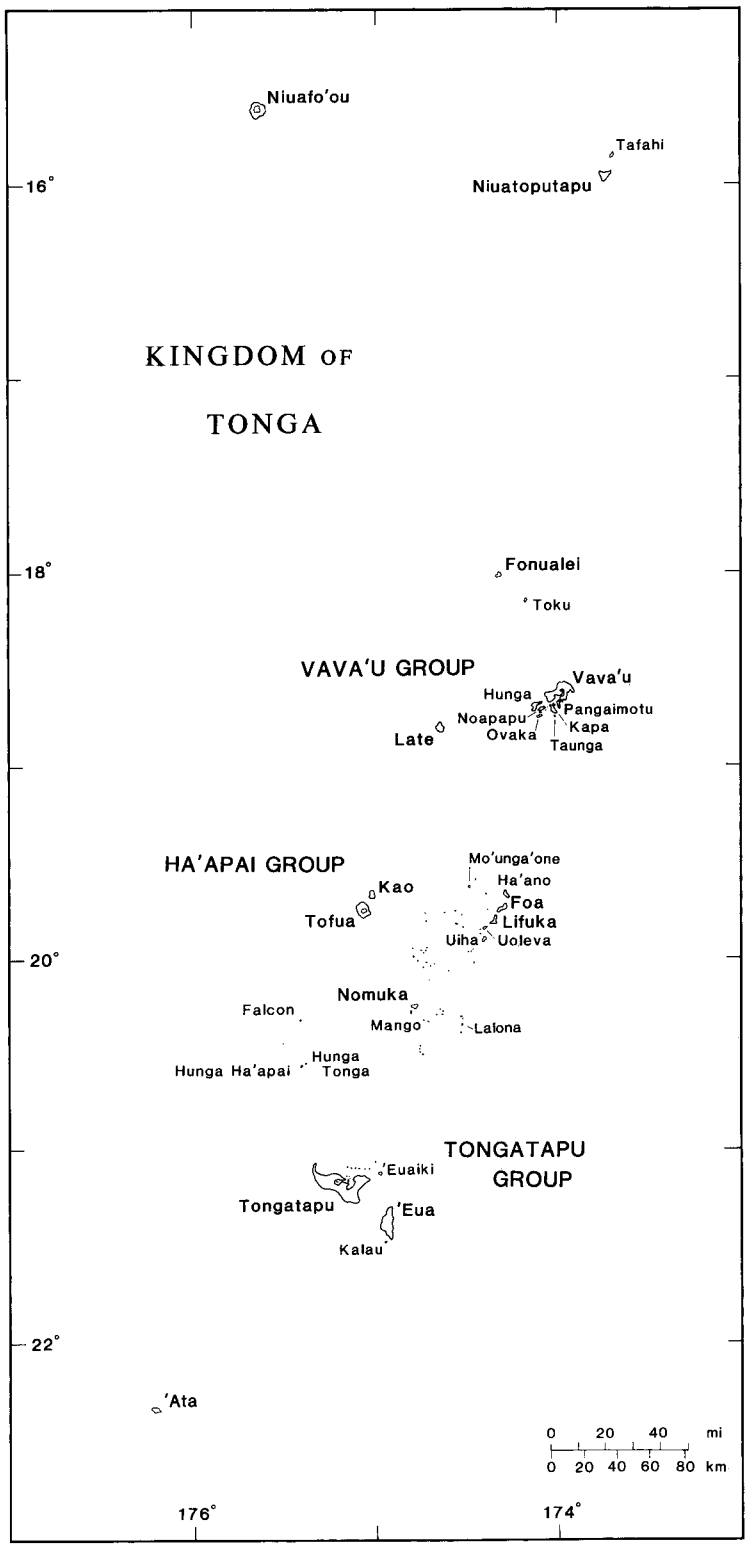

FIGURE 1. The Kingdom of Tonga.

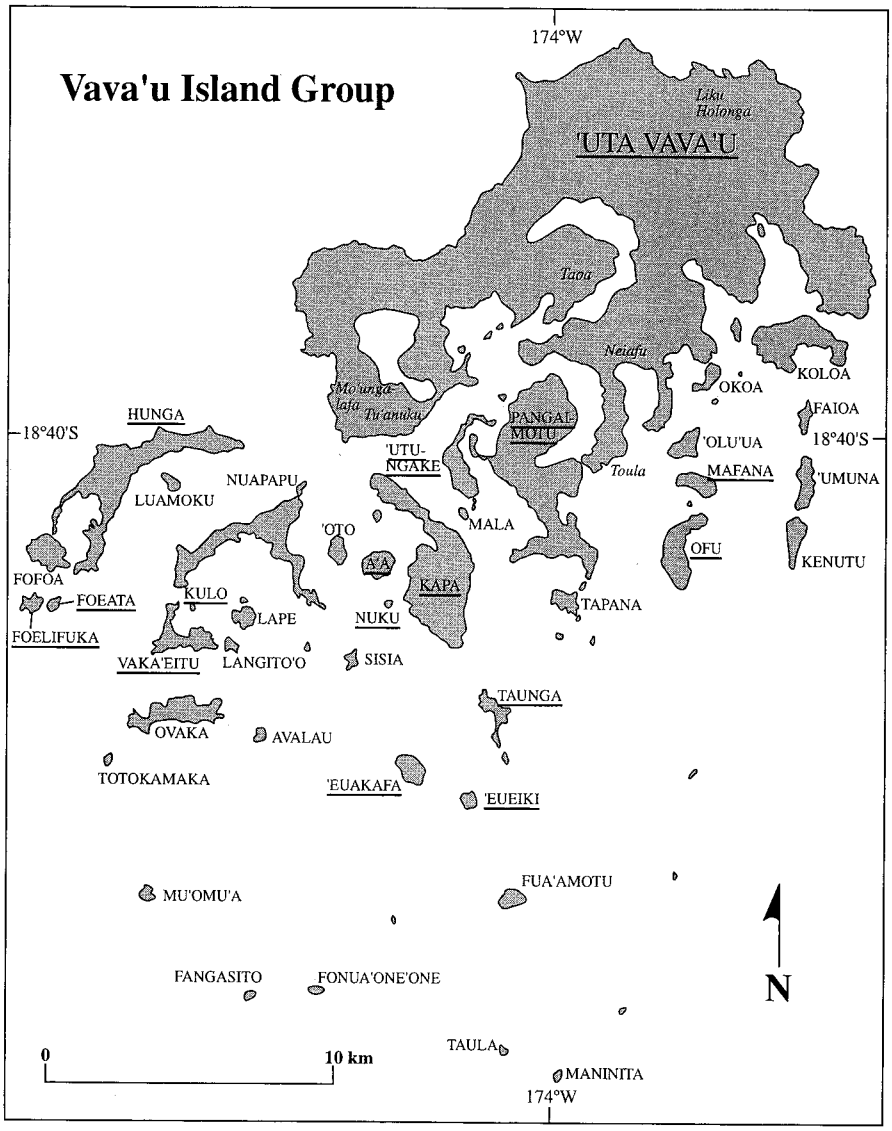

FIGURE 2. Vava`u Group, Tonga. Islands surveyed are underlined.

plots. Crops in Vava`u are usually grown beneath an overstory of coconut trees. Most of the cultivars are species introduced or managed prehistorically in West Polynesia, such as breadfruit *Artocarpus altilis,* paper mulberry *Broussonetia papyrifera,* Indian mulberry *Morinda citrifolia,* kava *Piper methysticum,* Tahitian chestnut *Inocarpus fagifer,* sweet potato *Ipomoea batatas,* ti *Cordyline fruticosa,* yams *Dioscorea* spp., sugar cane *Saccharum officinarum,* kape *Alocasia macrorrhiza,* taro *Colocasia esculenta,* pandanus *Pandanus* spp., and bananas *Eumusa* spp., *Australimusa* spp. (sequence and nomenclature follow Kirch 1994). Modern crops also include species introduced to Polynesia within the past 200 years, such as mango *Mangifera indica,* citrus *Citrus* spp., manioc *Manihot esculenta,* papaya *Carica papaya,* pineapple *Ananas comosus,* and tannia taro *Xanthosoma sagittifolium.* Woody but weedy exotics include *Adenanthera pavonina* and *Mimosa pudica.* Coconut, pandanus, and Indian mulberry are indigenous to Ton-

TABLE 1. Summary of characteristics of islands surveyed. Areas are rounded to the nearest 0.01 km², elevations rounded to the nearest 5 m, and distances rounded to the nearest 0.1 km. * Transect surveys were not conducted on Nuku or Kulo, although habitat assessments and counts of all birds were made. Habitat categories defined in Table 2. ** Includes Pangaimotu (connected by a causeway).

Island	Area (km²)	Max. elev. (m)	Distance to `Uta Vava`u (km)**	No. of stations in each habitat type					Dates surveyed
				1	2	3	4	5	
`Uta Vava`u	95.95	215	0	18	2	41	37	41	2, 8, 9, 14, 21–25, 29 July 1995, 7 July 1996
Pangaimotu	9.24	70	0	—	7	12	—	—	7 July 1996
Kapa	6.06	100	1.2	—	—	10	6	—	26 July 1995
Hunga	5.34	90	2.8	—	—	20	—	—	11–12 July 1995
Ofu	1.32	30	2.1	—	—	16	—	—	1 August 1995
`Utungake	1.09	80	0.2	6	—	—	6	—	8 July 1996
Vaka `eitu	0.85	45	7.0	—	—	—	5	6	4 July 1995
`Euakafa	0.70	62	6.8	—	—	—	7	15	19 July 1995
Taunga	0.56	40	4.0	2	—	23	—	—	20 July 1995
A`a	0.54	45	3.4	—	—	—	2	10	7 July 1995
Mafana	0.46	25	1.5	—	—	8	8	—	31 July 1995
`Eueiki	0.24	35	6.6	—	—	—	3	—	18 July 1995
Foelifuka	0.21	40	10.1	—	—	14	—	—	28 July 1995
Foeata	0.06	30	9.8	—	—	4	—	—	28 July 1995
Nuku	0.04	20	3.8	—	—	—	—	*	30 July 1995
Kulo	0.02	30	6.8	—	—	—	*	—	6 July 1995
Totals				26	9	148	74	72	329 Stations

ga, although they are managed to provide food, matting, cordage, medicine, and other products. After coconut, mango is the second most common large tree in the plantations.

Definition of our habitat categories 3–5 (Table 2) is enhanced by quantitative inventories of forests in Vava`u by Franklin et al. (in press) at the same time that we surveyed birds. Franklin et al. sampled forest vegetation in 44 plots of 600 m² each (20 × 30 m) on 13 islands, using methods and nomenclature described by Franklin and Merlin (1992), Bolick (1995), and Drake et al. (1996). They typically studied nearby pairs of plots in secondary and mature forest. All plant species listed for these habitat categories are indigenous unless stated otherwise. By identifying and recording all vascular plant species and measuring all woody stems > 5 cm, they calculated the basal area for 85 species of trees (11–29 species per plot). Their data classified

TABLE 2. Characteristics of habitat types in Vava`u. "Proportion native vegetation" refers to the approximate percentage of woody stems (> 5 cm diam.) that represents native species.

Habitat type	Proportion native vegetation	Structural characteristics
1. Village	<20	Isolated trees; largest trees non-native; ground cover grass, bare soil, buildings, or roads; no regeneration by native species.
2. Open plantation	<20	Open canopy (6–18 m); largest trees non-native; active cultivation of non-native crops; no regeneration by native species.
3. Wooded plantation/early successional forest	20–90	Semi-open to closed canopy (6–20 m); largest trees and understory both native and non-native; few or no trees > 40 cm diam.; all regeneration by native species.
4. Submature/disturbed mature forest	>90	Closed or nearly closed canopy of native species (10–22 m); understory open to dense; few trees > 40 cm diam.; all regeneration by native species.
5. Mature forest	>90	Closed canopy of native species (10–24 m); rather open understory; many trees > 40 cm diam.; all regeneration by native species.

the overstory vegetation into forest types that correlate with our categories 3–5 of bird habitat.

3. Wooded plantation/early successional forest refers to abandoned plantations. Native woody species begin to reoccupy plantations after several years, although on inhabited islands such land usually is cleared again within 30 years (often only 5–10 years), before or just as the native species begin to develop a canopied secondary forest. In these situations the indigenous trees tend to occur as scattered individuals or small groups, seldom with stem diameters > 40 cm. Franklin et al. (in press) distinguished two grades of early to mid-successional forest based on species composition: (a) *Rhus taitensis-Alphitonia zyzyphoides* early successional rain forest, found on gently sloping (0–15°) sites between 10–125 m elevation on large or small islands, with cultivated species such as *Cocos nucifera, Adenanthera pavonina, Citrus sinensis, Morinda citrifolia,* and *Artocarpus altilis* present; and (b) *Cryptocarya turbinata-Elattostachys falcata-Rhus taitensis-Alphitonia zizyphoides* mid-successional rain forest, with higher basal area and higher density than the first type, and most cultivated species absent from the overstory, which is co-dominated by *Zanthoxylum pinnatum, Pleiogynium timoriense, Elattostachys falcata, Elaeocarpus tonganus,* and *Cocos nucifera.*

4. Submature/disturbed mature forest refers to habitat with a closed or nearly closed canopy of native trees, but primarily with individuals of early successional species found in the largest size classes. This habitat type corresponds to two forest types described by Franklin et al. (in press): (a) *Cryptocarya turbinata-Ellatostachys falcata-Zanthoxylum pinnatum-Maniltoa grandiflora* disturbed mid- or late-successional rain forest, found in sites with some evidence of disturbance or past cultivation, with subdominants *Dysoxylum forsteri, Rhus taitensis,* and *Alphitonia zyziphoides,* the last two suggesting that this forest type is late-successional rather than mature; and (b) transition beach forest-lowland rain forest, found at elevations of 7–50 m in a narrow (20–60 m wide) perimeter around large, protected islands but covering much or all of the islands lying near the margins of the Vava`u Group, such as Foeata, Foelifuka, and Hunga. Influenced somewhat by salt spray, these forests are taller and richer in woody species on leeward than on windward coasts, although much of the leeward forest has been lost to village sites or fishing camps. Characteristic species include those usually associated with beach forest (*Pandanus tectorius, Casuarina equisetifolia, Guettarda speciosa, Neisosperma oppositifolia, Ochrosia vitiensis, Hibiscus tiliaceus,* and *Excoecaria agallocha*) as well as some species associated with lowland rain forest (*Planchonella grayana, Xylosma simulans,* and *Zanthoxylum pinnatum*). Evidence of past cultivation may be minimal. In category 4, we also place tracts of forest that we would have judged to be mature forest (category 5) except for evidence of selective logging during recent decades.

5. Mature forest has a closed canopy, many large (> 40 cm dbh) trees, no evidence of recent logging, and is dominated by native species. This corresponds to the following type described by Franklin et al. (in press): *Maniltoa grandiflora-Pleiogynium timoriense-Planchonella grayana* late-successional rain forest, found on steep, rocky slopes on both large and small islands from 50–180 m elevation. Co-dominants include *Garuga floribunda, Chionanthus vitiense,* and sometimes *Elattostachys falcata, Xylosma simulans,* and *Zanthoxylum pinnatum.* This forest type is considered mature and relatively undisturbed based on composition (low or no cover by early-successional species or cultivars), site characteristics, and in a few cases from air photos taken in 1968 showing no clearing since at least that year.

Banyans (*Ficus obliqua, F. prolixa*) are a patchily-distributed but significant component of habitat categories 4–5. Although seldom recorded in plots because they are usually found on steep slopes or cliffs, *Ficus* spp. are an important food resource for tropical frugivores (Frith et al. 1976, Snow 1981, pers. observ.).

BIRD SURVEYS

The scientific, English, and Tongan names for each species are given in the Species Accounts below, which also review previous records from Vava`u. We surveyed birds on 16 islands in Vava`u during 2 July–1 August 1995 and 7–8 July 1996 (Table 1), a season in which West Polynesian birds are vocally conspicuous (pers. observ.). To estimate relative abundance and distribution of birds among islands and in different forest types, we conducted 5-min, fixed-radius counts along transects (Hutto et al. 1986). Time and logistical constraints did not allow us to cen-

TABLE 3. Mean number of birds per station for each island or locality sampled. UV = `Uta Vava`u localities. Totals are calculated without White-rumped Swiftlet. Nuku and Kulo not surveyed.

Island/Locality (no. stations)	Banded Rail	Purple Swamp-hen	West Polynesian Ground-Dove	Purple-capped Fruit-Dove	Pacific Pigeon	White-rumped Swiftlet	Collared Kingfisher	Polynesian Triller	Tongan Whistler	Polynesian Starling	Wattled Honeyeater	Totals
UV-Taoa (16)	0.13	0.06	0.00	1.88	0.69	1.38	0.75	1.88	0.56	3.69	1.38	11.00
UV-Liku Holonga (7)	0.00	0.00	0.00	1.29	1.71	0.14	0.43	1.29	2.14	0.86	1.00	8.71
UV-Mo`ungalafa (59)	0.05	0.00	0.05	1.76	1.80	0.15	0.69	0.81	2.12	1.41	1.75	10.44
UV-Neiafu (30)	0.13	0.03	0.00	0.60	0.00	0.70	0.07	1.20	0.07	1.33	0.43	3.86
UV-Tu`anuku (24)	0.00	0.46	0.00	1.33	0.25	1.54	0.21	1.50	0.67	1.08	0.38	5.88
UV-Toula (3)	0.67	0.00	0.00	1.67	0.00	1.00	0.67	1.67	1.00	1.67	0.00	7.33
Pangaimotu (19)	0.05	0.05	0.00	0.53	0.26	1.78	1.05	0.74	0.47	1.26	0.05	4.47
Kapa (16)	0.00	0.00	0.00	1.31	0.56	0.38	0.19	1.25	0.69	1.38	0.31	5.69
Hunga (20)	0.00	0.00	0.00	1.10	0.65	0.35	0.35	0.95	0.35	1.25	0.25	4.90
Ofu (16)	0.00	0.00	0.00	1.00	0.38	0.81	0.56	1.00	0.00	2.13	0.00	5.06
`Utungake (12)	0.00	0.00	0.00	1.33	1.00	0.67	0.67	1.42	0.67	1.17	0.08	6.33
Vaka`eitu (11)	0.00	0.00	0.00	1.00	2.09	0.27	0.27	1.55	0.91	0.73	0.18	6.73
`Euakafa (22)	0.00	0.09	0.00	0.50	0.59	0.08	0.64	0.36	1.23	0.82	2.18	6.41
Taunga (25)	0.00	0.00	0.00	0.28	0.04	0.37	0.04	1.16	0.00	1.16	0.20	2.88
A`a (12)	0.00	0.00	0.00	2.25	2.25	0.25	0.33	0.83	0.25	0.50	0.17	6.58
Mafana (16)	0.31	0.00	0.00	0.81	0.69	0.69	0.44	1.75	0.00	1.63	0.06	5.69
`Eueiki (3)	0.00	0.00	0.00	0.67	1.00	0.10	0.00	0.67	1.00	1.33	2.00	6.67
Foelifuka (14)	0.00	0.00	0.00	0.57	0.14	0.29	0.57	1.50	0.64	0.43	0.00	3.86
Foeata (4)	0.00	0.00	0.00	0.50	0.00	0.00	0.25	1.50	0.50	0.00	0.00	2.75

sus the birds equally in each of the five habitat categories. Rather, we emphasized sampling the birds in forested habitats.

All counts were done between 07:00 and 12:00. We also recorded all bird observations, regardless of the time of day. Surveys were not conducted in rainy or windy conditions. The locations of transects were recorded on air photos using acetate overlays, copies of which are available from Steadman. Most islands were surveyed on only one day (Table 1). Because of its greater size and diversity of habitats, `Uta Vava`u was surveyed at six localities on 11 different days.

The transects in disturbed habitats followed existing trails or one-lane dirt roads to facilitate rapid but quiet travel between stations (Ralph et al. 1993). Transects in mature forests generally followed topographic contours, which provided the most continuous, linear routes over the extremely rugged limestone terrain. Stations were 100 m apart. At each station we recorded each bird detected within a 50 m radius during a 5-min period. Each bird was recorded as being heard or seen. Birds detected at distances > 50 m were noted but were not included in our analyses. Individual birds recorded at the previous station were monitored during travel between stations to avoid recounting the same bird at two stations. This is most easily done for species that vocalize consistently, such as the Purple-capped Fruit-Dove or Tongan Whistler. Our calculations are based on "birds per station," which is simply the mean number of birds seen or heard per station, regardless of age, sex, behavior, or vocalization.

Aquatic species, such as herons, ducks, and migrant shorebirds, as well as seabirds flying overhead, are excluded from the analyses. The White-rumped Swiftlet is a silent aerial feeder that is much easier to detect (visually) in open habitats than in forests. Therefore we have not included the transect data for this swiftlet in the totals for Table 3 or in any subsequent calculations.

RESULTS

The transect data (Table 3, Fig. 3) reveal major inter-island differences in the total abundance of birds and in the presence and/or abundance of individual species. Birds are scarcest on Foeata and Taunga (mean total abundance = 2.75 and 2.88 birds/station, respectively) and are most abundant on `Uta Vava`u and Vaka`eitu (mean total abundance = 7.87 and 6.73 birds/station, respectively).

Among the 12 indigenous species of resident landbirds that survive on the 16 islands sur-

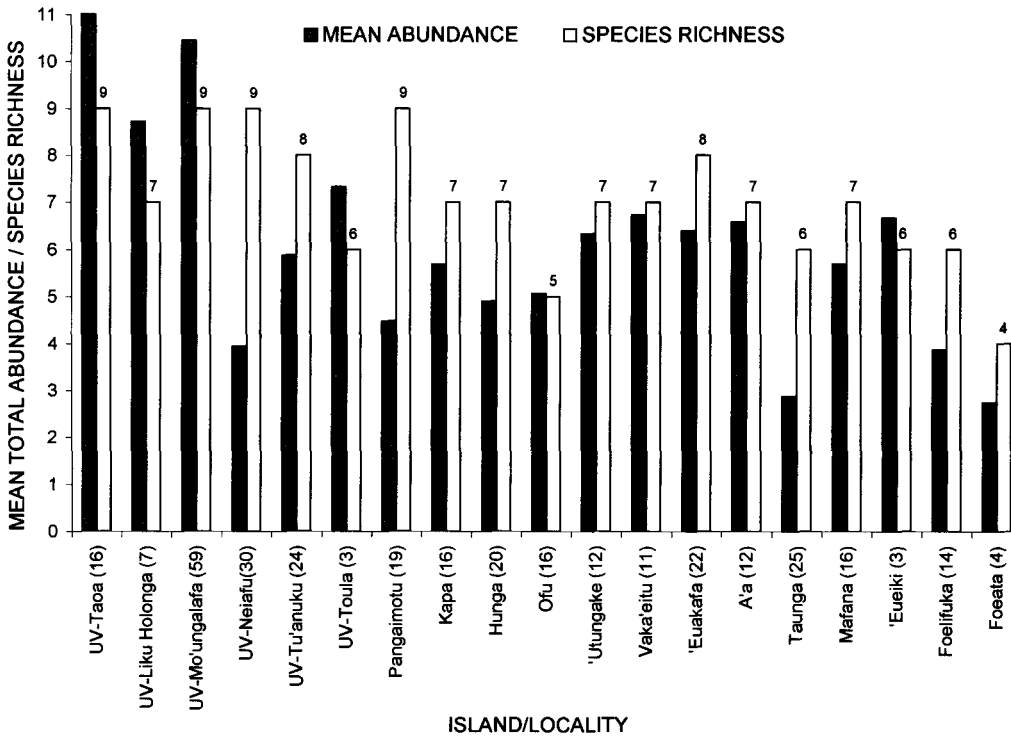

FIGURE 3. Relative abundance and species richness of indigenous landbirds on islands in Vava`u, Tonga. Based on data in Table 3. "UV-" refers to localities on `Uta Vava`u. Number of stations in parentheses.

veyed, 11 are widespread and at least locally common in the Vava`u Group. Seven of these (Purple-capped Fruit-Dove, Pacific Pigeon, White-rumped Swiftlet, Collared Kingfisher, Polynesian Triller, Polynesian Starling, and the nocturnal Common Barn-Owl) certainly or probably occur on most or all islands surveyed (Table 4). These six species (White-rumped Swiftlet excluded) make up 83 to 100% of the birds in each of the four localities where mean total abundance is fewer than four birds/station (Table 3).

Species richness per transect varies from four (Foeata) to nine species (four localities on `Uta Vava`u). Species richness is lowest in Village and greatest in the three forest categories (Fig. 4). The mean relative abundance is inversely related to habitat disturbance, again with lowest values for Village and a stepwise increase in less disturbed (older) habitat categories (Fig. 4). In general, this pattern among habitats holds for islands of varying sizes (Fig. 5). The patterns of relative abundance among habitats for individual species are highly variable (Fig. 6). Five species (West Polynesian Ground-Dove, Purple-capped Fruit-Dove, Pacific Pigeon, Tongan Whistler, Wattled Honeyeater) show a trend of increasing abundance with less habitat modification (Fig. 6). The opposite trend is true for Banded Rail and White-rumped Swiftlet. The Purple Swamphen, Collared Kingfisher, Polynesian Triller, and Polynesian Starling are habitat generalists of similar relative abundance regardless of habitat type (Fig. 6). Considering feeding guilds of arboreal species, both frugivores and passerine insectivores show the general trend of increasing abundance with less habitat disturbance (Fig. 7).

SPECIES ACCOUNTS

Throughout the Species Accounts, refer to Tables 3 and 4 and Figure 6 for details of the distribution and relative abundance of individual species.

Gallus gallus (Chicken, *moa*). A non-native gamebird introduced prehistorically through most of Oceania (Steadman 1993), the Chicken is abundant in villages in Vava`u. Feral birds occur regularly in all habitat categories.

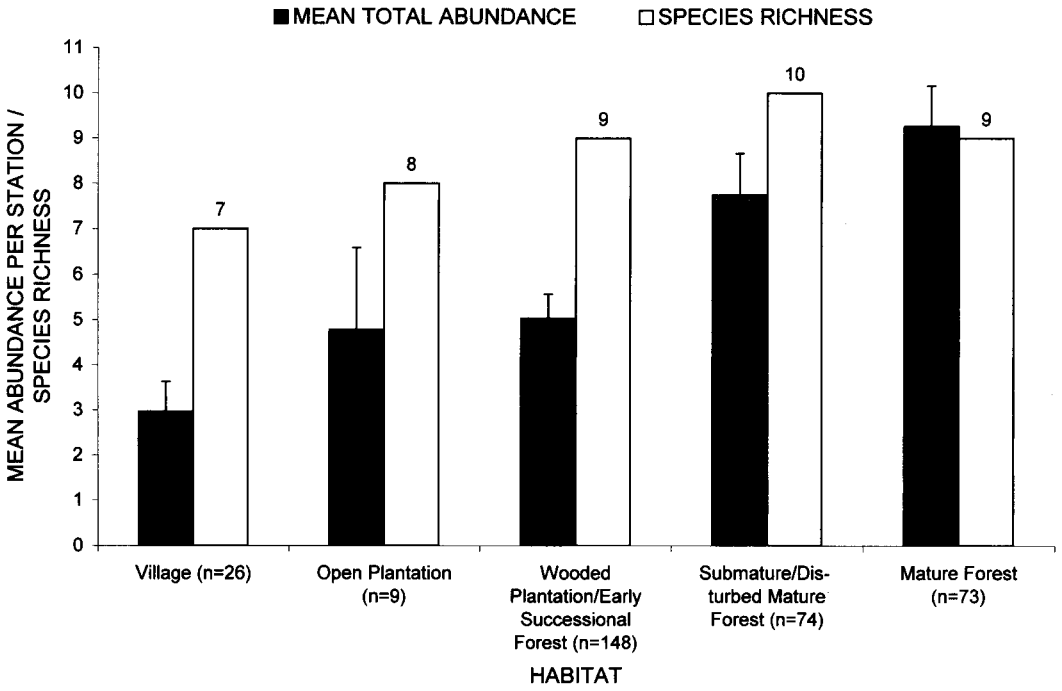

FIGURE 4. Total relative abundance (mean ± SE) and species richness of indigenous landbirds in the five habitat categories (defined in Methods; see also Table 2).

Gallirallus philippensis (Banded Rail, *veka*). This terrestrial rail thrives in disturbed habitats (Engbring and Ramsey 1989), favoring thick grassy areas during the day and venturing into more open places to forage in the early morning and late afternoon. We did not record the Banded Rail on uninhabited islands. Its absence on the four smallest islands (Table 4) probably results from the scarcity of grasses and sedges on these goat-infested islands. Our relative abundance values for the Banded Rail probably are underestimates as this species vocalizes irregularly. Specimens: ?`Uta Vava`u (Layard 1876). Sight records: `Uta Vava`u, Koloa (Gill 1990).

Porphyrio porphyrio (Purple Swamphen, *kalae*). This large rail prefers wetlands, especially those with wooded margins. Thus islands such as `Uta Vava`u (which features the royally protected Ngofe Marsh, where Gill [1990] saw 15 swamphens) and Hunga (with a smaller marsh) probably sustain the core population of the Purple Swamphen in Vava`u. We recorded this species only on three islands and never in mature forest. Our relative abundance values for the Purple Swamphen probably are underestimated as this species vocalizes only irregularly and can be shy because of hunting. Specimens: `Uta Vava`u (Layard 1876). Sight records: `Uta Vava`u (Gill 1990).

Gallicolumba stairii (West Polynesian Ground-Dove, *tu*). A forest obligate in Tonga, the West Polynesian Ground-Dove is difficult to see in the understory but is readily detected by its call (described by Beichle 1991). We encountered only one population of West Polynesian Ground-Dove (six different calling and apparently territorial birds, two of which we also saw), in the relatively large remnant of mature forest at Mo`ungalafa on `Uta Vava`u. This area was being cleared for agriculture in July 1995. Given the abundance of rats, cats, dogs, and pigs on `Uta Vava`u today, the prospect for survival of ground-doves there is slight. Elsewhere in Tonga, the West Polynesian Ground-Dove survives only on the volcanic islands of Late, Hunga Ha`apai, and perhaps Hunga Tonga and Tofua (Rinke 1991, Rinke et al. 1992). Populations of this West Polynesian endemic have been extirpated on `Eua, Lifuka, and Nomuka`iki (Steadman 1993, 1997b, 1998). No specimens of this species have ever been collected in the Vava`u

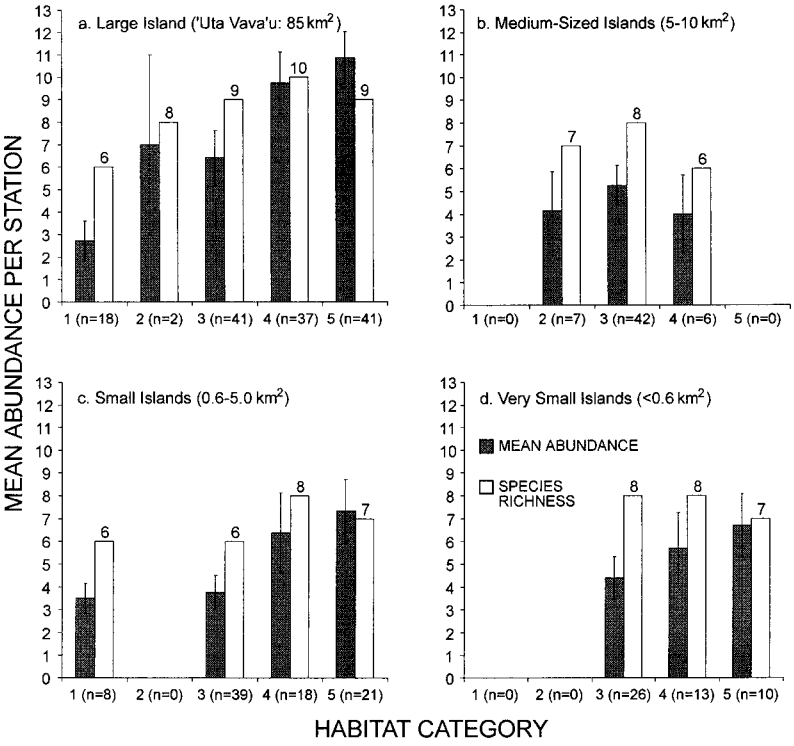

FIGURE 5. Relative abundance and species richness among habitat categories on islands in different size classes. Numbers in parentheses following habitat category refer to the number of stations in that habitat for that island size class. Large island (a) is `Uta Vava`u. Medium-sized islands (b) are Pangaimotu, Hunga, and Kapa. Small islands (c) are Ofu, `Utungake, Vaka`eitu, `Euakafa, and Taunga. Very small islands (d) are Mafana, A`a, `Eueiki, Foelifuka, and Foeata. Data are from Tables 1 and 3.

Group (Amadon 1943), where our sight/sound records are the first evidence of its presence.

Ptilinopus porphyraceus (Purple-capped Fruit-Dove, *kulukulu*). This vocally conspicuous frugivore is very common and widespread in Vava`u. It occurs in all habitats, but is consistently more abundant with increased maturity of the forest, an observation corroborated by data from Ha`apai (Steadman 1998). The distinctive call of the Purple-capped Fruit-Dove is given all day (and often in the night) from the forest canopy or high in isolated trees. Fruit-doves congregate in fruiting trees (especially *Ficus* spp.) but maintain separate breeding territories. Specimens: `Uta Vava`u (Layard 1876, Townsend and Wetmore 1919); WSSE `Uta Vava`u, Kapa, Ovaka (Ripley and Birckhead 1942). Sight records: `Uta Vava`u, Pangaimotu, `Utungake, Kapa (Gill 1988, 1990).

Ptilinopus perousii (Many-colored Fruit-Dove, *manuma`a*). This West Polynesian endemic is a canopy- and subcanopy-dwelling fig specialist (Engbring and Ramsey 1989, Steadman 1998). The reasons for its extirpation in Vava`u are not clear. The Many-colored Fruit-Dove apparently occurred in Vava`u in the 1870s but was rare and not collected or seen by Layard (1876). In Ha`apai in 1995–1996, the only individuals of this fruit-dove detected were on Tofua (a large, forested volcanic island) and in Pangai Village on Lifuka, where four pairs were observed foraging in the banyan *Ficus obliqua* (Steadman 1998). Large *Ficus* trees (*F. obliqua, F. prolixa*) are much more common in Vava`u than in Ha`apai, yet we never heard the distinctive vocalization of Many-colored Fruit-Doves in spite of being especially attentive for it.

Ducula pacifica (Pacific Pigeon, *lupe*). This large, vocal frugivore is abundant and conspicuous in the canopy of mature forests in Vava`u. The relative abundance of the Pacific Pigeon increases sharply in mature forests regardless of

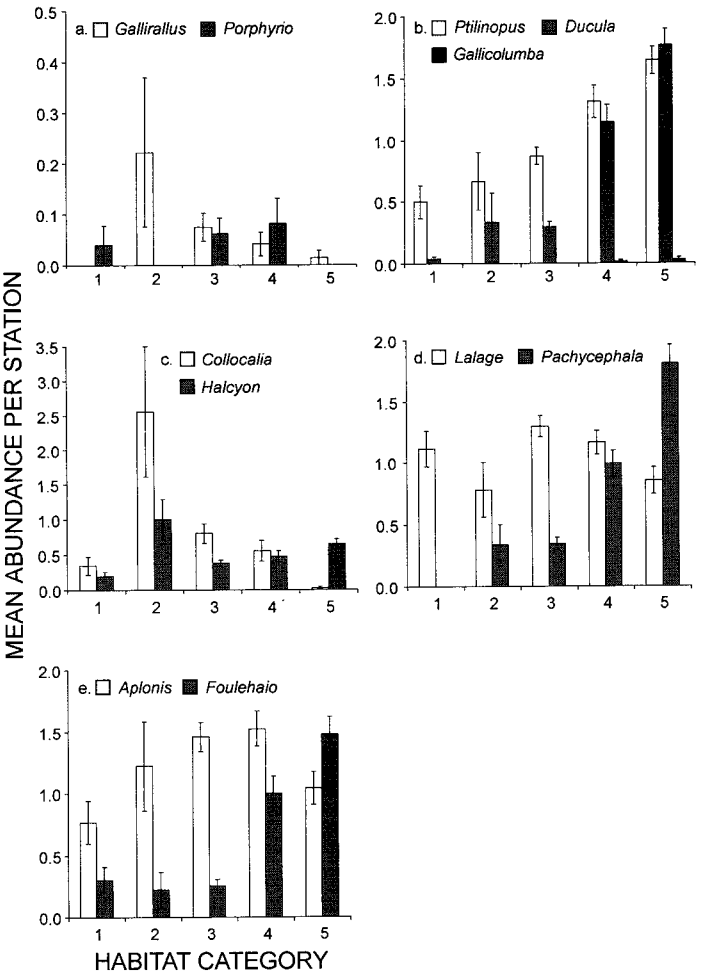

FIGURE 6. Relative abundance (mean ± SE) of indigenous landbirds in five habitat categories. 1 = village, 2 = open plantation, 3 = wooded plantation/early successional forest, 4 = submature/disturbed mature forest, 5 = mature forest.

island size. The Pacific Pigeon is less territorial than the Purple-capped Fruit-Dove, with one to four birds typically encountered. That it has survived 3,000 years of hunting in Tonga (Burley 1996, Steadman 1989, 1993, 1997a) is at least in part because of an excellent ability to disperse between islands (Diamond 1974, Franklin and Steadman 1991, Steadman 1997b). Specimens: `Uta Vava`u (Layard 1876, Amadon 1943). Sight records: `Uta Vava`u, Pangaimotu, `Utungake, Koloa, Kapa (Gill 1990).

Vini australis (Blue-crowned Lorikeet, *henga*). This West Polynesian endemic (Amadon 1942) is no longer found on many of the islands that once made up its range (Rinke 1985, Steadman 1993). There is no record of the Blue-crowned Lorikeet for Vava`u during the 20th century, although Layard (1876) had described this species (his *Coriphilus fringillaceus*) as "very abundant" in Vava`u in the 1870s. Layard (1876) also ". . . heard of a small parrot with two long feathers in its tail, which formerly existed in the group [Vava`u], but has become quite extinct." The identity of this parrot is unknown but might possibly be *Charmosyna amabilis* (Red-throated Lorikeet), confined today to Fiji (Pratt et al. 1987). The Blue-crowned Lorikeet consumes nectar and pollen gathered with its brushy-tipped tongue. Every individual of this species recorded by Steadman in Ha`apai in

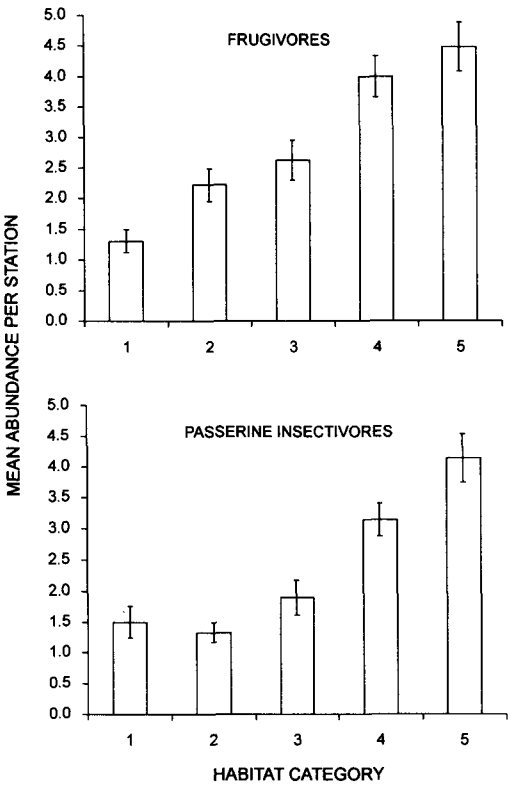

FIGURE 7. Relative abundance (mean ± SE) of frugivores and passerine insectivores in habitat categories. Frugivores are *Gallicolumba, Ptilinopus, Ducula,* and *Aplonis.* Insectivores are *Lalage, Pachycephala,* and *Foulehaio.* Habitat categories are as in Figure 6.

1996 was either perched in or flying between coconut trees. Given the abundance of coconut trees in Vava`u, poor quality habitat seems unlikely to account for its absence or extreme scarcity there. Rats and pesticides have been suggested to account for population declines of Blue-crowned Lorikeet elsewhere, although the evidence is equivocal (Steadman 1998). Specimen: `Uta Vava`u (Layard 1876). Sight records: `Uta Vava`u (Layard 1876).

Tyto alba (Common Barn-Owl, *lulu*). Barn-owls are common in Vava`u. Night surveys would probably record them on virtually every island. One or two species of non-native rats (*Rattus exulans, R. rattus*) occurs on each island we visited, providing ample food for the Common Barn-Owl. Sight records: `Uta Vava`u (Layard 1876, Gill 1990).

Collocalia spodiopygia (White-rumped Swiftlet, *pekepeka*). This small aerial insectivore is widespread and common in Vava`u because caves (required for roosting and nesting) are numerous on certain islands. As stated earlier, White-rumped Swiftlets are not amenable to auditory censusing from within the forest, therefore our data on relative abundance contain a major sampling artifact. Although their recorded abundance is highest in open, disturbed habitats (typical group size of one to five birds), swiftlets forage silently above the forest canopy as well, where they cannot be censused accurately. Specimens: `Uta Vava`u (Layard 1876, Townsend and Wetmore 1919). Sight records: `Uta Vava`u, Pangaimotu, `Utungake, Okoa, Koloa, Kapa (Gill 1990).

Halcyon chloris (Collared Kingfisher, *sikota*). Conspicuous on nearly every island surveyed, the Collared Kingfisher is a habitat generalist that feeds primarily on large insects and small lizards, although it occasionally takes small fish over the reef at low tide. Usually encountered as single birds or pairs, the mean abundance of Collared Kingfishers is highest in open plantation but the small number of stations (9) in that habitat and the large standard error preclude stating that this species in fact prefers this habitat over others. Specimens: `Uta Vava`u (Layard 1876, Townsend and Wetmore 1919). Sight records: `Uta Vava`u, Pangaimotu, `Utungake, Okoa, Koloa, Kapa (Gill 1990).

Lalage maculosa (Polynesian Triller, *sikiviu*). An omnivorous gleaner of the subcanopy and occasionally the understory, the Polynesian Triller is common and widespread in Vava`u, where typical group size is two to three birds. It is the only species that we recorded unequivocally on each island surveyed. The relative abundance data reveal no well-defined habitat preference. Specimens: `Uta Vava`u (Layard 1876, Townsend and Wetmore 1919); WSSE `Uta Vava`u, Ovaka, Kapa, `Euakafa (Mayr and Ripley 1941). Sight records: `Uta Vava`u, Pangaimotu, `Utungake, Okoa, Koloa, Kapa (Gill 1990).

Clytorhynchus vitiensis (Fiji Shrikebill, *fuiva*). This species is a gleaning understory omnivore that probably is extirpated from Vava`u. The only record of Fiji Shrikebill from Vava`u is two specimens collected on `Uta Vava`u in the 1860s (Finsch and Hartlaub 1870). In Ha`apai, this West Polynesian endemic and forest obligate seems to have disappeared by 1991 from eight islands where it was recorded in 1925 (Mayr

TABLE 4. Summary of landbird status, Vava`u, Tonga. X, recorded July 1995 or July 1996; —, not recorded in 1995/1996 and presumably truly absent; A, not recorded in 1995/1996 but likely occurs; * breeding unlikely; i, introduced species (not included in vertical totals).

Species	`Uta Vava`u	Pangai-motu	Kapa	Hunga	Ofu	`Utun-gake	Vaka`ei-tu	`Euakafa	A`a	Taunga	Mafana	`Eueiki	Foelifuka	Foeata	Nuku	Kulo	Totals X	Totals X + A
Chicken (i) *Gallus gallus*	X	X	X	X	X	X	X	A	A	X	X	X	X	X	—	—	12	14
Banded Rail *Gallirallus philippensis*	X	X	A	A	A	A	—	—	A	A	X	—	—	—	—	—	3	9
Purple Swamphen *Porphyrio porphyrio*	X	X	A	A	—	A	A	X	A	—	—	A	—	—	—	—	3	9
West Polynesian Ground-Dove *Gallicolumba stairii*	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Purple-capped Fruit-Dove *Ptilinopus porphyraceus*	X	X	X	X	X	X	X	X	X	X	X	X	X	X	A	X	15	16
Pacific Pigeon *Ducula pacifica*	X	X	X	X	X	X	X	X	X	X*	X	X	X*	A*	A*	X*	14	16
Common Barn-Owl *Tyto alba*	A	A	A	X	A	A	A	X	A	A	A	A	X	X	A	A	4	16
White-rumped Swiftlet *Collocalia spodiopygia*	X	X	X	X	X*	X	X	X	X	X*	X*	X	X*	A*	A*	A*	13	16
Collared Kingfisher *Halcyon chloris*	X	X	X	X	X	X	X	X	X	X	X	A	X	X	A	A	13	16
Polynesian Triller *Lalage maculosa*	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	16	16
Tongan Whistler *Pachycephala jacquinoti*	X	X	X	X	—	X	X	X	X	—	—	X	X	X	—	—	11	11
Polynesian Starling *Aplonis tabuensis*	X	X	X	X	X	X	X	X	X	X	X	X	X	A	A	X	14	16
Wattled Honeyeater *Foulehaio carunculata*	X	X	X	X	—	X	X	X	X	X	X	X	—	—	—	—	11	11
Red-vented Bulbul (i) *Pycnonotus cafer*	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Total indigenous species																		
X	11	10	8	9	6	8	8	10	8	7	8	7	8	5	1	4		
X + A	12	11	11	11	8	11	10	10	11	9	9	10	8	8	7	7		

1933, Rinke et al. 1992). By 1996, it could not be found on two other islands where it was recorded in 1991 (Steadman 1998); eight other small islands where it was found in 1991 were not visited by Steadman in 1996. Elsewhere in Tonga, two small populations of the Fiji Shrikebill may survive on the islets of `Eueiki (off Tongatapu) and Kalau (off `Eua), although it once occurred on both Tongatapu and `Eua (Rinke 1987, Steadman 1993). The only large populations are on the volcanic islands of Niuatoputapu, Tafahi, Kao, Tofua, and Hunga Ha`apai. The small populations of shrikebills that may still exist on nonvolcanic islands in Ha`apai are vulnerable to extinction, probably within years or decades. Population declines probably result from a blend of deforestation, understory clearance by pigs and goats, and predation by cats and rats. Specimens: `Uta Vava`u (Finsch and Hartlaub 1870). Sight records: none.

Pachycephala jacquinoti (Tongan Whistler, *hengehenga*). Strictly territorial and vocally conspicuous, the omnivorous Tongan Whistler is common in the understory of mature forests. Rinke et al. (1992) found this Tongan endemic to be the most common passerine in the mature forests on Late Island and at Liku Holonga on `Uta Vava`u. Our data are corroborative, with the Tongan Whistler being the most common species in the two largest tracts of mature forest (UV-Liku Holonga, UV-Mo`ungalafa). Overall, it is much more abundant in mature forest than in disturbed mature forest, wooded plantation/early successional forest, or open plantation. The Tongan Whistler is absent from village habitat. We also note that it occurs in successional habitats only if they are adjacent to a tract of mature forest. Specimens: `Uta Vava`u (Layard 1876, Townsend and Wetmore 1919); WSSE `Uta Vava`u, Kapa A`a, `Euakafa (Mayr 1932b). Sight records: `Uta Vava`u, Pangaimotu, `Utungake, `Euakafa, A`a, Kapa (Rinke 1986, Gill 1990, Rinke et al. 1992).

Aplonis tabuensis (Polynesian Starling, *misi*). This highly frugivorous omnivore is common virtually throughout Vava`u. Typically encountered in groups of two or three birds, the Polynesian Starling is a generalist in habitat and food habits in Tonga. The fruit it consumes in Tonga includes the native species *Ficus* spp., *Grewia crenata, Rhus taitensis, Pleiogynium timoriense, Guioa lentiscifolia, Alphitonia zizyphoides,* and *Cryptocarya turbinata,* and the non-native *Carica papaya, Psidium guajava,* and *Lantana camara* (Rinke 1987, Steadman 1998; pers. observ.). Specimens: `Uta Vava`u (Layard 1876, Townsend and Wetmore 1919); WSSE `Uta Vava`u, `Euakafa (Mayr 1942). Sight records: `Uta Vava`u, Pangaimotu, `Utungake, Okoa, Koloa, Kapa (Gill 1990).

Foulehaio carunculata (Wattled Honeyeater, *fuleheu*). A West Polynesian endemic, this canopy dweller is a noisy, conspicuous, aggressive nectarivore/insectivore (Whitmee 1875, Engbring and Ramsey 1989, Steadman 1998). The Wattled Honeyeater occurs in Vava`u in groups of two to six birds (usually three or four), much as on `Eua (Rinke 1984). The highest numbers are sustained by the two mature forest habitat categories, a pattern found as well in American Samoa (Freifeld 1998). Outside of the forest, the Wattled Honeyeater is attracted to isolated flowering trees such as coconuts and *Erythrina variegata.* It is absent or scarce on many small islands in Vava`iu; the only island $< 0.5$ km$^2$ where we recorded it regularly is the largely forested `Eueiki. Specimens: `Uta Vava`u (Layard 1876); WSSE `Uta Vava`u, Kapa, `Euakafa, Maninita (Mayr 1932a). Sight records: `Uta Vava`u (Gill 1990).

DISCUSSION

FACTORS INFLUENCING COMMUNITY COMPOSITION

Our knowledge of the landbird communities in Vava`u lacks direct prehistoric perspective. Based upon data from elsewhere in Tonga (`Eua and five islands in Ha`apai), however, we know that a typical island avifauna in Tonga included at least 25–30 species of landbirds when humans first arrived (Steadman 1993, 1995, 1998). Thus we assume that many species of landbirds have become extinct in Vava`u during the past three millennia of human occupation. The extant forest-obligate species in Vava`u, such as the Pacific Pigeon, West Polynesian Ground-Dove, and Tongan Whistler, are remnants of a once much larger set of species that probably required forested conditions. The present-day variation in landbird communities among habitats and islands in the Vava`u Group is the product of long-term anthropogenic influences on island landscapes and on individual species. Interpretation of our survey data rests on understanding how these processes have operated.

The mean relative abundance of landbirds is

greater in mature forest than in any other habitat (Fig. 4). This has been documented as well in nearby Samoa (Bellingham and Davis 1988, Freifeld 1998) and Cook Islands (Franklin and Steadman 1991). The dearth of autecological information about Polynesian landbirds constrains us to speculative discussion of the requirements underlying the apparent habitat preferences of particular species. Nevertheless, we explore five factors that may help to explain the patterns of habitat preference, relative abundance, and distribution that we observed.

1. Seasonally variable associations between bird and plant taxa. Frugivores may occupy certain forest types seasonally in continental environments to exploit particular food resources (Levey 1988, Innis 1989, Levey and Stiles 1992). Because many forest trees in Tonga seem to reproduce seasonally, birds exploiting their fruits may be expected to frequent selected habitats at a particular time of the year. If this is the case for the Pacific Pigeon and the Purple-capped Fruit-Dove, for example, our determination that these columbids are more abundant in mature forest than in other categories (Fig. 7) may only be part of an annual cycle of intra-island movement that cannot be represented in our seasonally limited data set.

For three reasons, however, we reject this suggestion of much seasonal movement among habitats in Vava`u. First, there are no strong intra-island environmental gradients that fruiting phenology seems to track, not even on the largest and highest island (`Uta Vava`u). Second, although the fruiting phenology of certain forest trees seems to be fairly synchronous within and between islands in Vava`u, many species of native trees were not setting flowers or fruit at the time of our study even in the habitats where landbirds were most abundant (*Alphitonia zyziphoides, Cryptocarya turbinata, Pleiogynium timoriense, Elattostachys falcata,* and the aseasonal *Ficus* spp. are notable exceptions). Finally, year-round censuses of some of the same species of frugivorous birds across a comparable range of forest types in American Samoa do not reveal seasonal movements or systematic changes in abundance between habitat types (Freifeld 1998).

2. Vegetation structure. The relative overall abundance of both frugivores and insectivores consistently increases with forest maturity (Fig. 7). For understory birds such as the Tongan Whistler, the presence of a well-developed shrub layer may be a critical habitat component. The understory plants in less-disturbed forests may sustain a richer prey base for insectivorous birds. A similar concept may apply for frugivores not restricted to the canopy, such as the Polynesian Starling (Fig. 6), that is, mature forest provides a greater diversity of food plants in the understory and subcanopy as well as in the canopy.

Human activities (deforestation, cultivation) restrict the extent of structurally complex forests. The escarpments that separate the limestone terraces in Vava`u restrict human activities and thus act to preserve bands of relatively intact forest between plantations. If deforestation and agriculture were as feasible on the escarpments as on terraces, Vava`u probably would lack mature forest altogether. Under such conditions, the West Polynesian Ground-Dove certainly would be extirpated, and the Pacific Pigeon and Tongan Whistler would be rare or gone. In contrast, some native forest birds seem to have adapted well to the spread of agricultural and disturbed forests. The Polynesian Triller and Polynesian Starling are more abundant in wooded plantation/early successional forest and submature/disturbed mature forest than in mature forest (Fig. 6d, e).

3. Intensity of predation by humans and other mammals (rats, cats, dogs, and pigs). Tongans have hunted birds for several thousand years with slings, snares, bird lime, thrown rocks, and bows and arrows (Gifford 1929, Steadman 1995, 1997a, Burley 1996). The species most often pursued today (with guns, snares, thrown rocks) are the Purple Swamphen, Banded Rail, Pacific Pigeon, and Purple-capped Fruit-Dove. Even for these four species, however, current hunting is not intense and may have little effect on distribution or population size. Nevertheless, the stations designated as mature forest tend to occur farther from villages and other sustained human activity than other habitat categories. For species subjected to hunting, distance from human habitation may reduce hunting pressure and thus improve habitat quality. Mortality of birds from toxic chemicals is a form of indirect human predation that has not been studied in Tonga. Pesticides are used on crops regularly in Vava`u, with an unknown influence on food webs involving birds.

Various species of non-native mammals occur on each of the 16 islands visited. These include

the prehistorically introduced Pacific rat *Rattus exulans,* dog *Canis familiaris,* and pig *Sus scrofa,* as well as the historically introduced black rat *R. rattus,* house cat *Felis catus,* horse *Equus caballus,* goat *Capra hircus,* and cow *Bos taurus.* The islands inhabited by people tend to have most or all of these species. The uninhabited islands have rats (usually *R. rattus*) and sometimes goats or pigs. Understory birds probably are subjected to more predation by non-native mammals than canopy species, a situation exacerbated when goats or pigs damage the understory vegetation. This sort of damage may be especially harmful to the West Polynesian Ground-Dove, Fiji Shrikebill, and Tongan Whistler.

4. Ability to disperse between islands. A good ability to disperse between nearby islands allows populations to come and go as circumstances change on any one island. This is not long-distance dispersal but is within the Vava`u Group, among islands within sight of each other (see distances in Table 1). Species more strictly confined to mature forest, especially understory birds, tend to be poor dispersers. For example, the West Polynesian Ground-Dove, Many-colored Fruit-Dove, and Fiji Shrikebill are three Tongan species with relatively poor inter-island dispersal abilities (i.e., species that we have never seen flying over the ocean anywhere in Oceania) and a strong preference for mature forest (Steadman 1998). These three species already are gone or rare on nonvolcanic islands in Vava`u and throughout Tonga.

The Pacific Pigeon is unusual in preferring mature forest yet being an excellent disperser over water (Diamond 1974). Rarity also may affect the relationship between distribution and observed dispersal of species. With all else equal, a rare species is less likely to be recorded crossing water than a common species. The Tongan Whistler, however, is common on forested islands within sight of each other in Vava`u, but was never recorded over water during our numerous inter-island boat trips.

5. Interactions (disease, competition, predation) with non-native birds. This topic is unstudied in Tonga. The chicken (native to Southeast Asia) is the only non-native species of bird firmly established in Vava`u. This domesticate has lived in Tonga since human colonization (Steadman 1993). The Red-vented Bulbul *Pycnonotus cafer* (native to Southeast Asia) is abundant today on Tongatapu and Niuafo`ou. In 1995, we observed it regularly in Neiafu Village on `Uta Vava`u, the most urbanized place in the Vava`u Group; this small population of bulbuls should be eradicated before it becomes established and spreads. Vava`u does not yet have populations of three other non-native species that are established elsewhere in Tonga: Rock Dove *Columba livia,* European Starling *Sturnus vulgaris,* and Jungle Myna *Acridotheres fuscus* (Rinke 1986, 1987, Gill 1988, 1990, Steadman, pers. observ.).

In Tonga's capital of Nuku`alofa, the Red-vented Bulbul and European Starling are now the two most common species of birds. This unfortunate condition may apply as well to all of Tongatapu, the largest island (325 km^2) in Tonga. Unless the spread of non-native species is contained, such could be the eventual fate of other Tongan islands.

COMPARISONS WITH LANDBIRD COMMUNITIES IN HA`APAI

Steadman (1998) conducted methodologically identical surveys of landbirds in the Ha`apai Group of Tonga in 1995–1996. The Vava`u and Ha`apai groups (Fig. 1) share 10 species of indigenous landbirds today. Five species of landbirds (Swamp Harrier *Circus approximans,* Many-colored Fruit-Dove, Blue-crowned Lorikeet, Pacific Swallow *Hirundo tahitica,* and Fiji Shrikebill) currently occur in Ha`apai but not in Vava`u. Both the Swamp Harrier and Pacific Swallow prefer to forage near fresh water or brackish wetlands, the scarcity of which accounts for their absence or extreme rarity in Vava`u. Two of the three remaining species (Many-colored Fruit-Dove, Fiji Shrikebill) are extirpated or rare on nonvolcanic islands throughout Tonga. On the 13 nonvolcanic islands Steadman surveyed in Ha`apai, the Many-colored Fruit-Dove and Fiji Shrikebill occurred on only one and zero islands, respectively. These species seem to require mature forest, although Many-colored Fruit-Doves can exist in limited numbers without mature forest if large *Ficus* trees are available. We are unable to explain why the nectarivorous Blue-crowned Lorikeet thrives on certain islands in Ha`apai yet is absent throughout Vava`u, where there is abundant seemingly suitable habitat (open plantation, wooded plantation/early successional forest).

Two forest obligates, the West Polynesian Ground-Dove and Tongan Whistler, are the only

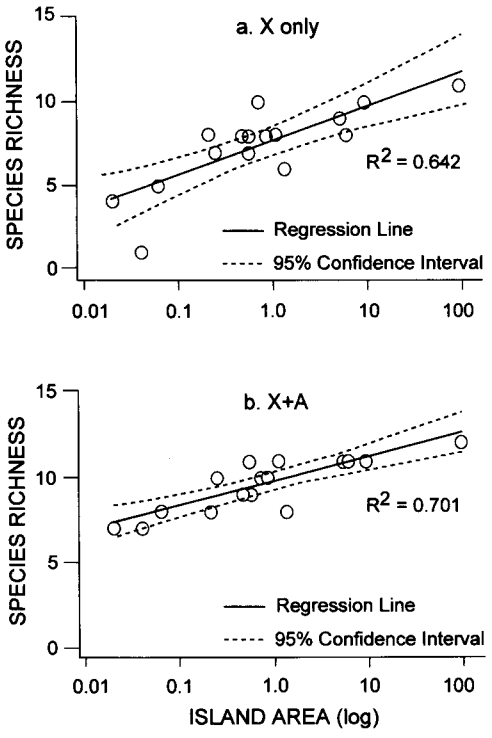

FIGURE 8. Species richness vs. island area for individual islands in Vava`u. Island areas (km^2) are from Table 1. Species richness values (X, X + A) are from Table 4. For 8a, $F_{1,14} = 25.1$, $P < 0.001$, z = 0.212. For 8b, $F_{1,14} = 32.8$, $P < 0.001$, z = 0.142.

species that we recorded in Vava`u but not in Ha`apai, where most islands lack submature/disturbed mature forest as well as mature forest. The White-rumped Swiftlet has a much broader distribution in Vava`u than in Ha`apai because this species requires caves or rockshelters for roosting and nesting. Such features are absent on all islands surveyed in Ha`apai except Tofua and to a very limited extent on Nomuka.

SPECIES-AREA RELATIONSHIPS

The values for species richness (S) versus island area (A) for all islands surveyed in Vava`u prescribe an overall positive relationship (Fig. 8). We use a semi-log rather than log-log plot of species-area values in order not to dampen the inter-island variation in S (Gilbert 1980). Our use of logA rather than A conforms to standard practice. This treatment emphasizes the influence of very large and very small islands on the relationship between S and A, here expressed as z, the slope of the line fitted to the points through linear regression (Fig. 8). The positive relationships shown, however, are weak (low z values), in spite of the inclusion of islands that span nearly five orders of magnitude of change in A.

Relatively low values for z are expected for remote island groups that have depauperate modern avifaunas (Diamond and Mayr 1976). We believe that this trend toward low z values is reflected in our data from Vava`u, where z = 0.212 for the less comprehensive S data (Fig. 8a) versus z = 0.142 for the more complete S data (Fig. 8b). Based on our knowledge of modern Polynesian avifaunas and the limitations of our surveys, we believe that the S values in Figure 8b reflect the actual avifaunas of islands more accurately than those in Figure 8a. Both values, however, consider only modern records. If prehistoric data were available, the values for S undoubtedly would be much greater. How z would be influenced by the prehistoric data is speculative, although preliminary data from Ha`apai and `Eua suggest that, in the absence of human impact, z would approach zero for Tongan islands > 1 km^2 (Steadman 1998, unpubl. data).

Except for the large island of `Uta Vava`u and the extremely small islands of Kulo and Nuku, the influence of A on S seems to be minimal in Vava`u. Much of the overall positive relationship between S and A may only reflect that it has been more difficult for humans (through both direct and indirect means) to extinguish populations of birds on large islands than on small islands (Steadman 1995). That habitat modification is an important variable is suggested by examining the points in Figure 8b that deviate the most from the fitted regression line, i.e., those that lie outside the 95% confidence intervals. Those lying below are the highly disturbed islands of Ofu and Foelifuka. Those lying above the line are islands retaining much forest in categories 4 or 5, such as `Utungake, A`a, and `Eueiki.

As island area approaches zero, it is intuitively obvious that one after another resident species must drop out as home range requirements are not met for even one pair. If all islands in Vava`u were still largely forested, however, the minimum size required to sustain the complete modern avifauna seems to be only about 1 km^2 or less (Fig. 5). Whether this was true in the past, when species richness undoubtedly was much

greater, awaits paleontological tests on multiple islands in Vava`u.

CONSERVATION IMPLICATIONS

The overall species richness and relative abundance of land birds in Vava`u today are greater in native forests than in other habitat categories. The remnant patches of mature forest sustain the remaining populations of species such as the West Polynesian Ground-Dove and Tongan Whistler. The populations of the Pacific Pigeon, Purple-capped Fruit-Dove, and Wattled Honeyeater also depend on native forests and are most abundant in mature forest. That these species were recorded at lower levels in more disturbed habitats may reflect a more transient use of these habitats or a "source-sink" situation (sensu Pulliam 1988, Brawn and Robinson 1996) in which breeding populations are sustained only by the less disturbed source areas.

The most vulnerable species of birds already have been lost throughout Tonga (and all of Polynesia) to anthropogenic predation, habitat loss, and perhaps disease (Steadman 1989, 1993, 1995). Land-use by humans is intense on most islands in Vava`u today, and during our field surveys some of the last significant tracts of mature forest on `Uta Vava`u were being cleared for agriculture. Given the evident importance of mature forests for some species and the large number of extinctions that already have occurred in Tonga, protection of the native forests of Vava`u (as well as those on `Eua and the various volcanic islands) may be essential to preserve what little remains of Tonga's indigenous avifauna.

Finally, the fundamental aspects of behavior and ecology are unknown or poorly documented for most species of Tongan birds. Detailed nesting and feeding studies of individual species are needed to understand their role in terrestrial ecosystems and their responses to disturbance and alteration of these systems.

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