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# NOTES ON THE NATURAL HISTORY, TAXONOMY, AND CONSERVATION OF THE ENDEMIC AVIFAUNA OF THE SAMOAN ARCHIPELAGO

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ABSTRACT.—The Samoan Archipelago is an important area of avian diversity and endemism within the tropical Pacific. Here, we summarize observations on the natural history and vocalizations of Samoan birds based on fieldwork conducted over the course of five visits to Samoa and American Samoa from 1977 to 2006 with particular emphasis on the Manu'a Islands and the highlands of Savai'i. We interpret our findings in light of modern understanding of the biological species concept to identify seven Samoan forms as previously unrecognized endemic species: Samoan Wood Pigeon *Columba* [vitiensis] castaneiceps, Peale's Kingfisher *Todiramphus* [chloris] pealei + manuae, Manu'a Shrikebill *Clytorhynchus* [vitiensis] powelli, Samoan Myzomela *Myzomela* [cardinalis] nigriventris, Samoan Robin Petroica [multicolor] pusilla, Manu'a Starling Aplonis [tabuensis] manuae, and Samoan Thrush *Turdus* [poliocephalus] samoensis. The number of endemic species in the archipelago thus increases from 10 to 17. Field surveys on Savai'i reveal significant differences between highland and lowland bird communities, with several lowland species reaching their upper elevational limit at 1,200 m. We conclude that the critically endangered Samoan Woodhen *Gallinula pacifica* has been extinct for over a century, and suggest that recent reports are based on misidentifications. We found the Tooth-billed Pigeon *Didunculus strigirostris* to be Critically Endangered and in urgent need of conservation action. *Received 26 January 2015. Accepted 9 August 2015.* 

Key words: conservation, endemic species, Samoan birds, Samoan Woodhen, Tooth-billed Pigeon.

The Samoan Archipelago comprises four island groups divided politically as independent Samoa (Savai'i and Upolu) and American Samoa (Tutuila and the Manu'a group). Home to 32 indigenous land birds (Watling 2001), including five classified as globally threatened (BirdLife International 2014b), it is one of the richest areas for avian diversity in Polynesia, and an important priority for conservation efforts both regionally and globally. Several authors (Mayr 1945, duPont 1976, Pratt et al. 1987, Watling 2001) have summarized the distribution and status of birds in the Samoan archipelago in a regional context and others (Amerson et al. 1982a,b; Muse and Muse 1982; Goldin 2002; Beichle and Baumann 2003) have focused solely on the archipelago. Over a decade has passed since the most recent general review (Beichle and Baumann 2003), and that one offered little new information on American Samoa.

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Here, we summarize findings based on field observations and sound recordings made in independent Samoa and American Samoa over the course of five visits between 1977 and 2006, totaling  $\sim$ 75 field days. We provide new information on the vocalizations, distribution, and conservation status of indigenous forest birds, particularly those in two understudied regions, the montane forests of Savai'i and the Manu'a Islands, and review the taxonomy of Samoan endemics using new methods for applying the biological species concept (BSC).

The island of Savai'i is an old shield volcano whose uplands support a large forest tract ( $\sim$ 720  $km^2$ ) in the island's interior from  $\sim 500$  m to the summit of Samoa's highest peak, Mt. Silisili (1,858 m; Conservation International et al. 2010). Savai'i's central rainforest is among the largest remaining intact forests in Polynesia, and as such is a critically important priority for conservation in the region (Atherton and Jefferies 2012). Nevertheless, ornithological research on Savai'i's upland birds has been limited; short papers by Reed (1980), Bellingham and Davis (1988), as well as a 2012 rapid assessment survey (Butler 2012) are all that have been published about birds in this habitat. The Manu'a Islands have also received relatively little ornithological attention despite being home to two distinctive endemic taxa. The group comprises a trio of small, volcanic islands: Tau 44 km<sup>2</sup> (max elevation: 931 m). Ofu 7.2 km<sup>2</sup> (491 m), and Olosega 5.4 km<sup>2</sup> (629 m); the latter two are often referred to as Ofu-Olosega, because they function as a single island and are connected by a short bridge. The Manu'a Islands are isolated from Tutuila and the rest of the Samoan archipelago by  $\sim 100$  km, and are its easternmost and geologically oldest islands.

Taxonomy has significant implications for conservation (Agapow et al. 2004, Mace 2004, Peterson 2006, Pratt 2010), and accurately assessing the species status of range-restricted taxa is particularly important in threatened island ecosystems such as those of the tropical Pacific. Following development of the BSC, Mayr (1945) revised the taxonomy of birds in the region and grouped many island populations into large polytypic species based on the presumption that they would interbreed in sympatry. The BSC (i.e., reproductive isolation) is still the most widely used species concept in ornithology (but see Sangster 2014). Since the mid-20th century, however, the basic paradigm for inferring genetic isolation among allopatric populations has shifted from Mayr's concept, which essentially considered all birds conspecific unless proven otherwise, to one in which all evolutionary end points are considered potential species (Helbig et al. 2002, Pratt 2010, Tobias et al. 2010, Gill 2014). Recent molecular studies (e.g., Cibois et al. 2007, 2011, 2014; Lerner et al. 2011; Andersen 2013; Andersen et al. 2014) have revealed that patterns of colonization, divergence times, and degree of genetic differentiation among island birds are often very different from historical hypotheses. With the exception of Hawaii, application of these new methods in Polynesia has lagged, and many Samoan birds have not been assessed taxonomically for over half a century. Furthermore, over-lumping of species has led to conflation of ecological and behavioral information from "subspecies" on different islands, obscuring potential isolating mechanisms. While a review of avian taxonomy is currently underway (del Hoyo et al. 2014), the methods of that study remain controversial (Peterson and Moyle 2008, Remsen 2015), and in many cases fail to include relevant behavioral and ecological data.

# METHODS

Our fieldwork in Samoa included three visits by HDP in 1977 (21 June-3 July, with P. L. Bruner), 1992 (7-8 July, with M. Lambarth and S. Fisher), and 1995 (6 June, with the cruise ship World Discoverer), together with longer expeditions totaling 60 days in the field by JCM in 2005 and HDP in 2006. In June-August 2005, JCM conducted ornithological surveys and made field observations at eight localities on Savai'i, Upolu, and the offshore island of Nu'utele. The focus of this project was to follow up a report of the Samoan Woodhen (D. Hobcroft, pers. comm.), and specific effort was made to search for this species. Observations were primarily on Savai'i, especially the higher elevations of the A'opo cloud forest (17 field days) and near Sinaloa falls, north of Sili village (6 field days). In 2006, HDP traveled to American Samoa under the sponsorship of the Wildlife Division of the Department of Marine and Wildlife Resources (DMWR) to train department personnel in field recording techniques and to collect sound recordings, particularly from the Manu'a Islands where no such recordings had been made before. This included work on Tutuila and Ofu-Olosega, from 12-23 and 29-30 November. HDP also visited Upolu and Savai'i from 14-28 November 2006 with J. O. Seamon and P. S. Fa'aumu of DMWR, with assistance from T. Foliga of the Samoa Division of Environment and Conservation, Ministry of Natural Resources and the Environment. Locality details and dates from expeditions are listed in Table 1.

On all trips, field observations began at dawn and continued opportunistically throughout the day. HDP made his recordings in 2006 with a NAGRA ARES-BB+ digital recorder with Telinga Parabola, while his earlier recordings were made on cassette tape using a Sony parabola and a Marantz PMD221 portable recorder (Sony Corp, Tokyo, Japan; Marantz, Kawasaki, Japan). JCM used a Marantz PMD660 with Sennheiser ME67 directional microphone (Sennheiser Electronic GmbH, Wedemark, Germany). Our series of over 220 recordings of Samoan birds, 17 species in American Samoa and 25 species in independent Samoa, is the most comprehensive collection of bird recordings from the archipelago, and includes many previously undescribed vocalizations. The collection is archived and publicly accessible at the Macaulay Library, (Cornell University, Ithaca, NY, USA; macaulaylibrary.org). We also reviewed recordings made by others and available online from both Macaulay Library and xeno-canto (xeno-canto.org), the online resource of the Xeno-canto Foundation Naturalis Biodiversity Center, Leiden, the Netherlands. Catalog numbers are designated as ML or XC respectively.

Our taxonomic treatments follow Pratt's (2010) paradigm in which allopatric populations with potential isolating mechanisms in two or more qualitatively different character states (e.g., differences in plumage color and voice, or voice and choice of nest site, diet and plumage), are regarded as separate biological species. This model differs from the quantitative approach of Tobias et al. (2010) in its emphasis on the biological functions of differences. We also support Gill's (2014) proposal to shift the burden of proof so that obviously different populations are considered species unless proven otherwise, but we suggest no revisions on that basis alone.

Several Samoan taxa belong to species complexes with wide distributions through Polynesia and the tropical Pacific. In this study, we focus on the Samoan members of these complexes (i.e., we do not treat all twelve subspecies within the Fiji Shrikebill *Clytorhynchus vitiensis* complex but focus specifically on the Samoan endemic *powelli* and its status relative to the other taxa). Several such widespread complexes, including Purple Swamphen Porphyrio porphyrio (see del Hoyo et al. 2014), Polynesian Triller Lalage maculosa, and Wattled Honeyeater Foulehaio carunculata (Andersen et al. 2014), warrant taxonomic re-evaluation, but we limit our discussions here to those taxa that potentially qualify as endemic Samoan species. We recognize several budding species (Frey 1993) wherein a small isolate, such as an island population, rapidly develops reproductive isolation while the components of its parent species do not, rendering the parent species paraphyletic. We note that listmakers are often reluctant to recognize such species without a review of the parent complex, but we argue that delaying the recognition of such species, solely because a larger complex has not been completely analyzed, both slows understanding of the speciation process and can have serious negative consequences for conservation of biodiversity (Mace 2004, Pratt 2010).

#### RESULTS

We found 48 bird species, including all native land birds except the Samoan Woodhen, plus three introduced and invasive species, Red-vented Bulbul Pycnonotus cafer, Jungle Myna Acridotheres fuscus, and Common Myna A. tristis. Across 10 sites that received >1 full day survey effort, the lowland forest around Sinaloa Falls was the most diverse with 24 species, followed by the upper elevations of the A'opo cloud forest (22 species), the A'opo forest trail (20) and Lake Lanoto'o on Upolu (20). While lowland and highland sites on Savai'i had comparable overall diversity, we did not find three common lowland species (Purple Swamphen, Flat-billed Kingfisher Todiramphus recurvirostris, and Samoan Flycatcher Myiagra albiventris) above 1,200 m. Conversely, we did not find three common highelevation species (Samoan White-eye Zosterops samoensis, Samoan Thrush Turdus samoensis, and Mao Gymnomyza samoensis) below 500 m (but note that HDP found the Mao near Sauniatu Village in 1977).

Among indigenous Samoan land birds, we observed but do not provide separate accounts for Banded Rail *Gallirallus philippensis*, Spotless Crake *Porzana tabuensis*, Many-colored Fruit Dove *Ptilinopus perousii*, Blue-crowned Lorikeet *Vini australis*, Barn Owl *Tyto alba*, White-rumped Swiftlet *Aerodramus leucopygia*, Polynesian Triller *Lalage maculosa*, Samoan Starling *Aplonis* 

	TABLE 1. Localitie	s in the Samoan Archipelago	visited by authors, with comments on local habitat and elevation.
Locality	Coordinates	Survey dates	Description: habitat and altitude (m)
Savai'i, Samoa 1. A'opo forest trail	13.571°S 172.507°W	6,11, 23–24 Jun 05, 24–26 Nov 06	Trail from A'opo village climbing to the lower limits of montane forest; gardens, secondary habitat, selectively logged forest (250-1000m)
2. A'opo cloud forest	13.610°S 172.506°W	10-23 Jun, 29-31 Jul 05	Upper reaches of the Above trail, Mata o le Afi, and Mt Silisili; montane primary forest, open earth around recent lave flows (1000–1850m)
3. Sinaloa Falls	13.674°S 172.426°W	13–16 Jul, 3–5 Aug 05	Valley between Siliv linge and the base of Sinalog falls; gardens, river edge, disturbed lowland ferror with extension encode financial solution (2000, 500m)
4. Tafua Crater, Falelologo Peninsula	13.787°S 172.251°W	1–2 Aug 05 26–27 Nov 06	torest with extensive areas of invasive metremut penatu (200-2001) Coastal forest reserve; gardens, disturbed lowland forest (sea level)
Upolu, Samoa 5. Lake Lanoto'o and upper Cross-island hichway	13.910°S 171.827°W	25 Jul, 14 Aug 05	Forest surrounding the lake; montane forest, secondary growth (ca. 700m).
6. Mt Vaca 7. Apia	13.865°S 171.765°W 13.834°S 171.750°W	5 Jun, 15 Aug 05 4-7, 25-28 Jun, 20-24	Small reserve located near Apia; gardens, lowland forest (ca. 400m) Capital city of Samoa; urban and suburban gardens, coastal habitat (sea level)
8. Nu'utele island 9. Sauniatu village	14.063°S 171.425°W 13.926°S 171.622°W	27–29 Jun 77	Small offshore island; coastal habitat, lowland primary forest (sea level). Small village with nearby waterfalls and forest; agricultural fields, pastures, low hills with primary forest (ca. 170m).
American Samoa Tutuila	14.295°S 170.700°W	10-12 Aug 05 12-15,	Governmental center (Pago Pago) of American Samoa. Entire island road-surveyed; urban and
Ofu-Olosega	14.175°S 169.618°W	22-22, 29-20 INOV UD 15-21 Nov 06	suburban garderns, secondary lorest, primary rannorest in rotational rank of American barnoa. Steep-sided twin islands with mostly primary rainforest; narrow flat sandy area on south side of Ofu supports small village with coconut-breadfruit agroforest.

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*fuscus*, and Wattled Honeyeater *Foulehaio car-unculatus*.

#### Species Accounts

Samoan Woodhen (Gallinula pacifica).-[Note: We prefer "woodhen" (Pratt et al. 1987, Dickinson 2003, Gill and Donsker 2014), over "moorhen" (Monroe and Sibley 1993, Taylor 1998, Clements et al. 2013), "gallinule" (Hume and Walters 2012), and "wood rail" (Mayr 1945, Ripley 1977). It provides a unique epithet for the distinctive forest rallids formerly placed in the genus Pareudiastes.] The Samoan Woodhen is known from three study skins and a single egg; the first specimen was collected in 1869, and the last two were given to the Challenger expedition in 1873 (Taylor 1998, Steadman 2006). Assertions that the species persisted until 1907 derive from a remark by K. Stoentzer in Apia, who "confirmed that this species is extinct, probably since 1907" (Reed 1980:155). However, hope that the woodhen might persist was revived by Bellingham and Davis (1988) who in 1984 reported two observations of a medium-sized rallid with "long red legs and a dark gray back and wings" in forest  $\sim 1 \text{ km}$ west of Mt. Elietoga. More recently, Dion Hobcroft and members of a 2003 birding tour reported an encounter with two 'black rallids' that were calling near the A'opo forest trail at 990 m on 5 October 2003 and were "possibly the Samoan Moorhen as the size, color, shape, behavior and the distinctive calls did not tally to anything else" (D. Hobcroft, pers. comm.).

The possibility that the woodhen might survive depends on a population persisting in undisturbed areas of Savai'i's montane forest where the species could escape human observation as well as persecution by introduced predators. Locations sufficiently remote to meet these criteria are almost exclusively above 1,200 m in Savai'i's interior highlands. However, we find no evidence that the woodhen ever occurred in montane environments. Mayr (1945:112) discounted the idea, stating that the woodhen "has been reported to live in the mountains in self-excavated holes, but [is] obviously confused with some species of Tubinares [i.e. petrels]." We agree with Butler (2012) that many lowland species, including other Samoan rallids such as Purple Swamphen and Buff-banded Rail Gallirallus philippensis, do not occur in the highlands of Savai'i above 1,200 m. The unconfirmed observations by Bellingham and Davis (1988) and Hobcroft were at the upper elevational limits of swamphens and Buff-banded Rails (Bellingham and Davis [1988] do not give a specific elevation for their sightings, but the slopes west of Mt Elietoga are all below 1,000 m). Thus, the survival of a population of woodhens in the highlands relies on the species surviving in a habitat where there is no confirmed evidence that it ever occurred.

Second, the two reports described by Bellingham and Davis (1988:123-124) both mention "red legs" as a conspicuous field mark and describe the bird's plumage as either "dark grey back and wings with a lighter grey rump" or simply "dark grey." Hobcroft, meanwhile, describes the birds seen by him as entirely "black" and "blackish" but makes no mention of leg color. In addition to being somewhat contradictory, both of these descriptions fail to eliminate two other native rallids, Spotless Crake and juvenile Purple Swamphen, which are either black, in the case of the crake, or dark gray, in the case of the swamphen. Hobcroft compared the vocalizations he heard with those of Buff-banded Rail and feral chickens, but did not consider Spotless Crake, which HDP heard calling at night near the same location. More significant is that neither observation matches specimen descriptions of Samoan Woodhen. The woodhen was never described in life, but on museum specimens, the feet and bill are dull vellow. The idea that the feet might have been red originates from a comment by Mayr that the yellow of specimens was "probably red in life" (Mayr 1945:111), a common color change that occurs as study skins dry and age, but both he and Ripley (1977) are careful to note that this may not actually have been the case. Ripley (1977:273) describes the bill and feet as "(probably) red" but illustrates the bill and frontal shield as yellow (Ripley 1977: Plate 34). Pratt et al. (1987) purposely illustrated the species in black and white because of uncertainty regarding the soft part colors. In plumage, Ripley describes the color as: "above dark olive, with a somewhat greenish tinge...lower rump, upper tail-coverts, and tail black" (Ripley 1977:273). In this context, one would expect a field observation of Samoan Woodhen to describe the bird as dark olive with brightly-colored legs (red or yellow) and a conspicuous frontal shield, something not done by either of the recent reports. In our view, neither the Hobcroft (pers. comm.) nor the Bellingham and Davis (1988) reports meet the standards for acceptance by modern bird records committees.

Finally, the status of the Samoan Woodhen must be considered in context of other flightless rails across Polynesia and the Pacific. Steadman (2006) estimates that between 500-1,600 species of flightless rails inhabited Pacific islands prior to the first human colonization. Today, not a single species of flightless rail survives on inhabited islands in Polynesia outside of New Zealand. The Henderson Crake Porzana atra persists only on uninhabited Henderson Atoll, and the Fijian Bar-winged Rail Nesoclopeus poecilopterus has recently been declared extinct (BirdLife International 2014a), despite an unconvincing 1970s report (Holyoak 1979). These extinctions began with the arrival of the first Polynesians (Steadman 1995, 2006), followed by a second wave associated with the advent of European colonization and introduction of additional predators (Blackburn et al. 2004). The last confirmed reports of Samoan Woodhen correspond closely with increased European contact and the likely arrival of domestic cats to Samoa. In July 2005, JCM found direct evidence of predation by feral cats (see Samoan Thrush account, below) in Savai'i's montane forest above 1,200 m, as did Butler (2012) during surveys of the area in 2012, indicating that these feral invaders have reached even the most remote places on the island.

Despite a concerted effort, neither we nor Butler (2012) found any trace of Samoan Woodhens, nor did we hear any reports of sightings from local villagers in A'opo and Sili. A public awareness campaign that included newspaper articles and requests for information (Tavita 2010) also turned up no new evidence of the species' survival. In summary, (1) no one has produced a confirmed report of Samoan Woodhen since 1873 despite repeated searches over the course of the twentieth century; (2) timing of the bird's decline coincides with the arrival and spread of European invasive species; and (3) current distribution of invasive predators throughout Savai'i argues against the survival of a flightless rail on the island. Therefore, we conclude that the Samoan Woodhen is extinct.

Samoan Wood Pigeon (Columba castaneiceps).—The Samoan taxon castaneiceps has previously been regarded as the easternmost subspecies of the White-throated or Metallic Pigeon *C. vitiensis* complex, distributed from the Philippines to southern Melanesia and Samoa (Gibbs et al. 2001). This complex shows strong geographic variation in both plumage and voice, and the differences follow roughly parallel lines of demarcation suggesting that at least four species may be involved, of which the Samoan Wood Pigeon is one. The white-throated forms in the complex range from the Moluccas eastward through Melanesia to Samoa with halmaheira (Moluccas to Solomons), leopoldi (Vanuatu), hypoenochroa (New Caledonia) and vitiensis (Fiji) all exhibiting various shades of rich pinkish chestnut on the breast and neck, with the crown a darker slaty brown. The nominate Fiji form is the palest of the group. To the east, the Samoan castaneiceps reverses the color pattern and has a dark chestnut crown (as reflected in its Latin epithet) contrasting with glossy, slate underparts such that it appears at a distance to be all dark with a white throat (for direct comparison, see Plate 26 in Pratt et al. 1987).

Earlier literature often conflated vocal descriptions from several different forms, obscuring geographically based differences. In fact, neither Pratt et al. (1987) nor Watling (2001) describe the voice of Samoan Wood Pigeon, their descriptions applying to Fiji birds only. Samoan Wood Pigeons are usually rather quiet, with their songs easily overlooked in a chorus of other columbids. The vocalist is often not in view, and the song has rarely been recorded. Beichle (1991) was the first to accurately describe the voice of the Samoan Wood Pigeon and illustrate it with sonograms, and McPherson (1995) published the first sound recording (made by T. G. Lovegrove in 1982). The "song" (ML 139951) is a series of low coos, similar to, but slower paced (6/10 sec; Beichle and Baumann 2003) than the song of the Tongan Ground Dove Gallicolumba stairii (18/10 sec), and reminiscent of the hooting songs of fruit doves Ptilinopus spp. This song is unique within the vitiensis complex, and completely different from the variably syncopated, short burst of rather staccato hoots, whup! hoo-doo, with variations in pitch and rhythm, given by Fijian birds, or a low moaning hooo-ooo uttered by all members of the complex (Coates and Bishop 1997; Kennedy et al. 2000; Gibbs et al. 2001; HDP, pers. obs.), except apparently, castaneiceps. In a survey of limited available recordings, HDP found no examples of the latter call from Samoan birds.

The vocal differences between Samoan Wood Pigeon and other populations of "White-throated" Pigeon are so striking that when HDP, at the time more familiar with Fijian birds, first recorded the Samoan form, he mistook the song for that of a ground dove (*Gallicolumba* sp.). With striking potential isolating mechanisms in color and vocalizations, the Samoan Wood Pigeon clearly satisfies modern standards as a Samoan endemic species separate from the rest of the *C. vitiensis* complex. We encourage the use of the epithet "wood pigeon," already widely used among Indo-Pacific *Columba* (Gill and Donsker 2014), to distinguish the members of this complex from other columbid groups in the region.

This newly recognized endemic is restricted to Savai'i, Upolu and the small offshore islands of Apolima and Manono (duPont 1976). Earlier reports (Keith 1957, Ashmole 1963) of its presence on Tutuila have been discounted (Amerson et al. 1982b). In June and July 2005, JCM found Samoan Wood Pigeons to be fairly common near Sinaloa falls and in montane forest above 1,000 m on the A'opo trail. Butler (2012), however, only observed wood pigeons at two of three survey localities in the interior and HDP found it only at low elevation in November 2006, suggesting that these frugivores may engage in seasonal movements. Although this species remains relatively common, hunting of native pigeons is widespread in Samoa and Samoan Wood Pigeons undoubtedly suffer some degree of hunting pressure.

Tongan Ground Dove (Alopecoenas stairi).-This species is widely distributed in western Polynesia, but its current range is patchy and in many archipelagoes it is confined to small offshore islands. Such appears to be the case in Samoa, where despite earlier authors' listing it as present on both Savai'i and Upolu (Mayr 1945, duPont 1976), it appears now to be absent from the larger islands. A population in central Upolu was studied in the 1980s (Beichle 1991, Beichle and Baumann 2003), but we know of no certain records for that island within the past decade. Thus, within the Samoan archipelago, the Tongan Ground Dove appears to be confined to Ofu-Olosega and the tiny island of Nu'utele off Upolu (Freifeld et al. 2001). JCM observed a single individual foraging on the forest floor on Nu'utele in July 2005; on Ofu-Olosega, HDP saw one individual in November 2006 and J. O. Seamon obtained a recording (ML 139864) on the rough road that leads to the ridge above the main village at the western end of Ofu. The species is considered Vulnerable by BirdLife International (2014a), and is a candidate for threatened status in American Samoa (US Fish and Wildlife Service 2013). Our limited observations bear out the species' rarity in the Samoan Archipelago. This species, along with other Polynesian and Melanesian congeners, has traditionally been placed in *Gallicolumba*. Here we follow Jønsson et al. (2011), and our English name follows Gill and Donsker (2014).

Tooth-billed Pigeon (Didunculus strigirostris).— The Tooth-billed Pigeon or Manumea is Samoa's most distinctive endemic bird, and one of the region's conservation icons. Its global conservation significance is reflected in its ranking as one of the top 50 bird species worldwide in terms of evolutionary distinctness and rarity (Jetz et al. 2014). Tooth-billed Pigeon is known only on Savai'i, Upolu, and Nu'utele (Beichle 1987, 1991; Freifeld et al. 2001; O. Langrand and J. Thomsen, pers. comm.), and it was recently uplisted to Critically Endangered based on apparently severe recent declines (BirdLife International 2014a).

Our work produced two certain and three probable detections of Tooth-billed Pigeons. On 21 June 2005, JCM heard but did not record calls from a pigeon calling near the Mata o le Afi crater at 1,600 m in the early evening. Based on the pacing of the notes and the location of the caller inside dense forest, he thought the bird was likely a Tooth-billed Pigeon. On 21 November 2006, HDP saw a single individual in flight in recently logged forest just below 1,000 m on the A'opo trail and later the same day recorded a vocalization that his Samoan colleagues identified as this species (ML 139881). The following day, P. S. Fa'aumu observed a bird perched overhead near the base camp when he was alone there, and on 24 November, HDP recorded another unseen pigeon (ML 139904) that, based on pace of the notes and a direct comparison with the vocalizations of Pacific Imperial Pigeon Ducula pacifica, was almost certainly a Tooth-billed Pigeon, despite the lack of visual confirmation. Note that only JCM's audio record was above 1,200 m. Similarly, Butler (2012) had only one "uncorroborated" sighting of Tooth-billed Pigeon in montane forest (at 1,300 m) despite targeted searches and the presence of abundant fruits of its preferred food trees, Dysoxylum spp. Thus, higher elevations may provide only marginal or seasonally-specific habitat for this species.

The Tooth-billed Pigeon's low moaning calls sound very much like some calls of the much more common Pacific Imperial Pigeon, a fact that is under-appreciated and that has likely resulted in erroneous voice-only reports of the species. According to Beichle (1991), the main difference is in the pace, or spacing, of the individual notes, but we have found this difference to be unreliable (see Pacific Imperial Pigeon below). Relatively little is known of the behavior and ecology of the Tooth-billed Pigeon, but Beichle (1987) and Gibbs et al. (2001) have speculated that the birds spend significant time foraging and perhaps nesting on the ground, which would make it especially susceptible to invasive predators. Two other ground-dwelling native species in Samoa have declined (Tongan Ground Dove) or gone extinct (Samoan Woodhen) over the last century. A juvenile Tooth-billed Pigeon photographed in December 2013 (Fowlie 2014) provides the first visual documentation this century and indicates that the species is still breeding. Given the recent population decline, the bird's potential vulnerability to invasive predators, and likelihood that previous population estimates included erroneous voice-only reports, the Tooth-billed Pigeon is clearly Samoa's most endangered bird.

Crimson-crowned Fruit Dove (Ptilinopus porphyraceus).-The Samoan endemic subspecies fasciatus of Crimson-crowned Fruit Dove has previously been included in a species complex together with porphyraceus (small islands of Tonga, Fiji, Niue), graeffei (Wallis and Futuna, Niuafoou) and the Micronesian taxa hernsheimi (Kosrae), and ponapensis (Chuuk and Pohnpei). Recently, del Hoyo et al. (2014) have proposed elevating four taxa to species status (with graeffei discounted as a hybrid form) based primarily on morphological criteria. The separation of the Polynesian (fasciatus and porphyraceus) and Micronesian (hernsheimi and ponapensis) taxa into separate species is well supported by molecular (Cibois et al. 2014), vocal, and morphological data (Hayes et al. 2016). Note that both "Crimsoncrowned" and "Purple-capped" have been used as English names for the larger P. porphyraceus complex, but they should now apply only to Polynesian and Micronesian species respectively. We believe, however, that del Hoyo et al.'s (2014) results with regard to porphyraceus and fasciatus are an artifact of their scoring system, which in this case amplifies subtle color differences. They also fail to consider vocal similarities and clear evidence of possible unrestricted hybridization and gene flow.

Beichle (1991), Beichle and Baumann (2003), and Hayes et al. (2016) give detailed descriptions of the vocalizations in this complex. The three Polynesian taxa all utter a variable but always halting series of hooting notes *hooo*, *hup-hoo*, *hup*- hoo, hoo-hoo-hoo that often sounds like the bird is stuttering, or stopping then starting again. HDP examined all published recordings and found little differentiation among the Polynesian subspecies. In contrast, the two Micronesian taxa have striking differences in voice which, coupled with plumage differences, justify ranking them as two species (Hayes et al. 2016). When compared morphologically, Samoan fasciatus show a yellowish-white band at the tail tip, a red rather than deep purple (as in *porphyraceus*) belly patch, and red-orange rather than yelloworange undertail coverts-differences significant enough to suggest incipient speciation. However, graeffei whose range lies between Fiji and Samoa. exhibits highly variable coloration with elements of both the nominate taxon and *fasciatus* and thus looks very much like a hybrid population, as suggested by del Hoyo et al. (2014). This situation may indicate either ongoing gene flow (fruit doves have been observed flying away from islands during fruit crop failures; V. Masibalavu, pers. comm.) or that the parent taxa have not yet completed the process of speciation despite their plumage differences, or both. Unfortunately, Cibois et al. (2014) did not sample fasciatus, so taxonomic decisions must be based solely on phenotypic and natural history data for the time being. Crimson-crowned Fruit Doves are common at all elevations throughout the Samoan Archipelago, although Beichle (1991) suggested that high concentrations of birds around preferred fruiting trees might give the false impression that populations are locally greater than they are.

Pacific Imperial Pigeon (Ducula pacifica).-This large pigeon is distributed from Melanesia across central Polynesia to the Cook Islands, including the Samoan Archipelago. These populations are undifferentiated taxonomically, which may suggest ongoing gene flow. Despite considerable hunting pressure, Pacific Imperial Pigeons remain fairly common and conspicuous (at least vocally) in the Samoas. As stated above, we believe that inadequate descriptions of the voice of this species may, in the past, have led to inflated population numbers of the rare and similarsounding Tooth-billed Pigeon. The most common call is usually described as a growl or moan, punctuated by a trill of sharper tones, like the sound of plucking the teeth of a comb (ML 140746). This higher-pitched growl is unlikely to be confused with the low moans of the Tooth-billed Pigeon, but a secondary low moan of D. pacifica

may at times be indistinguishable. An important difference is that a series of moans from a Pacific Imperial Pigeon usually varies in both pattern and cadence, and almost always include some growls if the sequence is long enough (ML 139884). In our recordings, we have not been able to duplicate the steady pace reported by Beichle (1991) but rather find that the spacing of the individual notes is usually irregular, unlike the steadier pace of the Toothbilled Pigeon, whose individual moans are much more stereotyped, a smoothly rising and descending *mooOOOooo*. Often, Pacific Imperial Pigeon moans are more structured, and may seem multisyllabic *ooo-WOOO-oo* (ML 5745, 01:00 and onwards).

Flat-billed Kingfisher (Todiramphus recurvirostris).-Flat-billed Kingfisher is common throughout the lowlands and coastal areas on Savai'i and Upolu. Whereas previous references (Muse and Muse 1982, Watling 2001) describe this species as occurring at all elevations, we found that it was absent from upland forest above 1,200 m on Savai'i. This pattern was also observed by Butler (2012), who recorded Flat-billed Kingfisher up to 1,200 m on the A'opo trail but did not find it in the highland interior above this elevation. Bellingham and Davis (1988) found kingfishers to be less common in upland habitats around 1,000 m, but as noted above, apparently did not survey higher than 1,200 m. A similar elevational limit occurs with kingfisher species on other tropical islands (e.g., Coates and Bishop 1997) and is likely because of paucity of food items such as large insects and lizards in cooler montane forests.

The Flat-billed Kingfisher's most common advertising "song" comprises loud, rapidly ( $\sim 3/$ sec) repeated notes *pio-pio-pio-pio-e*tc. that rise, then remain at a level pitch, then descend again (2–3 notes in rising or falling portion). These notes are uttered in bursts of 10–25 iterations. Beichle and Baumann (2003) show sonograms of four variants of this call. A less frequent vocalization, but the only one described by Pratt et al. (1987) and Watling (2001), is a slower series of 8–10 lively double notes *to-flee, to-flee, to-flee* etc. that may end in a series of 3–4 raspy hissing notes. The entire repertoire can be heard on ML 64535 (02:30 to end).

This Samoan endemic has long been considered a relative of the Sacred Kingfisher *T. sanctus*, with Fry and Fry (1992) even regarding it as conspecific. A robust molecular study by Andersen et al. (2015), however, found that this species is sister to the Pohnpei and Guam "subspecies" of the Micronesian Kingfisher *T. cinnamominus*, a group Pratt and Etpison (2008) previously suggested actually comprises three species. Other than the fact that all have strongly rusty or ocher-tinged plumage (restricted to juveniles in *reichenbachii* of Pohnpei), these forms do not closely resemble each other and their relationship to the Flat-billed Kingfisher is by no means visually or behaviorally obvious.

Peale's Kingfisher (Todiramphus pealei).-The two taxa of Peale's Kingfisher pealeii (Tutuila) and manuae (Manu'a Islands) are the easternmost geographic outliers of the complex of Collared Kingfishers and are separated geographically from the rest of the group by the intervening Flat-billed Kingfisher (above). With nearly 50 nominal subspecies distributed from the Red Sea to Samoa, this complex is one of the most polytypic of nominal avian species. Recent molecular analyses by Andersen et al. (2015), however, indicate that this complex is in fact highly paraphyletic, and comprises 26 or more species. Andersen et al. (2015) found Peale's Kingfisher to be a distinct lineage, but since the clade had been incompletely sampled decided to take a conservative approach, pending further scrutiny, and recommend including these taxa with other members of the Collared Kingfisher complex found from eastern Melanesia to American Samoa as a single species, Pacific Kingfisher T. sacer. Our observations of potential isolating mechanisms in plumage and voice, when considered in light of genetic distinctiveness, suggest that Peale's Kingfisher is probably better considered a distinct biological species with two subspecies.

Peale's Kingfisher is smaller than other Pacific taxa of the *chloris* complex, but larger than the Flat-billed Kingfisher. The blue-and-white plumage pattern of the nominate subspecies, with a white forehead and only a blue skullcap surrounded by white and a broken eye stripe (Fig. 1a), is reminiscent of that of the Chattering Kingfisher T. tutus of the Cook and Society Islands to the east, while the *manuae* subspecies has a head pattern more like those of Tongan and Fijian forms, with the blue of the crown extending through the forehead to the base of the bill, a pale eyebrow (broader than in others), and a prominent dark eye stripe (Fig. 1b). Peale's Kingfisher resembles sacer (Tonga) and marina (Lau Group, Fiji) in having pure white underparts, a feature that differs from other members of the Pacific Kingfisher group, which tend to have ochre-tinged underparts. This difference may indicate a species-level boundary, but note the much larger size of Tongan birds (duPont 1976, Pratt et al. 1987).



FIG. 1. Presumed adult male Peale's Kingfishers *Todiramphus pealei*: a) *T. p. pealeii* of Tutuila and b) *T. p. manuae* of the Manu'a Islands, showing the characteristically large amount of white above the eye. Both photos by HDP, November 2006.

The vocal repertoire of Peale's Kingfisher is generally similar to that of other taxa in the Pacific Kingfisher group, but with subtle differences. The louder of its two "songs" is a lengthy, paced series of identical slightly upslurred notes: weep-weep-weep-etc., or twee-twee-etc. at ~2/sec (ML 139812 pealei, XC 180839 manuae). It is slower and more plaintive, with less incisive individual notes, than the presumably homologous vocalization of the Fijian vitiensis (ML 139742). The other song includes a short introductory note followed by an extended high-pitched quavering one: chip-weeah, chip-weeah, chip-weer, etc. (ML 139824) that sounds much like similar notes heard in Fiji. The alarm call begins with a series of toneless raspy hisses that gradually morph into long shrieks similar to the second note of the second song: ssch-ssch-ssch-ssch-ssch-sschreshreeeah-shreeeah-shreeah (ML 139822). It is quieter and less vigorous than similar calls in Fiji. Tongan kingfishers have not been adequately sampled vocally to make meaningful comparisons. Peale's Kingfisher is common throughout its range and occurs throughout coastal areas and human-modified habitats. As such, it is not a species of conservation concern.

*Mao* (Gymnomyza samoensis).—This Samoan endemic is globally Endangered (BirdLife International 2014a) and found only in upland habitats on Savai'i and Upolu; a population that once occurred on Tutuila is now apparently extinct (Higgins et al. 2008). Despite, or perhaps because of, its rarity, it is among the best studied of all Samoan endemics (Beichle 2010) and is the focus of ongoing research (Leaman 2014). As did previous authors (e.g., Butler 2012), we found this species to be patchily distributed but relatively common in some areas of Savai'i's highland forest; at least five territories were present in the vicinity of the Mata o le Afi volcano in June-August 2005. In 2005 and 2006, we found the Mao only in highland rainforest, but HDP and P. L. Bruner observed and recorded it in forest edge adjacent to pastures near the village of Sauniatu (185 m) on Upolu in 1977. Beichle (2010) reported it from similar habitats as well as suburban areas with large trees, and Watling (2001) suggested it may opportunistically visit coastal coconuts in times of ecological stress, such as after hurricanes.

The vocal repertoire of the Mao has been described as catlike or wailing (Orenstein 1979, Pratt et al. 1987) with louder notes interspersed, often with an eerie or even maniacal quality. Beichle and Baumann (2003) give 6 sonograms of representative variations. Paired birds often sing back and forth, sometimes engaging in true duets (XC 110574). Bruner's recording (ML 5736) resulted when a pair of birds responded to playback of their sounds by approach and loud *tchowp!* calls and mewing wails. A wide variety of songs and calls, recorded by M. Feuersenger at two localities on Upolu in 2012, can be heard on xeno-canto.

Songs are highly variable, but most involve slowly upslurred or downslurred humanlike whistles. They vary from simple (XC 110559) to complex (e.g., XC 110447, 110558). Foraging birds utter a variety of quieter yelps, chirps, and short whistles, sometimes given as a rhythmic series (ML 139924). The Mao tends to be particularly vocal in the late afternoon and early evening.

Samoan Myzomela (Myzomela nigriventris).-Current taxonomic arrangements place the Samoan taxon nigriventris within the Cardinal Myzomela M. cardinalis complex, the other components of which inhabit the Solomons, Vanuatu, and the Loyalty Islands (Higgins et al. 2008, Dutson 2011). The Cardinal Myzomela group previously included both Micronesian M. rubratra and Rotuma Myzomela M. chermesina (Mayr 1945), which are now usually recognized as separate species (Pratt et al. 1987, Higgins et al. 2008, Hayes et al. 2016). As presently constituted, the Cardinal Myzomela has a disjunct distribution with the Samoan form isolated from supposed conspecifics by a large geographic distance, as well as two intervening congeners: Rotuma Myzomela and Orange-throated Myzomela M. jugularis of Fiji. More importantly, this taxonomic arrangement overlooks significant vocal and morphological differences among the Micronesian, Melanesian, and Samoan taxa. In light of these differences, we recognize the Samoan Myzomela as a distinct species. The Samoan Myzomela occurs throughout the Samoan Archipelago, where it is common in forested habitats as well as towns and villages at all elevations where it is often seen in flowering trees.

Males of all members of the Cardinal Myzomela complex are red and black, and fall roughly into two groups, those with red extending down the flanks and mingling with black along the margin, and those with a sharply defined head and breast (Higgins et al. 2008). Samoan males are of the second type. Females are far more varied within the complex, some resembling dull versions of their respective males, whereas others are mostly brown or gray with only tinges or patches of red. We suspect the female phenotype is likely a better indicator of species boundaries than males in this complex. Samoan females are unique in being plain dark gray above and buffy below, with a bright red rump patch. Samoan birds are also slightly smaller than most other forms, with relatively smaller bills.

Many, but not all, *Myzomela* possess distinctive, complex dawn songs that function primarily for mate attraction rather than territorial defense (van Balen 2008). Hayes et al. (2016) cited striking differences between the dawn songs of the Micronesian (ML 55634, ML 55659) and the Samoan Myzomela as one of the justifications for splitting the former from the original complex (Pratt et al. 1987). Similar comparisons between dawn songs of Samoan Myzomela and other members of the cardinalis complex, however, are impossible because all except sanfordi of Rennell Island apparently lack dawn songs altogether (Dutson 2011). This striking difference probably signals a species boundary. Like dawn songs of the Micronesian Myzomela, those of the Samoan taxon are heard only at dawn, and cease abruptly at the moment the light level is sufficient for human vision. They differ from the rather jerky Micronesian songs in being much more melodic, with up- and down-slurred whistles, sometimes paired and some with a burry quality, and occasional low raspy notes or short trills (ML 139807, best at 01:35). This song may last several minutes. During the day, the most frequent vocalizations are short phrases of usually two elements, the first either a quick dropping whistle or a buzzy sound, the second a sharply rising whistle: jeeer-zeeet or brrr-zheet or fee-er-zeet. These notes seem to be used more as contact calls than primary songs, as they are usually given by actively foraging birds. Beichle and Baumann (2003) give sonograms of six examples. Also heard is a raspy scold or alarm note jeee-jeee etc. Similar calls are given by most other members of the *cardinalis* complex. Occasionally a few of these notes are combined into a short songlike vocalization, but only the Melanesian members of the complex appear to have a true daytime song (Dutson 2011; ML 64459). The wide range of vocal and plumage differences in the cardinalis complex suggest that several more species may be imbedded within it, especially lifuensis of the Loyalty Islands, whose vocalizations and plumages are the most distinctive.

Samoan Triller (Lalage sharpei).—This Samoan endemic is found mostly above the normal range of the common lowland Polynesian Triller, although they overlap broadly. While the Polynesian Triller forages in low trees and on the ground, the Samoan Triller is a forest bird that frequently forages in the canopy of the tallest trees (we have never seen it on the ground). Trillers are named for their songs, which comprise rapidly reiterated notes, but in the case of Samoan Triller, previous authors (Pratt et al. 1987, Watling 2001) have only mentioned a weak, squeaky, up- or downslurred trill. Beichle and Baumann (2003), as well as our recordings, reveal that the vocal repertoire of the Samoan Triller is far more varied and extensive than previously appreciated, and that the aforementioned squeaky trill (ML 5722) is probably a call note rather than a song. Indeed, the Samoan Triller sometimes utters a trill nearly as loud and conspicuous as that of Polynesian Triller (see ML 139943 at 02:53), but more often, it utters a quieter short burst of usually five clear notes twee-twee-twee-twee (ML 139936). While foraging, it also utters short two- or threenote whistles that could be transliterated as fee-ertseet, sooee-tseu, or sweet-seet, as well as quicker notes in pairs or triplets, ti-di-dit (ML 139936) or chi-chit (ML 139913). Other whistled notes are up-slurred with a buzzy quality sooeet or tasweee (ML 139938). A single bird may go through nearly the whole repertoire over several minutes of vocalizing (ML 139902), and differentiating calls and songs among the variations is not possible. A less frequent call is a single very high-pitched hiss-like zheeet given at a rate of 1/ 1.5sec (ML 139914; sonogram in Beichle and Baumann 2003:89). Beichle and Baumann (2003) consider the entire repertoire to be very quiet, audible for only <15 m, but HDP found that birds singing while foraging in the canopy could be clearly heard from the ground.

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Samoan Whistler (Pachycephala flavifrons).-We have little new to add for this common endemic except to point out a previously misfiled 1992 HDP recording (ML 64534) of dawn song, first described by Beichle and Baumann (2003). The song was given by a bird obscured by predawn darkness, and ceased abruptly when the light became bright enough to see. It was a lengthy performance (11 mins) with only brief pauses, and involved rapid reiteration of the normal territorial song with pauses between each phrase of <1 sec. Each phrase was a series of quick whistles such as sweet-oh-sweeter-sweetie-sweet! building to an emphatic loud note, equivalent to the "whiplash" ending of songs of other whistlers of the region (Watling 2001). Beichle and Baumann (2003) consider this species' song very similar to that of the Wattled Honeyeater, but we never confused the two in the field.

Samoan Fantail (Rhipidura nebulosa).—Endemic to Savai'i and Upolu, Samoan Fantails are common in forested habitats on both islands. Mayr described birds on Savai'i as a distinct subspecies altera on the basis of lighter overall coloration and plumage characters including "white marks more pronounced; the white postocular stripe broader and longer; the white supraloral spot more pronounced; most specimens with a distinct whitish throat which is exceptional in nebulosa" (Mayr 1931:13). Our observations suggest that differences between these populations are not as clearcut as previously reported, and that they may more accurately reflect individual, rather than geographic, variation (Fig. 2). White-throated individuals are not uncommon on Upolu, while dark-throated ones seem about equally common on Savai'i. Indeed, one can find examples on Upolu that could pass for extreme examples of altera (e.g., Fig. 2c). Further research will be needed to confirm the validity of the two named subspecies.

Manu'a Shrikebill (Clytorhynchus powelli).-The Lesser, or Fiji, Shrikebill Clytorhynchus vitiensis is a polytypic and variable species with twelve recognized subspecies distributed widely in Fiji and western Polynesia but absent from most of the Samoan Archipelago except for an outlier in American Samoa's Manu'a Islands, where the outlier taxon powelli has traditionally been considered part of this complex despite its geographic isolation and substantial morphological differences. Pratt (2010) reviewed the Polynesian shrikebills as an example of how complexes of allopatric subspecies should be treated under his suggested new paradigm. That preliminary analysis found that the core group of subspecies in Fiji (including Rotuma) and Tonga were, with the possible exception of compressirostris on Kadavu, too similar among themselves to suggest any lines of speciation, and that some taxa might not even qualify as subspecies. However, three geographic outliers, fortunae in Wallis and Futuna, keppeli on the remote islands of Niuatoputapu and Tafahi (between the main islands of Tonga and the Samoan Archipelago), and powelli were each distinctive enough in a variety of traits to qualify "unequivocally" as full species. We present here some of Pratt's (2010:87) "details to be published elsewhere."

The Manu'a Shrikebill is much darker than all other forms of Polynesian shrikebills, with the exception of *keppeli*, and shows a gray throat that helps to make the very dark crown and cheeks especially noticeable. Despite a tawny tinge in the flanks, the overall impression is of a sooty or dark gray bird, whereas shrikebills in Fiji and Tonga



FIG. 2. Head pattern variation in the Samoan Fantail: Pale gray throat with auricular tuft only, a) from Savai'i, b) from Upolu; white throat with both auricular and loral tuft, c) from Upolu; dark throat with auricular tuft only, d) from Savai'i. All by HDP, a,d 2006; b–c 1977.

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generally look brown. In most of the complex, the lower mandible has a pearly or white base that reaches its extreme expression in the nearest neighbor taxon keppeli. In contrast to keppeli, the bill of Manu'a Shrikebill is entirely black except for a narrow white edge on both tomia (Fig. 3). Perhaps more significant, the bill shape in the Manu'a Shrikebill differs from that of other Clytorhynchus, which are named for their oddly upturned lower mandibles and hooked upper mandibles. The Manu'a bird has a more "conventional" passerine bill resembling those of other monarch flycatchers but retains a slight hook. This unique bill shape undoubtedly signals significant differences in foraging behavior and diet, but these have not yet been studied for any shrikebill.

To these morphological and ecological potential isolating mechanisms, we can add vocal differences. Manu'a Shrikebills have a harsh chatter *chi-chi-chi*-etc, presumably an alarm call, and a more frequent raspy rick-rick-ricky-dicky or rickrick-ricky-dear (ML 139844) that are distinctive, but not strikingly different from comparable calls of other Pacific monarchs (Pratt et al. 1987; HDP, pers. obs.). Songs are short high-pitched whistles <1 sec in duration. One is a quavering wee-wee-WEE-WEET with a slight rise in pitch and volume at the end, another has an introductory note followed by a whistle that rises then falls as per-weeer, another is a simple humanlike upslurred whistle wheee. The first example may be repeated every other second as a dawn song that may last >5 mins (ML 139844, 139850). Pairs of birds may sing a duet in which the first bird gives an up-slurred whistle and the other answers with a reverse whistle: wheee - wheeer, like a slow "wolf whistle" (ML 139848, 02:42 and onwards). This entire repertoire is distinct from those of shrikebills heard in Fiji, whose songs are long quavering "melodious but melancholy" (Watling 2001) whistles >1 sec. (see for example ML



FIG. 3. Three views of Manu'a Shrikebill *Clytorhynchus powelli*, a newly recognized endemic species. Ofu, American Samoa, October 2006. Photos by HDP.

139767) that may slur up or down. To our knowledge, duetting has not been reported in any other *Clytorhynchus*, but vocal sampling has been limited.

The Manu'a Shrikebill is found on all three of the Manu'a Islands (Ta'u, Ofu, and Olosega). At one time, it was believed extirpated from Ofu and Olosega (Amerson et al. 1982b), but HDP found it fairly common and frequently encountered in primary and secondary forest on both islands. It can even be heard from coconut agroforest along beaches where the lower edge of the forest clothes nearby steep hillsides, as in the national park unit on eastern Ofu. Manu'a Shrikebills often forage in pairs, near the ground among vine tangles and leaf clusters, and rarely, if ever, venture into the canopy. HDP observed at least one example of aerial-sally feeding. We recommend classifying this newly recognized species as Near Threatened on the basis of its extremely restricted distribution (~56 km<sup>2</sup>).

Samoan Flycatcher (Myiagra albiventris).-Samoan Flycatcher is a common and widespread species endemic to Savai'i and Upolu. Most current references describe this species as occurring at all elevations, but we found it to be absent from highland forest above 1,200 m on Savai'i, an observation also supported by Butler (2012). It seems particularly common in coastal mangroves. The Samoan Flycatcher is currently classified as Near Threatened, a higher threat category than many of Samoa's other endemic passerines, because of a presumed decline following the cyclones of 1990-1991 which substantially reduced forest cover in many parts of Samoa (International Union for Conservation of Nature 2014). In 1992, HDP's party could find only one bird on Upolu despite diligent searching. In contrast, in 2005-2006, we found Samoan Flycatchers to be common in mangroves and disturbed habitat around villages and plantations. It is clearly resilient following habitat damage, seems to be among the least threatened of Samoa's endemic bird species, and as such probably does not warrant its current status of Near Threatened.

The vocal repertoire of the Samoan Flycatcher has been inadequately described in field guides. Pratt et al. (1987) reported a whistled *feeuweet* and a buzzy *bzerr-it*, both of which may be repeated 2–3 times. We can add a raspy double note *szhrick-szhrick* and a raspy whistle *fweeeitfweeit* to the repertoire. All of these notes have many variations (see sonograms in Beichle and Baumann 2003 as well as ML 139949). The latter recording also includes a lengthy courtship ritual that immediately followed an afternoon rain shower. A pair sat close together, and the apparent male went through most of the vocal repertoire over several minutes. Meanwhile, the presumed female sang a whisper song of squeaky whistles and chirps that was nearly inaudible at a distance of <4 m. The male also displayed by fanning his tail and quivering wings like a begging chick.

Samoan Robin (Petroica pusilla).-The Samoan taxon *pusilla* was originally part of a widespread Scarlet Robin P. multicolor species complex (Mayr 1945), which has since been split into the continental Australian Scarlet Robin P. boodang. and the Pacific Robin P. multicolor with six allopatric island subspecies (Schodde and Mason 1999). Christidis and Boles (2008:202) suggested that these insular taxa might "merit further subdivision." Recent contributions to xeno-canto include all taxa in this complex, and reinforce the idea that multiple species are involved. The Samoan pusilla (Fig. 4) is distinctive both morphologically (smaller forehead and wing patches, different female color) and vocally, and is the easternmost outlier of the complex.

Previous descriptions have often conflated the Samoan Robin's song with that of Fijian birds, but the song of the Samoan differs in being entirely whistled, without burry or mechanical sounds. Beichle and Baumann (2003) provide sonograms. The song exhibits considerable individual variation and could be transliterated as seet-see-seet-chippysweet-treat (ML 140742), ter-wheet-ee-tu-wheet (ML 139899), or fee-tee-ti-wher-twee-tweechew (ML 20507). Kearns et al. (2015) revised subspecies of Pacific Robins in Vanuatu based on genetic and morphological data but did not examine vocalizations or compare this cluster of subspecies to others in the complex. Importantly, they found that variation in plumage may not be a good indicator of boundaries among these taxa. Species limits among the three Fijian forms likewise require further research. Samoan Robins are fairly common, mostly at higher elevations, on Savai'i and Upolu only.

Samoan White-eye (Zosterops samoensis).—This species is endemic to the highlands of Savai'i and is currently classified as globally Vulnerable on the basis of its restricted distribution and assumed small population size (BirdLife International 2014a). Existing references variously report



FIG. 4. The newly split Samoan Robin *Petroica pusilla*, adult male showing reduced white wing patch. Photo by HDP, October 2006.

the lower elevation limit of this species as 1,300 m (duPont 1976, Muse and Muse 1982), 900 m (Pratt et al. 1987), and 780 m (van Balen 2008). We found Samoan White-eyes to be common in highlands >1,100 m with additional sightings down to  $\sim 1000$  m along the A'opo trail where HDP observed them at dawn but not later in the day. However, Hobcroft (pers. comm.) found them at an unspecified lower elevation along the same trail in the afternoon. These observations suggest that Samoan White-eyes may conduct daily or seasonal movements between different elevation zones. Samoan White-eyes frequently visited the secondary scrub on the Mata o le Afi lava flow where they foraged in low bushes up to several hundred meters from the forest edge.

Vocalizations include a high-pitched *tchee* or *cheeer* sometimes with a buzzy or gurgling quality similar to notes of the House Sparrow *Passer domesticus* (ML 140745) uttered almost constantly by roaming flocks, and a previously undescribed dawn song (ML 139931) that comprises doubled notes, similar to the calls, but strung together in sequences of 3–5 pairs: *tee-deer, tee-dee, tee-deer,* 

*tee-dee, tee-deer.* The dawn song is apparently uttered only at first light, when the bird may be impossible to see. Many species of *Zosterops* have dawn songs (HDP, pers. obs.). While this species is restricted in its distribution, the Savai'i highlands remain one of the best preserved areas of forest in the region, with portions of the area included within three national parks (Conservation International et al. 2010). As such this species appears to be relatively secure, and we concur with Butler (2012) that it likely warrants being reclassified from Vulnerable to Near Threatened.

*Polynesian Starling* (Aplonis tabuensis).—The Polynesian Starling complex (Frontispiece) comprises eleven subspecies (not including *manuae*, see below) distributed from eastern Melanesia to Samoa (Feare and Craig 1999). They are potbellied, short-tailed, and short-billed compared to most starlings (Pratt et al. 1987), and in Samoa differ strikingly from the ubiquitous grackle-like Samoan Starling (Frontispiece). Samoa harbors two subspecies, *brevirostris* (Savai'i and Upolu) and *tutuilae* (Tutuila). Pratt (2010:84) used this complex, and specifically its Samoan members, as an example of a taxon that might comprise "previously unappreciated species." Placing them in geographic context, the Samoan forms are the easternmost members of the complex and represent the extreme end of a west to east shift in eye color, from brown to yellow, with the transition occurring in southeastern Fiji where some populations have both eye colors (Mayr 1945, Pratt 2010); color of upperparts from uniform chocolate brown to dark sooty olive with pale feather edges that create a scaly look; crown color from dark brown to green-glossed black; and throat color from dark to ochre-tinged to nearly white. These features vary independently, but for each character, island populations resemble snapshots taken along a cline, although no cline exists. Except for the aforementioned eye color, little intra-island variation is apparent. All forms have pale shaft streaks on the underparts; the prominence of the shaft streaks varies from buffy and less prominent in the west to white and very prominent in the east. Subspecies brevirostris is smaller than tutuilae, but both are yellow-eyed and white-throated, with the underparts showing pale edges to feathers as well as very prominent shaft streaks. All populations exhibit pale outer vanes on the secondaries that form a noticeable longitudinal pale streak in the middle of the folded wing, a distinctive feature of this species within the genus Aplonis.

Vocalizations of the Polynesian Starling complex have been rather poorly described, with considerable conflation of descriptions of different subspecies (Pratt et al. 1987, Feare and Craig 1999, Watling 2001), and the full range of variation has not been documented. Beichle and Baumann (2003) provide sonograms of several examples. In general, and in the context of other starlings, Polynesian Starlings are rather quiet birds whose songs and calls are not prominent in the avian ensemble. All forms utter various harsh screeches (ML 139825 at 01:53) as contact calls. Most authors refer to a two-element primary song, but that is an oversimplification, and the song is so highly variable individually that differences among populations are difficult to discern. The first element is usually a quick up-slurred whistle that covers a wide pitch range from low to high, often transliterated as sweee, followed by a shorter lower-pitched warble or a cluster of short whistles that sometimes extend in a trill with either a rattling or buzzy quality as *tzeeip-brree* (Pratt et al. 1987), but the elements may be reversed so that the quieter notes precede the loudest whistle (ML 5760 at 05:58). Songs in Fiji and Tonga tend to be simpler and more stereotyped than those of Samoan birds (HDP, pers. obs.).

All populations for which recordings are available have quiet vocalizations uttered during foraging. Some of these are comparatively complex, and could be considered songs (ML 139825 at 00:17 tutuilae; ML 139894 at 00:13 brevirostris). HDP recorded a flight song (ML 139833 01:50) of tutuilae that could be transliterated as sweee-see-terrrrr with a rising then falling inflection. Whether it represents a distinct song type or simply an advertising song uttered in flight we cannot say. On 3 July 1977, HDP recorded a remarkable performance of a complex whisper song (ML 5760) by a Polynesian Starling on the cross-island highway south of Apia. Had it been louder, the song would resemble those of American Mimidae, to which starlings are related (Sibley and Ahlquist 1984, Jetz et al. 2012). It is also very similar to whisper songs of some Hawaiian honeycreepers, which likewise include mimicry (Pratt 2005, 2009). The first recorded song bout lasted ~3.5 mins. Included, among others, are recognizable imitations of Wattled Honeyeater, Samoan Fantail, Flat-billed Kingfisher, and even White Tern Gygis alba. This recording was mentioned by Pratt et al. (1987), but as far as we can determine, no whisper song has otherwise been reported for the Polynesian Starling.

Manu'a Starling (Aplonis manuae).-This small starling has long been considered a subspecies of the widespread Polynesian Starling (Frontispiece), but the Manu'a Starling breaks nearly all of the geographical trends of that species (see above). If included in the complex, it would be the smallest and darkest member (while its neighbor tutuilae is the largest and palest), lacking shaft streaks on the breast feathers altogether. Instead, these feathers have pale gray edges that impart a scaly look. Interestingly, the only two starlings found east of the Manu'a Islands, the extinct Mysterious Starling (A. mavornata) of Mauke and the Rarotonga Starling (A. cinerascens), both from the Cook Islands, show a similar scaly, rather than streaked, breast pattern. Manu'a Starlings (Fig. 5) also lack, or have only a slight hint, of the pale secondary edges characteristic of Polynesian Starlings contra the illustration in Pratt et al. (1987).

HDP made the first recordings of the Manu'a Starling, and found noticeable differences from



FIG. 5. Manu'a Starling *Aplonis manuae*, a newly recognized American Samoan endemic showing characteristic scaly color pattern and lack of white wing stripe. Photo by HDP, Ofu, American Samoa, October 2006.

vocalizations of the Polynesian Starling across the repertoire. All of its vocalizations are higher pitched than similar, presumably homologous, vocalizations of Polynesian Starlings, which may be related to its smaller size. It has a two-element song, but the introductory note tends to be less prominent and on about the same volume level as subsequent elements. Most songs, however, are more complex and have a "sweeter" quality than those of Polynesian Starlings. Exemplary ones include tur-sweee-tu (ML 139894) and swee-chiptutu (ML 139855), or a more complex sweep-wertweet-wee-tweeet-wer-chee (ML 139845 at 02:49). ML 139863 features a light, high-pitched song much longer and more complex than those of Polynesian Starlings (except for the aforementioned whisper song) that includes up- and down-slurred whistles, rattling trills, and phrases similar to those given in shorter bursts. On Tau in February 2014, S. Jones (pers. comm.) recorded a Manu'a Starling whisper song that is somewhat similar to, but longer and livelier than, this longer song that might be the homologue of the whisper song of the Polynesian Starling. It appears unique to the Manu'a Starling.

The Manu'a Starling inhabits primary and secondary rainforest on all of the Manu'a Islands. HDP found it uncommon and infrequently seen on Ofu, and never in villages or coconut agroforest. In this respect it differs from Polynesian Starlings, which readily use a variety of secondary habitats. Given its morphological, vocal, and ecological potential isolating mechanisms, the Manu'a Starling certainly qualifies as a distinct biological species. While its total area of occurrence is relatively small (ca. 56 km<sup>2</sup>), the population appears to be stable, so Near Threatened would be an appropriate conservation status.

Samoan Thrush (Turdus samoensis).—The Island Thrush Turdus poliocephalus is a highly polytypic complex with >50 allopatric subspecies found in isolated montane habitats and small islands from Taiwan and Sumatra across the East Indies through Melanesia to Fiji and Samoa. It is characterized by a dozen or more striking plumage variations that appear intermingled in a mosaic fashion throughout the distribution, with little geographic basis (Clement 2001). Archipelagoes such as Fiji and the Philippines may have representatives of as many as five of the plumage variants; in the latter locality, molecular data reveal that similar morphotypes may not be each other's closest relatives (Jones and Kennedy 2008). Vocal sampling of Island Thrushes has been spotty, with most forms unrepresented in sound collections and sound samples heavily weighted toward call notes rather than territorial songs. However, even these limited samples reveal vocal variation at least as great as that in plumage color. Tissue sampling has likewise been limited, but virtually all recent authors agree that the "Island Thrush" comprises several species (e.g., Peterson 2007, Jones and Kennedy 2008).

Using phenotypic characters, Peterson (2007) suggested splitting the Island Thrush into 31 biological species, but this approach has not been widely adopted, presumably because of the lack of molecular and vocal data. Unfortunately, complete taxon sampling of DNA in this complex is not likely to be achieved any time soon, because many of the populations live at high elevations on remote and seldom-visited islands. Likewise, vocal sampling is hampered by the fact that many populations sing sparingly (in contrast to others that are highly vocal). Absent sufficient molecular and vocal data, we can either maintain the status quo with a single species, which nearly everyone acknowledges is incorrect, or accept the species limits suggested by Peterson (2007) as a working hypothesis to fine tune as more data become available. Like Gill (2014), we believe the burden of proof should shift to those who would argue for a single polytypic species, inasmuch as the current taxonomic arrangement means that any distinctive populations that are declining will be overlooked by conservationists who focus solely on species (Jones and Kennedy 2008, Pratt 2010). Peterson (2007) considered the Samoan Thrush a species, and we provide additional ecological and vocal data to support his conclusion.

The Samoan Thrush is found only on Savai'i and Upolu, and is the easternmost outlier of the complex of Island Thrushes. It is sooty black with yellow legs, "candy-corn orange" bill, and fleshy eye-rings, which in the past have been incorrectly depicted as yellow (duPont 1976, Muse and Muse 1982, Pratt et al. 1987). It is common in highland forest above 1,000 m on Savai'I, and JCM saw it frequently visiting the secondary growth on the Mata o le Afi lava flow in June–July 2005. On 22 June 2005, JCM found a nest of Samoan Thrushes along the inside edge of a crater in the Mata o le Afi successional habitat. It was located >100 m from the forest edge and placed on a volcanic cliff face  $\sim 3$  m above the ground on a small ledge under an overhang. It consisted of an open cup 9 cm in diameter made of moss and lined with grasses. A single egg (3  $\times$  2 cm) was light blue with dense brown speckling toward the larger end.

On some islands, such as Taveuni, Fiji, Island Thrushes are conspicuous components of the soundscape (HDP, pers. obs.), but in others they seem to sing rarely. The Samoan Thrush falls into the latter category. Its harsh tchack-tchack alarm calls, illustrated in sonograms by Beichle and Baumann (2003), are often uttered by birds startled in dense cover. But although both authors have spent considerable time in places where the species is common, at seasons when all other birds were in full song, neither has heard its primary song. Likewise, R. Stirnemann (pers. comm.), who has spent >4 years working in Samoan rainforests (Leaman 2014), has also heard call notes, but no song. In fact, the song of the Samoan Thrush has never been described (except as a conflation with songs from other islands). Does the Samoan Thrush lack a territorial song altogether? Does the song resemble that of another Samoan bird so closely that previous observers have misidentified it? Note that "Island Thrushes" in Fiji often sing from concealment in the underbrush, where getting a look at the singer is a challenge. Perhaps a dedicated study of a nesting pair will solve this mystery. For now we can only say that this species' vocal behavior is very different from that of other Turdus in the Pacific and elsewhere, with potentially significant implications for taxonomy.

We always saw the Samoan Thrush on or near the ground, as is typical of "Island Thrushes." In July 2005, JCM found a single Samoan Thrush that had been killed recently by a feral cat (Fig. 6) near Mata o le Afi. Although the impact of feral cats on Samoan Thrushes may be less severe than on other ground-feeding birds (e.g., Tongan Ground Doves, Tooth-billed Pigeons), the continued spread of these invasive predators could represent a threat. Although Watling (2001) considered this species to be of conservation concern, the Samoan Thrush appears to be relatively secure as long as habitats in Savai'i's central rainforest remain protected.

Samoan Parrotfinch (Erythrura cyaneovirens).— Samoa is home to two marginally differentiated (duPont 1972) taxa of parrotfinch, *cyaneovirens* 



FIG. 6. Samoan Thrush *Turdus samoensis*, long regarded as a subspecies of Island Thrush *T. poliocephalus*, killed by a feral cat on Savai'i, July 2005. Photo by JCM.

(Upolu) and gaughrani (Savai'i), which form part of a species complex that includes the Royal Parrotfinch E. regia of Vanuatu and the Fiji Parrotfinch E. pealii of Fiji. Mayr (1945) considered all these populations conspecific as Redheaded Parrotfinch E. cyaneovirens. However, Ziswiler et al. (1972) split the Fijian pealii as a distinct species, but retained regia and cyaneovirens as conspecific, whereas Immelmann et al. (1977) split regia and cyaneovirens, primarily on the basis of their widely separated distributions. More recent authors have been inconsistent, variously following Ziswiler et al.1972, Goodwin 1982, and Clements 2007, or Immelmann et al. 1977, Gill and Donsker 2014, or Mayr 1945, Pratt et al. 1987, Clement et al. 1993, and Payne 2010. Lack of clarity has been increased by use of the English name "Red-headed Parrotfinch" which has been variably applied to cyaneovirens including pealii and regia (Mayr 1945, Watling 1982, Payne 2010), cyaneovirens and regia excluding pealii (Clements 2007), cyaneovirens excluding both regia and pealii (Gill and Donsker 2014), and even an entirely different species, E. psittacea of New Caledonia (Goodwin 1982). For clarity, we recommend the names Fiji Parrotfinch (E. pealii), Royal Parrotfinch (E. regia), and Samoan Parrotfinch (E. cyaneovirens) for these taxa.

Most authors consider the vocalizations of all parrotfinches to be similar, and only Ziswiler et al. (1972) have analyzed them in any detail (but did not include any Samoan examples). Beichle and Baumann (2003) report and illustrate the song of the Samoan Parrotfinch as a rapid high-pitched metallic trill that trails off in volume and pitch over about 1.5 secs. HDP recorded a very similar vocalization at  $\sim$ 1,000 m on the A'opo trail (ML 139891), as well as variations in which the trill has an introductory note, or rises and falls in pitch (ML 139944). Call notes appear to be shorter bursts similar in quality to the longer song. Watling (2001) reports the song of the Fiji Parrotfinch as a "persistent double note," and M. Andersen recorded this and longer iterations of a single metallic note (ML 181335), none of which closely resemble the songs or calls of Samoan Parrotfinches. Based on Bregulla's (1992) descriptions (we found no published recordings), the vocalizations of the Royal Parrotfinch may be most similar to those of the Samoan Parrotfinch.

Ecology and behavior offer some additional points of difference among these taxa. Both Royal and Samaon Parrotfinches are most often found in pairs or small groups in primary rainforest. Samoan Parrotfinches sometimes feed in secondary forest edge, and their diet is eclectic (Beichle and Baumann 2003), but we have not seen them feed on the ground, nor have we seen any large flocks although Ziswiler et al. (1972) reported flocks of up to 40. In contrast, the Royal Parrotfinch appears to be a non-flocking specialist on figs (Ficus spp.) and feeds almost entirely in the canopy of tall trees (Bregulla 1992), while the Fiji Parrotfinch is a common and familiar bird found in large flocks of dozens of individuals in city parks and suburban habitats, as well as open fields where it has adapted to feed on seeds of introduced grasses (Goodwin 1982), often on the ground (HDP, pers. obs.). Further vocal data from parrotfinches in Vanuatu as well as molecular studies should provide more clarity on the relationships among these populations. But absent such evidence, we concur with Gill and Donsker (2014) that these geographically isolated and morphologically, behaviorally, and ecologically distinct populations are best treated as three species.

The Samoan Parrotfinch is among the least common of Samoa's endemic passerines (Muse and Muse 1982, Watling 2001, Butler 2012), and Watling (2001) suggests that, as with several other Samoan species, parrotfinches declined following the cyclones of 1990-1991. While that may be true, HDP did not find parrotfinches to be significantly more common in 1977. JCM and Butler (2012) did not find Samoan Parrotfinches in highland habitats on Savai'i and instead observed it to be uncommon and patchily distributed at lowland sites, including the forest around Sinaloa falls north of Sili village. In contrast, HDP found it uncommon at  $\sim 1000$  m on the A'opo Trail, and observed it at the crest of the cross-island highway at roughly the same elevation on Upolu in both 1977 and 1992. Somewhat surprisingly given the body size of parrotfinches, local villagers near Sili described opportunistic slingshot hunting of parrotfinches for food. The Samoan Parrotfinch is justifiably listed as a species of conservation concern in Samoa and likely deserves recognition as Near Threatened on a global scale.

#### DISCUSSION

Our results highlight important differences among lowland and highland bird communities on Savai'i. Bellingham and Davis (1988) also found elevational differences in bird communities, but their upland forest surveys in the areas west of Mt Elietoga (1,033 m) were apparently in forests below 1,200 m, which we observed to be the upper elevational limit for several lowland species. On the A'opo trail, this 1,200-m elevational boundary is marked by a visible change in forest structure and tree composition. While Bellingham and Davis (1988) observed both Samoan Flycatcher and Flat-billed Kingfisher to be uncommon or rare in the uplands, we and Butler (2012) found both species entirely absent from the highest elevations.

Our taxonomic review of Samoa's endemic taxa identified seven current subspecies that warrant recognition as full biological species: Samoan Wood Pigeon, Peale's Kingfisher, Manu'a Shrikebill, Samoan Myzomela, Samoan Robin, Manu'a Starling, and Samoan Thrush. In the case of the Crimson-crowned Fruit Dove, we found that vocal and behavioral data failed to support a recent split based on morphological scoring (del Hoyo et al. 2014). These changes increase the total number of species endemic to the Samoan archipelago from 10 to 17. Of these, three are endemic to American Samoa (Peale's Kingfisher, Manu'a Shrikebill, Manu'a Starling), where there had previously been no endemics; two of the species occur in both Samoa and American Samoa (Samoan Myzomela and Samoan Starling); and the rest are restricted to independent Samoa. In five cases (Samoan Wood Pigeon, Peale's Kingfisher, Samoan Robin, Samoan Thrush, and Samoan Myzomela), newly split species belong to larger complexes that, in our opinion, warrant further scrutiny.

We recommend changes in the conservation status of three currently recognized species: Samoan Woodhen (Critically Endangered to Extinct) Samoan Flycatcher (Near Threatened to Least Concern), and Samoan White-eye (Vulnerable to Near Threatened). Among our newly recognized species, Manu'a Starling and Manu'a Shrikebill may warrant consideration as Near Threatened on the basis of their tiny geographic distributions, although they are not uncommon within available habitat, much of which is within the National Park of American Samoa. Samoan Parrotfinch, currently unlisted because of confusion regarding its taxonomic status, appears to be uncommon and patchily distributed and also warrants being listed as Near Threatened. We provide additional support for the conclusion of Butler (2012) that the Samoan White-eve and Samoan Flycatcher are more common than their current designation suggests. Further, the Samoan Woodhen, currently considered Critically Endangered,

is almost certainly extinct. While it is impossible to prove extinction, particularly of a secretive forest rail, we believe conservation effort would be better invested in Samoa's other threatened birds. Most concerning is the Tooth-billed Pigeon, which should be an immediate priority for conservation efforts. Differences in elevational distribution have been addressed in the design of a reserve system within Samoa, where protected areas have been established in both the lowlands and highlands on Savai'i and conservation proposals have rightfully highlighted the need to preserve the unique montane habitats on Savai'i (e.g., Conservation International et al. 2010, Atherton and Jefferies 2012), but the roles these differences play in determining the status of particular species is also important. Lowland habitats in Samoa suffer greater degradation and exposure to invasive species, and as a result, lowland species may in some cases be more threatened despite occurring over a larger area. Furthermore, species that occur in both the lowlands and the highlands may exist at much lower (and possibly unsustainable) densities in one or other. This is particularly relevant in the case of the Tooth-billed Pigeon, inasmuch as we found only two unconfirmed reports of the species above 1,200 m.

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