Using Samoan traditional ecological knowledge to identify calls of the critically endangered endemic tooth-billed pigeon (*Didunculus strigirostris*)

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Abstract. The tooth-billed pigeon (*Didunculus strigirostris*) is an endemic and highly cryptic bird of the rainforest canopy of Samoa. According to the recently released Tooth-billed Pigeon Recovery Plan (2020–2029), one of the greatest obstacles to conservation efforts is the inability of ornithologists to reliably separate its advertising coo call from that of the common and sympatric Pacific imperial pigeon (*Ducula pacifica*). Because tooth-billed pigeons are very rarely seen, acoustic methods of identifying them, which have been problematic for ornithologists, would be helpful for population surveys. Our study examines the traditional ecological knowledge and skill of Samoan hunters, peer selected for knowledge and reliability from six villages located on Upolu and Savaii islands, to determine whether they can consistently identify the species based on the calls. Through use of automatic devices, we recorded pigeon coo calls at nine forest sites recommended by reliable hunters within four key biodiversity areas of the islands of Upolu and Savaii from March to June 2016. We isolated and filtered 104 clear coo call sequences from these recordings. The two top hunters separately and confidently identified which of the two pigeon species were calling for 80 of the 104 sequences. On 54 of these 80 call sequences the hunters were in agreement, both assigning a call to the one species. We measured seven sonographic variables on each of the coo calls of each of these 54 sequences in order to investigate potential differences between the calls of *Didunculus* and *Ducula*. Two clear differences emerged: a strongly statistically significant difference in the highest frequency of the coo call, and the more regular spacing of the coo calls of *Didunculus* than of *Ducula*. Only the second rhythm outcome is consistent with a recent independent analysis by other authors. This regularity of the intervals between coo calls in a sequence may be the key to separation of the two species in the field.

Keywords: call overlap, *Didunculus strigirostris*, *Ducula pacifica*, local ecological knowledge, oceanic rainforest, Pacific imperial pigeon, Polynesia, Samoa, sympatric pigeons, tooth-billed pigeon, traditional ecological knowledge.

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Introduction

The tooth-billed pigeon (*Didunculus strigirostris*), locally known as 'Manumea' (MNRE 2006, called '*Didunculus*' hereafter), a Samoan endemic, is evolutionarily distinctive (Jetz *et al.* 2014). It has been assessed as Critically Endangered in the IUCN Red List since 2014 (BirdLife International 2015). Ecological and behavioural knowledge about this species is scant and scattered (Beichle 1982*a*, 1982*b*, 1987*a*, 1987*b*, 1989; Beichle and Baumann 2016; Pratt and Mittermeier 2016). All the available information on *Didunculus* was reviewed and collated recently by Collar (2015).

The precipitous decline of *Didunculus* was brought to the attention of the conservation community by Beichle (2006), who reported that only a 'few hundred' birds survived at the time, implying a 90% reduction in numbers since the mid-1980s

(Stattersfield and Capper 2000; Beichle and Baumann 2016). The perilous conservation status of *Didunculus* was confirmed by a survey in 2012 of the species' presumed stronghold in the remote uplands of Samoa's largest island, Savaii, that found no *Didunculus* (Butler 2012). *Didunculus* has been listed as Endangered since 2000 (BirdLife 2015) and a recovery plan was approved for implementation in 2006 (MNRE 2006) although very few of its recommendations have been implemented (Serra 2017; U. Beichle, pers. comm.).

Didunculus is highly cryptic in rainforest habitat. Serra *et al.* (2017) found that medium to intensive surveys by Government or international experts produced one sighting every 3–5 years. The situation has been summarised by Collar (2015), who stated 'The great difficulty throughout this century has simply been to find even a single representative of the species', and

Pratt and Mittermeier (2016) stated that *Didunculus* has turned into 'an immediate conservation priority' for Samoa.

Further complicating the issue of assessing the occurrence and conservation status of *Didunculus* is the extreme difficulty of reliably identifying its call in the field. The advertising coo call of *Didunculus* (*sensu* Baumann and Beichle 2020) is similar to a call of the relatively common sympatric Pacific imperial pigeon (*Ducula pacifica*, called '*Ducula*' hereafter). The similarity in calls between the two species was first noted by Butler (2012) and then confirmed by Beichle and Baumann (2016), Pratt and Mittermeier (2016) and Serra (2016).

This 'under-appreciated similarity' (Pratt and Mittermeier 2016) was evidenced through use of traditional ecological knowledge (TEK): selected 'reliable' hunters (see definition in the Methods) showed an unexpected difficulty distinguishing the recorded vocalisations of the two species (Serra *et al.* 2017). Moreover, little consensus was found in terms of key differences between *Didunculus* and *Ducula* calls when consulting local hunters, and Government or international experts, including the *Didunculus* authorities (Ulf Beichle and Sabine Baumann) (Serra *et al.* 2017).

The distinguishing feature on which all agreed is that ~20% of *Ducula* coo call sequences present an introductory syllable and/or a brief modulation within the first third of the call (Beichle and Baumann 2016). The same authors indicated that *Didunculus* has shorter intervals between coo calls within a given sequence (Beichle and Baumann 2016).

Based on recordings of birds identified visually (9 *Didunculus* and 16 *Ducula*), Baumann and Beichle (2020) suggested that the coo call of *Didunculus* is higher pitched than that of *Ducula* and proposed a pitch higher than 400 Hz as a criterion for identifying the call of *Didunculus*. The same authors state that only *Didunculus* repeats the call more than 20 times, especially during the breeding season, presumed to be the dry season between April and August (Beichle and Baumann 2016; Baumann and Beichle 2020).

TEK mastered by the indigenous communities typically goes unrecorded and is often downplayed as 'anecdotal information' in the scientific literature (Blair 2005). The 'observational value', however, of TEK was underlined by Sinclair *et al.* (2010), while its relevance in relation to detecting rare birds was emphasised by Serra *et al.* (2004) and Blair (2005). Sourcing this type of knowledge requires spending a considerable amount of time establishing a trusting and viable working relationship with indigenous holders of TEK. By contrast, the 'rapid' survey methods popular nowadays such as the BIORAP (Conservation International 2016), reliant mainly on scientific ecological knowledge, are not ideal for the detection and assessment of the status of rare and elusive fauna (Powell 2008). In the present study, we regarded as TEK all the information we managed to collect, decode and verify from a rigorously selected sample of senior and experienced pigeon hunters based in the Samoan villages.

Given the present extreme challenge of detecting *Didunculus* visually in the field, this study adopts an indirect approach. We used TEK of experienced hunters to separate the coo calls of *Didunculus* and *Ducula*, based on automatically recorded forest sounds. We analysed sonographically independent sound recordings ascribed to the two species by hunters and identified spectral and temporal differences.

Materials and methods

Detailed information about this section is available as Supplementary Material online (refer to underlined words within the text).

Study areas

The study areas were in four of the eight designated terrestrial Key Biodiversity Areas (KBAs) of Samoa (Conservation International *et al.* 2010), namely Uafato-Tiavea Coastal Forest and Apia Catchments on Upolu island (Fig. 1) as well as Central Savaii Rainforest and Falealupo Peninsula on Savaii island (Fig. 2).

Selection of reliable pigeon hunters

Between November 2015 and February 2016 we designed a questionnaire to selected hunters holding reliable TEK of their ancestral forests (Serra 2016). The questionnaire was in the Samoan language and we followed customary protocols (Grattan 1985) before requesting to interview the hunters of the village. The respondents were not randomly selected (Text S1); they were identified by the village council of elders as 'the most knowledgeable about native biodiversity and sincere'. We followed design recommendations to minimise response biases (White *et al.* 2005).

We used special care to test the ability of interviewees to identify birds (Text S2), the most biologically diversified taxonomic group targeted by hunters in Samoa, in an attempt to determine their credibility (Serra 2016). We aimed to obtain detailed anatomical, ecological and behavioural descriptions from interviewees, without influence from published images or use of local names.

The reliability and skills of each interviewee were independently assessed by three interviewers by scoring their replies on a scale of 1 (low) to 10 (high). The purpose of these assessments was to ensure that interviewees could consistently and accurately distinguish different bird species (with a focus on pigeons), and to gauge the quality of other information they related while answering the questionnaire.

We considered any interviewee who scored 6 or better to be a reliable source of TEK, hereafter indicated as 'reliable hunter'. In total, 40 hunters from seven villages located within the mentioned four KBAs were interviewed and their bird identification skills assessed (refer to Serra *et al.* 2017, table 1). Based on their performance, we then selected 19 hunters whom we regarded as reliable (refer to Serra *et al.* 2017, table 2).

Automatic forest sound recording, in locations based on TEK

From the 19 selected hunters we chose one or two reliable hunters from each village. These hunters were then asked to lead field observations (Text S3) over 1 or 2 days in their ancestral forests (refer to Serra *et al.* 2017, table 1). During these field visits, we recorded all TEK about rare native species based on informal unhurried discussions; we double checked and 'ground truthed' any key information gathered during previous interviews and from questionnaires as much as feasible (refer to 'consistency' in Serra *et al.* 2017, table 2).

We deployed two autonomous recording units (ARU, Wildlife Acoustics SM3), each equipped with two non-directional

Fig. 1. Distribution of villages sampled for traditional ecological knowledge on the vocalisations of the critically endangered *Didunculus strigirostris* in the two terrestrial KBAs of Upolu island (borders in yellow): Apia Catchments (AC) and Uafato-Tiavea Coastal Forest (UTCF). Image courtesy of Google Earth.

Fig. 2. Distribution of villages sampled for traditional ecological knowledge on the vocalisations of the critically endangered *Didunculus strigirostris* in the two terrestrial KBAs of Savaii island (borders in yellow): Central Savaii Rainforest (CSR) and Falealupo Peninsula (FP). Image courtesy of Google Earth.

microphones, for 7–15 days at two locations recommended by the reliable hunters within the forests of Uafato, Aopo, Taga and Falealupo (so across three different KBAs of Samoa) (Text S4).

Only in the Malolelei forest (Apia Catchments KBA) were two sets of ARUs set up at sites selected not based on TEK but on possible/probable identifications of *Didunculus* calls attempted by Government and international experts
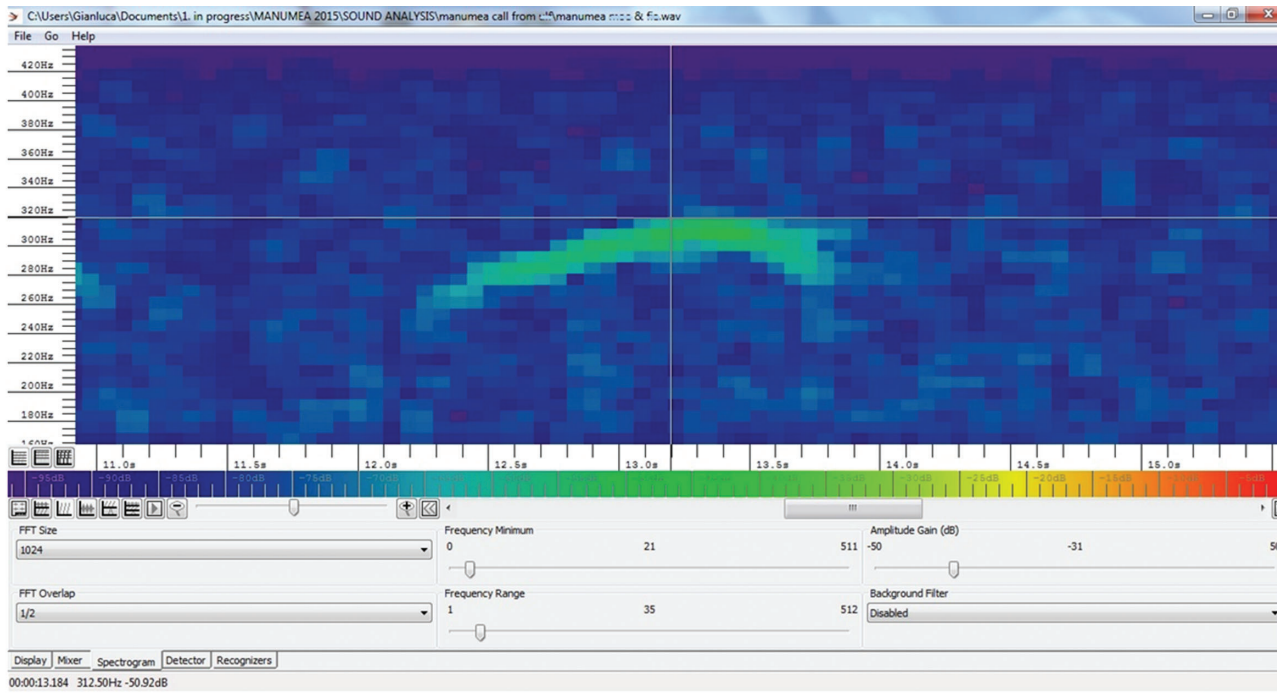
Fig. 3. Program Song Scope (ver. 4.1.3 A) workspace for spectrographic analysis showing a coo call (identified as *Didunculus* by Ulf Beichle in assistance to MNRE). The two crossed lines, moving through the cursor, were used to measure the sonographic variables with accuracy. For instance, the highest frequency of the coo call shown was measured as 320 Hz.

(Text S5). The ARUs were recording continuously, from sunrise to sunset, and recordings were saved as WAV files at a sampling frequency of 1 h.

Coo call sequence detection using Song Scope

The advertising vocalisation of the two pigeon species in question, *Didunculus* and *Ducula*, consists of a sequence of repeated 'coo calls' (*sensu* Beichle and Baumann 2016). The two ARUs, deployed at different sites at different times, recorded 1290 h of forest sounds that were scanned using the program Song Scope 4.1.3 A (Wildlife Acoustics 2016) in order to capture *Didunculus* and *Ducula* coo call sequences (Fig. 3). We developed a coo call recogniser for the purpose using Song Scope functions, which isolated 201 unidentified coo call sequences, belonging to *Didunculus* or *Ducula*; from these, we selected 104 coo call sequences on the basis of favourable signal to noise ratio.

Testing the hunters on coo call sequences

During July–August 2017 10 hunters with the highest reliability and consistency scores (Serra *et al.* 2017, table 2), from five villages of Upolu and Savaii, attempted to identify (Text S6) each of the selected 104 coo call sequences automatically recorded at the forest sites. The order of presentation of sequences to each hunter was carefully shuffled before each session.

We obtained a matrix of 104 coo call sequences by 10 hunters, with entries recording the hunter's identification of the call. During the process hunters were further assessed for reliability (Text S7).

Coo call sequence identification through TEK

We assessed the level of agreement for each pair of hunters using the following four-stage process:

(1) In order to explore the degree of dependence between sequences recorded at the same location within a period of 3 days, we tested the 104 sequences for independence using a one-way analysis of variance. Both being frugivourous (Watling 2001), *Didunculus* and *Ducula* may be bound to a certain territory only over short-term periods, at least at certain times of the year, such as during the breeding season or the fruiting of certain trees. The analysis of variance tests did not provide consistent evidence of dependence within the same-location 3-day sets of sequences (Text S8).

(2) We omitted from further analysis a row of the 104-row by 2-column matrix if either of the hunters was uncertain about the identification, or if the identification was other than *Didunculus* or *Ducula* (so leaving a 'cleaned' set).

(3) We assembled the identifications (*Didunculus* or *Ducula*) for each pair of hunters in a 2 × 2 contingency table, as shown in the example of Table 1. Counts on the leading diagonal are numbers of sequences on which the classification of the two hunters agreed. The best agreement performance we obtained was for the pair of hunters Fiu and Afaese: specifically, they agreed that 32 of the calls were *Didunculus* and that 22 of the calls were *Ducula*.

(4) We tested each table for independence using a Chi-square test; in this context, when most entries lie on the leading diagonal, evidence against independence is indicative of hunter agreement and so the presence of TEK.

Table 1. Contingency table showing identifications of coo call sequences for the top hunter pairwise combination

A cross-classification of the 80 sequences identified as either *Didunculus* or *Ducula* by hunters Fiu and Afaese; the hunters agree on 54 (67%) of these sequences (Pearson's Chi-square test for independence with Yates' continuity correction: 8.600, $P = 0.0034$)

| | | Afaese | | |
		Didunculus	*Ducula*	Total
Fiu	*Didunculus*	32	9	41
	Ducula	17	22	39
	Total	49	31	80

Table 2. Measurements of the coo calls of each sequence used in the sonographic analysis, with abbreviations and units

Description	Abbreviation	Units
Length	LC	s
Highest frequency	HF	Hz
Lowest frequency	LF	Hz
Frequency of the decibel peak	FP	Hz
Duration of the decibel peak	DP	s
Position of the decibel peak	PP	ratio (of s)
Average duration of the intervals following all coo calls within the sequence	DI	s

The subset of the cleaned coo call sequences on which a pair of hunters were in agreement is termed their 'TEK identified' set; these are coo call sequences for which there is TEK evidence for the identification. With the aid of a cell colour coding (Text S9), the level of agreement in each matrix was identified. We then followed an analogous process for the three hunters Fiu, Afaese and Livingstone, considered all together. The most successful combination among all studied was the pair of Fiu and Afaese, with a TEK-identified set of size $n = 54$, seen in the total of leading diagonal entries of Table 1.

Data analysis

In order to improve statistical independence of the data, we grouped coo call sequences identified as the same species by a hunter combination and recorded within 3 days of each other at the same location. We retained the sequence in a group with highest signal-to-noise ratio. As a result, the Fiu and Afaese TEK-identified set was reduced from 54 to 30 coo call sequences (19 *Didunculus* and 11 *Ducula*).

For each coo call of these 30 independent sequences, and the interval following, we used Song Scope to measure seven sonographic variables (Text S10), described in Table 2.

We measured the above-defined seven variables from a total of 73 and 56 coo calls, included in 19 and 11 sequences previously TEK-identified by the two mentioned selected hunters (F, A) as *Didunculus* and *Ducula*, respectively. We calculated the average for each variable for each sequence; we then determined the average and standard deviation across sequences of these within-sequence average values.

In order to evaluate the extent of the variation of the duration of the between-call intervals (DI), we measured the standard deviation, across sequences, of the standard deviation of DIs for each sequence. In order to do so, from the 30 sequences selected, we discarded those with ≤3 calls and ≤2 intervals: therefore we performed this exercise on 8 sequences of *Didunculus* and 5 of *Ducula,* TEK-identified by Fiu and Afaese ($n = 13$).

We used a two-sample *t*-test to detect differences between *Didunculus* and *Ducula* coo call sequences in the seven averaged sonographic variables. When the data were not normally distributed, we used a non-parametric Mann–Wilcoxon test.

Results

The 10 hunters tested did not agree on the classification of the 104 coo call sequences. Three, however, showed remarkable pairwise agreement ranging from 67% down to 51% over all their clearly identified coo call sequences. The analysis was thus narrowed down to these three reliable hunters: Fiu (F), Afaese (A) and Livingstone (L). Additionally, these three hunters scored as the top three amidst the selected 10, based on the reliability and consistency tests.

Fiu and Afaese showed highest identification agreement of coo call sequences: they agreed on the classification of 54 (67%) of the 80 sequences for which they both had clear identifications. Of the total of 80 sequences, note that the hunters agree on 32 *Didunculus* sequences and 22 *Ducula* sequences. We therefore largely focus on this pair (notated F, A) in the sequel to TEK-identify coo call sequences. Table 1, a contingency table, summarises the results of their identifications of *Didunculus* and *Ducula*.

Table 3 reports the averages and standard deviations of the seven sonographic variables (already averaged across individual coo calls within each sequence) measured from the 30 independent coo call sequences on which F and A agree. The *Didunculus* and *Ducula* difference in highest frequency (HF) of the call is highly statistically significant (332 Hz vs 372 Hz, respectively, with $P = 0.001$). This difference corresponds to a full tone, roughly from E to F sharp above middle C. Supporting this finding, a *t*-test performed on the same seven variables based on the agreement coo call sequence sets of the other combinations of hunters (F, L; A, L; A, F, L) revealed consistent statistical significance ($P < 0.05$) for HF. Additionally, for F and A, the decibel peak of the call (FP) and its position within the call (PP) are also statistically significant (*P*-values of 0.013 and 0.026 respectively).

The final measure studied was DI, the average duration (in seconds) of intervals between coo calls within a sequence. For *Didunculus* these averaged (across sequences) 12.30 s and for *Ducula*, 22.37 s, mildly suggesting that the between-coo call interval duration is longer for *Ducula* than for *Didunculus*, but not quite reaching significance (*P*-value = 0.067). Table 4, however, reports that DI does vary significantly less in *Didunculus* than in *Ducula*. Simply stated, this says that the coo calls of *Didunculus* are more regularly spaced than those of *Ducula*.

In summary, the TEK-based sonographic analysis indicates that the coo calls of *Didunculus* are lower in pitch and more regularly spaced within a sequence than those of *Ducula*.

Finally, we tested two key criteria for *Didunculus* identification proposed by Baumann and Beichle (2020): namely,

Table 3.   Average and standard deviation (s.d.) of seven sonographic variables of coo calls found in sequences identified through TEK

Traditional ecological knowledge identifications, as either *Didunculus* or *Ducula*, were based on consistent and independent identifications by reliable hunters Fiu and Afaese ($N = 30$ independent sequences identified in agreement). Average: average across sequences of the within-sequence averages. The two rightmost columns report the *P*-value and significance of the associated two-tailed *t*-test. See Table 2 for explanation of abbreviations for sonographic variables. ***, $P < 0.005$; *, $P < 0.05$; n.s., not significant

Sonographic variables	*Didunculus* ($n = 19$)		*Ducula* ($n = 11$)		*P*	Statistical significance
	Average	s.d.	Average	s.d.		
LC (s)	1.37	0.22	1.52	0.23	0.102	n.s.
HF (Hz)	331.67	22.64	371.62	29.92	0.001	***
LF (Hz)	249.75	13.81	259.40	18.40	0.150	n.s.
FP (Hz)	304.88	13.41	326.04	21.73	0.013	*
DP (s)	3.30	0.81	2.70	0.99	0.122	n.s.
PP (ratio)	0.41	0.08	0.53	0.15	0.026	*
DI (s)	12.30	4.62	22.37	8.92	0.067	n.s.

Table 4.   Variation across sequences of the within-sequence average duration (DI) of coo call intervals

s.d., standard deviation across sequences of DI values (s.); n.s., not significant

	Didunculus ($n = 8$)	*Ducula* ($n = 5$)	*P*	Statistical significance
Average	12.30	22.37	0.067	n.s.
s.d.	4.62	8.92	0.017	*

Didunculus' HF is >400 Hz, and *Didunculus*' repetitions can be >20. These two criteria were tested on the set of 104 unidentified coo call sequences recorded and used in the present study. Out of the only six sequences from our dataset with HF > 400 Hz five included either the introductory syllable or the brief modulation during the first third. These are the criteria used to identify *Ducula* by the same authors and by several other experts, local and international. On the other hand, the average HF of the only 10 sequences from our dataset with >20 repetitions of coo calls is 366 ± 26 Hz (and two of them, again, presented either the syllable or the modulation). Also noteworthy is that the average HF of the four coo call sequences identified as *Didunculus* by the same authors in the past upon request of the Samoa Ministry of Environment is 334 ± 16 Hz.

Discussion

Didunculus is a highly secretive and extremely rare bird living in the dense canopy of primary and secondary rainforests of Samoa. Relying on the identification of the call appears to be the only option available in order to survey and monitor this iconic and critically endangered species (MNRE and SCS 2020).

Results of the present study suggest that the coo call of *Didunculus* is lower in pitch and more regularly spaced within a sequence than that of *Ducula*: the sound analysis approach used in this study showed that the two top hunters, Fiu and Afaese, attribute these characteristics to *Didunculus* coo call sequences. These acoustic differences provide a preliminary step in the process of reliably separating the calls of these sympatric species in the field.

The complexity of the challenge is reflected by the fact that even the TEK shared by 10 reliable Samoan pigeon hunters, with an average rainforest pigeon hunting experience of over 28 years, appears only partially able to differentiate the recorded coo calls of the two sympatric rainforest pigeon species. This fact has an important conservation implication: *Ducula* hunting, still a common practice in Samoa, is confirmed to be a dire threat to survival of *Didunculus*, consistent with the findings of Serra *et al.* (2017) and Stirnemann *et al.* (2018).

The best TEK identification performance we obtained is the 67% agreement based on 80 sequences tested, with hunters Fiu and Afaese. While the analysis of variance tests on the original 104 sequences do show some hint of call homogeneity within same-location 3-day sets, this evidence is weak (refer to the table of Text S9). On the other hand, the Chi-square test *P*-value (Table 1) is highly significant, so we conclude that there is a satisfactory degree of agreement between F and A.

The TEK-based analysis of the acoustic parameters revealed that the call of *Didunculus* had lower HF than that of *Ducula*. Interestingly, this particular difference in HF was orally described and reported on two separate occasions by two other reliable hunters during the 2015–2016 TEK survey (Serra 2016; Serra *et al.* 2017). This 40 Hz difference may be hard to detect by the human ear in the forest. Hunters proficient at TEK must be using a combination of acoustic characteristics: for instance, they may be able to also pick and assess the variability of the intervals between coo calls within a sequence and possibly their length.

The difference in pitch between *Didunculus* and *Ducula* found in this study is inconsistent with results from Baumann and Beichle (2020). The mentioned inconsistency may be explained by the limited sample size of both analyses. These same authors report a difference of ~80 Hz between male and female *Didunculus* (where male shows a lower pitch). A bias of sampling toward male *Didunculus* individuals in the present analysis versus a bias by the Baumann and Beichle (2020) analysis toward female individuals would be sufficient to explain the inconsistency of results (especially if combined with an opposite bias by both analyses in relation to *Ducula* male and female calls).

The average and variation of the length of intervals between adjacent coo calls within a sequence were smaller in *Didunculus* than in *Ducula*, meaning that the intervals are shorter, more

frequent and more regularly spaced in *Didunculus*. The shorter length of intervals in *Didunculus* is consistent with Beichle and Baumann (2016) and with statements by one of the reliable hunters (Serra *et al.* 2017). Also, the variation of the intervals is consistent with results from Baumann and Beichle (pers. comm.). This consistency of outcomes between two independent studies with very different approaches presents an opportunity for a conservation field application: the regularity of intervals separating coo calls in a sequence, if confirmed by further observations, holds the potential to be used as a simple and yet efficient method to identify *Didunculus* directly in the field, without need of *a posteriori* digital and spectrographic analysis.

Noteworthy, and unlike Baumann and Beichle (2020), the present study used ARU and non-directional microphones to automatically record forest sounds over periods of weeks. This method has substantial application potential as it could be used to design and implement standard surveys and monitoring programs over the whole *Didunculus* distribution range at reasonable cost.

Certainly, as noted also by Baumann and Beichle (2020), the two calls are extremely similar. If a set of coo call sequences is randomly recorded from the Samoan forest the chances are that only a portion with the more extreme sonographic values can be identified through TEK. Based on the present study, we believe that the two calls may be differentiated statistically only over a substantial sample size, since there probably exists considerable within-species variability.

On top of the extensive call overlap the possible reasons why TEK identification has proven not to be highly efficient in this specific field may include:

(1) Some audio recordings we played may have not been of a sufficient quality and clarity for an elderly ear (10 hunters, 53 years old on average).
(2) Pigeon coo call identification through listening to digitally recorded sounds, via a headset, may be challenging and partially confusing for a local hunter accustomed to direct acoustic identification in the field.
(3) The challenging acoustic separation of the two species in the field may not be a critical need for the average Samoan hunter, as until relatively recently they were both targeted as food (Appleton 1871; U. Beichle, pers. comm.). A consensus, however, among reliable hunters interviewed in recent surveys (Serra *et al.* 2017) could not be reached regarding whether the meat of *Didunculus* tastes good.

The discrepancy between the estimated rate of visual detections of *Didunculus* by Government or international experts, mentioned in the Introduction (Serra *et al.* 2017), versus the rate of audio identifications of the same species by the hunters, from the sample of recorded sequences of the present study, can be explained by two possible factors. Firstly, it seems reasonable and likely that the visual detection rate of *Didunculus* by local hunters in the field may be higher than that by Government or international experts. Secondly, and more importantly, the visual versus audio sampling efforts are not comparable. Visual encounters were attempted during search efforts in the field lasting from a few hours to a few days maximum (on average, lasting from a few hours to a half/full day in the field). On the other hand, audio

identifications were based on ARUs continuously recording from dawn to sunset for 7–15 days in a row, for a total of 90 full days or 1290 h of forest recordings. In addition, the audio recorders worked with zero noise in the forest: this is a very important aspect, taking into account that *Didunculus* is highly cryptic and actively hiding in the dense canopy when hearing distant noise associated with people moving through the forest.

We are aware that the sonographic differences found in this study may simply reflect what distinguishes *Didunculus* and *Ducula* in the minds of the hunters; this may be only their memory of the *Didunculus* call. It is also possible that a portion of the 54 (reduced to 30) TEK identifications were incorrectly identified (i.e. both hunters gave the same wrong identifications). We do not have the means to assess the proportion of possible TEK-based wrong identifications. Despite this 'background noise' (i.e. the possible hunters' 'interpretations' and the possible wrong identifications), statistically significant differences emerged in relation to HF and to the average and variation of intrasequence coo call intervals. We regard these differences found in the present study to be interesting and unique TEK information and we strongly doubt that they are the result of pure coincidence.

Perfecting this knowledge through future more focused studies, either science-based or TEK-based (or, ideally, through a mix of the two approaches), may allow identification of forest areas with sufficient density of *Didunculus* to enable implementation of urgently needed conservation work (such as local community engagement, forest protection and restoration, invasive predator and hunting control) (*sensu* MNRE and SCS 2020). Additionally, it will allow the assessment of *Didunculus* population size and distribution across the whole historical range and allow population trend and conservation status to be monitored.

A recommended next stage would be to record coo call sequences of *Ducula* on Tutuila Island (American Samoa) where *Didunculus* has never been recorded, in order to better assess intraspecies variability. Also helpful would be to test, using the playback technique, samples of automatically recorded coo call sequences (including those of *Didunculus*) with different *Ducula* individuals in the field in Samoa in order to record their behavioural responses using already established protocols (Wolfenden *et al.* 2015).

In general, the advertising calls of sympatric species are not similar due to selection for species-specific signals (Wilkins *et al.* 2013). Exceptions to this general pattern are species that are not ecological competitors (Price 2008), rare cases where species have adapted to similar soundscapes (Cardoso and Price 2010), or situations where range expansion has led to recent sympatric occurrence of previously allopatric species (Johnson *et al.* 2001; Wolfenden *et al.* 2015).

Currently, there is insufficient ecological and zoogeographic information to assess the situation for *Didunculus* and *Ducula* in Samoa. It is conceivable that these two sympatric species are ecological competitors, although the former's beak structure suggests a specialised diet (Beichle 1987*a*). It is also possible that *Ducula* is a relatively recent arrival in Samoa, but there are no records to support this hypothesis. Thus why two sympatric pigeon species have such similar vocalisations remains a mystery.

Overall, the present study proposes an original approach, using traditional ecological knowledge to separate the calls of *Didunculus* and *Ducula*. Two main results emerge. First, the two identification criteria proposed by Baumann and Beichle (2020) (*Didunculus* indicated by HF > 400 Hz or >20 repetitions) appear not to be as definitive and clearcut as hoped. On the other hand, the study confirms that the regularity of the intervals between coo calls in a sequence may be the key to separation of the two species in the field.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

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