From wetlands to islands: morphological variation, plumage and song in Pacific island *Acrocephalus* warblers

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Abstract: *Acrocephalus* warblers occur across Eurasia, Africa, and Australasia, where they are typically migratory, wetland species, but also occur on islands as sedentary endemics in drier habitats, including forest and scrub. External morphology and song amongst Pacific island *Acrocephalus* warblers were investigated and comparisons made with *Acrocephalus* species elsewhere. There was a range of sizes between Pacific island *Acrocephalus* warblers, many being larger than migratory continental species. Bill:wing length ratios were higher in most Pacific species, and their wings more rounded, than most continental species, but less rounded than swamp-warblers of Africa and adjacent islands. Plumages of W and N Pacific species resembled reed-warblers elsewhere, but in SE Polynesia were more varied, brown or grey dorsally, shaded olive, yellow or rufous, and pale ventrally, shaded white, yellow or buff-white, with a melanistic morph on Tahiti. Spectrographic analysis showed a gradient of song complexity from continental and Marianas/ Micronesia species (*A. hiwae, A. syrinx*), through to *A. taiti* and *A. vaughani* on the Pitcairn islands, which had no song. The mean frequency of Pacific island reed-warbler songs was inversely correlated with mean body size.

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**Key words:** *Acrocephalus*, body-size, evolution, islands, Pacific, reed-warbler, song

INTRODUCTION

Many *Acrocephalus* warblers (Passeri: Acrocephalidae) are well-known summer migrants that breed across the Palaearctic, and over half of the recognised species (55%) are endemic sedentary island species confined to islands or archipelagos (Dyrcz *et al*. 2016). Of 42 recognised *Acrocephalus* warbler species, 19 are continental, often migratory species, 19 occur (or occurred) on islands in the Pacific, and 4 occur on islands off Africa (Baker 1997; Dyrcz 2006; Kennerley & Pearson 2010; Leisler & Schulze-Hagen 2011; Dyrcz *et al*. 2016; Thibault

& Cibois 2017). The 19 continental species typically inhabit wetlands, selecting breeding habitats in and around reeds or in other dense swamp or marshland vegetation (Dyrcz 2006; Kennerley & Pearson 2010; Dyrcz *et al*. 2016). Some may select drier habitats, such as trees with dense herbaceous undergrowth or scrubby thickets, e.g. *A. orinus, A. dumetorum* and some *A. palustris. Acrocephalus newtoni* on Madagascar also occurs in reeds and other wetland habitats, but *A. rodericanus* on Rodrigues Island and *A. sechellensis* on the Seychelles both occupy dry forest and scrub, while *A. brevipennis* on the Atlantic Cape Verde Islands occupies a broad range of dry habitats, as well as wetter situations in giant reed (*Arundo donax*) (Komdeur 1992; Showler *et al*. 2002;
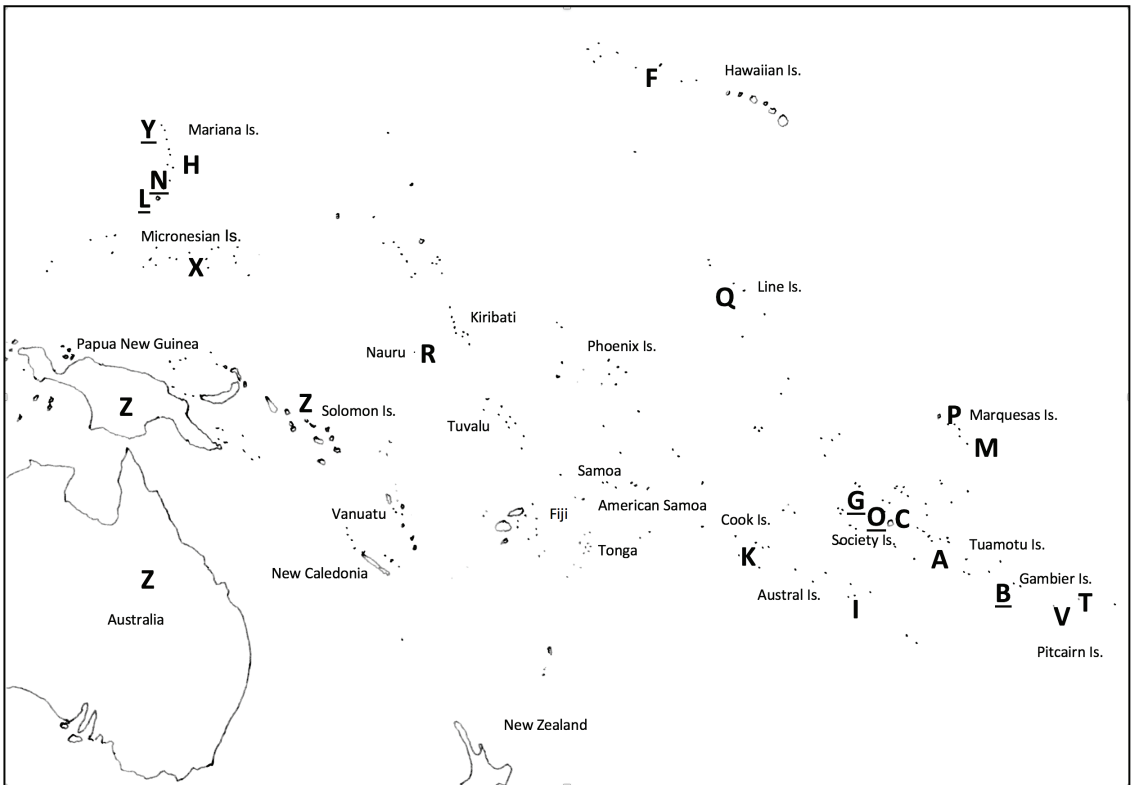
Figure 1. Indicative distribution of 20 *Acrocephalus* warbler species across the Pacific islands. Letter codes for species are: A = *atyphus*; B = *astrolabii*; C = *caffer*; F = *familiaris*; G = *musae*; H = *hiwae*; I = *rimitarae*; K = *kerearako*; L = *luscinius*; M = *mendanae*; N = *nijoi*; O = *longirostris*; P = *percernis*; Q = *aequinoctialis*; R = *rehsei*; T = *taiti*; V = *vaughani*; X = *syrinx*; Y = *yamashinae*. For reference, the broad distribution of *Acrocephalus australis* (coded Z) in Australia, Papua New Guinea, and the Solomon Islands is also shown. Codes for six extinct species are underlined.

Kennerley & Pearson 2010).

The Pacific islands (Fig. 1) on which 19 endemic *Acrocephalus* (formerly *Conopoderas*) warblers are known range from the Mariana Islands and the Hawaiian Leeward Islands in the north, south to the Line Islands (Kiritimati), Eastern Polynesia including the Cook Islands, then further south to the Austral, Gambier and Pitcairn islands (Pratt *et al.* 1987; van Perlo 2011; Thibault & Cibois 2017). In addition, *Acrocephalus* species occur in Australia, New Guinea, the Solomons, and SE and E Asia (Dyrcz 2006; Kennerley & Pearson 2010). No *Acrocephalus* species breed in New Zealand, although a vagrant male *A. australis* sang near Cheviot in November 2004 (Allen 2013; Heather & Robertson 2015). *Acrocephalus* warblers are absent from the larger, species-rich islands of Melanesia and Hawaii (Kennerley & Pearson 2010), apart from *A. australis* represented on Pacific islands in Melanesia by the subspecies *A. a. sumbae* (Dyrcz *et al.* 2016). Most Pacific island *Acrocephalus* warblers occupy dry habitats, such as forest and scrub, although

some species also occupy habitats alongside lakes, ponds or rivers, e.g. *A. kerearako* and *A. syrinx*. In the Marianas, *A. luscinius* once occupied cane thickets near freshwater ponds, and *A. hiwae* occupies woodland and tall wetland vegetation and even mangroves (Kennerley & Pearson 2010), with habitat loss a leading factor limiting its populations (Mosher 2006; Camp *et al.* 2009). *Acrocephalus caffer* (Tahiti) and the extinct *A. longirostris* (Moorea) select (or selected) patches of Polynesian bamboo (*Schizostachyum glaucifolium*) near forest (Kennerley & Pearson 2010; *pers. obs.*), although this bamboo is considered as introduced in the Society Islands (Larrue *et al.* 2010).

The Pacific island *Acrocephalus* taxa have been the focus of increased research over recent years, resulting in re-interpretation of their phylogeny and taxonomic changes (Holyoak & Thibault 1977; Leisler *et al.* 1997; Thibault & Cibois 2006, 2017; Fregin *et al.* 2009, 2012; Cibois *et al.* 2007, 2008, 2011a,b; Leisler & Schulze-Hagen 2011; Fregin 2012; Saitoh *et al.* 2012). Kennerley & Pearson (2010)

Table 1. Pacific island *Acrocephalus* species and their IUCN Red List status (IUCN 2017).

Name	Species	Pacific region	Red List status	Population trend
Australian reed-warbler	*australis*	Melanesia	Least Concern	Stable
Guam reed-warbler	*luscinius*	Micronesia	Extinct	—
Saipan reed-warbler	*hiwae*	Micronesia	Critically Endangered	Decreasing
Aguijan reed-warbler	*nijoi*	Micronesia	Extinct	—
Caroline reed-warbler	*syrinx*	Micronesia	Least Concern	Stable
Kiritimati reed-warbler	*aequinoctialis*	Eastern Polynesia	Endangered	Decreasing[1]
S Marquesas reed-warbler	*mendanae*	Eastern Polynesia	Least Concern	Stable
Pagan reed-warbler	*yamashinae*	Eastern Polynesia	Extinct	—
Mangareva reed-warbler	*astrolabii*	Eastern Polynesia	Extinct	—
Nauru reed-warbler	*rehsei*	SE Micronesia	Vulnerable	Stable
Millerbird	*familiaris*	Hawaiian Islands	Critically Endangered	Stable
Pitcairn reed-warbler	*vaughani*	Eastern Polynesia	Endangered	Unknown
Henderson reed-warbler	*taiti*	Eastern Polynesia	Vulnerable	Stable
Cook reed-warbler	*kerearako*	Eastern Polynesia	Near Threatened	Decreasing
Rimatara reed-warbler	*rimitarae*	Eastern Polynesia	Critically Endangered	Decreasing
Forster's reed-warbler	*musae*	Eastern Polynesia	Extinct	—
Tahiti reed-warbler	*caffer*	Eastern Polynesia	Endangered	Decreasing
Moorea reed-warbler	*longirostris*	Eastern Polynesia	Extinct[2]	—
N Marquesas reed-warbler	*percernis*	Eastern Polynesia	Least Concern	Stable
Tuamotu reed-warbler	*atyphus*	Eastern Polynesia	Least Concern	Stable

[1] however, no declines on Kiritimati Island noted since 2007 (VanderWerf *et al.* 2016; Thibault & Cibois 2017)
[2] changed from IUCN Critically Endangered, following Thibault & Cibois (2017)
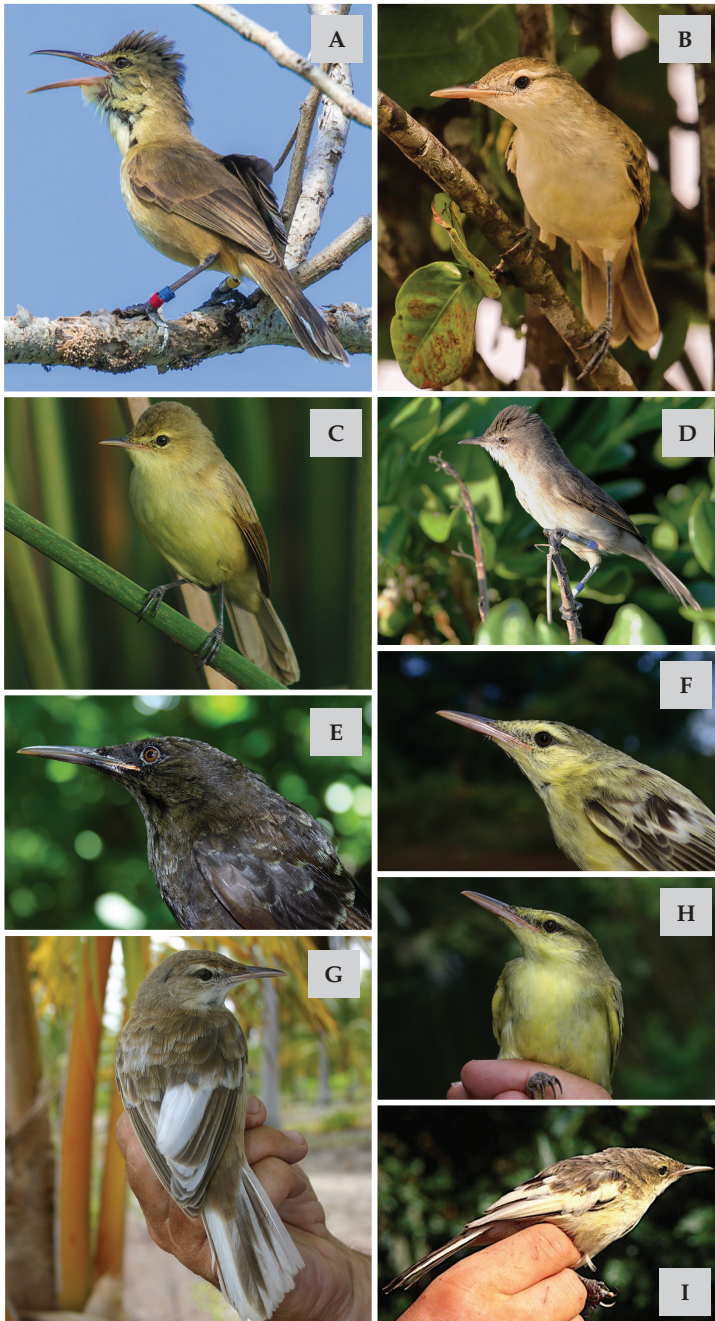
Figure 2. A selection of nine Pacific island *Acrocephalus* warblers. (A) *A. hiwae*, Saipan (photo: Lainie Berry); (B) *A. syrinx*, Weno, Chuuk (photo: Lainie Berry); (C) *A. kerearako kerearako*, Mangaia (photo: Gerald McCormack); (D) *A. familiaris kingi*, Laysan (photo: Cameron L. Rutt); (E) *A. caffer*, dark phase, Tahiti, (photo: A. Cibois & J-C. Thibault); (F). *A. percernis idae*, Ua Huka, (photo: A. Cibois & J-C. Thibault); (G) *A. atyphus atyphus*, showing leucism (white feathers), Takapoto, (photo: A. Cibois & J-C. Thibault); (H) *A. mendanae dido*, Ua Pou, (photo: A. Cibois & J-C. Thibault); (I) *A. vaughani*, Pitcairn, (photo: Elizabeth Bell, WMIL). The colour banded *A. familiaris kingi* (D) had been translocated from Nihoa to Laysan, the location of the extinct subspecies *A. familiaris familiaris*, to re-create a second millerbird population (Freifeld *et al.* 2016; Cameron L. Rutt, *pers. comm.*).

discussed the origin, distribution and extinction of Pacific island *Acrocephalus* warblers, regarding them as 'supertramp' species (Diamond 1974), but Cibois *et al.* (2011a) concluded that, while these species meet some of the 'supertramp' criteria in their aptitude for colonising remote archipelagos, their life-history characteristics do not fit the model. Leisler & Winkler (2015) examined *Acrocephalus* warblers on islands in the Atlantic, Indian, and Pacific Oceans, emphasising that their evolution pertained to more than the hitherto studied body size and bill dimensions.

Here, I follow the names and classification of Dyrcz *et al.* (2016), using additional information from Kennerley & Pearson (2010). Of the 20 species of Pacific island *Acrocephalus* warblers, which include *A. australis* from the Solomons (Fig. 1), six (30%) are extinct, eight (40%) are threatened, one (5%) is near threatened and five (25%) are of least concern; eight extant species are stable, five are decreasing and the population trend of one species is unknown (Table 1; IUCN 2017; Thibault & Cibois 2017).

Morphologically, these Pacific island *Acrocephalus* warblers vary widely across their area of distribution, such as in size, wing shape, and colour. For instance their lengths, from Dyrcz (2006), range from the 13 cm millerbird (*A. familiaris*) from Nihoa and Laysan to the 18 cm *A. luscinius* of Micronesia and 17–19 cm *A. atyphus, A. caffer, A. mendanae,* and *A. percernis* from Eastern Polynesia. More sedentary *Acrocephalus* warblers, including those on islands, have more rounded wings, while *Acrocephalus* warblers that migrate long distances have more pointed wings (Kennerley & Pearson 2010; Leisler & Schulze-Hagen 2011). However, Komdeur *et al.* (2004) found the Seychelles Warbler (*A. sechellensis*) did not differ from migratory warblers in its wing shape and wing loading, arguing that it showed morphological structures required for sustained flight, and may have a behavioural reluctance to disperse across the sea. More recently, Leisler & Winkler (2015) reported that *A. sechellensis* — freed from requirements of long-distance flight — was better able to adapt to highly cluttered habitats by having, *inter alia,* rounder, more slotted and broader wings than migratory *Acrocephalus* species.

Continental *Acrocephalus* warblers have streaked or uniform brownish plumage, but Pacific island species may have: yellow underparts (e.g. *A. caffer, A. kerearako, A. mendanae, A. percernis*), white (leucistic) feathers (e.g. *A. taiti, A. vaughani, A. rimitarae*), predominantly grey and white plumage (*A. aequinoctialis*), or, in *A. caffer,* a melanistic as well as typical colour morph (Fig. 2; Dyrcz *et al.* 2016).

Many *Acrocephalus* warblers exhibit a high degree of song complexity (Catchpole 1980; Parmenter & Byers 1991; Cramp *et al.* 1992; Kennerley & Pearson 2010), including mimicry of other species, e.g. the marsh warbler (*A. plaustris*) that breeds in Europe (LeMaire 1974; Bairlein *et al.* 2006; Catchpole & Slater 2008; Leisler & Schulze-Hagen 2011). Delivery rates and diversity of song syllables have been studied in various migratory *Acrocephalus* species (e.g. Catchpole 1980, 1983; Hasselquist *et al.* 1996; Bell *et al.* 1997, 2004; Borowiec & Lontowski 2000), as well as in some island species (e.g. Catchpole & Komdeur 1993). Island *Acrocephalus* species are reported to have simpler songs than mainland relatives, and variations in their song patterns across the Pacific have been briefly presented (Bell & Perfect 1994; McPherson 1998; Bell 2001; Bairlein *et al.* 2006; Kennerley & Pearson 2010). The song frequency of birds is negatively correlated with body-size in some species (e.g. Wallschläger 1980; Badyaev & Leaf 1997; Mahler & Gil 2009), and as Pacific island *Acrocephalus* species vary in size (Dyrcz 2006), they provide an opportunity to test this inverse size-song frequency relationship.

Here, I examine in further detail morphological variation and song patterns in Pacific island *Acrocephalus* warblers, comparing them with congeneric species elsewhere. Two broad questions are addressed: (1) How variable are shapes, sizes and colours of Pacific island *Acrocephalus* species, and how do they compare with *Acrocephalus* species elsewhere? (2) How variable and complex are Pacific island *Acrocephalus* warbler songs, how do they compare with *Acrocephalus* species elsewhere, and how do their song frequencies relate to body size?

METHODS
Measurement of museum specimens
To obtain data on size variation among Pacific island and continental *Acrocephalus* species, morphometric data were obtained from seven museums (Bishop Museum, Honolulu; British Museum of Natural History, Tring; California Academy of Sciences, San Francisco; Muséum National d'Histoire Naturelle, Paris; Museum of Vertebrate Zoology, Berkeley; Smithsonian Institution National Museum of Natural History, Washington DC; Te Papa Tongariro Wellington).

With measurements following Svensson (1975), the following variables were recorded, where available, from most specimens: data entry number (chronological), taxon code, location code, museum code, sex code, age code, year collected, wing-length (mm) using maximum flattened chord, tail length (mm), tail graduation as outer-tail feather tip to longest tail feather tip (mm), bill to skull (mm), bill to feathers (mm), bill to nostril (mm), bill depth (mm), bill width (mm), tarsus length (mm), 1st toe claw length (mm), 1st toe claw depth (mm), 1st toe

length excluding claw (mm), 1st toe length including claw length (mm), 3rd toe claw length (mm), 3rd toe claw depth (mm), 3rd toe length excluding claw (mm), 3rd toe length including claw length (mm).

Plumage condition of each specimen was noted, including whether or not it was in moult (if so, which area – body, wings or tail), and the degree of feather wear from fresh to abraded. Damaged or moulting museum specimens resulted in some measurements not being taken so these data were unavailable for multivariate analysis. For each specimen, the colours of the plumage and soft-parts were recorded, and for comparison with additional mainland *Acrocephalus* species, supplementary data were obtained from Kennerley & Pearson (2010).

The ascendant system of numbering primaries (from outer distal to inner proximal) was used in wing feather examination, e.g. to measure wing-formulae (see Witherby *et al.* 1943; Svensson 1975; Williamson 1976; Kennerley & Pearson 2010; Shirihai & Svensson 2018), rather than the descendent system generally used in moult studies and elsewhere (see Ginn & Melville 1983; Jenni & Winkler 1994; Deutsche Ornithologen-Gessellschaft 2011; Bell 2015). In *Acrocephalus* warblers, the first primary is small or minute (Kennerley & Pearson 2010) and its length was compared to that of the longest primary covert (mm: greater or less than). The wing formula was recorded for ascendant primary feathers 2–10, including relative feather-length (mm) from wing point, as well as primary emargination (primary nos. and emargination lengths (mm)), primary notching (primary nos. and notch lengths (mm)), and the position of the 2nd primary relative to other primaries. From examination of wing data, wing shapes can be compared. For analysis, where a range of primaries was recorded between individuals of a species, the mid-point primary number was taken, (e.g. 5 if range 4–6; 3.5 if range 3–4) to simplify graphical representation of the relationship between the position of the wing-point primary and the inner primary (occasionally secondary) equivalent to the tip of the 2nd primary (Fig. 5).

Recording of songs and calls

Field recordings of songs of Pacific island *Acrocephalus* warblers were made as follows: *A. kerearako kaoko* on Mitiaro (Cook Is.) and *A. caffer* on Tahiti (Society Is.) by the author; *A. kerearako kerearako* on Mangaia (Cook Is.) by members of the Ornithological Society of New Zealand; *A. familiaris kingi* on Nihoa (Hawaiian Leeward Is.) by Sheila Conant; *A. percernis percernis* on Nuku Hiva (N. Marquesas Islands) and *A. mendanae mendanae* on Hiva Oa (S. Marquesas Is.) by Rod Morris; *A. vaughani* on Pitcairn Is. by Bruce Robertson; and *A. taiti* on Henderson Is. by Jim Jolly. Sound

spectrograms from a selection of these recordings were reproduced by Kennerley & Pearson (2010) after being lodged in the McPherson Sound Library (McPherson 1995, 1998). The late Ralph Shreiber kindly supplied song information for *A. aequinoctialis* from Kiritimati Is. (see Milder & Schreiber 1989).

In the Pacific, both cassette and DAT tape recorders were used to record warbler songs and calls, particularly a portable Sony TCD-D10 ProII DAT recorder with a Telinga parabolic microphone. Other *Acrocephalus* song recordings were made in Europe (e.g. Bell *et al.* 1997, 2004), while songs (or calls) were also sourced from the following bird sound libraries: the British Library of Wildlife Sounds, London, UK; the Florida Museum of Natural History Bird Sounds Library, University of Florida, Gainesville, Florida USA; the Macaulay Library of Bird Sounds, Cornell University Laboratory of Ornithology, Ithaca, NY, USA; the McPherson Natural History Unit Sound Archive, Ashburton, NZ; the Television New Zealand Natural History Unit sound library, Dunedin, NZ; and the National Biodiversity Center's Xeno-canto web-site. The quality of these library sound recordings varied, but those of better-quality were selected to provide samples additional to the field recordings described above.

Morphometric analysis

For statistical comparison of Pacific island *Acrocephalus* warbler morphometrics, principal component analyses (PCA) using XLSTAT were undertaken, while other statistical analyses were done using both XLSTAT and StatPlus:mac Pro. A wide range of combinations of variables were run using PCA and the most informative set used to compare morphometrics across species (Figs. 3 & 4). The chosen combination of PCA variables balanced good representation of both species and variables, given that some had to be excluded in damaged and/or moulting specimens.

Bioacoustic analysis

Songs (or calls) of a selection of individual *Acrocephalus* warblers from Pacific islands and adjacent mainland areas were analysed using AviSoft SASLab and Raven Pro version 1.5 sound analysis software on PC and Mac computers. A song-element coding system, previously used for European *Acrocephalus* species, was used to identify and classify individual syllable element types on printed output of spectrograms (see e.g. Catchpole 1979; Bell *et al.* 1997, 2004; Catchpole & Slater 2008). The following song variables were calculated: mean maximum frequency (kHz); mean minimum frequency (kHz); mean frequency (kHz); and frequency range (kHz). For visual comparison,

3–3.5 second sound spectrograms were compared, and for quantitative comparison, samples over a standard 36 second recording period were analysed to provide data on: mean time in song (seconds); mean no. syllables; mean no. syllable types; mean no. syllables per second overall (36 second sample); mean no. syllables per second of song; and percentage of time in song.

RESULTS
External morphometrics
Morphometric variation
From 139 museum specimens, morphometric data were obtained for 16 Pacific island *Acrocephalus* species (following Dyrcz *et al*. 2016) as follows: 6 Guam reed-warblers (*A. luscinius*, extinct); 9 Saipan reed-warblers (*A. hiwae*), 5 Caroline reed-warblers (*A. syrinx*), 5 Kiritimati reed-warblers (*A. aequinoctialis*), 6 Southern Marquesas reed-warblers (*A. mendanae*), 7 Pagan reed-warblers (*A. yamashinae,* extinct), 2 Mangareva reed-warblers (*A. astrolabii,* extinct), 1 Nauru reed-warbler (*A. rehsei*), 51 millerbirds (*A. familiaris*, including 16 of the extinct nominate subspecies *familiaris* from Laysan), 11 Pitcairn reed-warblers (*A. vaughani*), 3 Henderson reed-warblers (*A. taiti*), 6 Cook reed-warblers (*A. kerearako*), 1 Forster's reed-warbler (*A. musae*, extinct), 8 Tahiti reed-warblers (*A. caffer*), 4 Northern Marquesas reed-warblers (*A. percernis*), and 14 Tuamotu reed-warblers (*A. atyphus*). A principal component analysis plot for measurements of museum specimens from the 16 Pacific island *Acrocephalus* species illustrates morphometric variation amongst them (Fig. 3).

The first two axes explained 96.9% of the variance. Increasing size is evident along PC axis 1 which corresponded to all measurements and explained most of the variance (85.8%). Axis 2 was mainly composed of bill lengths and tail length, explaining 11.1% of the variance (Fig. 3), and a bivariate plot of two of these measurements (tail-length and bill-to-feathers length) was used to further illustrate their relative sizes (Fig. 4). *Acrocephalus familiaris* was distinctly smaller than other taxa (PC1 axis), while *A. caffer* and single *A. astrolabii* and *A. musae* specimens were largest (Fig. 3). *Acrocephalus mendanae*, *A. percernis*, *A. atyphus*, *A. luscinius*, and *A. hiwae* were also relatively large, while species clustered in an intermediate position were *A. syrinx*, *A. rehsei*, *A. aequinoctialis*, *A. yamashinae*, *A. kerearako*, *A. vaughani*, and *A. taiti*. Contributing to shape variation (PC2 axis) were particularly *A. luscinius*, and *A. hiwae* with relatively long bills, and *A. taiti* and *A. vaughani* with relatively longer tails and tarsi and relatively smaller bills (Figs. 3 and 4).
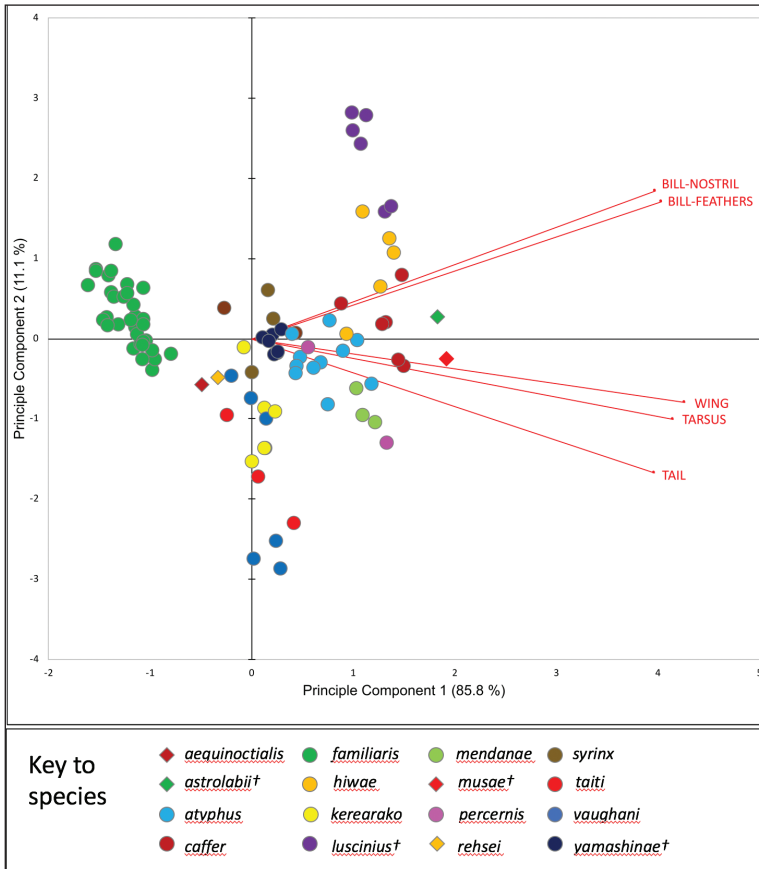
A feature of many Pacific island *Acrocephalus*

species was their relatively large bill size (Figs. 2–4; Dyrcz 2006; Kennerley & Pearson 2010; Dyrcz *et al*. 2016). For comparison with other *Acrocephalus* warblers, ratios of mean bill-to-skull length to mean wing-length were determined for all the world's *Acrocephalus* species (see Appendix). Ratios were highest in Pacific island species, except for *A. taiti*, *A. vaughani* and *A. aequinoctialis*, reflecting the proportionately larger bills in most Pacific island *Acrocephalus* warblers. Clearly both wing-size and wing-shape also affect these ratios, and wing-shape is considered next.

Wing formula and wing-shape
Wing-formulae were determined for a range of *Acrocephalus* species. Resident species, including those on islands, had more rounded wings, and generally, they have primaries 3–6 emarginated, often primaries 3–5. Long-distance migrants tended to have longer wings with fewer primaries emarginated, usually primary 3, sometimes 4 (Kennerley & Pearson 2010). Consequently, the position of the wing-point, and of the inner primary (or secondary) equivalent in length to the 2nd primary, tended to be more proximal on the bird in resident species, and more distal in migratory species.

When positions of the wing-point and the flight feather equivalent to the tip of the 2nd primary were compared (Fig. 5) for four *Acrocephalus* species groups — resident African species (including islands), resident Pacific island species, round-winged migratory or sedentary continental species, and long-winged continental migrants — there was a significant correlation between the two wing measures (Pearson r = 0.8691, df = 34, p < 0.001) and differences occurred between most groups for both wing measures (Mann-Whitney U-tests, p = 0.124 to p < 0.001).

Continental migrant *Acrocephalus* warblers with longer, more pointed, wings had equivalent primary measures most distally positioned (*arundinaceus, griseldis, orientalis, paludicola, palustris, schoenobaenus, scirpaceus*). Next in the sequence were rounder-winged migratory or more sedentary continental species (*agricola, australis, bistrigiceps, dumetorum, melanopogon, orinus, sorghophilus, stentoreus, tangorum*). Resident Pacific island reed-warblers (*aequinoctialis, atyphus, caffer, familiaris, kerearako, luscinius, mendanae, rimitarae, syrinx, taiti, vaughani*) were round-winged, but less so than the African species (*brevipennis, gracilirostris, newtoni, rodericanus, rufescens, sechellensis*) which had markedly rounded wings. The aptly named 'blunt-winged warbler' (*A. concinens*), a continental species, fell amongst some Pacific island species (Fig. 5; Kennerley & Pearson 2010).

Figure 3. Principal component analysis plot for five log-transformed measurements of museum specimens from 16 Pacific island *Acrocephalus* species. The measurements were wing-length, tail-length, bill-to-feathers, bill-to-nostril, and tarsus-length. The five lines show the projections of the five variables in the factors space. Symbols for most species are circles, but diamonds are used for four single individuals. † indicates extinct species.
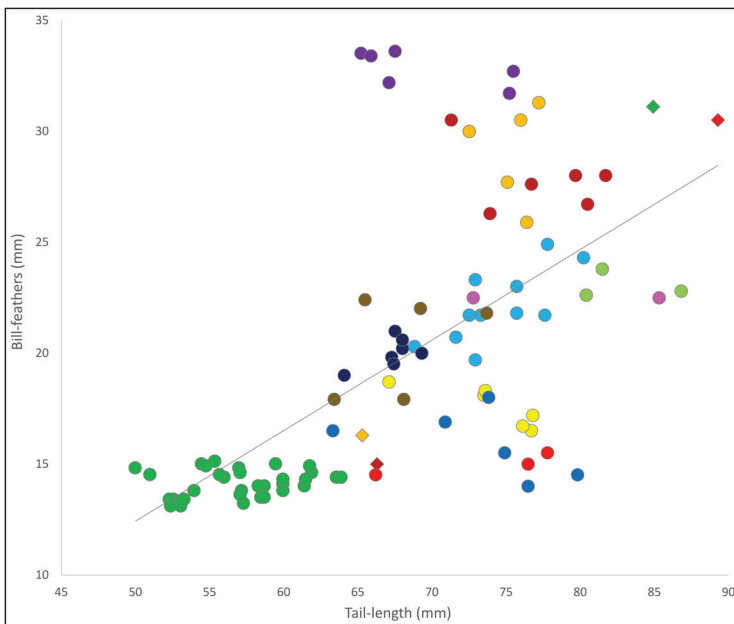

Figure 4. Scatter plot (with regression line) of tail-length and bill-to-feathers length for museum specimens of 16 Pacific island *Acrocephalus* species. Symbol codes for species are shown in Fig. 3.
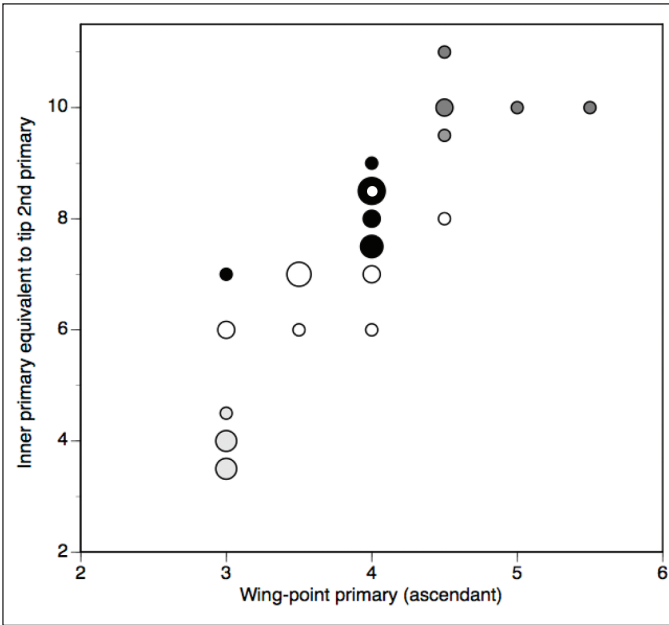
Figure 5. The positions of the wing-point primary plotted against the inner primary (occasionally secondary) equivalent to the tip of the 2nd primary (numbered ascendantly) in *Acrocephalus* warblers, the size of circles indicating the number of species (range 1–4). Four main *Acrocephalus* groups are differentiated: light grey = long-winged continental migrants; white = other continental species, often migratory; black = Pacific island species with rounded wings; dark grey = species from Africa and its offshore islands with markedly rounded wings. Those species with rounder wings tend to have both the wing-point and the primary equivalent to the 2nd primary more proximally positioned on the bird, while these primaries are more distal in species with longer wings, especially some long-distance migrants (r = 0.8691, df = 34, p < 0.001). Data from Kennerley & Pearson (2010) and present study.
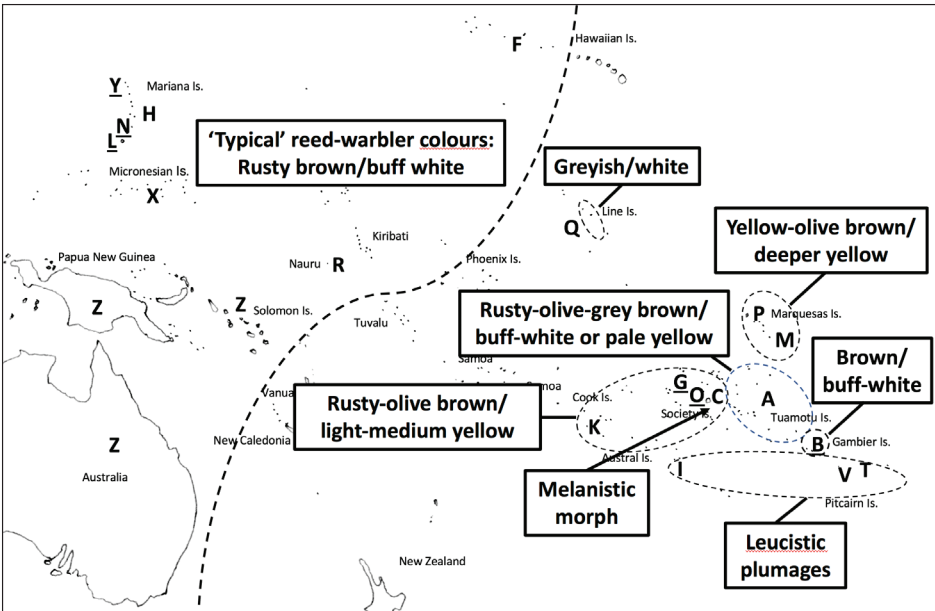
Figure 6. Predominant colours of *Acrocephalus* warblers across the Pacific based on examination of museum specimens, expressed mostly as dorsal colour/ventral colour. Letter codes for species as in Fig. 1. Data from present study, supplemented with information from Dyrcz (2006), Kennerley & Pearson (2010) and Dyrcz *et al*. (2016).

Plumage colour

The colours of Pacific island *Acrocephalus* warblers (Figs. 2 & 6) fell into two main groups: (1) species from the N and W Pacific islands (Hawaii, Marianas, Micronesia, and Solomons) which were uniform brownish dorsally and pale buff ventrally, akin to *Acrocephalus* species outside the Pacific (Fig. 2A,B,D; Dyrcz *et al*. 2016); (2) species that occur across E Polynesia which departed from the typical and relatively uniform 'reed-warbler' pattern, which were predominantly brown or grey dorsally, variously shaded olive, yellow and rufous, and paler ventrally, variously shaded white, yellow or buff — *A. percernis* and *A. mendanae* of the Marquesas islands (Fig. 2F,H) were particularly yellow ventrally, while in Kiritimati *A. aequinoctialis* was distinctly greyish dorsally and whitish ventrally (Fig. 6). In *A. atyphus* large colour variation was found in almost all atolls (Cibois *et al*. 2011c; A. Cibois *pers. comm.*).

South east Polynesian species also had pale edgings to the feathers, particularly on the mantle and upper wing coverts. In N and W Pacific species (group 1), these edgings appeared more uniform, although slightly paler brown edging occurred (in *australis, familiaris, hiwae, luscinius, nijoi, rehsei, syrinx* and *yamashinae*); also in *A. astrolabii*, evidently from Magareva in the Gambier Islands, SE Polynesia (Dyrcz 2006; Cibois *et al*. 2011b; Thibault & Cibois 2017). Some populations of adjacent *A. atyphus* in the Tuamotus also showed less marked feather edging, as did *A. aequinoctialis* and *A. kerearako* (Fig. 2C). In remaining, often larger, Polynesian species, pale yellow or yellow-white edging to dorsal feathers were clearly evident. The occurrence of white feathers (leucism) was a feature of the southern *A. rimitarae, A. taiti,* and *A. vaughani* (Fig. 2I & Fig. 6). In some specimens of *A. atyphus* (Fig. 2G), *A. caffer, A. familiaris* (Laysan subspecies *familiaris*), *A. kerearako, A. mendanae* and *A. percernis* some white feathers were also seen. On Tahiti *A. caffer* was dimorphic, being either a 'typical' olive brown/light yellow or, less frequently, a melanistic dark brown (Fig. 2E). In some species predominant colours differed between and within islands, e.g. in *A. atyphus* (Cibois *et al*. 2011c), and with age, e.g. in *A. vaughani* and *A. rimitarae* (Thibault & Cibois 2006).

Song patterns

Song spectrograms

Short sound spectrogram samples of song (or calls) of ten Pacific island *Acrocephalus* warblers and, for comparison, two continental species from the W Pacific (*A. australis, A. orientalis*), exemplify differences between species (Fig. 7). There was a gradient of song complexity from continental and Marianas/Micronesia species (*hiwae, syrinx*),

through to *A. taiti* from Henderson and *A. vaughani* from Pitcairn, which had no song but simpler harsh calls. Short bursts of song with intervals of no song were a feature of *A. familiaris* from Nihoa and *A. aequinoctialis* from Kiritimati, while a characteristic of the song repertoires of SE Polynesian *Acrocephalus* species (*kerearako, caffer, mendanae, percernis*) was the inclusion of 'churr' syllables. The relatively accomplished song of the 'nightingale' reed-warbler (*A. hiwae*) from Saipan was evident (Fig. 7).

Song complexity and delivery rate

Analyses of 36-second sound spectrogram samples of 13 Pacific island *Acrocephalus* warblers, plus *A. australis* and *A. orientalis* for comparison, revealed clear variation across the Pacific region, with similarity between some geographically adjacent groups (Table 2).

The most southern species on Henderson and Pitcairn evidently lacked a complex song and only uttered simple calls, generally varying only slightly in duration and amplitude — 1–3.5 syllable types s^{-1}, rather than the more complex series of syllables typical of the songs of most other Pacific island *Acrocephalus* species (Fig. 7; Table 2). No songs, only calls, of *A. rimitarae* were analysed. Amongst the other species examined, song syllable diversity and delivery rates varied, but overall most had less diversity than the migratory *A. orientalis* which had a higher syllable count and rate of syllable delivery (Table 2). The mean syllable diversity was highest in *A. hiwae* from Saipan; however, again reflecting its popular name 'nightingale reed-warbler' (e.g. Mayr 1945; Pratt *et al*. 1987).

The percentage of time in song was highest in *A. orientalis, A. kerearako* and *A. percernis*, but relatively low in song samples of *A. aequinoctialis, A. familiaris* and *A. rehsei*. Despite *A. familiaris* having a low song delivery rate overall, when syllable delivery was measured in relation to the time in song, it had the highest value – short, fast syllable deliveries with long intervals between them (Table 2). *Acrocephalus aequinoctialis* from Kiritimati had a distinctive and much simpler song than most *Acrocephalus* species (see Milder & Schreiber 1989), with the lowest percent time in song and low syllable diversity – the poorest of the Pacific island *Acrocephalus* songs, excluding *A. taiti* and *A. vaughani* with no song, and perhaps *A. rimitarae* with limited song (see Thibault & Cibois 2006). Although data were limited, the mean syllable delivery rate and syllable diversity were lower in *A. mendanae* from the S Marquesas than in *A. percernis* from the N Marquesas. *Acrocephalus caffer* was intermediate between the two Marquesan species. *Acrocephalus australis*, from both E Australia and the Solomons, had a relatively high syllable diversity but a relatively moderate delivery rate (Table 2).

Table 2. Song syllable diversity and delivery rates from 36-second samples of Pacific island *Acrocephalus* warbler songs. For comparison, samples from *A. orientalis* (Japan) and *A. australis* (E Australia and Honiara Island) are also included. Species are ordered by declining mean no. of song syllables over the 36-second period.

Species	Location	Sample size (n)	Mean (±SE) song time (seconds)	Mean (±SE) no. syllables	Mean (±SE) no. syllable types	Mean (±SE) no. syllables per second overall	Mean (±SE) no. syllables per second of song	Percent time in song
orientalis	Japan	2	31.3 ± 2.3	126.5 ± 3.4	18.0 ± 0.4	3.5 ± 0.3	4.0 ± 0.0	86.9
hivae	Saipan	5	27.4 ± 1.8	124.8 ± 4.9	32.8 ± 0.6	3.5 ± 0.3	4.5 ± 0.1	76.1
percernis	N Marquesas	4	30.9 ± 0.8	119.5 ± 3.1	20.0 ± 0.4	3.3 ± 0.2	3.9 ± 0.1	85.7
kerearako	Mangaia & Mitiaro	9	31.0 ± 0.6	114.9 ± 5.9	14.9 ± 1.1	3.2 ± 0.2	3.7 ± 0.2	86.1
syrinx	Truk	5	23.8 ± 2.6	94.0 ± 7.2	15.2 ± 0.6	2.6 ± 0.5	3.8 ± 0.2	66.2
australis	Australia & Solomons	5	19.9 ± 1.9	89.2 ± 9.5	20.2 ± 3.2	2.5 ± 0.3	4.5 ± 0.1	55.4
rehsei	Nauru	3	17.3 ± 4.0	89.0 ± 11.1	19.7 ± 1.3	2.5 ± 0.6	5.0 ± 0.1	48.1
caffer	Tahiti	5	29.6 ± 1.4	82.4 ± 0.3	13.2 ± 0.3	2.3 ± 0.3	2.8 ± 0.1	82.2
atyphus	Tuamotus	2	28.1 ± 7.9	80.5 ± 9.7	18.0 ± 1.9	2.2 ± 0.9	2.7 ± 0.2	78.0
familiaris	Nihoa	3	13.5 ± 2.9	75.7 ± 11.5	12.0 ± 0.6	2.1 ± 0.5	5.3 ± 0.4	37.4
mendanae	S Marquesas	5	25.4 ± 2.3	71.8 ± 4.2	10.6 ± 0.4	2.0 ± 0.4	2.8 ± 0.1	70.5
*rimitarae**	Rimatara	2	33.3 ± 2.7	38.0 ± 2.9	1.0 ± 0.0	1.1 ± 0.4	1.1 ± 0.4	92.5
aequinoctialis	Kiritimati	2	9.0 ± 2.1	35.5 ± 5.4	3.5 ± 0.1	1.0 ± 0.2	3.9 ± 0.3	24.9
*taiti**	Henderson	2	23.3 ± 5.7	30.0 ± 0.6	3.5 ± 0.6	0.8 ± 0.1	1.4 ± 0.3	64.8
*vaughani**	Pitcairn	2	23.7 ± 8.8	28.0 ± 0.3	1.0 ± 0.0	0.8 ± 0.0	1.4 ± 0.7	65.8

* only simple calls, no song
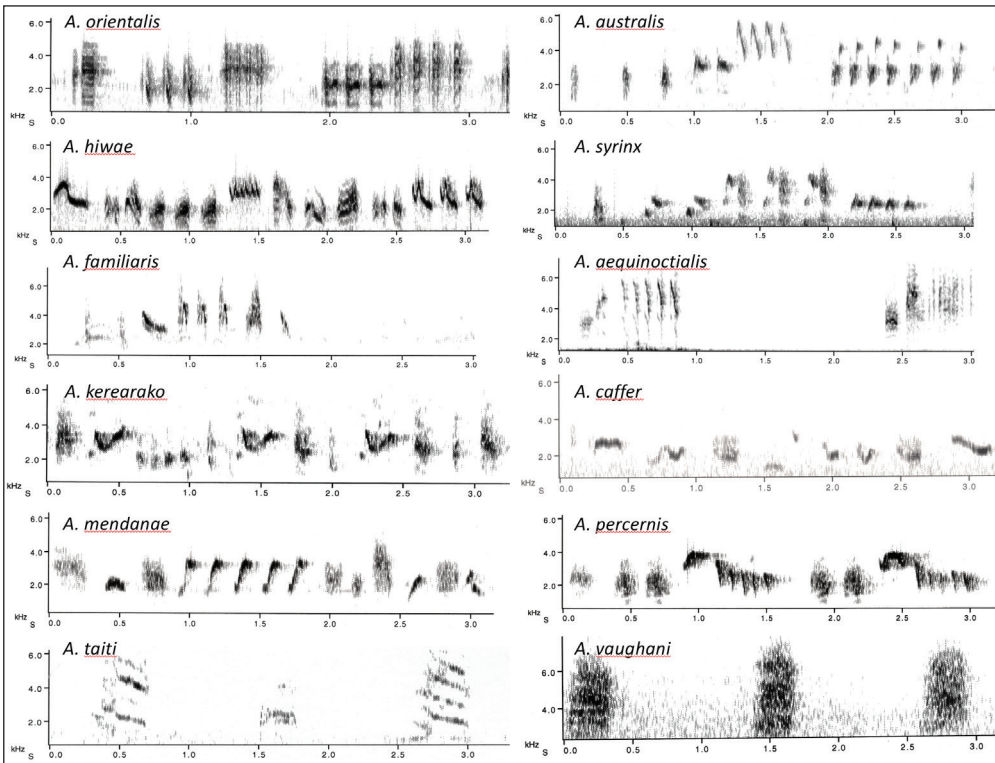
Figure 7. Sound spectrograms of ten Pacific island *Acrocephalus* warblers and, for comparison, two continental species from the W Pacific (*A. australis, A. orientalis*). Note harsher 'churr' notes in many species (e.g. *A. caffer, A. kerearako, A. mendanae, A. percernis*).
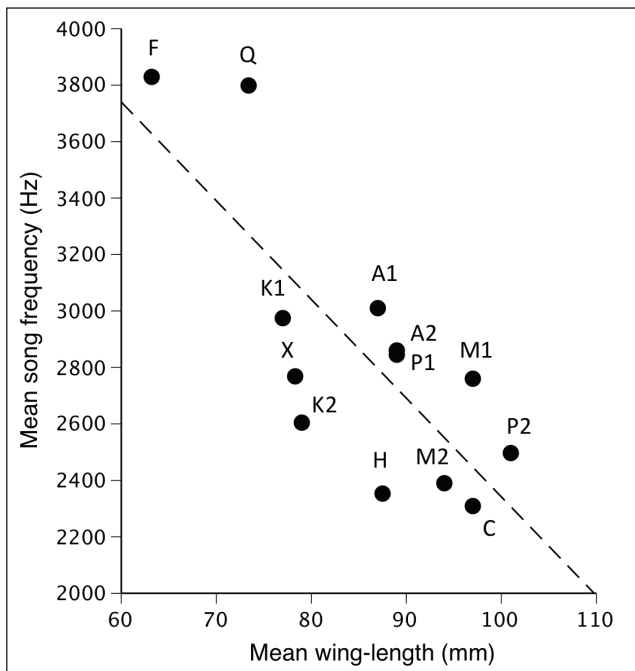
Figure 8. Mean song frequency is inversely correlated with mean wing-length in Pacific island *Acrocephalus* warblers (Pearson r = –0.608, df = 11, p < 0.02). Viewed downwards with decreasing mean frequency, the points plotted represent: F = *A. familiaris kingi* (Nihoa); Q = *A. aequinoctialis aequinoctialis* (Kiritimati), A1 = *A. atyphus eremus* (Anuanurunga); K1 = *A. kerearako kerearako* (Mangaia); A2 = *A. atyphus ravus* (Makatea); P1 = *A. percernis idae* (Ua Huka); X = *A. syrinx* (Chuuk); M1 = *A. mendanae consobrina* (Mohotani); K2 = *A. kerearoako kaoko* (Mitiaro); P2 = *A. percernis percernis* (Nuku Hiva); M2 = *A. mendanae dido* (Ua Pou); H = *A. hiwae* (Saipan); C = *A. caffer* (Tahiti). Samples of *A. taiti* (Henderson), *A. vaughani* (Pitcairn) and *A. rimitarae* (Rimatara) were excluded as no song was recorded.

Song frequency and body-size

While there was variation in the frequency range of different syllables in the song, overall the mean frequencies of song syllables for Pacific island populations were inversely correlated with mean body size: for example, the smallest species, *A. familiaris* of Hawaii (Nihoa) had the highest mean frequency and larger species, like *A. caffer* (Tahiti) and *A. hiwae* (Saipan), had song syllables in the lower mean frequency range (Fig. 8).

The frequency 'sound window' (mean maximum frequency – mean minimum frequency) was 4.8 kHz in the continental *A. orientalis*, but narrower in Pacific island *Acrocephalus* warblers. In songs or calls of *A. aequinoctialis, A. taiti* and *A. vaughani* the mean frequency range was 3.4–4.3 kHz. In other Pacific island species, it was lower, in descending order: 3.2 kHz (*A. familiaris*); 3.0 kHz (*A. atyphus*); 2.7 kHz (*A. australis* and *A. mendanae*); 2.3 kHz (*A. percernis*); 2.0 kHz (*A. kerearako*); 1.7 (*A. syrinx*); 1.5 (*A. hiwae*); and 1.3 (*A. caffer*).

DISCUSSION

The focus of this study was to quantify and inter-relate measures of morphological variation and song patterns in Pacific island *Acrocephalus* warblers, recognising that there have already been a range of studies describing their biology, phylogeny, systematics, behaviour, and ecology (e.g. Holyoak & Thibault 1977; Kennerley & Pearson 2010; Leisler & Schulze-Hagen 2011; Leisler & Winkler 2015; Thibault & Cibois 2017). In some instances, these warblers are the sole passerines on an island (e.g. *A. aequinoctialis, A. rehsei, A. taiti, A. vaughani*), and as residents on isolated islands or archipelagos, they differ behaviourally, ecologically, and morphologically from most *Acrocephalus* warblers elsewhere in the world. Over much of their global range, *Acrocephalus* warblers are migratory and associate with wetland habitats, including reeds from which reed-warblers get their name. On Pacific islands, such habitats are often not available, so these 'reed-warblers' have adapted to drier situations, including rank vegetation, scrub and forest (Dyrcz 2006; Kennerley & Pearson 2010; Leisler & Schulz-Hagen 2011; *pers. obs.*).

Morphologically, Pacific island reed-warblers ranged in size from the relatively small *A. familiaris* (superficially resembling the migratory common reed-warbler *A. scripaceus*), to relatively large warblers of Micronesia (e.g. *A. hiwae* and *A. luscinius*) and Eastern Polynesia (*A. caffer, A. longirostris, A. mendanae, A. musae*). Craig (1992) noted that greater size is typical of island forms that may confront competitively impoverished or food-limited environments, although the small *A. familiaris* also inhabits a food-limited environment.

The relative bill size was also greater in these species (*A. caffer, A. hiwae, A. luscinius, A. longirostris, A. musae*). In general, Pacific island *Acrocephalus* warblers had shorter, more rounded, wings than their continental counterparts (Fig. 5; Kennerley & Pearson 2010), suggesting different flight capability (Leisler & Schulze-Hagen 2011; Leisler & Winkler 2015). Pratt *et al*. (1987) described the flight as 'weak and fluttering' in *A. aequinoctialis* and *A. familiaris*, and 'slower and weaker than that of larger reed-warblers' in *A. atyphus*. On Tahiti, fluttering flight was a feature of *A. caffer*, while on Mitiaro Island in mid-February, an *A. kerearako* in heavy moult was virtually flightless (*pers. obs.*). Leisler & Schulze-Hagen (2011) remind us that in temperate continental *Acrocephalus* species, the longer the migration route, the longer and more pointed their wings, while in dense vegetation rounded wings are an advantage. Regarding tarsus length, Murphy & Matthews (1929) noted that *A. vaughani* is 'set well apart from other [Pacific] members of the genus by at least one structural characteristic, namely, the greater proportionate length of the tarso-metatarsus' (tarsus) — a difference evident in this study (Fig. 3).

Leisler & Schulze-Hagen (2011) suggested that overall the morphologies of island *Acrocephalus* warblers point towards terrestrial living and a more acrobatic use of the substrate (tarso-metatarsus diameter), a reduction in longer flights but greater manoeuvrability (wing traits), as well as a diminished role for aerial feeding and closer contact with various substrates during extractive foraging (rictal bristles). Leisler & Winkler (2015) later noted that the evolution of island *Acrocephalus* warblers is beyond just 'bills and masses', stressing that their evolution pertained to all functional complexes, and not only previously studied body size and bill dimensions, concluding that shape-related morphological evolution of island species is characterised by changes in the hind limb, flight, and feeding apparatus. Birds on islands converged to a morphology with strong legs, shorter rictal bristles, and rounder, more slotted and broader wings. However, body size and bill dimensions did not contribute to the separation of continental and island forms because of their high variance among islands, although bills tend to be longer on islands. They suggested that 'vegetation clutter' is the major driving force for variation in body size (Leisler & Winkler 2015). Wings of island birds hardly varied among islands; Leisler & Winkler (2015) concluding that this was not surprising due to a lack of adaptive features associated with long distance flights, and attributed a tendency towards shorter rictal bristles in island warblers to the diminished role of aerial feeding, and to closer contact with various substrates in the course of extractive foraging.

Noting a shift towards stronger legs in several insular species, they saw this as remarkable, as reed-warblers on continents have even stronger legs than other passerines of comparable size, noting that this trait correlates with feeding techniques associated with broad habitat use (Leisler & Winkler 2015).

The colour of the more northern island *Acrocephalus* species in the Marianas, Micronesia and Hawaii broadly resembled the colour of reed-warblers elsewhere, but in SE Polynesia their colouration was more varied, including more yellow and/or white in the plumage (Fig. 6). Such shifts from 'typical' reed-warbler colours suggests different selection pressures on reed-warblers that generally no longer live in reeds. In the Line Islands (Kiritimati) the plumages were shades of grey and white (*A. aequinoctialis*; Fig. 6), while on Pitcairn, Henderson and Rimatara, leucism (white feathers) occurred (*A. taiti, A. rimitarae, A. vaughani*; also in some *A. atyphus* – see Fig. 2G,I). On Tahiti, *A. caffer* had a less common melanistic morph (Kennerley & Pearson 2010; Cibois *et al*. 2012; Fig. 2E; *pers. obs.*). A dark morph also occurs in *A. stentoreus* in the Middle East, forming approximately 5% of the population there (Laird 1992; Svensson 2009; Kennerley & Pearson 2010; Shirihai & Svensson 2018). The pattern of leucism was different between *A. taiti, A. rimitarae* and *A. vaughani*, affecting primarily the anterior body plumage, secondaries, and rectrices of *A. taiti*, the primaries, secondaries, and rectrices of *A. vaughani*, and scattered parts of the plumage of *A. rimitarae* (Murphy & Mathews 1929; Holyoak 1978; Graves 1992; Thibault & Cibois 2006). In all three taxa, leucism appeared to progress with age. Graves (1992) suggested that there was no evidence that leucism was a consequence of songlessness or vice-versa.

While the complexity and delivery rate of song syllables have been studied in a range of migratory *Acrocephalus* species (e.g. Catchpole 1980, 1981a; Hasselquist *et al*. 1996) and a few island taxa (e.g. Catchpole & Komdeur 1993), song complexity in resident Pacific island reed-warblers has received less attention (but see, e.g. Milder & Shreiber 1989). The generally more complex songs of the Old World warblers, including the Acrocephalidae, may have evolved under the pressures of sexual selection or during the process of speciation (Barlein 2006).

Song contrasts are most striking when they concern close relatives, as within the genus *Acrocephalus,* and whether or not a bird migrates has been identified as an important factor influencing song learning strategies (Catchpole & Slater 2008). While here 49 individual song spectrograms were examined for various Pacific island *Acrocephalus* species, and comparisons made with *A. australis* and *A. orientalis*, only a few individuals were sampled for some species. But, given this qualification, contrasting and comparable trends did emerge from spectrographic analysis (Fig. 7; Table 2). Song syllable diversity and delivery rates varied, but overall they had lower syllable diversity than the migratory *A. orientalis* (Table 2). On Kiritimati in the Line Islands *A. aequinoctialis* had a relatively simple song (see Milder & Schreiber 1989), on Nihoa Island *A. familiaris* gave rapid bursts of song at intervals, and on Saipan *A. hiwae* had the most complex song — Mayr (1945) described the 'nightingale' reed-warbler of the Marianas as a 'beautiful singer', implying such a varied and musical repertoire. The three southernmost species had either no song (*A. taiti* and *A. vaughani*), or limited song (*A. rimitarae*), mostly uttering simpler, harsh call notes (Fig. 7; Table 2; Thibault & Cibois 2006).

How do Pacific island *Acrocephalus* songs compare with long-distant migrant *Acrocephalus* species other than *A. orientalis* (Table 2)? Two well-researched European species that winter in Africa, known to have elaborate song repertoires, are the marsh warbler (*A. palustris*) and the sedge warbler (*A. schoenobaenus*; Lemaire 1974; Catchpole 1980, 1981a; Simms 1985). Males of both species have greater song syllable diversity and delivery rates than the resident Pacific island *Acrocephalus* warblers (Table 2). For example, in Poland the mean (± SE) song syllable delivery rate of 23 male *A. palustris* was 5.00 (± 0.17) syllables s^{-1} (range 3.11–6.30 syllables s^{-1}; data from Bell *et al*. 2004), while over 15 min of continuous song a male *A. palustris* in Worcestershire, UK, sustained a generally linear output of 66.2 *new* syllable elements min^{-1} (Bell *et al*. 2004). This comparison is at the higher level of syllable diversity for *Acrocephalus* warblers, Simms (1985) noting (p. 220) that a top singer among marsh warblers 'has no real peer among the *Acrocephalus* warblers'. The migratory *A. shoenobaenus* also has a complex repertoire (Catchpole 1980, 1981a; Simms 1985). In Poland, males had a mean (± SE) overall syllable delivery rate of 3.61 (± 0.24) syllables s^{-1} overall (range 2.02–4.69 syllables s^{-1}), and 4.24 (± 0.22) syllables s^{-1} (range 2.40–5.14 syllables s^{-1}) if between-song intervals were excluded (Bell *et al*. 1997). In this comparison, song complexity and delivery rates were generally higher than in Pacific island *Acrocephalus* species, except for *A. australis, A. familiaris, A. hiwae* and *A. rehsei* which had higher mean syllable delivery rates for time in song, but not higher mean syllable delivery rates overall (Table 2).

Numerous studies indicate that large repertoires are driven by sexual-selection, some field studies showing correlations between repertoire size and breeding success (e.g. Searcy 1984; Catchpole *et al*. 1986; Baker *et al*. 1987; Searcy & Yasukawa 1990;

Searcy 1992; Mountjoy & Lemon 1996; Bell *et al.* 1997, 2004; Buchanan & Catchpole 1997; Lampe & Espmark 2003), but that was not always the case (e.g. Beecher *et al.* 2000), or has been questioned (e.g. Darolová *et al.* 2012). Amongst *Acrocephalus* species, the migratory *A. palustris* with its particularly complex and varied repertoire, appropriates syllables from other species into its repertoire, both from its European breeding grounds and from its African winter quarters (Dowsett-Lemaire 1979). It is the latest trans-Saharan migrant *Acrocephalus* species to arrive on its European breeding grounds (Catchpole 1980, 1981a), and there is a high premium placed on the male to quickly attract a mate, which might have driven sexual selection for development of its particularly complex song. Song functionally therefore evolved primarily for mate attraction (inter-sexual selection), more than for territorial advertisement (intra-sexual selection), more elaborate songs resulting in higher breeding success, involving polygyny in some species, and invoking the idea of male song being an 'acoustic peacock's tail' (Catchpole 1980, 1981a,b; Hasselquist *et al.* 1996; Bell *et al.* 1997, 2004). Other migratory *Acrocephalus* warblers, including *A. orientalis* and *A. schoenobaenus*, also face pressures of time to attract a mate and initiate breeding. In a review of the relationship between latitude, migration and the evolution of bird song complexity, Najar & Benedict (2018) concluded that there was no strong evidence that song complexity increases with latitude and/or migration in all birds, although it did in some species, as evidenced by *A. palustris* and *A. schoenobaenus*.

For resident island *Acrocephalus* species, the situation is very different, as such time constraints do not apply in tropical and subtropical regions where extended breeding throughout much of the year occurs (Kennerley & Pearson 2010). In an island study of *A. sechellensis* on the Seychelles, Catchpole & Komdeur (1993) found that this resident reed-warbler is a cooperative breeder in a saturated, island environment, with a song structure differing significantly from migratory European marshland *Acrocephalus* species. Song was transmitted within a more restricted frequency range which propagated more effectively through tropical forest. Males had a relatively short, simple song, used for territorial defence throughout the year, but they also had a complex repertoire of song types, with song activity peaks before and declines during breeding, suggesting an inter-sexual function — mate-attraction. Catchpole & Komdeur (1993) concluded that the demands of tropical island life are reflected in both the structure and function of male song in *A. sechellensis*. Leisler & Schulze-Hagen (2011) suggested that simpler songs in Pacific island *Acrocephalus* populations,

comprising shorter signals, might have been selected for to facilitate individual recognition of familiar resident neighbours. They noted that such songs are more strongly coded for estimating distance and for individual recognition, with a much-reduced function of attracting a partner through greater song complexity.

On Kiritimati, Milder & Shreiber (1989) reported that in the absence of other Pacific land birds and natural predators, vocal signals of *A. aequinoctialis* were simple compared to most *Acrocephalus* species, and suggested that this was the result of a lack of interspecific interactions, a monogamous life-style, large permanent territories, open dry habitat and limited interaction among neighbouring individuals. On Saipan, however, *A. hiwae* is extremely territorial, singing from exposed treetops, interior thickets, or stems of elephant grass (*Pennisetum purpureum*), male defensive behaviour including song and pursuit (Craig 1992; Rounds & Radley 2018). Contrasting with mainland *A. orientalis* and *A. arundinaceus*, *A. hiwae* had polygyny largely or entirely absent, much larger territories, upland rather than marshes as the principal breeding habitat and body size, particularly bill size, greatly increased. A shift to upland habitats may account for these differences in social behaviour and territory size. Mosher & Fancy (2002) found nests of *A. hiwae* within three habitat types: upland introduced tangan-tangan (*Leucaena leucocephala*) forest, a native mangrove (*Bruguiera gymnorrhiza*) wetland, and a native reed (*Phragmites karka*) wetland. Nesting substrates included five native and two introduced tree species and one native reed species. Kennerley & Pearson (2010) noted that *A. hiwae* showed a distinct preference for tangan-tangan woodland, and mosaics of tangan-tangan and sword grass (*Miscanthus floridulus*) or elephant grass, but otherwise chose wetlands.

Holyoak (1978) reported that on Henderson *A. taiti* gave a variety of chirping calls but no song. However, Graves (1992) suggested that the lack of song may be a matter of interpretation, noting that most of its vocalisations were high pitched (4–8 kHz) single notes of short duration (<0.13 set), but there were also series of thin, longer notes (l–5 set) given by adult territorial birds, albeit in an unknown context, that resembled song (his Fig. 6). He observed that these vocalisations could be clearly heard at 25 m above the white noise of wind and surf (both predominately 0–3 kHz) along beaches, and probably functioned in inter-territorial communication, given the small territory size of *A. taiti*.

There have been conflicting reports about whether *A. rimitarae* has a song. It was reported as emitting a variety of chirping calls, but no song by Barlein (2006). Thibault & Cibois (2006), however, reported that males sang regularly in

the early morning, the evening, or during bright moonlit nights, but rarely during midday, even during the breeding season, quoting Quayle (ms) who wrote: 'Here is a warbler singing with all the variation and harmony of Marquesan or Tahitian varieties'. Kennerly & Pearson (2010) noted that *A. rimitarae*, unlike its counterparts on Pitcairn and Henderson, has a recognisable song described as a succession of low and short whistling notes, less powerful and elaborate than songs of *A. caffer* or *A. atyphus*, and was typically of shorter duration. Dyrcz & Sharpe (2018) report its description as a loud 'chack-chack', with a variety of chirping calls, and noted that while the latter are recognised as a song by some authors, 'true song' was not recorded.

Tameness is another feature of many endemic island birds, and is evident in some Pacific island reed-warblers. For example, on the extinct Laysan millerbird, *A. familiaris familiaris*, Schauinsland (1899), quoted by Bailey (1956), remarked that 'one of these little singers once chose the edge of my open book for its perch, and gave forth its best song'. Elsewhere, *A. aequinoctialis* and *A. vaughani* were described as 'bold and inquisitive' and *A. atyphus* and *A. mendanae [percernis]* as 'easily "squeaked up" ...', while, in contrast, *A. luscinia* [*hiwae*] and *A. syrinx* were described as skulkers, the Nihoa millerbird *A. familiaris kingi* as 'A secretive denizen' and *A. caffer* as 'usually shy and difficult to observe' (Pratt *et al.* 1987), although I found the song posts of *A. caffer* were typically high up (usually in bamboo) rather than in a skulking position lower down. On Mitiaro Island *A. kerearako* was relatively approachable (pers. obs.).

Body size is known to be negatively correlated with song frequency measures in birds (e.g. Wallschläger 1980; Badyaev & Leaf 1997; Mahler & Gil 2009; Tietze *et al.* 2015). The low frequency range of a species may be limited by body size (Ten Cate 2004) — e.g. in the small leaf warblers (Phylloscopidae) body size was a constraint on song frequencies, independent of phylogeny (Tietze *et al.* 2015). Frequency (or pitch) not only indicates body size across different species, but also within a species — e.g. the larger the male purple-crowned fairy-wren (*Malurus coronatus coronatus*) the lower the pitch of its song (Hall *et al.* 2013). In Pacific island reed-warblers, the song of the 13 cm long *A. familiaris* from Nihoa was described as 'metallic and bubbling' (Shallenberger 1981) and the 15 cm *A. aequinoctialis* had songs of limited syllables usually beginning with a distinctive 'cha chĕ', with the 'chĕ' high-pitched (Milder & Shreiber 1989). In contrast, the song of the 17–19 cm *A. caffer* on Tahiti was of lower frequency, with mellow notes (reminiscent of some *Turdus* thrushes), while the song of *A. hiwae* was described as a slow, loud, varied but simple melody, range 1–5 kHz, not dissimilar to the song of

a Eurasian blackbird (*Turdus merula*), but sounding harsher and less melodic and containing short and fluty warbling sections (Kennerly & Pearson 2010). Over a range of measurements of frequency and size, there was therefore an inverse relationship (see Fig. 8).

However, size alone does not influence song frequency, the environment through which the sound is transmitted also plays a part (Morton 1975; Catchpole & Slater 2008). When comparing *A. sechellensis* with the migrant *A. scripaceus*, Catchpole & Komdeur (1993) found that the frequency range was much reduced in the island species, and approximated the 'frequency window' for optimal transmission in tropical forest (Morton 1975). Many Pacific island *Acrocephalus* species also inhabit forest and scrub habitats, rather than more open wetland habitats (Kennerley & Pearson 2010), and their frequency ranges (Fig. 7) are also relatively narrow and generally reflect the <4 kHz sound window that Morton (1975) described for low forest. The higher frequencies in *A. aequinoctialis* and *A. familiaris* songs may also reflect their more open habitats (Morton 1975), while the harsh, high frequency calls of *A. taiti*, *A. rimitarae* and *A. vaughani* may facilitate sound transmission against a background of wind and ocean noise in SE Polynesia, as Graves (1992) suggested.

Using sequences of mitochondrial DNA (cytochrome *b*, ND2, and ATP8 genes), Cibois *et al.* (2011a) concluded that Pacific island *Acrocephalus* warblers did not form a monophyletic group, since the extinct *A. luscinius luscinius* from Guam fell outside the main Pacific radiation. The remaining Pacific taxa were divided into two clades: one clade including all other reed-warblers from Mariana/Micronesia and Australia, and two Polynesian taxa from the Line Islands (*A. aequinoctialis*) and S Marquesas (*A. mendanae*); the other clade including all remaining Polynesian taxa. Adding to earlier studies of Pacific island *Acrocephalus* species (e.g. Holyoak & Thibault 1977; Thibault & Cibois 2006; Cibois *et al.* 2007, 2008), they revealed a more complex pattern of colonisation of the Pacific islands by *Acrocephalus* warblers than stepping-stone colonisation previously invoked, notably that the Mariana, Marquesas and Society taxa are polyphyletic and that the Australian reed-warbler (*A. australis*) represents 'reverse colonisation' from island to continent. The present study found some similarities between *A. australis* and Pacific island *Acrocephalus* species (Fig. 6; Table 2), but the phylogenetic difference between the northern (*A. percernis*) and southern Marquesas (*A. mendanae*) was not evident from their broadly similar morphometrics and colouration (Figs. 2–4), but *A. mendanae* had a less elaborate song (Table 2). Although data were limited, the mean syllable

delivery rate and syllable diversity were lower in *A. mendanae* than in *A. percernis*, but sampling from a greater number of islands in the Marquesas Archipelago could possibly show different dialects rather than a clear difference between two species. Similar morphological characters may reflect their broadly similar environments as the two species are in close geographical proximity (Fig. 1). Thibault & Cibois (2017) suggested that for these two species this similarity reflected a higher influence of ecology than of phylogeny and that within the Marquesas Archipelago birds on dry and smaller islands tend to be smaller than those on larger islands, irrespective of their phylogenetic origin. The *Acrocephalus* species across Micronesia, while manifesting some marked differences (e.g. in body and bill size – see Mayr 1945), are collectively more typical *Acrocephalus* species in terms of their general colouration and type of song.

In conclusion, insularity has resulted in extensive speciation of *Acrocephalus* warblers across the Pacific. Since Darwin's studies of finches on the Galapagos Islands (Darwin 1859; Lack 1947; Grant *et al*. 1985), studies of avian evolution have often focussed on islands and archipelagos, including elsewhere in the Pacific such as Hawaii and New Zealand (e.g. Fleming 1962, 1975; Bock 1973; Lerner *et al*. 2011). Islands are simplified, isolated ecosystems, providing an ideal set-up to study evolution, including bird song (Morinay *et al*. 2013). The Pacific island reed-warblers are more widely distributed than on single archipelagos, and there are further opportunities for behavioural, ecological and evolutionary research on them across a range of spatial scales, adding to studies already undertaken (e.g. Cibois *et al*. 2007, 2008, 2011a; Leisler & Schulze-Hagen 2011; Leisler & Winkler 2015), and addressing how the birds might have adapted to island environments far removed from the wetland habitats occupied by their continental counterparts.

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Appendix. Ratios of bill (to skull) length/wing-length in the world's *Acrocephalus* species. Species are in increasing order of ratio values. Ratios are highest in most Pacific island species (shown in bold), although they are lower in *A. taiti, A. vaughani* and *A. aequinoctialis*. Species names follow Dyrcz *et al*. (2016), data are sourced from this study and from Kennerley & Pearson (2010), Cibois *et al*. (2011b) and Saitoh *et al*. (2012).

Species	Bill/wing ratio	Status
paludicola	0.215	Palaearctic migrant
schoenobaenus	0.220	Palaearctic migrant
taiti	**0.226**	**Resident (Pacific island)**
palustris	0.231	Palaearctic migrant
arundinaceus	0.237	Palaearctic migrant
vaughani	**0.244**	**Resident (Pacific island)**
sorghophilus	0.248	Asian migrant
scirpaceus	0.256	Palaearctic migrant
bistrigiceps	0.256	Asian migrant
agricola	0.256	Palaearctic migrant
aequinoctialis	**0.260**	**Resident (Pacific island)**
griseldis	0.261	Palaearctic migrant
melanopogon	0.261	Partial migrant
gracilirostris	0.264	Resident (Africa)
sechellensis	0.265	Resident (Seychelles Is.)
orientalis	0.270	Asian migrant
newtoni	0.272	Resident (Madagascar Is.)
australis	0.273	Resident (Australasia)
dumetorum	0.274	Palaearctic migrant
concinens	0.274	Asian migrant
tangorum	0.280	Asian migrant
rimitarae	**0.282**	**Resident (Pacific island)**
rodericanus	0.284	Resident (Rodrigues Is.)
rufescens	0.294	Resident (Africa)
kerearako	**0.296**	**Resident (Pacific island)**
familiaris	**0.300**	**Resident (Pacific island)**
stentoreus	0.302	Migrant
brevipennis	0.305	Resident (Cape Verde Is.)
percernis	**0.307**	**Resident (Pacific island)**
rehsei	**0.313**	**Resident (Pacific island)**
orinus	0.314	Palaearctic migrant
atyphus	**0.315**	**Resident (Pacific island)**
yamashinae†	**0.317**	**Resident (Pacific island)**
mendanae	**0.323**	**Resident (Pacific island)**
nijoi†	**0.324**	**Resident (Pacific island)**
syrinx	**0.329**	**Resident (Pacific island)**
caffer	**0.360**	**Resident (Pacific island)**
longirostris†	**0.364**	**Resident (Pacific island)**
musae†	**0.371**	**Resident (Pacific island)**
astrolabii†	**0.379**	**Resident (Pacific island)**
hiwae	**0.400**	**Resident (Pacific island)**
luscinius†	**0.432**	**Resident (Pacific island)**

† extinct