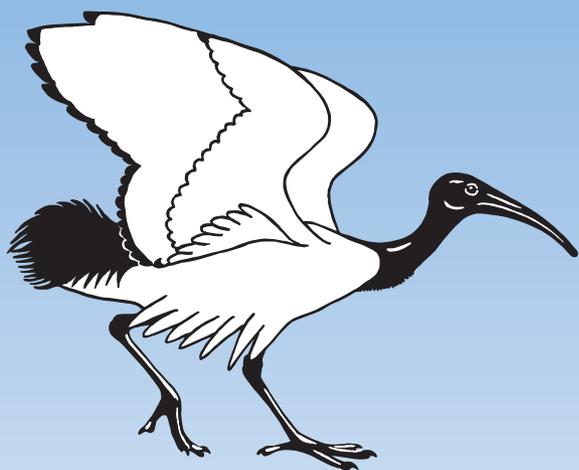


Bulletin of the British Ornithologists' Club



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CLUB ANNOUNCEMENTS

FORTHCOMING MEETINGS

See also BOC website: <http://www.boc-online.org>

The next meeting is a Zoom event. It is free to attend, but pre-registration is essential: <https://www.eventbrite.co.uk/e/abernethy-forest-its-history-and-ecology-tickets-138519045193?ref=estw>

Monday 29 March 2021—6.30 pm—Ron Summers—*Abernethy Forest: its history and ecology*

Abstract.—Abernethy Forest is a nature reserve managed by the Royal Society for the Protection of Birds. The forest has more Caledonian pinewood than any other area in Scotland. The trees in these remaining fragments are lineal descendants of an ancient forest that once spread across the Highlands of Scotland. Since the Bronze or Iron Age, the forest has been used by people for hunting, exploitation of timber, farming and now nature conservation. This talk will describe the changes caused by people and the natural processes that have shaped the forest, providing an environment for an astonishing diversity of wildlife (3,800 species of plants, fungi and animals). The lives and status of the 'big three' birds of pinewoods will be described: Western Capercaillie *Tetrao urogallus*, Crested Tit *Lophophanes cristatus* and crossbills (*Loxia* spp.). Comparisons will be drawn with natural forests in continental Europe, revealing the conservation measures that need to be taken to restore lost features in an attempt to create a present-natural forest.

Biography.—Dr Ron Summers is a Principal Conservation Scientist at the Royal Society for the Protection of Birds and, over the past 30 years, has been involved in studies of a range of Highland birds, particularly in pinewoods. Having attained a Ph.D. at the Univ. of Aberdeen on the ecology of European Flounder *Platichthys flesus*, he undertook post-doctoral work at the Univ. of Cape Town, where he studied sandpipers on Langebaan Lagoon, providing data that supported the case to designate the area a national park. Subsequently, he studied the effects of Upland Geese *Chloephaga picta* on sheep farming in the Falkland Islands, followed by work with the Ministry of Agriculture, Fisheries and Food, initially on the movements of European Starlings *Sturnus vulgaris* in relation to the spread of pig diseases, and latterly on the effect of grazing by Brent Geese *Branta bernicla* on fields of winter wheat. He further outlined a hypothesis about the role of lemmings in determining the breeding success and population growth of these geese; this link also applied to the waders he had studied in South Africa, and he subsequently travelled to Siberia to help test his theory on the birds' breeding grounds. The Arctic has always held an appeal and he has made many trips there, notably as part of a long-running study of Purple Sandpipers *Calidris maritima*, which will culminate in a forthcoming monograph.

Friends of the BOC

The BOC has from 2017 become an online organisation without a paying membership, but instead one that aspires to a supportive network of Friends who share its vision of ornithology—see: <http://www.boc-online.org/>. Anyone wishing to become a Friend of the BOC and support its development should pay UK£25.00 by standing order or online payment to the BOC bank account:

Barclays Bank, 16 High Street, Holt, NR25 6BQ, Norfolk
Sort Code: 20-45-45
Account number: 53092003
Account name: The British Ornithologists' Club

Friends receive regular updates about Club events and are also eligible for discounts on the Club's Occasional Publications. It would assist our Treasurer, Richard Malin (e-mail: rmalin21@gmail.com), if you would kindly inform him if you intend becoming a Friend of the BOC.

The *Bulletin* and other BOC publications

Since volume 137 (2017), the *Bulletin* of the BOC has been an online journal, published quarterly, that is available to all readers without charge. Furthermore, it does not levy any publication charges (including for colour plates) on authors of papers and has a median publication time from receipt to publication of five to six months. Prospective authors are invited to contact the *Bulletin* editor, Guy Kirwan (GMKirwan@aol.com), to discuss future submissions or look at <http://boc-online.org/bulletin/bulletin-contributions>. Back numbers up to volume 136 (2016) are available via the Biodiversity Heritage Library website: www.biodiversitylibrary.org/bibliography/46639#/summary; vols. 132–136 are also available on the BOC website: <http://boc-online.org/>

BOC Occasional Publications are available from the BOC Office or online at info@boc-online.org. Future BOC-published checklists will be available from NHBS and as advised on the BOC website. As its online repository, the BOC uses the British Library Online Archive (in accordance with IZCN 1999, Art. 8.5.3.1).



A reassessment of issues surrounding the Hastings Rarities, with particular reference to supposed fraud by George Bristow

by Pat Morris

Received 15 April 2020; revised 19 August 2020; published 9 March 2021

<http://zoobank.org/urn:lsid:zoobank.org:pub:A80704E8-3C70-4547-939C-D2016826B39C>

SUMMARY.—In 1962, a special issue of *British Birds* alleged that the number and pattern of records of rare birds from around Hastings, in southern England, between 1892 and 1930 were so improbable that fraud was the only reasonable explanation. A press conference resulted in absurdly exaggerated reports that encouraged general acceptance of the alleged fraud and in particular that George Bristow, a local taxidermist, was responsible. There are potential weaknesses in the statistical analysis of the purported fraud, and the case against Bristow was based on probability and innuendo, not solid evidence. Plausible information from Bristow and the respected ornithologist Norman Ticehurst was largely ignored, as were the practicalities of fraud, especially during wartime and in the absence of modern deep-freeze facilities. The lead author was apparently prejudiced against taxidermists. The allegations unfairly tainted Bristow and his profession, and have encouraged some distrust of historical datasets.

In 1962 two papers (Nelder 1962, Nicholson & Ferguson-Lees 1962) and an editorial (Hollom *et al.* 1962) formed a special issue of *British Birds*, which proposed the deletion of 542 specimen and 53 sight records of rare birds from the Hastings area of Sussex, in southern England, between 1892 and 1930. Among them were 16 taxa that, at the time, had not otherwise been recorded in Britain. The 595 records were listed numerically and became known as the Hastings Rarities, allegedly involving fraud by a local taxidermist, George Bristow (1862–1947). A press conference on 10 August 1962 resulted in widespread dissemination of greatly exaggerated reports and misinformation. For example, *The Yorkshire Post* stated that 600 birds had been struck off in ‘The biggest hoax in ornithological history, a birdwatcher’s Piltdown fraud’. It also commented that ‘if Hastings was not an El Dorado from the bird lover’s point of view it may well have been for Bristow’, quoting Nicholson as saying that rare birds could fetch as much as £30 apiece. *The Daily Telegraph* even quoted Bristow directly (despite that he had been dead for 15 years): ‘all of them [the birds sold to museums and collectors] said George Bristow as he briskly sold 542 specimens at up to £300 a time were found dead or shot in Britain’. *The Daily Sketch* claimed the so-called ‘Bird Detectives’ had ‘found that ... Mr George Bristow ... made good money’ and asserted that ‘the specimens may have been smuggled ashore by pilot boat’. No evidence was ever advanced to support either statement. *The West Sussex Gazette* reported that Bristow had shot the birds, although this was untrue. Few would have read the issue of *British Birds*, but the press reports were seen by millions, including syndications abroad.

The August 1962 issue of *British Birds* was a profound shock to many ‘old school’ ornithologists, including David Bannerman who wrote a scathing critique (Bannerman 1963). Another was Norman Ticehurst, co-author of *The handbook of British birds* (Witherby *et al.* 1938–41), who first expressed dismay at being duped by Bristow, then became indignantly critical. He protested that during 1900–16 he had ‘... thrashed out the whole

matter ... with Howard Saunders, Bowdler Sharpe, Meade-Waldo, Witherby and Hartert, and in 1952 with Bannerman and all were completely satisfied with the bona fides of the records'. He also confirmed that he and colleagues 'were constantly on the lookout for any evidence of fraud' (letter to James Harrison, 23 August 1960, Harrison Archives, Sevenoaks, Kent) probably in response to a preliminary statement by Hollom (1960); see Nicholson *et al.* (1969: 377).

Nevertheless, whilst the original authors were not responsible for crass journalism, the accusation of fraud has been accepted for more than 50 years and misinformation persists. For example, Wikipedia ([https://en.wikipedia.org/wiki/George_Bristow_\(ornithologist\)](https://en.wikipedia.org/wiki/George_Bristow_(ornithologist))) claims that Nelder calculated Bristow made £7,000 from his fraudulent activities, although neither Bristow nor money was mentioned by Nelder (1962). Harrop (2019) referred to the 'Pre-Bristow era' of fraud as if dishonesty was a proven historical fact and Bristow the culprit. Coulson (2003) linked the Hastings Rarities with the (proven) Piltdown Hoax. Bristow's infamy has been officially recognised by erection of a blue plaque on his old shop in St. Leonards, and the opprobrium cast upon him posthumously smeared the man and his profession.

There will be exasperation in some quarters that the matter is being raised again, but rather than dismiss this revival of an old controversy, I hope readers will consider the issues raised, some highlighted for the first time. Approximately 70% of the disputed species have been seen since in Kent (Taylor *et al.* 1981), Sussex (Thomas 2014) or both, with others observed elsewhere in the UK, suggesting that many records could have been genuine, but I am not seeking to change the ornithological record. I seek a balanced judgement, particularly in relation to the taxidermist George Bristow. Vernacular names given here are as in the original Hastings Rarities list to avoid confusion resulting from subsequent taxonomic revisions.

Exaggeration caused by inclusion of genuine records

The Hastings Rarities comprised published records of rare birds from the 'area' (defined as a 20-mile radius from Hastings Pier) between 1892 and 1930 (hereafter the 'era'). The records for the area/era included some potentially genuine ones. This was justified on the grounds that, as one could not determine which were genuine British specimens and which were not, they would all be included in the list of 542 unacceptable records of dead birds. Harrison (1968) objected, as did others, that the veracity of records had not been considered before undertaking the analysis and this was both uncritical and unscientific. The approach resulted in the rejection of many records for which significant validation exists. Norman Ticehurst checked his diaries from half a century earlier and offered plausible substantiation for many of the rejected records (quoted by Harrison 1968, but brushed aside by Nicholson *et al.* 1969). He included details of at least some of the collectors who had obtained disputed specimens, described as suspiciously anonymous by Nicholson & Ferguson-Lees (1962).

Six Ferruginous Ducks *Aythya nyroca* and a pair of Night Herons *Nycticorax nycticorax*, obtained locally but not formally recorded, were not listed. They belonged to Edwin Catt, a part-time local taxidermist, and support the validity of the rejected records. Another Night Heron (with good provenance) shot within the area, but just after the era, questions the justification for including the seven on the Hastings Rarities list. There were additional genuine specimens of suspect species, including Sabine's Gull *Xema sabini*, Aquatic Warbler *Acrocephalus paludicola* and Slender-billed Nuthatch *Nucifraga caryocatactes macrorhynchos*, which were obtained by Guy Mannering (1881–1966), a resident of Dover (Anon. 1985). They were not formally recorded and therefore not part of the Hastings Rarities series.

Mannering's specimens confirm the presence of these species in the area/era. Other independent observers saw species listed among the Hastings Rarities within the area/era, including the Duchess of Bedford, who recorded them in her diary (Bedford 1938), and E. C. Arnold (headmaster of Eastbourne College) who published accounts of Hastings Rarities being seen or shot within the area/era (Arnold 1907, 1936). Harrison (1968) also listed many unrecorded examples of disputed species within both the area and era, as well as afterwards, weakening the case for treating all of the Hastings Rarities as false. The existence of so many additional examples of disputed species suggests that the rarities were perhaps not so rare in the area/era after all.

Records were on the Hastings Rarities list for no other reason than that they had been recorded within the area/era. Nicholson & Ferguson-Lees (1962) admitted that 'several' of the records could be genuine, conceding later that this could apply to nearly half of them (Nicholson *et al.* 1969), a subtlety that has been overlooked by many subsequent authors. Nicholson & Ferguson-Lees (1962) also extended the era by nine years beyond the period covered by Nelder's analysis, thereby adding 79 records to the list of Hastings Rarities. The longer that list of disputed birds became, the more authoritative it appeared to be, strengthening the case for adding still more (a circular argument). But every genuine record of a species that was included challenges the case for condemning others on the list. The consequences are discussed below.

Fifty-three sight records were declared 'unacceptable' by Nicholson & Ferguson-Lees (1962) because they were 'closely linked in various ways' with the list of dead specimens. They nevertheless mentioned a 'refreshingly informative sight record of a Mediterranean Black-headed Gull [*Larus melanocephalus*] being fed... by ladies on Hastings seafront', but despite this apparently acceptable observation, two sightings from 1915 were on the list of disqualified records of live birds, as were five dead ones from that year and another in 1913. Thirty-two of the rejected sight records (60%) turned up dead the same day or soon after, tending to confirm their validity. But both records were then treated as separate and added to the numbered list of rejections, although in most cases they probably referred to the same bird (see Table 1).

TABLE 1

Dates (as accurate as known) of the 53 sight records that were rejected as part of the Hastings Rarities (HR), and the date of the next subsequent specimen of the same species that was recorded. * = seen dead 'in the flesh'.

Species	HR	Seen alive	Seen dead	HR no.
Squacco Heron <i>Ardeola ralloides</i>	543	October 1913	13 November 1913*	35*
Red-crested Pochard <i>Netta rufina</i>	544	January–February 1911	10 February 1911*	53, 54, 55, 56, 57
Ferruginous Duck <i>Aythya nyroca</i>	545	2 January 1912	2 January 1912	58*, 59*
Sociable Plover <i>Vanellus gregarius</i>	546	3 May 1907	3 May 1907	106*
Sociable Plover	547	May 1910	25–27 May 1910	107*, 108*, 109*, 110*
Sociable Plover	548	30 April 1914	9–18 May 1914	111*, 112*, 113*
Killdeer <i>Charadrius vociferus</i>	549	12–16 November 1915	12 November 1915	121*, 122*
Asiatic Golden Plover <i>Pluvialis fusca</i>	550	23 April 1914	23 April 1914	128*, 129*, 130*
Upland Sandpiper <i>Bartramia longicauda</i>	551	12 July 1908	18 July 1908	140*
Slender-billed Curlew <i>Numenius tenuirostris</i>	552	September 1910	21–23 September 1910	142, 143, 144
Pectoral Sandpiper <i>Calidris melanotos</i>	553	1 August 1906	19 September 1906	184
Broad-billed Sandpiper <i>Limicola falcinellus</i>	554	27 August 1920		
Black-winged Stilt <i>Himantopus himantopus</i>	555	7 August 1903		

Species	HR no.	Seen alive	Seen dead	HR no.
Black-winged Stilt	556	3 October 1910	9 October 1910	
Great Black-headed Gull <i>Larus ichthyaetus</i>	557	July 1911		
Mediterranean Gull <i>Larus melanocephalus</i>	558	July 1915	15–21 July 1915	233*, 234, 235, 236*
Mediterranean Gull	559	11 November 1915		
Bonaparte's Gull <i>Larus philadelphia</i>	560	April 1914	20, 26 April 1914	239, 240
White-winged Black Tern <i>Chlidonias leucopterus</i>	561	29 May 1904	29 May 1904	245*, 246*, 247*, 248, 249
White-winged Black Tern	562	29 May 1911	29 May 1911	250*, 251*, 252*
Alpine Swift <i>Tachymarptis melba</i>	563	3 August 1908		
Alpine Swift	564	9 October 1923		
Alpine Swift	565	June 1925		
Black Lark <i>Melanocorypha yeltoniensis</i>	566	29 January 1907	29 January 1907	301*
Black Lark	567	31 January 1907	31 January 1907	302*
Black Lark	568	January 1915	16 February 1907	303
Calandra Lark <i>Melanocorypha calandra</i>	569	17 May 1916	16 May 1916	307* 308*
White-winged Lark <i>Melanocorypha leucoptera</i>	570	3 November 1915	10 November 1915	314
Slender-billed Nutcracker <i>Nucifraga caryocatactes macrorhynchos</i>	571	December 1912	26, 28 December 1912	332*, 333*
Dusky Thrush <i>Turdus eunomus</i>	572	Feb–Mar 1915	3 March 1915	344*, 345*
Isabelline Wheatear <i>Oenanthe isabellina</i>	573	August 1905		
Aquatic Warbler <i>Acrocephalus paludicola</i>	574	August 1906		
Aquatic Warbler	575	summer 1909		
Icterine Warbler <i>Hippolais icterina</i>	576	8 May 1900		
Icterine Warbler	577	14 May 1901		
Icterine Warbler	578	2 September 1902		
Barred Warbler <i>Sylvia nisoria</i>	579	31 October 1902		
Collared Flycatcher <i>Ficedula albicollis</i>	580	5 May 1922	5 May 1922	429
Richard's Pipit <i>Anthus novaeseelandiae</i>	581	7 September 1901		
Tawny Pipit <i>Anthus campestris</i>	582	May 1906		
Black headed Wagtail <i>Motacilla flava feldegg</i>	583	May 1902		
Lesser Grey Shrike <i>Lanius minor</i>	584	6 November 1901		
Woodchat Shrike <i>Lanius senator</i>	585	29 April 1898	1 May 1898	478
Woodchat Shrike	586	June 1902	29 June 1901	479
Rose coloured Starling <i>Pastor roseus</i>	587	23 March 1902	10 June 1902	491
Rose coloured Starling	588	8–14 August 1914	8 August 1914	493*
Rose coloured Starling	589	August 1914		
Pine Grosbeak <i>Pinicola enucleator</i>	590	25 October 1905	25 October 1905	502*
Pine Grosbeak	591	30 October 1905	30 October 1905	503
Two-barred Crossbill <i>Loxia leucoptera</i>	592	15 January 1914	15 January 1914	516*
Two-barred Crossbill	593	8 February 1917		
Black-headed Bunting <i>Emberiza melanocephala</i>	594	25 December 1900		
Snow Finch <i>Montifringilla nivalis</i>	595	21 February 1905	22 February 1905	537

Whilst such double-counting by Nicholson & Ferguson-Lees makes little difference to the total numbers involved (and there is no evidence of double-counting by Nelder), basic principles were ignored, exaggerating the case for fraud and the seriousness of the Hastings affair, a point overlooked at the press conference and by later authors.

The statistical case

Nelder's paper formed the bedrock of the case for fraud and has been widely accepted as conclusive (Greenwood 2012). The basic unit for analysis was a record published in the formal literature. Records were grouped into rarity classes based on the number of English occurrences in Witherby *et al.* (1938–41). Nelder wrote that details would be deposited at the Edward Grey Institute, Univ. of Oxford, but searches made recently at my instigation reveal they cannot now be traced and may never have been lodged there (S. Wilcox *in litt.* 2020). The many rarity records for the area/era appear improbable, but the focus of Nelder's argument concerned patterns of occurrence (see Table 2). He used Chi-squared tests to establish the probability of the observed patterns being due to chance, a probability of less than 5% suggesting that some form of intervention had occurred.

TABLE 2

Occurrence of rarities recorded in different areas and eras (Nelder's Table 2, with his notation in brackets for each area/era). Species were assigned to rarity classes based on the number of English reports in the *Handbook of British birds* (Witherby *et al.* 1938–41). Nelder wrote that he would deposit details with the Edward Grey Institute, but these cannot now be traced there (see main text). The dates of the 'Hastings era' given by Nelder (1895–1924) differ slightly from those used by Nicholson & Ferguson-Lees (1892–1930). The reasons for this were not explained, but the difference is immaterial in respect of Nelder's analysis.

Area/era	Class 1 rarities	Class 2 rarities	Class 3 rarities	Total
Hastings area, 1895–1924 (XA)	243	108	165	516
Hastings Area 1925–54 (XB)	54	51	103	208
Rest of Sussex 1895–1924 (YSA)	15	16	45	76
Rest of Sussex 1925–54 (YSB)	19	13	32	64
Rest of Kent 1895–1924 (YKA)	11	11	22	44
Rest of Kent 1925–54 (YKB)	26	28	53	107
Totals	368	227	420	1,015

Was the Hastings area/era different from other areas/eras?—Chi-squared tests require that the samples being tested compare like with like. It was assumed (and explicitly stated by Nicholson & Ferguson-Lees 1962) that nothing about the Hastings area/era could account for the extraordinary abundance of rare birds. However, that assertion is open to question. The area included >60 km of coastline, patrolled by semi-professional beachcombers, helping to account for the various rare seabirds recorded. It also included a diversity of habitats whose ornithological richness is still evident (Sharrock 1976, Lack 1986), even after habitat loss and increased disturbance since the era. Although this has little effect on the occurrence of vagrants, it certainly attracted bird collectors, one of whom described 'The Crumbles' (a coastal area west of Hastings) as 'almost to idealize the requirements of the collector' (Arnold 1907).

Inland areas (i.e. beyond the 20-mile radius from Hastings Pier) were probably less visited by bird collectors because access was more difficult and collecting less fruitful than in the wetlands and open fields near the coast. Inland areas included extensive woodland, an unlikely habitat for casual shooters to roam, and within which there was no need for farmers and market gardeners to carry a gun to protect their crops. Direct comparison of

the Hastings area with 'the rest of Kent' and 'the rest of Sussex' (YK and YS in Nelder's analysis) is therefore questionable.

A second distinctive feature was the presence of George Bristow, whose father was also a taxidermist. They had a widespread community of local men who were encouraged to shoot unfamiliar birds and offer them for sale. Their firm was the principal local taxidermists for 40 years even prior to the era, and postal directories show the business was operating for longer than any other in the rest of Kent or Sussex.

Crucially, during the era, Hastings was home to a number of dedicated collectors who were competitively engaged in securing rarities and creating the formally published records upon which the statistical analysis was based. Among them were Boyd Alexander, Ruskin Butterfield, Michael Nicoll, and Norman & Claude Ticehurst. Although they did not live there, J. L. Bonhote, A. F. Griffith, Ernst Hartert and Howard Saunders collected specimens from the area/era and published records in the *Bulletin of the British Ornithologists' Club* (BBOC) and elsewhere (*British Birds*, *The Zoologist* and *The Hastings and East Sussex Naturalist*). Other notable collectors who visited the area during the period included G. Mannering, E. C. Arnold, J. B. Nichols and the Duchess of Bedford. The British Ornithologists' Club (BOC) encouraged members to bring interesting specimens to its meetings and publish details in BBOC. It is not difficult to envisage that avid collectors vied with each other to exhibit notable specimens, promoting rivalry and an eagerness to publicise their latest acquisition, creating a positive feedback loop in which the appearance of interesting new items stimulated the search for still more. This scenario is supported by the disproportionate number of records (516) from the Hastings area published during the era (see Table 2), precisely the anomaly that Nelder identified.

Thus, it appears that the abundance of rarities in the Hastings area/era could have been the result of several factors combined: habitat diversity, a well-established taxidermist with a network of suppliers, and very active ornithologists dedicated to finding rare birds and publishing their records. Nowhere in the rest of Kent or Sussex were all three factors operating simultaneously during the era, and to such an extent, undermining the basic principle of comparing like with like using Chi-squared tests. In statistical parlance those factors would be termed 'confounding variables' because they each contribute to the data being analysed. Beyond question, Nelder's analysis demonstrated that the pattern of records in the Hastings area/era was statistically different from that elsewhere in Kent and Sussex. But it is impossible to establish the extent to which each of those factors may have contributed because of their interactions. Arguably, it is inappropriate to definitively attribute statistical significance to a single cause (e.g. fraud). An alternative interpretation might be that a statistically significant abundance of rare bird records in the area/era arose because the Hastings area was unusually likely to harbour rare birds and the era was a period when their occurrence was particularly likely to result in formal records being published.

A further statistical issue arises from the inclusion of genuine records in the Hastings Rarities list. Boosting the number of examples being analysed increases the likelihood of obtaining probability values that are statistically significant, simply because large samples are statistically more robust than small ones. The *proportions* of rare, genuine or fraudulent records may remain the same, but larger *numbers* effectively enhance probability values.

The pattern of different classes of rare birds.—Nelder's argument also focused on the relative numbers of records of birds in different categories of rarity. For example, the number of exceedingly rare (class 1) species within the Hastings area/era was improbably greater than that of 'commoner' rare birds (class 3). Extreme numbers within the area/era were improbable compared to the consistency witnessed in other areas and eras.

Here we must remember that the analysis was not based on occurrences, but published records. Records are not random samples, only occurrences that were formally recorded. Publication demands both that someone decided an account was worth producing and that an editor agreed it was sufficiently significant to merit publication. Thus, a filtering process was involved, a fundamental issue that has been overlooked. It is possible that class 3 rarities were no longer regarded as particularly special around Hastings, which was known to be an ornithologically rich area, and they were therefore less likely to be formally recorded from there. Records from the area submitted for publication might have been omitted or rejected because they were perceived as nothing special. Instead, attention there seems to have become focused on class 1 rarities, which were more likely to be published, especially by several local collectors dedicated to doing exactly that. Conversely, over the rest of Kent and Sussex, where bird collecting was evidently less intense, class 1 rarities were relatively more likely to escape notice and class 3 rarities more liable to be recorded because they had been less often observed hitherto.

For example, it appears suspicious that rare petrels were recorded from Hastings' beaches, but not Storm Petrels *Hydrobates pelagicus*. However, a Storm Petrel found on the beach at Hastings would scarcely merit publication as a formal record, whereas one found in Tunbridge Wells ('rest of Kent') probably would. Ticehurst (1909) commented it was 'not surprising' that Storm Petrel was a 'fairly frequent' visitor to the Kent coast. He then listed a dozen or so records in 120+ years, hardly a comprehensive list for a 'fairly frequent' visitor. Moreover, the records were clearly selective, those mentioned often being unusual occurrences that made an interesting story: 'shot with flock of hoopoes' and 'stunned with a stone', 'captured in the streets of Dover' for example. Ticehurst ended: 'while among other recent occurrences may be mentioned *one* [my italics] that is remarkable for the time of year...' (and found below a telegraph wire). Citing only that one from among the 'recent occurrences' clearly confirms editorial selectivity. Ticehurst also commented to Harrison: 'After all, the Tawny Pipit [*Anthus campestris*] is not such a very great rarity. I have over 60 subsequent records from our condemned area' (Harrison 1968: 107). It is impossible to know the extent to which these factors affected the patterns in Nelder's analysis, but it is clear that published records could involve a degree of editorial subjectivity, with a potentially significant effect on the designation of a species to a specific rarity class.

Other patterns were identified, including a bias towards males, potentially more valuable to a commercial taxidermist. But single-sex flocks can form seasonally (Cramp 1988, Catry *et al.* 2004, Lehtikoinen *et al.* 2017) and this would bias samples shot by collectors. 'Pairs' were also suspiciously frequent among the records, but many involved species of which male and female could not easily be separated by the shooter and were therefore probably not acquired intentionally as implied, e.g. Little Crake *Porzana parva* (Hastings Rarities 92–93), Scops Owl *Otus scops* (Hastings Rarities 277–278), Aquatic Warbler (Hastings Rarities 394–395), and various terns and sandpipers. If the 'pairs' were not natural occurrences, it is difficult to envisage a plausible alternative explanation that does not involve improbable expertise in the supply chain and wastage of excess specimens.

Nelder also drew attention to other anomalies that are more difficult to account for, such as the occurrence of multiple specimens of a rare vagrant. But this could have been due to small flocks arriving under exceptional weather conditions, e.g. the Black Larks *Melanocorypha yeltoniensis* (see below) or small flocks of Pine Grosbeaks *Pinicola enucleator*, from which four were shot in October 1905, two in March 1909 and three in January 1914. These numbers suggest some vagrants were formerly more common and Harrison (1971) quoted support for the patterns of irruptive behaviour in Pine Grosbeaks and Two-barred Crossbills *Loxia leucoptera*.

Many birders are unfamiliar with statistical tests and they were a novelty in 1962. Most readers would have been content to accept that Nelder had proved his point. But statistics measure the probability of a set of observations occurring by chance. To be clear, en masse the Hastings Rarities were never *proved* to be false, just improbably genuine. This may seem a pedantic distinction, but it is real. 'Proof' has been widely assumed and was explicitly claimed in a letter on *British Birds* notepaper: 'If you read our analysis right through I think you will agree that it has been proved that fraud took place' (I. J. Ferguson-Lees to Mrs W. H. O'Connor, 31 August 1962; Harrison Archives, Sevenoaks, Kent). Nicholson & Ferguson-Lees (1962) stressed they were not claiming that all of the disputed records were false, and later conceded that up to about 250 (c.46%) were statistically likely to be genuine (Nicholson *et al.* 1969). They clearly failed to communicate this at their press conference; nor did they consider the effect on the statistical analysis.

Was fraud actually feasible?

It is easy to allege fraud, but difficult to explain how it might have been carried out. The statistical improbability of all the contested records being genuine is matched by the unlikelihood of undertaking the alleged fraud and keeping it secret for decades. These points were ignored in 1962.

Bristow, or anyone else, would have needed agents to supply foreign birds from North America, North Africa and Eastern Europe / Central Asia). To avoid creating suspicion and wastage, they would have needed to select species rare in Britain but plausible vagrants. Frequent batches would have been required in order to have fresh birds in St. Leonards over a period of at least 30 years. The idea that they could have been imported alive and then shot (or otherwise killed) to be inspected 'in the flesh' is not credible.

Importing dead birds would have required refrigeration in transit. Mechanical refrigeration on board ship was first demonstrated as proof of concept in 1876 and began to be used commercially soon afterwards for importing meat (Capie & Perren 1980), but was not in regular use until the early 20th century (Moyer & Fittz 1932). The equipment was heavy and too bulky for domestic use. Efficient refrigeration, powered by compressors, was not portable on land or widely available during the early part of the era and could do little more than retard decay. Refrigeration machines could produce ice, but animal tissues contain salts that depress their freezing point below that of ice. They could not be 'frozen solid' as in modern deep-freeze facilities. Domestic refrigerators were unavailable until the 1930s and then were incapable of cooling much below c.4°C. Import 'on ice' (as alleged), especially in summer, or in refrigerated ships would not permit long-term storage. Cooling in a refrigerator (or ship's cold room) was sufficient to transport meat in fit condition to eat, and it is customary to allow chilled meat to 'hang' in transit. Preserving small birds (that thaw quickly) in a state suitable for skinning is a different matter as they decay rapidly, causing feathers and epidermis to 'slip', especially on the abdomen and around the eyes. Birds could be shipped on ice from the Middle East or America and arrive sufficiently fresh to market, at least in the colder months (Heath 1970), but such means of transport do not preserve objects for very long in a state suitable for taxidermy.

If the disputed birds had not arrived naturally, they must have been imported somehow. Nicholson *et al.* (1969) claimed that importation on ice was 'not an essential part of our case', despite having explicitly proposed it in 1962. In support, they reproduced a lengthy statement (>400 words) from a museum curator asserting that deep-frozen specimens could be transported and stored for long periods, yet remain suitable for taxidermy. This was misleading and irrelevant as modern deep-freeze facilities were unavailable during the era, yet there was an almost continuous supply of Hastings Rarities for 30 years. For Bristow to

perpetrate a fraud in the absence of such facilities he would have required regular deliveries and to have maintained the secrecy for decades. Importing birds, chilled to about 4°C on ice, was feasible but would not preserve them for long in a state suitable for taxidermy.

The most likely origin of suitable specimens was an established commercial source such as London's Leadenhall meat market. Foreign birds could certainly be obtained that way; other taxidermists did so (Bourne 1963) and the matter was extensively discussed (Aplin 1890). Collectors often visited markets in search of rarities and were aware of the opportunities (Collinson 2012) and the possibility of fraud. If using Leadenhall market, Bristow (or his agent) would have needed to avoid recognition by one of the collectors, all of them potential customers and also part of the gossip network represented by the BOC and personal friendships. Maybe Bristow sent someone on his behalf, or had batches delivered to him in St. Leonards, but the logistics involved would have been daunting, particularly to achieve frequent supplies, in summer, in secret, for 30 years. Nevertheless, evidence was published (Coombes 1970) stating that a ship's steward (Alfred Parkman) had imported birds from the Middle East and that his brother Sydney had delivered them to Bristow in St. Leonards. This was given national publicity by *The Daily Telegraph* (27 July 1970). Harrison (1971) subsequently established that Coombes' testimony was inaccurate and misleading. Delivery had not been to Bristow personally, involved just two birds, and occurred post-1930. The brothers publicly denied involvement with regular importation of birds and with fraud (*The Daily Telegraph*, 3 August 1970).

Could anyone acting for Bristow be trusted never to betray him through careless talk or grievance at not being adequately paid from the allegedly lucrative business? It is possible that Bristow could have added some imported birds to his stock, but why bother if they were turning up naturally? Any hint of dishonesty would have lost him his prime customers, for whom British provenance was of paramount importance. That it was possible for Bristow to obtain foreign birds is not evidence that he actually did so, repeatedly, for three decades and involving hundreds of specimens. Nor would it account for records of birds seen alive, or those that were not obtained by him but shot by others and retained by the collector. Nevertheless, they remain part of the implicit case against him.

Verification measures

To combat fraud, it was normal practice for rarities to be shown 'in the flesh' to an independent and respected expert, who could testify that the specimen was freshly dead and thus locally acquired. This procedure was applied to 283 of the 542 disputed specimens (52%). They were seen 'in the flesh' or freshly mounted by 11 local ornithologists, including the respected experts Norman & Claude Ticehurst. Two verifiers were medical doctors, others dedicated bird collectors used to handling dead birds. One (Thomas Parkin) was president of the local natural history society, another (W. Ruskin Butterfield) curator of Hastings Museum. Mullens was a respected naturalist, former Mayor of Bexhill, and Deputy Lieutenant of Sussex. Several had very extensive practical experience of handling freshly shot birds in the field. Twenty-two of the challenged specimens were inspected by two or more of these men. They knew each other, were well aware of the possibility of deception, and would suffer serious loss of face and social status if they erred or were shown to be implicated in fraud (see Table 3).

The verifiers looked for fresh blood, sunken eyes and stiffened toes, dryness in the eyelids and mouth. The epidermis and feathers 'slip' during decay, especially after thawing. The skin around the tarsi soon dries, making it difficult to mount a bird. Birds shot within hours of inspection would have appeared (and smelt) differently from any that had been cooled for a week or more on a sea journey. Fresh blood has a different colour and texture

TABLE 3
Local ornithologists who inspected half of the disputed Hastings Rarities 'in the flesh' (i.e. freshly dead)
or recently mounted.

Name(s)	Number of specimens inspected
W. B. Alexander & N. F. Ticehurst	1
J. L. Bonhote & N. F. Ticehurst	1
W. R. Butterfield	89
W. R. Butterfield & L. A. C. Edwards	4
W. R. Butterfield & H. W. Ford-Lindsay	4
W. R. Butterfield & J. B. Nichols	2
W. R. Butterfield & M. J. Nicoll	1
W. R. Butterfield & T. Parkin	1
L. A. C. Edwards	6
L. A. C. Edwards & N. F. Ticehurst	1
H. W. Ford-Lindsay	93
G. Knight	1
W. H. Mullens	1
J. B. Nichols	6
J. B. Nichols, L. A. C. Edwards & N. F. Ticehurst	1
M. J. Nicoll	18
M. J. Nicoll & L. A. C. Edwards	2
M. J. Nicoll & C. B. Ticehurst	1
M. J. Nicoll & N. F. Ticehurst	1
T. Parkin	14
C. B. Ticehurst	7
C. B. & N. F. Ticehurst	2
N. F. Ticehurst	26
Total	283

to older blood. Could all of the scrutineers have been complicit in fraud *and* kept it secret for 30 years? Could they be duped 283 times without becoming suspicious? Would such prominent men have risked their reputations by publishing some of the records if they thought they were being duped? Several were customers of Bristow. By authenticating his allegedly foreign specimens they would be fooling themselves and enabling him to charge them higher prices for his birds.

Nicholson *et al.* (1969) questioned the character of two of these men, stating that Butterfield 'deliberately destroyed every record of the rarities when questions began to be asked', but the specimens are still in the Hastings Museum, so it is unclear exactly what was destroyed and what significance this might have had. They also questioned the ornithological competence of Ford-Lindsay (a local solicitor, disparaged as a 'stamp collector who dabbled in rare birds'). But identification was not his role. He was testifying only that specimens were freshly killed, on which issue Nicholson *et al.* (1969) appeared not to have questions. Ford-Lindsay and Butterfield were responsible for 186 of the verifications and this is concerning. However, many inspections took place in wartime, when limitations on travel would have restricted the availability of other scrutineers.

Michael Nicoll was one of the verifiers and personally shot some of the disputed birds. This might have made him more confident of the specimens shot by other people. Bristow did not supply Nicoll's birds and would have received only the stuffing fee, yet Nicoll's specimens remain as implicit evidence against him. Nicoll annotated his own copy of

Borrer's *The birds of Sussex*, recording his role in obtaining some of the Hastings Rarities specimens.

Could natural events account for the Hastings Rarities?

Weather patterns, where extreme conditions prompt the arrival of vagrants, might explain part of the area/era argument. Groups of birds can be swept over the North Atlantic by depressions, and prevailing westerlies often bring American birds to Britain. But the Hastings Rarities dataset comprised a list of records shorn of context. In isolation, many appear highly improbable, but it is worth considering the background to three of the most contested species. Snow Finch *Montifringilla nivalis* occurs in southern and central Europe and had never occurred in Britain. The species was deleted from the British List in 1962 on grounds of improbability, without reference to the events described by Ticehurst (1909). The details of Ticehurst's observations on timing and wind direction demonstrate that he was paying close attention to the circumstances in which he saw the freshly dead Snow Finch that Bristow brought to him. Snow Finch occurs as far west as the Pyrenees and is a vagrant as far north as Heligoland (Cramp & Perrins 1994, Slack 2009). Is it more probable that the species arrived naturally or that Bristow managed to import some, even during the wartime blockade of British ports during which three were recorded in 1916 (Hastings Rarities 540–542)? Records of Black Lark and White-winged Lark *Melanocorypha leucoptera* also coincided with extreme cold weather on the Continent and strong easterly winds (Ticehurst 1909), although that contextual detail did not prevent the relevant records being disallowed in 1962. In June 2003, a Black Lark was well documented on Anglesey (Degnan & Croft 2005). Subsequently, others from Yorkshire in April 1984 (Degnan & Croft 2005) and Norfolk in April 2008 (Offord 2008) were also accepted by the *British Birds* Rarities Committee. White-winged Lark was formerly more abundant, especially in the west of its distribution, and westward 'invasions' occurred in years when five of the Hastings records were made (Lindroos & Tenovuo 2000). Given the known extent of habitat loss in the steppes, the occurrence of both species during the era is not inconceivable, especially as Ticehurst's description of weather conditions at the time could have enabled their arrival.

Ignoring contextual details highlights the indiscriminate nature of the Hastings Rarities list, creating an inflated picture of improbability. This was supported by stories of other improbable occurrences (Nicholson & Ferguson-Lees 1962), but unlikely stories are not evidence, and have no bearing on Bristow's integrity.

Nicholson & Ferguson-Lees (1962) claimed that many records occurred at improbable times of year, but some were not implausible. For example, Aquatic Warbler is mostly seen in August–September (Thomas 2014), as were all five Hastings examples. All three Wallcreepers *Tichodroma muraria* were recorded in winter, when the species most regularly retreats from its montane habitat. Comments about some records being 'out of season' or not matching perceived migratory patterns implicitly assumes that seasons and bird behaviour are inflexible. But the Hastings Rarities were vagrants, by definition sporadic and accidental occurrences, especially in atypical weather conditions. Given the instability of weather patterns, why should vagrancy patterns apparent by 1962 be the same as half a century earlier?

The problem posed by World War I

The difficulty of importing foreign birds during the Great War was never considered. The war lasted from 28 July 1914 until 11 November 1918. One hundred and eighteen records, 21%

of all 595 Hastings Rarities (including ten seen alive), date from that period. They included oceanic birds, two North American species, and at least ten from Eastern Europe.

For import to Britain, birds needed to be refrigerated or packed in ice during travel overland and at sea. Was this feasible during a war that engulfed most of Europe? International trade was restricted, many ports and shipping routes were closed, insurance for ships was difficult (Russell-Smith 1919) and cargoes closely scrutinised. Shipping was disrupted and there were long delays at congested ports, a serious problem for dead birds on melting ice. In February 1915, Germany declared that all ships in British and Irish waters would be sunk on sight and even some from neutral countries were lost (Hoehling 1967). Yet 1914–15 witnessed the largest number of disputed records.

Minefields were laid and the German U-boat blockade covered most of the Mediterranean and all of the waters around the British Isles (Dixon 1917). Entry to British ports that remained open required a pilot due to restrictions on navigable channels. Would pilots help to import dead birds even in wartime? The suggestion in 1962 was indignantly denied (Harrison 1968) and no evidence was forthcoming. Even small vessels, such as the fishing boats that operated at Hastings, were subject to stringent controls and heavy penalties (Dixon 1917). Clandestine activity would probably have been minimal, and it is surely unlikely that anyone would continue to import mere dead birds. Despite this, in 1962 it was considered more probable that 118 birds had been imported in wartime than that they arrived in Britain unaided.

Wartime also compromised trade at Leadenhall Market, weakening the case for acquiring foreign specimens there. I have checked the superintendent's annual reports and they reveal a 97% decrease in meat tonnage from Europe passing through Leadenhall following the outbreak of war. It is difficult to reconcile this with the number of allegedly imported Hastings Rarities specimens during this time. Could Bristow, with remarkable prescience, have stocked up on imported birds before the war, kept them 'on ice' and released them for sale over the ensuing years? This would have meant storing >130 birds (given that some may never have been formally recorded), and four years later still being able to produce 14 to be authenticated as freshly killed on various dates in 1918. Without modern deep-freeze facilities this was not feasible.

Importing birds during the war was clearly compromised, so it is possible that the 118 wartime records (of 63 taxa) were actually genuine, including those seen alive. If we accept that possibility, then the list of 595 disqualified records is reduced to 477. Nicholson & Ferguson Lees (1962) proposed that, as one could not be certain which records were genuine, all of the records for a species within the area/era must be rejected. If we accept that logic, then why not the reverse, namely that establishing the veracity of one record of a species undermines the case for denouncing the remainder. By that argument the 63 taxa recorded during World War I (including those 'seen') could be deleted entirely from the Hastings Rarities, removing another 310 records from the list of rejections. Moreover, if we also accept that seeing live birds effectively authenticates dead ones that appear soon afterwards, eight more species could be reinstated, along with 53 of their associated records. Any one of these reasonable adjustments results in a much-reduced case of potential fraud that does not justify the highly publicised attack on George Bristow or the implication of incompetence on the part of the scrutineers who had agreed to validate his specimens. Accepting the above reductions still leaves >100 potentially fraudulent records, but in the absence of direct evidence to the contrary they are also potentially genuine.

Was Bristow fairly accused of fraud?

H. F. Witherby, editor of *British Birds*, wrote to Bristow in 1916 insisting that no further records of rarities would be accepted unless specimens were shown 'in the flesh' to Norman Ticehurst. In 1962 much was made of Bristow's failure to fulfil this requirement, and the observed decline in records after he was challenged in 1916. Despite the implicit accusation of dishonesty, Bristow responded courteously and at length. He explained his reluctance to comply fully with requests to identify his sources. Subsequently, he also explained why the number of rarities declined after 1916, pointing out that many of his suppliers had gone to join the war. This was dismissed as 'defensive' in 1962, then ignored, although the memorials in many local churches show significant losses for the small villages, supporting Bristow's assertion. Actually, many more able-bodied men would have been absent from the villages and countryside during wartime, not just those recorded as killed. Table 2 confirms that numbers of records also declined in the rest of Sussex (Nelder's YSB), supporting Bristow's contention.

If a lucrative fraudulent network had been established pre-war, the cessation of hostilities should have resulted in business picking up. In fact, the number of rare birds recorded continued to decline. There are plausible reasons for this, including increased efforts by the Royal Society for the Protection of Birds to enforce the legal protection of birds at Dungeness. The former bird collectors were also getting old and the collecting ethos was coming to an end as ornithology began to focus on ecological and behavioural topics. These issues were ignored in 1962, and the post-war reduction in rarity records was attributed entirely to Bristow's activities being curtailed due to his being 'found out' in 1916. In their editorial, Hollom *et al.* (1962) stated: 'The record shows that faced with the requirement that all new specimens should be submitted to [Ticehurst's] independent expert scrutiny the deception finally collapsed. Had he been able to examine evidence while it was fresh, he must have undoubtedly found what we have established now'. Despite this negative portrayal, Bristow in fact submitted birds for examination by Ticehurst on at least 33 occasions (Table 3). They were all rejected in 1962. Following intervention by Norman Ticehurst a single record of a White-spotted Bluethroat *Luscinia svecica cyaneacula* was accepted in an addendum to Nicholson & Ferguson-Lees (1962), but nevertheless remained on their list of rejected records (Hastings Rarity 384).

Accusations of profiteering

The motive advanced for fraud was explicitly financial gain (Hollom *et al.* 1962, Nicholson & Ferguson-Lees 1962), a suggestion emphasised at the 1962 press conference, although not a single example was cited of the transaction cost for any bird bought from Bristow, rare or otherwise. By contrast, Harrison (1971) recorded that he paid Bristow just ten shillings for what was claimed to be the first British specimen of an Audubon's Shearwater *Puffinus lherminieri* and the Maidstone Museum paid Bristow £18 for 28 birds in 1911 and 1920, or less than 13 shillings each.

The case for financial gain rested entirely on inference and hearsay. However, what people privately paid would not have been a matter for public record nor considered a subject for polite enquiry, especially among gentleman collectors. Relevant information comes from the collector J. B. Nichols, who recorded what he paid in a simple code (Morris 2006), for example 12/6d for two Red-footed Falcons *Falco vespertinus* (Hastings Rarities nos. 77–78) bought direct from Bristow. Many of Nichol's birds were absorbed into the Auden collection (now in Birmingham museum) and Nichols' costs are still legible on most of their labels. Forty-two Hastings Rarities cost him an average £2-11-6d each. This is more

than double the prices Bristow charged museums for similar material (Harrison 1968), confirming that he did take advantage of an eager collector. Sixteen non-Hastings Rarities bought from other taxidermists cost Nichols an average of 9/9d, although he paid Bristow £1 for an Alpine Ring Ouzel skin *Turdus torquatus alpestris* (cf. Hastings Rarities 348) in 1914 (now in Colchester museum). Fourteen birds in the Royal Museum of Scotland, Edinburgh, were bought from Bristow in 1913–14. They include 11 Hastings Rarities, costing on average 30 shillings each (Collinson & McGowan 2011).

It is fair to record that Bristow was probably making the most of his specialist clientele, but he charged less than half the (unsubstantiated) amounts suggested in 1962, when Nicholson was quoted as saying at his press conference that a rare bird could cost £25–30. Nor was there evidence of a competitive scramble to buy, as alleged. Instead, old collections reveal there were even more specimens of the disputed species passing through Bristow's hands than previously stated, suggesting that these 'rarities' were perhaps not so rare after all (or that he managed an even larger supply without being discovered).

If buying foreign birds meant extra costs, Bristow could not have made the alleged additional profits unless he charged higher prices. No evidence was provided in 1962 to show that this occurred. More significantly, avid collectors were becoming fewer. It is unlikely that profits from a diminishing band of customers would have supported a complex smuggling operation, and perhaps not even paid for frequent supplies from Leadenhall market.

Was the principal Hastings Rarities author prejudiced?

Opprobrium has been heaped on George Bristow, but what of the others in this affair? John Nelder (1924–2010) was an accomplished statistician, who developed many of the standard analyses commonly used today, a Fellow of the Royal Society, and a keen ornithologist. James Ferguson-Lees (1929–2017) wrote several popular bird guides, edited *British Birds* for 20 years and was a key figure in the ornithological establishment, but he was the junior partner in the 1962 paper (Moore 2012). The lead author was Max Nicholson (1904–2003), a highly respected senior civil servant and a pillar of the naturalist community. He had a lifelong interest in birds and was one of the chief architects of the British Trust for Ornithology, President of the Royal Society for the Protection of Birds, and Editor of *British Birds* (1951–60). Perhaps, as a senior civil servant, he had neither time nor freedom to write the Hastings denunciation earlier. The long delay in doing so was a complaint made by those who objected to his assertions being made so long after the events (Harrison 1962, Bannerman 1963: 394).

Despite his distinguished career, Nicholson was not always the dispassionate scientific enquirer that might be supposed. In his youth he expressed intemperate opinions regarding taxidermists, equating them with receivers of stolen goods and describing taxidermy as a 'mischievous occupation' (Nicholson 1926). He also attacked bird collectors, verbally and in print, and many of the rarity records he found implausible had been accepted by the journal of which he became editor. Some of his language in 1962 suggests deep-seated hostility. For example (Nicholson & Ferguson-Lees 1962: 321) 'The *great majority* [my italics], at least of the records, was in the shop of Mr. George Bristow', but listed only 209 out of 542 specimens as 'taken to Bristow'. Describing 38% as a *great majority* suggests a determination to lay blame. Similarly, it was asserted (p. 323) 'if, as we claim to have demonstrated, there is no reasonable possibility of the Hastings Rarities being genuine', but only improbability was demonstrated, not impossibility. It was said many times that 'Bristow had persistently declined repeated opportunities...', but he had simply not acted as instructed, perhaps because there was a war on. Bristow was accused of 'repeatedly evading' the need to show

his birds to Ticehurst, although he did so at least 33 times and to others on more than 200 occasions.

Discussing financial gain, with the implication of profiteering by Bristow, Nicholson stated in print (Nicholson & Ferguson-Lees 1962) and at the press conference that a stuffed Great Auk *Alca impennis* was worth £300, a totally irrelevant remark in relation to the Hastings Rarities but clearly intended to bolster his case against taxidermists. Nicholson asserted in 1962 that ‘the Trinity of the casual gunner, the busy taxidermists and the wealthy collector ... formed the backbone of the system ... and the nexus between them was cash’. He made the same remark 50 years earlier using the same distinctive vocabulary (Nicholson 1926). It is difficult to escape the feeling that Nicholson had it in for Bristow and calling a press conference was a triumphal act to publicly expose the latter’s guilt.

Bristow was relentlessly portrayed as devious and dishonest, but given no credit for his polite replies or the honest (and potentially incriminating) statement that he had once used refrigerated foreign birds. His detailed (and plausible) explanation for reluctance to identify all of his suppliers was described as ‘deliberate suppression’ of their names. But this was because certain birds were obtained illegally by his suppliers. Bristow also recounted his salutary experience of naming names. In fact, he did name some of his suppliers and assisted A. F. Griffiths (of the Booth Museum, Brighton) to contact them. A prejudicial tone was also evident when Nicholson *et al.* (1969) dismissively described James Harrison (a family doctor) as a ‘skin collector’, whilst referring to Meinertzhagen and Witherby as ‘leading ornithologists’ of reliable competence. Witherby’s collection numbered 9,000 specimens, Meinertzhagen had 25,000 (Mearns & Mearns 1998).

There are other disquieting aspects to Nicholson & Ferguson Lees (1962). A map on pp. 332–333 includes ‘The Crumbles’, a coastal site within the area, but it is curiously excluded from the discussion and no mention is made of observations from within both the area and the era published by Arnold (1936) that do not support the case for fraud and were not associated with Bristow. After defining the ‘area’ as 20 miles from Hastings Pier, another species was added to the list (Great Shearwater *Puffinus gravis*, Hastings Rarities 18) from Shoreham, which is 43 miles away. When publishing a formal record, it was helpful to cite the nearest village, of which there were relatively few in the area, producing clusters of records around named places. It was explained that records ‘near’ somewhere were added to the total for that place, but the text deemed it ‘suspicious’ that so many records were associated with particular villages. This also overlooked that some place names served for whole parishes, thereby covering a larger area than just a village. Many records (31) were from St. Leonards, but it is neither surprising nor ‘suspicious’ that they were taken to Bristow, rather than to a more distant taxidermist. During the era it was customary for the identity of rare birds to be confirmed by shooting them. In a peculiar reversal of that principle, 53 sight records were declared ‘unacceptable’ because they were associated with suspect specimens. The logic is unclear, but including them augmented the number of allegedly fraudulent records, especially as some were counted twice—once dead and once alive (Table 1).

Conclusion

The claim in 1962 that a massive fraud had occurred has prompted wider scepticism regarding historical bird lists (Bourne 1963, Collinson 2019). Maybe we cannot believe anything now when considering early records for invasions by new species or investigating effects of long-term environmental change. Or maybe there was no fraud after all. Perhaps it was not necessary to import rare birds because they appeared naturally, as many species have done since, including Cetti’s Warbler *Cettia cetti*, which was a class 1 rarity in 1962, but

is now commonplace. Perhaps time and place are crucial, and Bristow benefitted from being active in a particularly favourable area/era.

The arguments advanced in 1962 make a strong case for some deception having occurred, but it is not the clear-cut issue that many have come to accept. The proposed fraud, involving several continents and sustained in secret for 30 years, stretches credulity. It requires acceptance of improbabilities on a par with those highlighted by Nelder (1962). Moreover, the practicalities of importing dead birds for fraudulent sale were never considered, especially the difficulty of doing so during a World War, during which a fifth of the disputed records occurred. Nor was any evidence offered to support the central claim of major financial benefit, only ill-informed innuendo.

The stated aim of Nicholson & Ferguson-Lees (1962) was to protect the integrity of the British List by eliminating unacceptable records. Their principal critic was Harrison (1968) who sought to defend the integrity of Bristow. In their critique of his book, Nicholson *et al.* (1969) recognised that these were different issues. Protagonists of each approach were unlikely to agree as they were contesting two different things. The same is true of the present paper. Accepting the conspicuously large number of records from the area / era as genuine, despite their statistical improbability, means perpetuating uncertainty and suspicion, hence their proposed deletion. Rejecting them implies 'a serious suspicion that deception had been practised' (Nicholson *et al.* (1969), who then claimed 'We left it at that'. But they did not. They named Bristow, repeatedly. Their agnostic stance was clearly unacceptable at the 1962 press conference: if fraud had occurred, someone must have been responsible for it and only one name was mentioned.

Genuine specimens of rarities from the era confirm that Hastings offered a rich seam for vagrant hunters. The period 1890–1914 was a particularly active time for local people supplying a long-established taxidermy business with specimens, spurred on by collectors (local and from further afield) keen to obtain rarities and gain kudos by publishing their records. Far from 'setting the record straight', as claimed, the opposite may have been achieved.

Inclusion of birds 'seen' and many genuine records exaggerated the affair and the extent of the implicit case against Bristow, tainting the taxidermy profession. But many of the disputed specimens were not supplied by him, and others have plausible provenance data. If those specimens were genuine, the only reason why others that passed through Bristow's hands were not is that they were statistically improbable.

The demonisation of George Bristow was collateral damage of little public concern, but the case against him was absurdly exaggerated in the popular press and widely promulgated. Nicholson *et al.* (1969) made no attempt to repudiate the absurdly inaccurate press coverage they had received. Bristow has been blamed ever since.

It was asserted that the era ended when Bristow's nefarious activities were curtailed by Witherby's challenge in 1916. A plausible alternative explanation, offered by Bristow, and consistent with evidence, was ignored.

After so much time, the deleted records should remain as 'unproven' but George Bristow's alleged duplicity should be treated the same way. Without question, he did not perpetrate the 'massive' fraud portrayed by the popular press in 1962 and asserted many times since. Bristow was not responsible for all 595 records that comprise the Hastings Rarities, nor even the majority. The records with which he was explicitly associated were not all fraudulently supplied, and there is a possibility that none were. Nevertheless, some of the patterns of records highlighted by Nelder's analysis are troubling, although not inexplicable. The status of the Hastings Rarities and the role of George Bristow will remain controversial, especially in the minds of those who believe the case was settled in 1962. On

the other hand, Bristow just might have been conducting a largely honest business in the right place at the right time. Presumption of guilt is unjust.

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EDITORIAL COMMENT.—Pat Morris, while not denying that fraud may have underlain at least a subset of the Hastings Rarities, argues that the vilification of the taxidermist George Bristow for his purported role in the affair is unjustified based on available facts. The paper is a work of advocacy, re-examining issues that many British birdwatchers have assumed, or at least wished, had been settled decades ago. No doubt some ornithologists may wish to contest its conclusions.

The fact that John Nelder's 1962 statistical analysis of the almost 600 individual Hastings Rarities records yielded some clear improbabilities regarding the distribution of the specimens in space and time is not contested. Rather, it is the array of facts and suppositions underlying these improbabilities that are re-considered, especially with regard to the nature of the involvement of George Bristow in bringing many of the records to public attention.

Presumably because of the sheer number of records involved, which would make it a daunting task, no systematic attempt appears to have been made to re-examine the Hastings Rarities on a case-by-case basis, in the manner that most rarity records are now routinely assessed. While this is understandable, such reconsideration would nevertheless seem essential. In at least one other case where evidence has pointed to large-scale fraud, notably that involving the Meinertzhagen collection, gradual implementation of this course of action is enabling the data for some specimens to be designated as almost certainly valid and for others as almost definitely fraudulent, though admittedly with a third grouping, which for now remains enigmatic and thus must continue to be flagged as doubtful (e.g. Rasmussen & Prÿs-Jones 2003, Prÿs-Jones *et al.* 2019).

To lay the basis for such a review, it might seem desirable to attempt to determine the current whereabouts of those specimens comprising the Hastings Rarities. Whereas many are held in just a few collections, others have been widely scattered and some may have disappeared beyond trace. Reassessment on an individual specimen basis could then begin, using standard records committee criteria, and perhaps initially focusing on records in which Bristow is known or suspected to have played a role. This would clearly involve considerable input by a group of knowledgeable people who would need to feel the results potentially justified the time invested, but without it the possibility of further progress in elucidating the problems underlying the Hastings Rarities appears slight.

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First record of Forbes-Watson's Swift *Apus berliozi* in southern Africa, with comments on vocal and visual identification

by Etienne Marais, Faansie Peacock & Gary Allport

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SUMMARY.—We report the first record of Forbes-Watson's Swift *Apus berliozi* for the southern Africa region from coastal southern Mozambique. Identification was primarily based on vocal characters using sonogram analyses, which show that voice is diagnostic compared to all seven possible confusion species in the region. Current knowledge of the distribution and life history of *A. berliozi* is summarised, which shows that the Mozambique record extends the non-breeding range c.1,700 km south and suggests that Forbes-Watson's Swift is a migrant to the littoral of Tanzania and northern and central Mozambique. Field identification of Forbes-Watson's Swift using visual characters is challenging, but information is presented to aid separation from the most likely confusion species, Common Swift *A. apus*.

Forbes-Watson's Swift *Apus berliozi* was originally described as a subspecies of Pallid Swift *A. pallidus* based on specimens from the Yemeni island of Socotra collected by A. D. Forbes-Watson in 1964 (Ripley 1966). Subsequently, Brooke (1969) treated it as a species, and this arrangement has persisted until the present. More recently, molecular phylogenetic work has placed Forbes-Watson's Swift in a clade with Nyanza *A. niansae*, Bradfield's *A. bradfieldi*, African Black *A. barbatus*, Plain *A. unicolor*, Pallid *A. pallidus* and Common Swifts *A. apus* (Päckert *et al.* 2012), but phenotypically it can be grouped with the 'paler brown' swifts including Pallid, Nyanza and Bradfield's Swifts and, less distinctly, the *pekinensis* subspecies of Common Swift.

Two subspecies of Forbes-Watson's Swift are recognised, both with restricted breeding ranges. *A. b. berliozi* is known only from Socotra, where it nests in two systems of caves in limestone cliffs, at sea level and at c.500 m. The population has been estimated at 1,000–2,400 birds but potential breeding areas on smaller islands nearby have not been surveyed (Porter & Suleiman 2013). Breeding seasonality on Socotra is not completely clear. Screaming and display flights have been regularly observed in February and March, but there was no evidence of breeding during the period 31 March–7 April 1993 (Porter *et al.* 1996). Forbes-Watson collected 32 birds, nearly all of them in breeding condition, on 9–14 May 1964 (Ripley 1966), and the species has been observed entering caves late February–May, which is presumably the local breeding season (Porter & Suleiman 2013). The species has not been recorded on Socotra between June and September during the peak monsoon, but this could simply reflect the lack of visits during this season of stormy weather. It has been suggested that the Socotran population is resident (Porter & Aspinall 2010, Kirwan 2010) but none was recorded in surveys during 20 December–19 February, when Porter & Suleiman (2013) considered it to be probably absent from the archipelago. If this is the case then it is a migrant, the non-breeding area of which is unknown.

The other subspecies, *A. b. bensoni*, is locally common, present all year and breeds in March–September in coastal and, perhaps, inland Somalia (Ash & Miskell 1983). Nesting records are mostly from sea caves, but a specimen from Borama, north-west Somalia

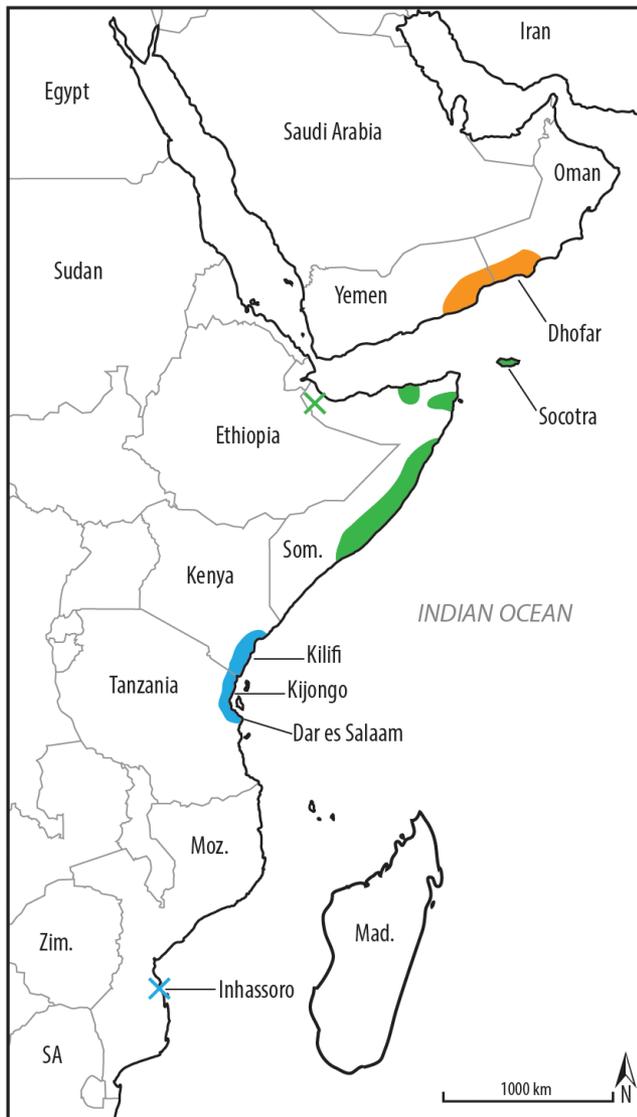


Figure 1. Distribution of Forbes-Watson's Swift *A. berliozii*, showing breeding range in Somalia ('Som.') and Socotra (green), southern Arabia (orange), and non-breeding range in coastal southern Kenya and northern Tanzania (blue). The location of the observation reported herein (Inhassoro, Mozambique) is indicated with a blue 'X'.

(09°53'37.5"N, 43°11'19.3"E; 122 km inland) was in breeding condition when collected on 27 June 1958, suggesting that inland nesting in Ethiopia and Djibouti is also possible (Brooke 1972, Ash & Miskell 1983; Fig. 1).

After more than 50 years of observations of 'mystery' swifts in south-west Oman and neighbouring eastern Yemen (since Smith 1956), birds which had been previously identified as *A. pallidus* or *A. apus pekinensis* were re-identified as Forbes-Watson's Swift *A. b. bensoni* by Grieve & Kirwan (2012), extending the known breeding range to southern Arabia. Observations in Oman span mid-April to late December, peaking between mid June and mid October (Eriksen & Victor 2013; <https://ebird.org/species/fowsw1/OM>), but the identity of birds seen, but not heard calling, after late September is uncertain (G. M. Kirwan *in litt.* 2020).

Specimen records from East Africa are all of this subspecies (see below) and, along with seasonal absence from Oman (Grieve & Kirwan 2012), show it to be at least a partial migrant

in parts of its range (Chantler & Driessens 2000), despite year-round occurrence in Somalia (Ash & Miskell 1983).

In the non-breeding season the species has been known from coastal southern Kenya since Forbes-Watson collected ten specimens in early December 1964 and late January 1966 (Brooke 1969). None of these birds—which form the type series of *A. b. bensoni*—was in breeding condition, whilst feather wear varied from worn, darker and ‘even browner’ plumage in the December series to freshly moulted plumage in those collected in January (Brooke 1969).

Since then there have been fairly regular sight records in coastal Kenya, almost all of them during November to February over forested areas at Kilifi, Gede Ruins, Gazi, Ribe, Tiwi, Arabuko-Sokoke and the Shimba Hills (Brooke 1969, Britton 1980, Fry 1988, Zimmerman *et al.* 1996, Chantler & Driessens 2000, Stevenson & Fanshawe 2002; D. A. Turner *in litt.* 2020), although there have been relatively few reports since 2010 (R. Nussbaumer *in litt.* 2020). It has also been noted further north at Kipini Conservancy, on the coast between the Tana River delta and the villages of Witu and Mpeketoni, where small numbers were seen during 1 November–26 December 2006 and the species was presumed to be seasonally resident or on passage (Dowsett-Lemaire & Dowsett 2014). The area around Malindi and Watamu is regularly used and apparently monospecific flocks have been seen flying out to sea at dusk, possibly to roost on Whale Island, a small rocky islet 2 km off the mouth of Mida Creek (Britton 1980, Zimmerman *et al.* 1996; D. A. Turner *in litt.* 2020).

There have also been reports of *A. berliozii* from Tanzania’s coast. The only published record was of a notably large flock of *c.*1,000 individuals near Dar es Salaam on 29 March 1996, moving north in a single, spiralling group (Fisher & Hunter 2014; B. Finch *in litt.* 2020, sound-recording on the *eGuide to birds of East Africa*, mydigitalearth.com). Unpublished records include unauthenticated sightings of two birds over primary montane evergreen forest at Mazumbai Forest Reserve, in the West Usambaras, in February 2009, and *c.*30 foraging over the East Usambara foothills *c.*10 km east of Siggi (Zigi) in March 2014 (J. Wolstencroft *in litt.* 2020), as well as two records documented with video, photographs and audio. One involved hundreds of birds around Kijongo Bay 26 km south-west of Pangani (05°38′49.8″S, 38°54′30.9″E) on 20–26 March 2017 (J. Haureljuk *in litt.* 2017; Fig. 2; <https://www.facebook.com/groups/241108492733888/permalink/764278667083532/>); the other of



Figure 2. One of hundreds of Forbes-Watson’s Swifts *A. berliozii* in a low-flying flock, Kijongo Bay, Tanzania, March 2017 (J. Haureljuk)

90 at Manta Resort, Pemba Island, Zanzibar (04°53'00.5"S, 39°40'44.4"E) on 12 April 2017 (J. Wolstencroft *in litt.* 2017; <https://www.facebook.com/groups/241108492733888/permalink/780996082078457/>).

The Tanzanian records involving large numbers of birds further south than previously recorded, and within a restricted period, suggesting possible passage, led to speculation that this species may be migrating to and from wintering localities further south than hitherto known (N. Baker *in litt.* 2018, 2020). It was this suggestion that prompted GA to consider the species as a possible migrant to Mozambique.

The field identification of Forbes-Watson's Swift is challenging. Grieve & Kirwan (2012) were the first to combine a review of specimen biometrics with analyses of both field photographs and vocal characters. They found that in general appearance this species is the palest of the paler brown group of swifts, but the only diagnostic field character is the better-defined triangular pale throat patch. Although the vocalisations of Forbes-Watson's Swift have been described previously (e.g. Zimmerman *et al.* 1996), it was only via sonogram analysis, and comparison with other swift species known or likely to occur in southern Arabia, that Grieve & Kirwan (2012) demonstrated that its screaming calls are clearly distinct. This was evident in high, low and mean peak frequency measurements—the calls showing less variation in frequency and with a significantly lower mean peak of 3.9 kHz, vs. 5.9 kHz for both Common and Pallid Swifts, resulting in a rasping scream relatively low and flat in structure. This represented a significant step forward in the field identification of Forbes-Watson's Swift.

Recent record from Mozambique

On the morning of 3 March 2017 EM was leading a bird tour in the Save Woodlands (21°16'8"S, 34°36'21"E), a tract of semi-disturbed forest c.350 km² in extent, 40 km inland of Inhassoro (21°31'52"S, 35°11'34"E) in southern Mozambique. A flock of what were assumed to be Common Swifts was seen above the forest and EM noted that they were calling intermittently, which is unusual for the species in southern Africa, but did not pay further attention.

Later that day the group returned to Inhassoro, on the coast c.50 km north of Vilanculos and due west of the northern tip of the Bazaruto archipelago. At sunset EM observed a flock of large dark swifts above a beachfront lodge. The birds were swirling around 30–100 m above ground. It was hard to estimate numbers as they formed a loose, fast-moving group, but there were at least 50. They were initially thought to be Common Swifts (possibly *A. a. pекinensis*, of which EM had previous experience) but they were uncharacteristically vocal, which prompted EM to study them. The swifts circled above the lodge for c.20 minutes, then moved north-east over the ocean. The following notes were compiled subsequently, from memory.

Description.—Similar in size to Common Swift. Flight a little slower and 'lazier' than typical of Common Swift; at the time, this was thought probably to be a function of calm conditions. The evening light was poor but some appeared to be paler (brownier) than Common Swift and to have a more obvious whitish throat patch. The screaming calls were unfamiliar to EM, albeit reminiscent of African Black Swift (known to EM at breeding colonies) but 'mellower' in comparison. EM considered that, given the locality, date and habitat, a migrating flock of African Black Swifts was extremely unlikely. He made a sound-recording using an Olympus voice recorder (WS-853).

Initial identification.—All possible species of swifts were considered for both encounters, and most were easily excluded; Mottled Swift *A. aequatorialis* on the basis of overall size and behaviour, as well as call, with which EM was very familiar, and Scarce

Schoutedenapus myoptilus, Alpine *A. melba*, Horus *A. horus*, White-rumped *A. caffer* and Little Swifts *A. affinis*, and African Palm Swift *Cypsiurus parvus*, by general appearance and flight action. After initially thinking that they were Common Swifts, EM subsequently felt that he was unable to identify them with certainty and planned to review the voice recording of the birds at the lodge. This was not done until late March 2020, when GA raised the possibility of Forbes-Watson's Swift occurring in Mozambique. An initial analysis revealed that the Inhassoro swifts' screaming calls were very similar to Forbes-Watson's Swift. A more thorough comparative analysis of the calls of potential confusion species was therefore undertaken. In hindsight, the birds seen over the Save Woodlands may also have been the same species, but no such claim is made here due to the cursory nature of the observations.

Identification

Four species of large swift with the potential to be confused with Forbes-Watson's Swift are currently known from the southern Africa and Madagascar region. These are discussed below in relation to the identification of the 'Inhassoro swifts'.

Bradfield's Swift breeds in western southern Africa and Angola. It is locally common, being the commonest swift in Namibia, and is thought to be resident and sedentary. *A. bradfieldi* occurs marginally in south-east Botswana and is found no further east than Kimberley, South Africa: there are no records from Mozambique (Hockey *et al.* 2005). It is relatively distinctive, being paler brown overall than other species (but see *A. a. pekinensis*). A previously accepted specimen record of Pallid Swift from the southern Africa region (Hockey *et al.* 2005) has since been re-identified as this species (Davies 2013).

The nominate race of African Black Swift *A. barbatus* breeds widely in mountainous regions of South Africa, Lesotho and Eswatini, with a minor presence in eastern Botswana. It is uncommon in the uplands of southern Mozambique and in the Lebombo Mountains, the highlands bordering Eswatini. There is also a population of the subspecies *oreobates* resident in the Chimanimani Mountains of Mozambique bordering Zimbabwe and this taxon is also reported from Mount Gorongosa (Brooke 1970, Clancey 1996, Hockey *et al.* 2005). The subspecies *hollidayi* has a very restricted range, in western Zimbabwe, where it is apparently resident. Nominate *barbatus* is mostly absent from large parts of its southern range between May and August, although some over-winter. It has been recorded on passage in Zimbabwe in May and August, with one record in Mozambique in April (Fry 1988, Hockey *et al.* 2005). The non-breeding range is unknown but is assumed to be tropical Africa (Hockey *et al.* 2005). Away from its colonies, this species represents an identification challenge in the region, being similar to *A. a. apus*, but is separable with good views of the upperparts (often difficult to achieve), showing a characteristic dark 'saddle' on the mantle contrasting with paler secondaries (less clear in *hollidayi*) (Hockey *et al.* 2005).

Malagasy Black Swift *A. balstoni* occurs throughout Madagascar and the Comoros, where it is generally presumed to be resident and sedentary. However, it is apparently highly mobile within this range, with fluctuations in numbers in several parts of Madagascar (Safford & Hawkins 2013, del Hoyo *et al.* 2020). Large flocks of swifts reported arriving off the sea in Mozambique have been suggested to be this species, rather than *A. barbatus*, but this is unproven and hypothetical (Chantler & Driessens 2000, del Hoyo *et al.* 2020). *A. balstoni* is smaller than African Black Swift with a blacker head and body, and smaller pale throat patch distinctly streaked dark (Safford & Hawkins 2013).

Common Swift (*A. a. apus* and *A. a. pekinensis*) is a Palearctic migrant present late October–March in the southern African region (Hockey *et al.* 2005, Chantler *et al.* 2020). The Western Palearctic-breeding *A. a. apus* is the darker of the two subspecies, similar in overall tone to African Black Swift, with a poorly defined pale throat patch. Eastern *A. a. pekinensis*

is more variable in tone but is normally a paler brownish bird which can show a ‘saddle’ on the mantle (Grieve & Kirwan 2012), similar to African Black Swift. This subspecies is not illustrated in most African field guides, contributing to its confusion with Bradfield’s and Forbes-Watson’s Swifts. The migratory ranges of the two forms in southern Africa are not well known; *A. a. apus* is considered to reach only the eastern part of the region whilst *pekinensis* is recorded over-wintering further south and west, especially in arid regions (Brooke 1975, Hockey *et al.* 2005). For more detail see section below on temporal occurrence in the subregion.

In Mozambique, Clancey (1996) described Common Swift (*sensu lato*) as ‘probably of fairly general occurrence, but so far known on the basis of three specimens’. It is unclear which specimens these are but they may be those collected by Pinto (1959) on 24 March at Funhalouro. Parker (2000, 2005) reported the regular occurrence of Common Swift in southern Mozambique, but only inland, from 24°S as far north as northern Tete province, in November–March (but with observations until May). However, it is unclear what criteria were used to identify these birds, and there was no mention of subspecies. More recently, Common Swift has been recorded regularly in Sofala province south of the Zambezi, particularly in the latter’s basin, west of Mount Gorongosa and in the Pungwe River catchment, between November and February (SABAP2 database: <http://sabap2.birdmap.africa/>) often in flocks of hundreds, possibly thousands, in stormy weather (EM pers. obs.; e.g. <https://ebird.org/checklist/S68018268>). At least ten *pekinensis* were seen together with the nominate in Sofala province, central Mozambique, on 6 December 2010 (EM pers. obs.; <https://ebird.org/checklist/S67277339>). Large swifts are generally very uncommon in the southern littoral of Mozambique. None was found there by Parker (2000) and GA recorded only three birds (in two observations) over nine years of birding in the region (see Allport 2018 for locations and effort), one of which was identified as *A. a. apus* (<https://ebird.org/checklist/S51956079>). However, there is an observation of 40 swifts logged as *A. apus* near Xai-Xai, in March 2016 (EM pers. obs.; <https://ebird.org/checklist/S68021013>), which is now in question.

Voice analysis

Methods.—Seven species of swift known, or thought possibly, to occur in southern Mozambique were included in the analysis; the four species discussed above, plus Pallid, Nyanza and Forbes-Watson’s Swifts. Pallid and Nyanza Swifts have not been recorded in the region but were included based on similarity in voice and plumage. The two subspecies of Common Swift were analysed separately.

Sound-recordings were located via online resources (Xeno-canto [XC] and the Macaulay Library of Wildlife Sounds) and personal contacts. The vocalisations chosen for comparative purposes were limited to flight calls, and no attempt was made to cover the full variety of vocalisations made in courtship and at the nest.

Adobe Audition was used to prepare sonograms for initial review. Analysis was attempted following the methodology of Grieve & Kirwan (2012), but the algorithm for maximum and minimum peak frequency used in their analysis was found to be heavily influenced by incidental sounds on many recordings, which resulted in readings from false signals. However, in trial analyses, the algorithm for frequency (kHz) at peak amplitude (Pk) yielded consistent results, and this algorithm was adopted for the comparative analysis.

Recordings were selected based on clarity and length of strophes of ‘screaming’ calls. Each ‘scream’ was individually analysed by selection in a hamming window with a fast Fourier transformation size of 2,048 points and the frequency at peak amplitude was measured.

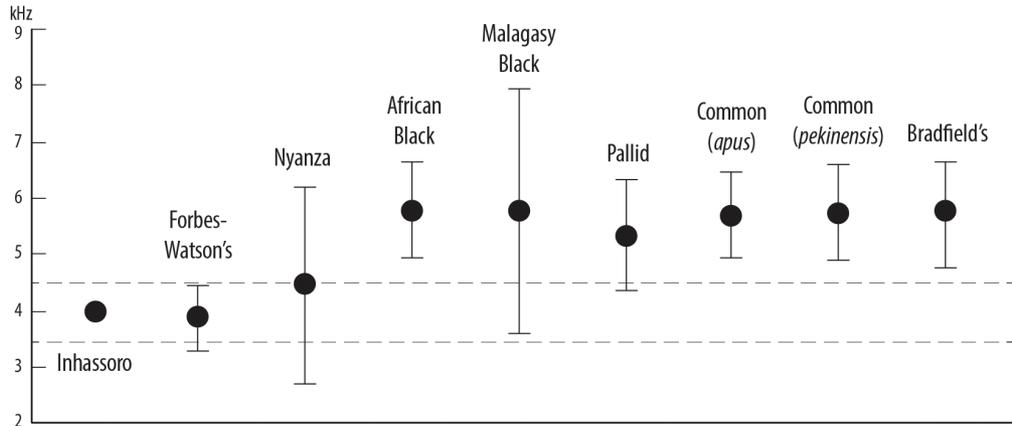


Figure 3. Comparison of mean (circle) frequency (kHz) at peak amplitude (Pk) of the screaming calls of 'Inhassoro swifts' with Forbes-Watson's *Apus berliozii*, Nyanza *A. niansae*, African Black *A. b. barbatus*, Malagasy Black *A. balstoni*, Pallid *A. pallidus*, Common (*A. a. apus* and *A. a. pekinensis*) and Bradfield's Swifts *A. bradfieldi*. Bars show 95% range in values (± 1.96 SD), and range for 'Inhassoro swifts' shown as broken lines.

It was noted that higher pitched harmonics in individual screams were evident on the best-quality recordings so only the lowest-pitched first-fundamental harmonic was considered, even if one or more overlying higher harmonics were visible in the sonograms. The data thus comprised a series of measurements of individual screams but were pooled to form a combined dataset for each taxon for the purpose of analysis.

Call series were assessed both visually on the sonograms and aurally at normal playback speed and with speed reduced by 0.3 \times ; the slower playback was found to aid characterisation of the rapid, complex screaming calls. The terminology of Robb & Pelikan (2020) was followed to describe the sound structure.

Results.—The recording of the 'Inhassoro swifts' was 39 seconds in duration and comprised 33 screams from multiple birds; each rasping scream was of a flat tone at c.4 kHz (Figs. 3–4; full call series XC543748).

Twenty-one recordings of screaming call sequences from the nine taxa were analysed (Appendix 1). There was no significant difference between mean frequency at peak amplitude of the calls of 'Inhassoro swifts' and Forbes-Watson's Swift, but all other swift species analysed vocalise at higher frequencies at the peak of the call (Table 1, Fig. 3). The nearest call within the range of both the Inhassoro recording and Forbes-Watson's Swifts was that of Nyanza Swift, which, along with Malagasy Black Swift, exhibited wider ranges of variation in this measurement (Fig. 3). However, there were reasonable sample sizes of these two species and *t*-tests revealed significant differences from the 'Inhassoro swifts' in both cases (Table 1).

The sonogram signatures of flight calls across the species tested are shown in Fig. 4. These high-pitched, rather frantic screams all sound quite similar to the human ear. Structurally, the long screams are 0.7–1.0 second in duration and often exhibit a rapid rise in frequency in the 'foreleg', which can form a very rapid spike. There is a crest, when frequency is highest, followed by a slightly less rapid decline in frequency towards the call terminus (the 'hindleg'). In several species the 'hindleg' is attenuated and has the effect of a notable down-slug. Many calls have very rapid oscillations in frequency or volume, and this modulation creates a 'buzz', 'rasping' note or a 'trill', as opposed to a smooth sound, which is often most pronounced in the 'hindleg'. Modulation also varies in the rate of oscillations: very fast modulation sounds shrill, whereas slower modulation is more like a trill with the vibration clearly audible. The calls of each species are described in Appendix 2.

TABLE 1
Comparison of mean frequency at peak amplitude of screaming calls of the 'Inhassoro swifts' (Fig. 4; XC543748) with Forbes-Watson's *Apus berliozi*, Nyanza *A. niansae*, African Black *A. b. barbatus*, Malagasy Black *A. balstoni*, Pallid *A. pallidus*, Bradfield's *A. bradfieldi* and Common Swifts (*A. a. apus* and *A. a. pekinensis*). See Appendix 1 for details of samples.

	Sample size (n)	Mean frequency at peak amplitude (kHz)	Standard deviation	Standard error	Comparison <i>t</i> -test with the Inhassoro birds
'Inhassoro swift'	33	3.945	0.259	0.045	
Forbes-Watson's Swift	33	3.846	0.290	0.050	NS
Nyanza Swift	17	4.465	0.896	0.217	$P < 0.001$
African Black Swift	44	5.795	0.430	0.064	$P < 0.001$
Malagasy Black Swift	32	5.801	1.123	0.198	$P < 0.001$
Pallid Swift	32	5.361	0.498	0.088	$P < 0.001$
Bradfield's Swift	35	5.681	0.461	0.078	$P < 0.0001$
Common Swift (nominate)	27	5.678	0.390	0.075	$P < 0.001$
Common Swift (<i>pekinensis</i>)	23	5.761	0.426	0.088	$P < 0.001$

Discussion

All swift species analysed had vocal characters significantly and diagnostically different from the 'Inhassoro swifts', except Forbes-Watson's Swift, to which they were almost identical (<https://www.xeno-canto.org/set/5842>; Table 1, Figs. 3–4). The vocalisations of *A. berliozi* are distinct from other species in both frequency and details (Fig. 4, Appendix 2; Grieve & Kirwan 2012). The recording from Inhassoro is thus consistent with Forbes-Watson's Swift, as also are the plumage characters observed.

This is the first record of Forbes-Watson's Swift for Mozambique and the southern African region (Hockey *et al.* 2005; T. Hardaker *in litt.* 2020). Although the species was not a widely anticipated new bird for the country, indeed it was little known to most birders in southern Africa (J. R. Nicolau *in litt.* 2019), the emerging pattern of records further north, particularly in Tanzania, indicate its occurrence probably could have been expected (N. Baker *in litt.* 2018, 2020; L. Kearsley *in litt.* 2020).

This record extends the non-breeding range *c.* 1,700 km south and suggests that Forbes-Watson's Swift may be found anywhere along the East African littoral, from Somalia to southern Mozambique. Whether the Inhassoro record is an example of a regular occurrence or vagrancy is yet to be established. It is noteworthy that there was a cluster of records on the East African coast in March/April 2017 with four observations in Tanzania (see above) in addition to the Mozambique occurrence. Together, these suggest that there may have been an unusual movement at the time. Plausibly, Forbes-Watson's Swift has an 'irruptive' population dynamic or migratory cycle (Newton 2006), but, equally, it may be that these are simply the first records of a previously unnoticed normal migration.

Large swifts are uncommon on the coast of southern Mozambique; for example, none has been reported on the relatively well-watched San Sebastian Peninsula, 70 km south of Inhassoro (Read *et al.* 2014; C. Read & D. Gilroy *in litt.* 2020). This suggests that Forbes-Watson's Swift is at least not widespread in this part of Mozambique. However, like its close relatives, the species might select airspace over forest for daytime foraging, but unlike Common Swift, which ascends in vesper flight at dusk and roosts on the wing (Dokter *et al.* 2013, Hedenström *et al.* 2016), Forbes-Watson's Swift may roost in caves on offshore islands (as suspected in Kenya—Zimmerman *et al.* 1996) or on the mainland, perhaps on coastal cliffs similar to those in which it breeds. In this case the daily foraging distance inland

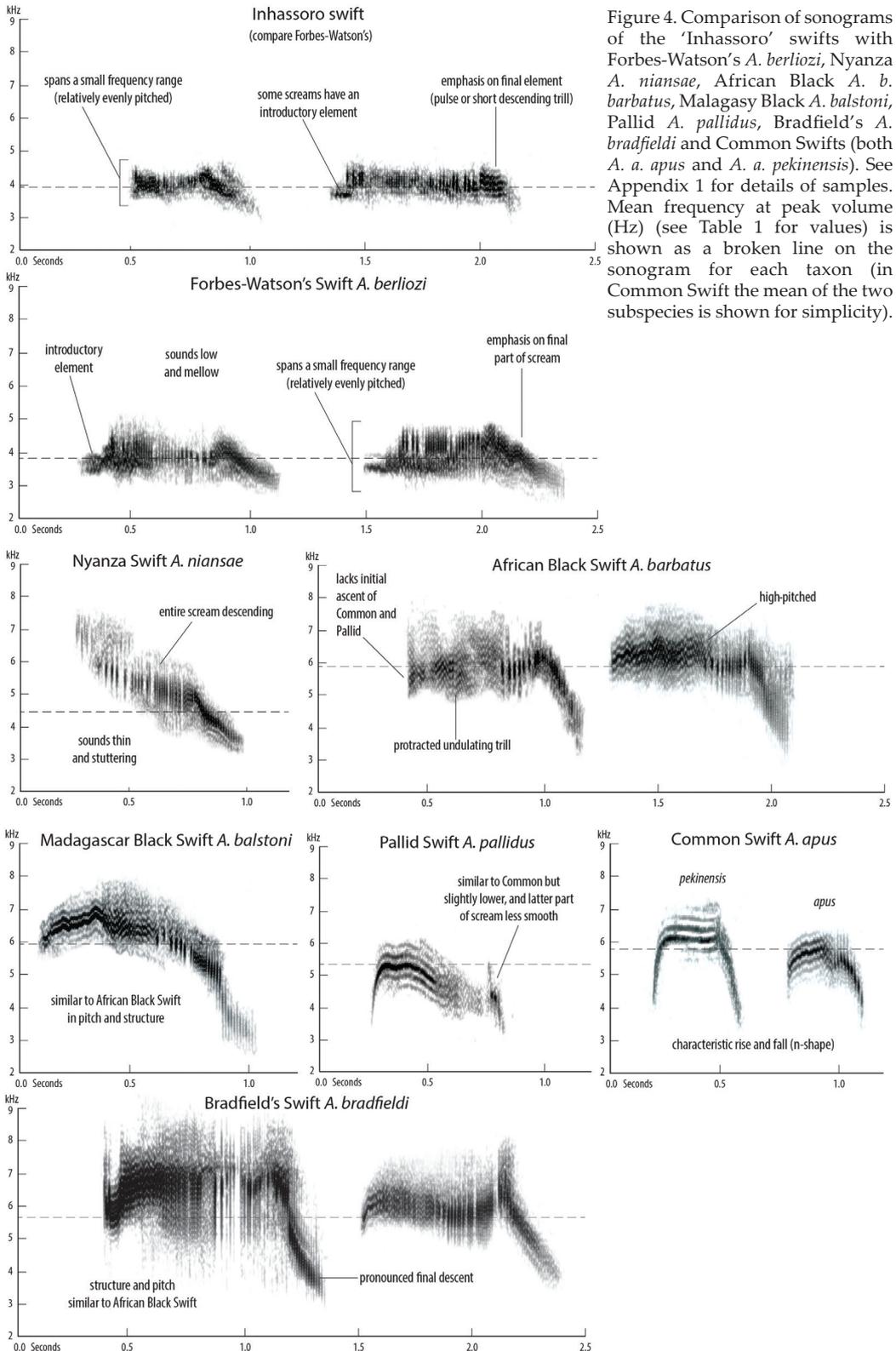


Figure 4. Comparison of sonograms of the 'Inhassoro' swifts with Forbes-Watson's *A. berliozi*, Nyanza *A. niansae*, African Black *A. b. barbatus*, Malagasy Black *A. balstoni*, Pallid *A. pallidus*, Bradfield's *A. bradfieldi* and Common Swifts (both *A. a. apus* and *A. a. pekinensis*). See Appendix 1 for details of samples. Mean frequency at peak volume (Hz) (see Table 1 for values) is shown as a broken line on the sonogram for each taxon (in Common Swift the mean of the two subspecies is shown for simplicity).



will be limited to those areas that can be reached during daylight from coastal roosts. It is possible that feeding over areas such as the Save Woodlands and use of offshore island roost sites in the Bazaruto archipelago, or on the cliffs north of Inhassoro, provides suitable non-breeding season habitat for *A. berliozi*. Such requirements may be met only at a limited number of localities in the coastal region.

The records of non-breeding *A. berliozi* reported here all involved monospecific flocks. It may be that the species occurs only or mainly in single-species groups, and is more likely to be identified under such circumstances, whereas if part of multi-species flocks they are more likely to go unnoticed especially if not vocalising. However, the observations reported here, although few, support the hypothesis that the species may have different habits and requirements to other swifts and so behaves independently, at least at certain times.

The timing of the 2017 records from Mozambique and Tanzania abut or overlap the reported breeding dates in Somalia and on Socotra. However, the precise timing of the species' nesting season is not well known; the population in Oman appears not to arrive at the breeding sites until early May (<https://ebird.org/species/fowswi1/OM>) and on Socotra they arrive in February but are not reported breeding until mid-May (Porter & Suleiman 2013). As Common Swifts are known to migrate rapidly, covering up to 300 km/day (Åkesson *et al.* 2012), assuming equivalent speeds for Forbes-Watson's Swift, it is possible that from Inhassoro they could reach the breeding areas in *c.*10 days.

Identification and temporal occurrence in southern Africa

The difficulty of identifying Forbes-Watson's Swift, in particular its separation from Common Swift, limits understanding of its occurrence in southern Africa. We review what is known of the seasonality of its occurrence in the East and southern Africa regions as well as that of, the most likely confusion species, Common Swift, and discuss how these species can be separated in the field.

Seasonality.—Forbes-Watson's Swift is absent from Socotra in December–February (Porter & Suleiman 2013) and there are very few records from Oman between January and late April (Grieve & Kirwan 2012, Eriksen & Victor 2013; <https://ebird.org/species/fowswi1/OM>). Records of migrants from Kenya are sparse and range from early November to early April, with a small peak in mid November (Brooke 1969; <https://ebird.org/species/fowswi1/KE>; R. Nussbaumer *in litt.* 2020). Thus, the broadest date range when migrants may be present on the east coast of southern Africa is likely to be November to April.

Common Swifts arrive in southern Africa in late October–November and depart between January and early March, with *pekinensis* present in the south-west and nominate *apus* in the north-east of the region (Hockey *et al.* 2005). However, these conclusions were based on limited data, and given the difficulty of subspecific identification and paucity of reliable observations over much of south-central Africa, this simple interpretation may be inaccurate.

Recent studies have investigated the migrations of Common Swifts. The results are mostly still unpublished but initial findings have shown that *A. a. apus* tagged in Western Europe travelled to East Africa, arriving in early December and departing in late January. Most of these remained in Kenya and Tanzania where they fed over forested areas, although many individuals reached northern Mozambique (Appleton 2012, Wellbrock *et al.* 2017) and one as far south as Beira before returning north-west to the Congo Basin (Klaassen *et al.* 2014). Individuals were found to return annually to specific localities (Wellbrock *et al.* 2017). In contrast, *A. a. pekinensis* tagged in Beijing, China, migrated via Central Africa to overwinter in south-west Africa in October where they stayed until mid-January. On their

return journey they passed through eastern South Africa and Mozambique, where present between mid to late January and February, and then moved to the Congo Basin by early March (Kearsley 2016, 2019). Nominat *apus* might therefore be expected to occur on the littoral of central and northern Mozambique from perhaps late November until early March, especially north of Beira, and *pekinensis* from mid January to late February. However, all of these tagged birds were adults, and juveniles may have a different pattern of occurrence (Common Swifts are thought to return to the breeding grounds in their second year, possibly arriving later than adults: Jukema *et al.* 2015). Furthermore, tagged individuals of the two subspecies were from the longitudinal extremes of the breeding range, and may not cover the full range of migration strategies.

Forbes-Watson's Swift may overwinter in the same areas as Common Swifts in East Africa and venture south at the same time as *A. a. apus* in December–January, and co-occur with *pekinensis* in February. Thus, flocks of swifts in the region merit particular attention in March–April when most Common Swifts should have departed. Previous records of Forbes-Watson's Swifts may have been overlooked in Mozambique, for there are reports of Common Swifts much later in the season than might be expected (Parker 2005) and the specimens collected in March by Pinto (1959; Coleção de Aves do Museu da História Natural de Maputo, CPMM.AVE.1958.15–16) warrant re-examination.

Moult.—Moult is a useful means to age birds in the field and can be critical in the identification of some swifts (Larsson 2018), but it is unclear to what extent it is relevant to the separation of Common and Forbes-Watson's Swifts. However, a summary of known data is presented here as an aid to interpreting swift plumages in the region.

Migrant *Apus* mostly time their moult cycles to coincide with arrival in the non-breeding quarters, either by starting primary moult on the breeding grounds and then suspending the process until they reach the non-breeding areas, or by delaying moult until after arrival (Cramp 1985, Ginn & Melville 1985, Chantler & Driessens 2000).

Adult Common Swifts commence a lengthy moult in August, taking 5–6 months to regrow their primaries and secondaries, completing the process in late December and January. Many Common Swifts—and possibly Forbes-Watson's Swifts—return north with an old outermost primary (p10), which is not replaced until the following winter (De Roo 1966, Brooke 1969, Ginn & Melville 1985). Such heavily worn outer primaries may result in a blunter than usual wing shape. First-winter Common Swifts moult their body feathers, lesser and median coverts, and (usually) rectrices and secondaries on the non-breeding grounds, so their primaries and greater coverts look increasingly worn and therefore slightly browner and more contrasting than adults as the non-breeding season progresses. The contrast in age is more evident once adults have replaced several inner primaries, which then contrast in tone with the outer wing (De Roo 1966, Cramp 1985).

The moult cycle of Forbes-Watson's Swift is largely unknown but photographs from Oman in November show a bird in worn plumage except three innermost primaries and median underwing-coverts (P. Kennerley *in litt.* 2019; <https://ebird.org/checklist/S49665050>), whilst December specimens from Kenya were in active primary moult but those collected in January were in completely fresh plumage (Brooke 1969). Photographs from Tanzania in March/April show birds in fresh plumage and none was in active wing moult (J. Haureljuk *in litt.* 2017; <https://www.facebook.com/groups/241108492733888/permalink/764278667083532/>; J. Wolstencroft *in litt.* 2017; <https://www.facebook.com/groups/241108492733888/permalink/780996082078457/>). This suggests its moult cycle is probably similar to Common Swift, at least in adults; there is no information for immatures.

Field characters

The generally fleeting nature of sightings of swifts, often against a bright sky, make accurate assessments of colour difficult, as apparent shades can change quickly depending on the light. For detailed reviews of judging the colour of swifts in the field see Ahmed & Adriaens (2010) and Roberts & Campbell (2015). They emphasised plumage and structural characters that are less dependent on light conditions, such as general shape, head pattern, patterns of scaling on the underparts, and contrasting features on both wing surfaces.

It is hoped that the following, which focuses on the appearance in the field of the three taxa concerned, with key features shown in Fig. 5, will help with identification. We stress, however, the value of good-quality photographs and indeed of sound-recordings in this process.

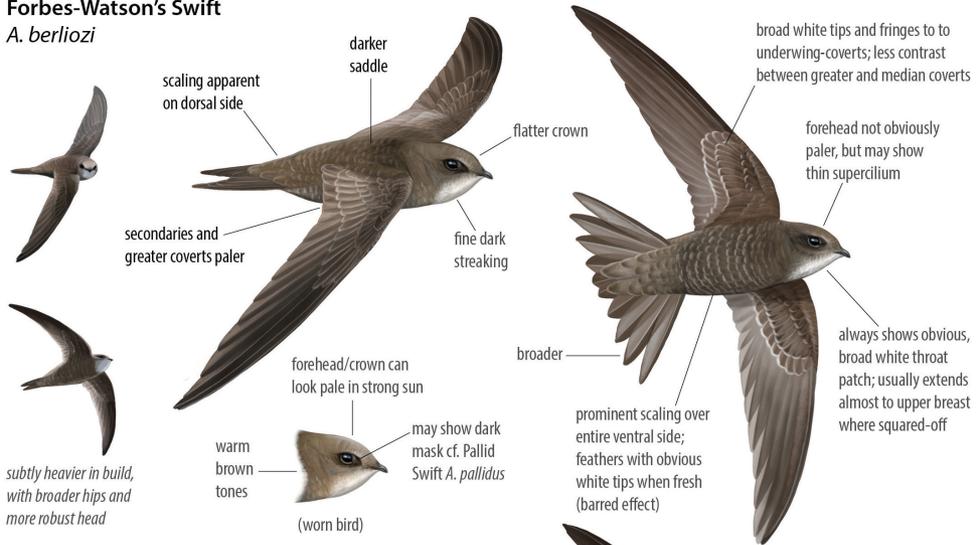
Common Swift.—Both subspecies are generally sooty brown in tone, bleaching with wear, but *pekinensis* is typically (but not always) paler (Larsson 2018). Features that separate *pekinensis* from nominate are the more extensive pale throat patch, often paler head (especially forehead) and variable but sometimes prominent ‘saddle’ effect, due to the mantle and scapulars appearing darker relative to the inner wing and greater primary-coverts, but never as contrasting as in African Black Swift. Most *pekinensis* exhibit clear scaling on the underparts, most pronounced on the vent and undertail-coverts, the latter sometimes appearing contrastingly pale when fresh (from early January), and aligned diagonally in neat rows on the breast and belly. Faint scaling is visible on the rump in certain lights (Fig. 5; see fresh adult *pekinensis* in February and March, Plates 5–6 in Roberts & Campbell 2015). Common Swift usually shows no scaling on the upper- or underparts, appearing uniformly dark, but can simultaneously possess both darker recently moulted and paler old bleached body feathers, thereby seeming to be irregularly mottled (but not scaled). Our own observations suggest that *pekinensis* appears slimmer and more cigar-shaped than *apus*, the wings held slightly straighter and less scythe-shaped than in *apus* (GA pers. obs.).

A. a. pekinensis vs. Forbes-Watson’s Swift.—The *pekinensis* subspecies is likely to be the main confusion subspecies with Forbes-Watson’s Swift as it is the paler form, but the features described below also apply to separation from *A. a. apus*.

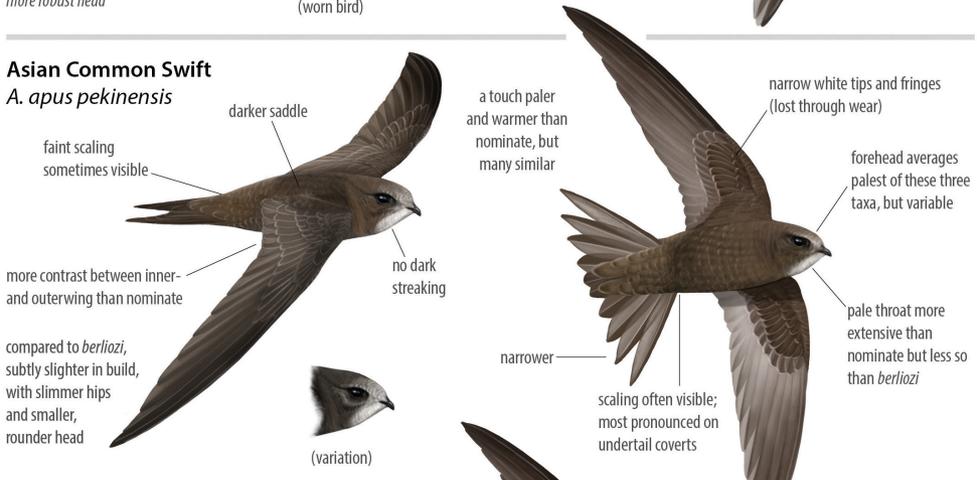
Grieve & Kirwan (2012) thoroughly reviewed this identification challenge and found the throat patch to be the most useful character. Although they found overlap in the range of measurements, the differences were statistically significant (Fig. 6). They described the throat patch in Forbes-Watson’s Swift as ‘Broad and deep, whitish or pale ... [which] extends almost to upper breast though slightly less extensive on some. Centres of throat feathers possess dark, fine, vertical streaking (which wears off) and an overall whiter shade of pale, as opposed to off-white in Common Swift. This feature was also noted in the field by Dowsett-Lemaire & Dowsett (2014) who described Forbes-Watson’s Swift as ‘showing [a] big white chin’. However, it can vary with the light and the throat patch may be extensive but have ill-defined boundaries (see Fig. 2) with the fine streaking possibly reducing the definition. In *pekinensis* Common Swift, ‘Narrower and less deep whitish or pale throat patch, extending to just over 50% down throat or even less extensive on some birds. Throat lacks fine streaking’ (Grieve & Kirwan 2012).

There is also a difference in the width of the outermost (or fourth) tail feather. This was found to be consistent and statistically significant but slight, being c.10% broader in Forbes-Watson’s Swift (Grieve & Kirwan 2012). This feature may be visible in good-quality digital photographs.

Forbes-Watson's Swift
A. berliozii



Asian Common Swift
A. apus pekinensis



Common Swift
A. apus apus

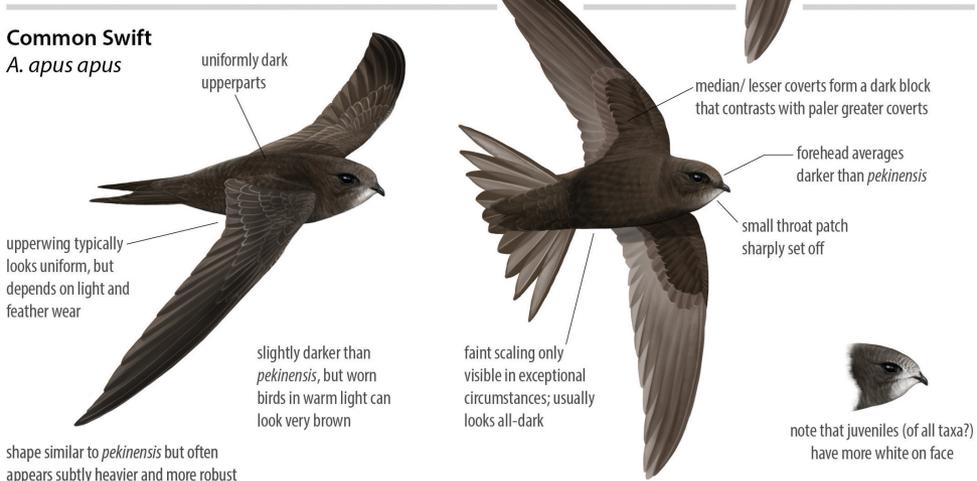


Figure 5. Identification characters of Forbes-Watson's *Apus berliozii*, Asian Common Swift *A. a. pekinensis* and Common Swift *A. a. apus* (Faansie Peacock)

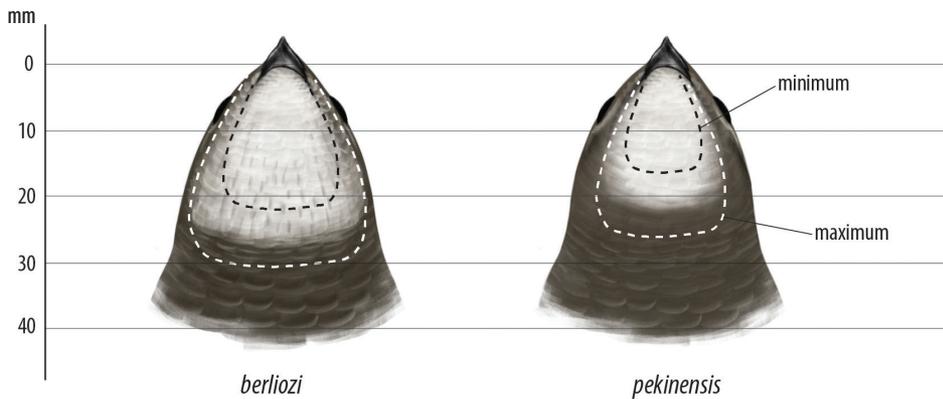


Figure 6. Comparison of throat patches of Forbes-Watson's Swift *A. berliozii* (left) and Common Swift *A. a. peginensis* (right). Dimensions from Grieve & Kirwan (2012); in *A. b. bensoni* depth (from base of bill): mean 25.5 mm (range 21.6–29.8 mm), width (at widest point): 22 mm (range 15.7–25.2 mm); in *pekinensis* depth: 22 mm (range 15.6–26.5 mm), width: 16 mm (range 12.1–20.7 mm). Minimum dimension indicates the lower ranges, maximum, upper ranges, and the illustrated throat patch the mean dimensions. Note slightly whiter ground tone and fine throat streaks in Forbes-Watson's Swift (Faansie Peacock)

Furthermore, Zimmerman *et al.* (1996) stated that the two species are diagnosable by bill length, citing measurements apparently repeated from Brooke (1969) for the 'chord of tomium' (presumably the length of the cutting edge of the bill, or the linear distance from bill tip to the base of the gape), which is 17.5–20.0 mm in *A. berliozii* and 16.0–19.0 mm in *A. apus* (subspecies and genders pooled). This is not therefore a clear-cut feature as suggested by Zimmerman *et al.* (1996), and is unlikely to be helpful in the field.

Other possible plumage characters to distinguish Forbes-Watson's Swift include a blackish mask, the so-called 'alien eye' characteristic of Pallid Swift (Larsson 2018), which is not usually evident in Common Swift (but is apparent in some images of *pekinensis* in China; T. Townshend *in litt.* 2020). In addition, photographs suggest that, like Pallid Swift, *A. berliozii* does not show a strong contrast between the darker lesser and median underwing-coverts and slightly paler, more silvery greater underwing-coverts, and therefore lacks the dark underwing-covert block found in both Common Swift subspecies (Larsson 2018).

Summary of identification features and likely occurrence

The key features that separate Forbes-Watson's Swift from Common Swift (Figs. 5–6) are listed below.

1. Larger and broader white throat patch, usually well defined, often extending almost to the upper breast and is squared-off, appearing triangular from below, with faint dark streaking.
2. Slightly heavier build with wider hips and a broader, flatter head. Build may be less useful in relation to *A. a. apus*, which can be more bulky than *pekinensis*.
3. Greater uniformity between the greater and median underwing-coverts.
4. Extensive and obvious scaling on the underparts—bolder than *pekinensis* when both are compared in fresh plumage (most evident later in the non-breeding season)—and on the dorsal side where the contrast between species is clearer, if more difficult to observe in the field (usually only very faint in *pekinensis* and not visible in nominate).

5. Most likely in monospecific flocks on the east coast of southern Africa during early December–late March, and probably especially obvious in March when most Common Swifts have departed. Likely over forested areas near the coast.

The use of voice and vocal analysis

Whilst many birding apps now provide samples of vocalisations, most field guides do not offer guidelines for identifying birds by sound that draw on the recent advances in digital recording and sonogram analysis. It is fortuitous that Forbes-Watson's Swift seems to be quite vocal and, given the obvious differences in voice from the most common large dark swifts in the region, these calls can significantly assist in the identification of this group. We hope that this paper will stimulate increased sound-recording in the field and sharing of information using online databases, as this has greatly facilitated the identification of the birds in this study, and our understanding of one of the least well-known members of this mysterious group.

Acknowledgements

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Appendix 1: sound-recordings used for comparative analysis of East and southern African large *Apus* swifts. XC denotes the Xeno-canto reference number (<https://www.xeno-canto.org>) and ML reference in the Macaulay Library of Wildlife Sounds (<https://www.macaulaylibrary.org/>).

Species	Recording	No. of screams analysed	Location	Recordist
‘Inhassoro swift’	XC543748	33	Inhassoro, Mozambique	E. Marais
Forbes-Watson’s Swift <i>A. berliozii</i> (subspecies unknown, but both presumably <i>bensoni</i>)	Forbes-Watson’s Swift; <i>eGuide to birds of East Africa</i> , mydigitalearth.com	5	Dar es Salaam, Tanzania	B. Finch
	XC488728	24	Khawr Rawri, Oman	J. Lidster
Forbes-Watson’s Swift <i>A. b. bensoni</i>	XC321549	4	Wadi Darbat, Dhofar, Oman	G. Kirwan
Nyanza Swift <i>A. niansae</i>	XC209974	17	Gemessa Gedel, Ethiopia	A. Spencer
African Black Swift <i>A. barbatus</i>	XC368196	33	Graskop, South Africa	O. Campbell
	XC279844	8	Memel, South Africa	P. Boesman
	XC413388	3	Mossel Bay, South Africa	L. Rudman
Malagasy Black Swift <i>A. balstoni</i>	Mad_Black_Swift-01 BF	7	Madagascar	B. Finch
	XC162908	1	Ranomafana National Park, Madagascar	M. Nelson
	ML93639	24	Toliara, Madagascar	L. Macaulay
Pallid Swift <i>A. pallidus</i>	XC493531	10	Migjorn, Spain	J. Fischer
	XC274847	11	Sevilla, Spain	‘Carlos W.’
	XC33948	8	Turin, Italy	G. Boano
	XC499549	3	Lagos, Portugal	J. Leitão
Common Swift <i>A. a. apus</i>	XC492936	15	Cheboksary, Russian Federation	A. Lastukhin
	XC480871	3	Tychy, Poland	I. Oleksik
	XC482476	6	Extremadura, Spain	C. Fernández
	XC486189	2	Faro, Portugal	N. Conceição
	XC487370	1	Gelderland, The Netherlands	J. van Bruggen
Common Swift <i>A. a. pekinensis</i>	XC451146	9	Tashkent, Uzbekistan	Ding Li Yong
	XC185710	7	Tashkent, Uzbekistan	A. Lastukhin
	XC185708	7	Tashkent, Uzbekistan	A. Lastukhin
Bradfield’s Swift <i>A. bradfieldi</i>	XC65278	10	Ugab River, Namibia	F. Bruneliere
	XC346607	6	Spitzkoppe, Namibia	P. Boesman
	XC337014	10	Windhoek, Namibia	C. Robertson
	Faansie Peacock Sound Library	9	Omaruru, Namibia	F. Peacock

Appendix 2: detailed descriptions of calls shown in sonograms (Fig. 4).

Forbes-Watson's Swift.—The scream is overall lower pitched and less harsh, with the least rise and fall of pitch of any of the species reviewed (Fig. 4). Modulation is obvious throughout the call and attenuated at the end. Max. volume occurs two-thirds of the way through the scream, before a slight final decline in pitch. The 'Inhassoro swifts' were inseparable from Forbes-Watson's Swift in the sonograms and aurally.

Nyanza Swift.—Lower pitched than all but Forbes-Watson's Swift, comprising a single steady 'down-slur', not showing the rise and fall in pitch of most of the other species. Max. volume was three-quarters through the call. Modulated throughout but attenuated towards the end of the scream.

African Black Swift.—Described as a high-pitched *shree*, higher pitched than Common Swift (Hockey *et al.* 2005); heard at breeding colonies in the region. Our analysis found screams to be similar in pitch to Common Swift, but longer (up to 800 milliseconds), more drawn-out and without the prominent 'foreleg' of the latter species. The 'hindleg' is very strong and the scream often ends at a much lower frequency than it commences. Max. volume is about two-thirds into the scream, as the long down-slur starts. Modulation is more obvious than in Common and Pallid Swifts, often with a stronger up-slurred trill just before the end. The stronger modulation makes the scream sound 'mellower' to the human ear. This species also utters much shorter screams, which consist of a fast spike and a fast 'hindleg'.

Madagascar Black Swift.—Described as a high-pitched, screaming trill, *zzzzziieewwww*, which falls at the end and lasts 1–2 seconds, often given in chorus, reportedly slightly lower in frequency than *A. apus* (del Hoyo *et al.* 2020; B. Finch *in litt.* 2020). Analysis showed this species' scream to be similar in pitch and structure to African Black Swift, although some of the shorter screams consist primarily of a strong downward slur with a pulse in volume at the start of the scream.

Bradfield's Swift.—Voice is little known but described as a harsh scream (Maclean 1993). The screams of this species are longer (0.8–0.9 seconds) than Common Swift, but possess a similar structure to African Black Swift, with a very small 'foreleg' followed by a flat section. The 'hindleg' is a strong down-slur, even more pronounced than in African Black Swift. Modulation is also pronounced throughout the scream, but more prominent on the 'hindleg'.

Pallid Swift.—The most distinctive call is described as a grating disyllabic *shree-er*, not as shrill as Common Swift (Chantler & Driessens 2000). Screams are slightly longer in duration and lower pitched, with a similar overall structure to Common Swift. The 'foreleg' is less pronounced and the 'hindleg' longer, with a slower decline and a pulse of energy towards the end. The scream sounds 'mellower' than Common Swift, with modulation obvious towards the end of the scream.

Common Swift (*A. a. apus*).—Described as a high-pitched *shree* (Cramp 1985) but both subspecies of Common Swift are largely silent in their African wintering grounds (Hockey *et al.* 2005). The scream is generally fairly short in duration, averaging 343 milliseconds (Malacarne *et al.* 1989) and sounds disyllabic. The call starts with a rapid spike in frequency, and the main part of the scream is flat in pitch or ascends slightly towards the crescendo, before the 'hindleg'. Modulation is most discernible at the max. volume just before the 'hindleg', as well as during the down-slur.

Common Swift (*A. a. pekinensis*).—Similar to nominate but, based on the samples analysed, this taxon sometimes produces screams without a 'hindleg' to the call.

Birds from Sumatra given by Sir Stamford Raffles to Lord Stanley: links to names, types and drawings

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<http://zoobank.org/urn:lsid:zoobank.org:pub:E499C581-87BC-4D3B-BA72-0859B169F618>

SUMMARY.—After escaping from the burning East Indiaman *Fame*, but losing all of his possessions, Sir Stamford Raffles, the Lieutenant-Governor of Bencoolen, hastily re-collected as many natural history specimens and drawings as he could before leaving Sumatra in April 1824. On his return to England Raffles was elected a Fellow of the Linnean Society and, with Lord Edward Smith Stanley and others, founded the Zoological Society of London. In 1825 Raffles gave 21 Sumatran birds to Stanley. Upon his death in 1851, Stanley (then 13th Earl of Derby) bequeathed his collection to the people of Liverpool, founding what is now the World Museum, National Museums Liverpool. Here I record these birds, 11 of which are still extant in the collection, including links to: the names and types from Raffles' (1822) 'descriptive catalogue' of a zoological collection from Sumatra; Raffles' post-*Fame* zoological drawings; and Nicholas Aylward Vigors' catalogue of Raffles' specimens in the Zoological Society Museum, published in Lady Sophia Raffles' memoir in 1830.

Sir Thomas Stamford Bingley Raffles, the name and face of British colonial history in South-East Asia, has been described as an 'icon of imperial mythology' (Barnard 2019). Raffles 'founded' modern Singapore in 1819 (Huang 2018) while working as Lieutenant-Governor of Bencoolen (= Bengkulu, Sumatra, Indonesia) (1818–24) for the East India Company. This followed ten years of postings in Penang (= Pinang, Malaysia), Malacca (= Melaka, Malaysia) and Java (= Jawa, Indonesia). Like many colonial officers, Raffles was an enthusiastic collector of natural history specimens and kept menageries at his various residences. However, his life in South-East Asia was also punctuated with personal tragedy. Raffles lost his first wife, four of his children and several close friends, including his natural history collectors, to sickness. These problems culminated in the sinking of the *Fame* in 1824, the East Indiaman which was to have transported himself, Lady Sophia Raffles and his collections to England, following his resignation from the East India Company (Glendinning 2012).

As far as is known, Raffles did not collect many birds, instead he mostly commissioned drawings of the birds he encountered during his postings (Sharpe 1906). Arguably the most important zoological work attributed to Raffles was the 'Descriptive catalogue of a zoological collection made in the island of Sumatra and its vicinity', which was read in two parts under his name at the Linnean Society (Raffles 1821, 1822). However, the manuscript was almost exclusively the work of Dr William Jack (Raffles' physician and naturalist, who died in 1822), based on collections made by Pierre-Médard Diard and Alfred Duvaucel (French zoologists in the service of Raffles; Weiler 2019) and Dr Joseph Arnold (also Raffles' physician and naturalist, who had died in 1818) (Bastin 1990). The paper was hastily assembled to avoid being scooped by the French zoologists (Raffles 1821) and was further edited in London prior to publication, with names from the preceding paper on Javan birds by Horsfield (1821) and new names nominally attributed to Raffles being added. The

specimens, which included the types of the new names, and associated drawings had been sent to London in 1820 and deposited in the East India Company Museum (Noltie 2009). After dividing triplicates between them, and concealing other valuable specimens, some birds collected by Diard and Duvaucel while in Raffles' service were sent from Sumatra to the Paris museum (Weiler 2019, MNHN & Chagnoux 2020). It is unclear whether specimens retained by Diard and Duvaucel would have featured in Raffles' catalogue, but it seems likely that the manuscript would have been prepared before the collection was divided. Duvaucel, without Diard, made further collections on Sumatra after they had both left Raffles' service in 1820 (Weiler 2019, MNHN & Chagnoux 2020).

Raffles continued to assemble collections in Singapore (Noltie 2009) and Sumatra, and commissioned more than 2,000 drawings, according to a letter by Raffles quoted by Sophia Raffles (1830). These were all lost with the sinking of the *Fame* on 2 February 1824. During the two months prior to securing fresh passage on the *Mariner*, Raffles partially re-built his collection and commissioned new drawings, including 44 of birds by J. Briois, which are now held in the British Library (in the Natural History Drawings [NHD] collection; Noltie 2009). Raffles knew the social capital of exotic curiosities; his collections and account of Java (Raffles 1817) had earned him a knighthood. On his return to England, Raffles was elected a Fellow of the Linnean Society and set about lobbying for the establishment of the Zoological Society of London (ZSL).

Lord Edward Smith Stanley, who became 13th Earl of Derby in 1834, was an archetype of the imperial elite. He travelled little himself, but with access to incredible wealth as heir to the Knowsley estate in north-west England, and a network of contacts and agents worldwide, assembled a menagerie and private museum at Knowsley Hall comprising exotic animals from across the empire and beyond (see Fisher & Jackson 2002). Stanley was the Member of Parliament for Preston and Lancashire from 1796, before joining the House of Lords in 1834 (Crosby 2002), and a member of the Linnean Society's Zoological Club.

Although Raffles and Stanley do not appear to have been close—no written correspondence between them is known—Raffles considered Stanley someone of 'weight', and both were founding members (subscribers) of the ZSL (Bastin 1970). During his campaign to be the Zoological Society's founding president, Raffles gave 21 of his Sumatran birds to Stanley. Raffles was elected the first president of ZSL in February 1826, a position Stanley himself would hold from 1831 until his death.

Stanley listed the birds 'given to me by Sir Stamford Raffles' in his unpublished manuscript entitled the 'General index of the birds in my collection at Knowsley' in 1825 (Fig. 1). Raffles died on 5 July 1826 and his remaining zoological material was donated to the ZSL Museum by Sophia Raffles in April 1827 (Wheeler 1997, Noltie 2009). Sophia Raffles subsequently published a memoir (Raffles 1830) to which a catalogue of Raffles' collections was appended—specimens in the East India Company Museum listed by Thomas Horsfield, and those in the ZSL Museum by the society's secretary, Nicholas Aylward Vigors (Tweeddale 1877, Wheeler 1997). Stanley added notes, which clearly originate from his reading of this appendix, to his own manuscript catalogue (Fig. 1).

ZSL began to dispose of its collection in the early 1850s. The British Museum had its pick of specimens and, in addition to the type material, selected 383 mounted birds and 100 relaxed skins (Wheeler 1997) which became part of the national collection in 1855 (Sharpe 1906). The remaining ZSL collection, which may have included some of Raffles' birds, was dispersed across provincial museums, dealers and private collectors (Wheeler 1997). Unfortunately, due to lack of adequate documentation most of these specimens are now effectively 'lost'. Further Raffles material arrived at the British Museum following the closure of the East India Company Museum in 1880. Therefore, other than a few notable



Figure 2. Specimens from Sumatra given by Sir Stamford Raffles to Lord Stanley in 1825 and extant in the collection of World Museum, National Museums Liverpool. From left: Thick-billed Green Pigeon *Treron curvirostra curvirostra* (NML D3636); Pink-necked Green Pigeon *Treron vernans* (NML D3641a); Crested Partridge *Rollulus rouloul* (NML D512g); Long-billed Partridge *Rhizothera longirostris* (female NML D2212b, male NML D2212); Crestless Fireback *Lophura erythrothalma* (NML D1583); Lesser Whistling Duck *Dendrocygna javanica* (NML D843b); Ferruginous Partridge *Caloperdix ocellatus ocellatus* (male NML D2179a, female NML D2179); Oriental Pratincole *Glareola maldivarum* (NML D3192b); Buff-rumped Woodpecker *Meiglyptes tristis grammithorax* (NML D3791) (© National Museums Liverpool [World Museum Liverpool])

2140. Red-crowned Barbet *Psilopogon rafflesii* (Lesson, 1839)

Listed as *Bucco versicolor* by Raffles (1822), a name also used for an unsexed specimen by Stanley in 1825. However, this name was already in use for a South American species, Versicoloured Barbet (now *Eubucco versicolor* Statius Muller, 1776). Stanley later annotated his manuscript with '*Barbu bigarrè* Pl. Col. 309', referring to Vigors' catalogue (Raffles 1830). Subsequently, while cataloguing the collection of Abeillé, Lesson (1839) named the Sumatran species eponymously as '*Bucco Rafflesii*'. Lack of a traceable specimen in NML, or a number in Moore's stock books, suggests it was not part of the 1851 bequest.

2141. Scarlet Minivet *Pericrocotus flammeus xanthogaster* (Raffles, 1822)

The species was listed twice by Raffles (1822), the male as '*Turdus flammeus - Muscivora flammea*, Gmel. [sic]' and the female (described as a male) under a new name, *Lanius xanthogaster*. In 1825, Stanley used *Muscivora flammea*, as in Vigors' catalogue (Raffles 1830), and 'Flammeous flycatcher' to list a male specimen. A male depicted among the post-Fame drawings (NHD 47.31; Noltie 2009; Fig. 3) could therefore represent Stanley's specimen. The population on Sumatra is recognised subspecifically under Raffles' name '*xanthogaster*'. Lack of a traceable specimen in NML, or a number in Moore's stock books, suggests it was not part of the 1851 bequest.

2142. White-rumped Shama *Kittacincla malabaricus tricolor* (Vieillot, 1818)

The species was listed as '*Lanius macrourus - Turdus macrourus*, Gmel. [sic]' by Raffles (1822). In 1825, Stanley listed a male specimen as '*Turdus macrourus*' and 'Longtailed thrush', although '*Lanius macrourus*' was used in Vigors' catalogue (Raffles 1830). A male depicted among the post-Fame drawings (NHD 47.22; Noltie 2009; Fig. 4) could represent Stanley's



Figure 3. Scarlet Minivet *Pericrocotus flammeus xanthogaster* (Raffles, 1822) by J. Briois in Bengkulu, 1824 (© The British Library Board; NHD 47.31)

Figure 4. White-rumped Shama *Kittacincla malabaricus tricolor* (Vieillot, 1818) by J. Briois in Bengkulu, 1824 (© The British Library Board; NHD 47.22)



specimen. Lack of a traceable specimen in NML, or a number in Moore's stock books, suggests it was not part of the 1851 bequest.

2143 [3791]. Buff-rumped Woodpecker *Meiglyptes tristis grammithorax* (Malherbe, 1862)
Listed by Raffles (1822) as *Picus tristis*, a name first used by Horsfield in 1821, and Stanley treated a male specimen under this name in 1825. Stanley annotated the entry with the synonyms '*P. strickup* (*P. poecilophos* = *pæcilophos*) Pl. Col 197' from Vigers' catalogue (Raffles 1830). The vernacular name used by Stanley is illegible (but is perhaps 'Striated crowned woodpecker'). The subspecies occurring on Sumatra is *grammithorax*, which was not described until 1862. The skin of the relaxed mount is at NML (accession number D3791).

2144 [512g]. Crested Partridge *Rollulus rouloul* (Scopoli, 1786)

Listed by Raffles (1822) as '*Tetrao viridis*, Gmel. [sic]'. The species was evidently a major source of taxonomic confusion (see Vigers 1829), with the male described as *Columba cristata* Pallas, 1764, and the female as *Perdix coronata* Latham, 1790. In 1825, Stanley matched the female specimen given to him by Raffles with a male he had obtained earlier from Melaka (no. 1693 in the 'General index') and listed the specimen under Temminck's (1815) genus as *Crytonyx coronatus* and the vernacular name 'Green Partridge'. The male specimen is still at NML (accession number D512c). The species is listed as *Crytonyx cristatus* Vigers in Vigers' catalogue (Raffles 1830). The skin of Raffles' relaxed mount is at NML (accession number D512g).

2145 [1583]. Crestless Fireback *Lophura erythrophthalma* (Raffles, 1822)

Described by Raffles (1822) under a new name, *Phasianus erythrophthalmus*, and Stanley listed a male specimen under this name in 1825. Vigers (Raffles 1830) transferred the species to *Gallus*. The skin of the relaxed mount is at NML (accession number D1583) and had been labelled with red tags as 'one of the types of the species'. However, the probable collection date of this specimen (1824) would make this impossible. There are two syntypes from the East India Company Museum at NHMUK, both also former mounts. Interestingly they both had been labelled (as *Acamus erythrophthalmus*) with the same accession number ([18]80.1.1.1810). Warren (1966) listed one adult male and one female syntype at NHMUK. However, the specimens are both male, one adult and one juvenile.

2146 [1582]. Malaysian Fireback *Lophura rufa* (Raffles, 1822)

Listed twice by Raffles (1822), the male as *Phasianus ignitus* Latham, the name Stanley used for a male specimen in 1825, and the female (described as a male) under a new name, *Phasianus rufus*. The taxon was listed solely as *Gallus ignitus* (presumably *sensu lato*) by Vigers (Raffles 1830). The population on Sumatra is recognised as a species by some taxonomies (del Hoyo & Collar 2014) under Raffles' name '*rufa*', distinct from *Lophura ignita* (*sensu stricto*). There are two depictions of the male among the post-Fame drawings (NHD 47.43 and NHD 47.44; Noltie 2009; Figs. 5–6), one, or both (if highly stylised), of which could represent Stanley's specimen. The existence of a number in Moore's stock books suggests the specimen was part of the bequest but has been lost post-1851.

2147. Hill Myna *Gracula religiosa* Linnaeus, 1758

The only *Gracula* listed by Raffles (1822) and by Vigers (Raffles 1830) was *G. religiosa* Linnaeus. In 1825, Stanley listed the unsexed specimen given to him by Raffles as 'Greater Mias *Gracula*' without a species epithet. Lack of a traceable specimen in NML, or a number in Moore's stock books, suggests it was not part of the 1851 bequest.

2148. Greater Racket-tailed Drongo *Dicrurus paradiseus* (Linnaeus, 1766)

Listed as *Lanius malabaricus* Latham with no notes by Raffles (1822) and Stanley used the same name for an unsexed specimen in 1825. Stanley later annotated his catalogue entry with '*Edolius retifer* of Temminck', following the synonyms listed in Vigers' catalogue



Figure 5. Malaysian Fireback *Lophura rufa* (Raffles, 1822) by J. Briois in Bengkulu, 1824 (© The British Library Board; NHD 47.43)



Figure 6. Malaysian Fireback *Lophura rufa* (Raffles, 1822) by J. Briois in Bengkulu, 1824 (© The British Library Board; NHD 47.44)

(Raffles 1830). Lack of a traceable specimen in NML, or a number in Moore's stock books, suggests it was not part of the 1851 bequest.

2149 [3192b]. Oriental Pratincole *Glareola maldivarum* Forster, 1795

In 1825, Stanley listed an unsexed specimen as '*Glareola Orientalis*' and 'Oriental Pratincola [sic]', but the species does not appear in Raffles' (1822) catalogue or seem to be in Vigors' catalogue (Raffles 1830). *Glareola orientalis* Leach was described and figured (Leach 1821) in the same volume of the Linnean Society transactions as Raffles' catalogue, based on a specimen in Paris brought from Java by M. Leschenault (Horsfield 1821). Stanley's *G. maldivarum* specimen is at NML (accession number D3192b). Oriental Pratincole is principally an uncommon migrant and winter visitor to Sumatra (van Marle & Voous 1988), but has bred in the north of the island (Eaton *et al.* 2016).

2150. Greater Coucal *Centropus sinensis bubutus* Horsfield, 1821

In 1825, Stanley listed an unsexed specimen simply as '*Polophilus*'. *Cuculus bubutus* (asterisked as *Centropus Bubutus* Horsfield) was listed by Raffles (1822), a name subsequently synonymised under '*Centropus Philippensis* Cuvier' by Horsfield and Vigors (Raffles 1830). This taxon seems to be the most likely to correspond with '*Polophilus*'. Lack of a traceable specimen in NML, or a number in Moore's stock books, suggests it was not part of the 1851 bequest, thereby precluding further determination.

2151. Bridled Tern *Onychoprion anaethetus* (Scopoli, 1786)

In 1825, Stanley listed an unsexed specimen as 'Panyan Tern' and '*Sterna Panay* [sic]'. Listed as '*Sterna panayensis?* Gmel. [sic]' by Raffles (1822), but the description clearly involves Bridled Tern (= *Onychoprion anaethetus*) which is resident in western Sumatra (van Marle & Voous 1988). The species was listed as '*Sterna Panayensis* Gmel. [sic]' by Vigors (Raffles 1830). Lack of a traceable specimen in NML, or a number in Moore's stock books, suggests it was not part of the 1851 bequest.

2152 [3641a]. Pink-necked Green Pigeon *Treron vernans* (Linnaeus, 1771)

In 1825, Stanley listed a male specimen as *Columba vernans* and 'Parrot Pigeon'. Treated as *Columba vernans* Linnaeus by Raffles (1822) and as *Vinago vernans* by Vigors (Raffles 1830). The skin of the relaxed mount is at NML (accession number D3641a).

2153 [3636]. Thick-billed Green Pigeon *Treron curvirostra curvirostra* (J. F. Gmelin, 1789)

In 1825, Stanley listed an unsexed specimen as *Columba curvirostra*. The species was listed as '*Columba curvirostra*, Gmel. [sic]' by Raffles (1822) and under *Vinago* by Vigors (Raffles 1830). Curiously, the extant skin of the relaxed mount accessioned in NML as D3636 had been incorrectly labelled with a red tag as 'Type of *Columba curvirostra* Raffles'. However, the name '*curvirostra*' was used by Raffles (1822) for a supposedly new species of partridge (see below).

2154 [2179a] and 2155 [2179]. Ferruginous Partridge *Caloperdix oculus ocellatus* (Raffles, 1822)

In 1825, Stanley listed single male (2154) and female (2155) specimens as 'Malacca Partridge' and '*Perdix Malaccensis*'. However, the species had appeared under a new name, *Tetrao ocellatus*, in Raffles' (1822) catalogue and later as *Crytonyx ocellatus* Raffles in Vigors' catalogue (Raffles 1830). The skins of the relaxed mounts are at NML, accession numbers D2179a (the male) and D2179 (female). The male had been labelled with a red tag as 'type of *Tetrao ocellatus* Raffles'. However, the probable collection date of these specimens (1824) makes this impossible. The two syntypes at NHMUK, 1880.1.1.4543 and 1880.1.1.4510,

have '*PERDIX OCULEA* Temm. Horsfield' written on Horsfield's labels. 'BM(NH)' labels had been added to the syntypes with the annotation '*Caloperdix sumatrana* Loc. Java Pres. by India Museum', which matches the NHMUK register entry for 1880.1.1.4543, showing the locality as Java (the other syntype lacks a locality in the register). However, according to Warren (1966), the types 'must have come from Sumatra as according to *MSS List of Birds received at India House* no examples of this bird were secured from Java whereas three *Perdix* came from Sumatra in the Raffles collection'. Likewise, the species is only listed from Sumatra (and not Java) in Sophia Raffles' (1830) appendix. To add further confusion, the Sumatran population was formerly known as '*sumatranus*' (Ogilvie-Grant 1893), with the type also held at NHMUK, but Raffles' name '*ocellatus*' has priority.

2156 [2212] and 2157 [2212b]. Long-billed Partridge *Rhizothera longirostris* (Temminck, 1815)

In 1825, Stanley listed a male (2156) and female (2157) of 'Curve-billed partridge' under the combination of the new epithet introduced by Raffles (1822)—*Tetrao curvirostris*—with the genus *Perdix* (i.e. *Perdix curvirostra*), as in Vigers' catalogue (Raffles 1830). The skins of the relaxed mounts are at NML, accession numbers D2212 (the male) and D2212b (female), and had been labelled with red tags as 'type of *Tetrao curvirostra* Raffles'. However, the probable collection date of these specimens (1824) would make this impossible. The two syntypes at NHMUK (female no. 1880.1.1.4552, male no. 1880.1.1.4557) are both labelled as 'co-types' on Horsfield's labels, which read '*Perdix curvirostris* Raffles, Raffles, Sumatra', and recorded in the register as 'Loc. Sumatra, Pres. by India Museum (Raffles)'. Besides the '*curvirostris*' types there appear to be no other specimens of this species collected for Raffles in NHMUK. An image of a female among the post-*Fame* drawings (NHD 47.40; Noltie 2009; Fig. 7) could represent Stanley's specimen.



Figure 7. Long-billed Partridge *Rhizothera longirostris* (Temminck, 1815) by J. Briois in Bengkulu, 1824 (© The British Library Board; NHD 47.40)

2158 [843b] and 2159. Lesser Whistling Duck *Dendrocygna javanica* (Horsfield, 1821)

In 1825, Stanley listed two unsexed specimens simply as *Anas*, which matches Raffles (1822). The only species of *Anas* listed by Vigors (Raffles 1830) was *Anas arcuata*, a Horsfield name from 1824. However, one skin of a relaxed mount (2158) is at NML, accession number D843b, and is a *D. javanica*. Lack of a second traceable specimen at NML, or a number in Moore's stock books, suggests it may not have been part of the 1851 bequest.

2160. Great Argus *Argusianus argus* (Linnaeus, 1766)

In 1825, Stanley listed a specimen as 'Argus pheasant' without a species epithet. Catalogued by Raffles (1822) as *Phasianus argus* Linnaeus, but as *Argus giganteus* Temminck by Vigors (Raffles 1830). Lack of a traceable specimen in NML, or a number in Moore's stock books, suggests it was not part of the 1851 bequest.

Concluding remarks

Since Raffles left Sumatra almost 200 years ago, the island has suffered rampant deforestation, which has intensified to unprecedented levels in the last 30 years with the expansion of oil palm *Elaeis guineensis* plantations (Margono *et al.* 2012). In addition to the profound impacts of habitat loss, the island's wild birds are vulnerable to trappers supplying the lucrative pet trade (Harris *et al.* 2016). Raffles' 'descriptive catalogue' (Raffles 1821, 1822) was recognised as the first systematic account of the avifauna of Sumatra (Tweeddale 1877) and provides the earliest records of birds on the island in the European literature. The contribution of local people, and their indigenous knowledge, to Raffles' catalogue, collections and drawings is uncredited and largely overlooked, but must have been vital. Raffles and Jack had organised a congress of local nobles to share their knowledge of, and names for, the native fauna (Noltie 2009). Consequently, Malay and Sumatran species names feature prominently both in the 'descriptive catalogue' (including in Jawi script) and the ZSL Museum catalogue, drawing additional attention to this critical contribution. Further linking the written accounts in the catalogues of Raffles' collections with extant specimens and drawings would be a highly worthwhile project, especially in light of the approaching anniversaries associated with South-East Asia's most prominent colonialist.

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The valid specific name of Sulawesi's Maroon-chinned Fruit Dove: *gularis* Quoy & Gaimard, 1832

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SUMMARY.—We present evidence demonstrating that the combination *Columba gularis* Quoy & Gaimard, 1832, is not preoccupied by *Columba gularis* Wagler, 1827, and is available. It should be used as the valid specific name of the taxon rather than the replacement name *Leucotreron epia* Oberholser, 1918.

The Maroon-chinned Fruit Dove of Sulawesi was originally described as *Columba gularis* Quoy & Gaimard, 1832¹, and for almost a century this name was invariably used for the taxon. However, a slightly earlier application of this same combination for an African bird was known, and because Quoy & Gaimard's name was thought to be preoccupied, the replacement name *epia* Oberholser, 1918, was introduced for the Sulawesi bird. The appropriateness of this action and the history of the case require examination to confirm the valid specific name for this taxon.

History of the names

In 1808, in his *Histoire naturelle des oiseaux d'Afrique* (pp. 116–118), François Levaillant described a new form of dove, accompanied by an attractive illustration, calling it 'Le Colombi-Caille', and stating that it came from Great Namaqualand. Levaillant was an adherent of Buffon and rejected the Linnaean naming system, considering that a vernacular French name was quite sufficient. He also remarked (p. 118) that he had made a special effort to complete the descriptions of his new pigeons so that Temminck could include them in his forthcoming monograph on the Columbidae.

Temminck (1811: 26–27) duly included Levaillant's 'Colombi-Caille' in the monograph, with a description almost identical to Levaillant's and a perhaps slightly inferior plate (Pl. XV). He called the bird 'Colombi-Galline Hottentot', but, more to the point, gave it a scientific name, *Columba Hottentotta*.

A few years later, Wagler (1827: [261]) listed within his genus *Columba* what was clearly the same bird, citing both Levaillant's and Temminck's names, again presenting a near-identical description, and naming it *C. gularis* (#90). Wagler was among those who considered that scientific names should be apt and that this outweighed the historically accepted principle of priority, which may explain why he provided a new name for a form that already had an apparently valid name. As a result, *gularis* Wagler, 1827, would have been a junior objective synonym of *hottentotta* Temminck, 1811.

Around the same time, during a French circumnavigation of the globe by the *Astrolabe* in 1826–29, a large number of specimens were collected including a new dove from near Manado, at the north-east tip of the Indonesian island of Sulawesi. When the ship's surgeons, Quoy and Gaimard, were writing up their results, they named the species *Columba gularis* (1832: 247), presumably unaware that Wagler had recently used the same name for a totally different bird in southern Africa.

¹ For dating to 1832, rather than 1830, see Mlíkovský (2012).

The best part of a century later, Oberholser (1918: 48) reached the conclusion that Quoy and Gaimard's name was preoccupied by Wagler's [objective] synonym of Temminck's name, despite noting that both names referred to 'a fictitious bird of Levaillant's'. At the time, the *Règles internationales de la nomenclature zoologique*, the forerunner of the present Code, had no provisions related to fictitious animals (see Hemming 1958). However, it was already accepted practice that such fabricated inventions had no place within the realms of zoological nomenclature, and such names were customarily ignored. Despite this, Oberholser went on to provide a replacement name for that of Quoy and Gaimard, calling the species *Leucotreron epia*².

Levaillant's bird

Levaillant's sparkling accounts of his travels in southern Africa caused an immediate sensation after his first publications in 1790, and he quickly became a celebrity in European society (Stresemann 1975: 88 ff., Bruce 2003: 21). However, from the outset there were sceptics, as revealed in a letter from Count von Hoffmannsegg to his sister, in 1797 (translation from Stresemann 1975: 89): 'It is quite possible that often in his tales he improves on nature as he observed it, but certainly not so vastly as many here [Paris] believe, and I do not know why all his stories should not basically be true.' At the same time, Hoffmannsegg also commented on how skilled and rapid Levaillant was at preparing skins.

As already noted, Wagler had renamed Levaillant's pigeon in his *Systema avium* of 1827. In the prologue to this book (p. [7]) he extolled Levaillant's work and criticised the small-mindedness and jealousy of those who cast doubt on its authenticity. But, just a few years later, by the time he was writing his *Monographia Psittacorum*, he too had become suspicious, having detected that some of Levaillant's birds were taken from plates in the works of Buffon and Edwards, skilfully altered and then claimed to occur in 'Lisbon, the Cape or some other remote location' (1832: 467). Perhaps he might have had more to say about the matter, and even the dove in question, but in August 1832 he died in an unfortunate accident (Gebhardt 2006: 375).

Some clear falsifications among Levaillant's birds were detected by Hartlaub and Jules Verreaux³, whilst Bonaparte (1857: 69) did not know what to make of '*Columba hottentotta*' and did not award it a species entry. It was left to Sundevall (1857) to reveal the true extent of Levaillant's falsehoods. As a child, Sundevall had been captivated by Levaillant's books, which had been important in his electing to become a zoologist. While working on collections of southern African birds made by Wahlberg and others, he was struck by the number of birds described by Levaillant as being common that were never encountered by subsequent visitors to apparently the same regions, in an area not notably given to local endemism. Amid growing doubts, Sundevall eventually examined all of Levaillant's 'species' one by one, checking various skins in Leiden with the help of Schlegel, and in Paris with Jules Verreaux. He concluded that of the 284 species covered by Levaillant, 134 were valid southern African species, but the rest consisted of large numbers found exclusively in other parts of the world (New Zealand, Australia, North and South America, China, India, Java, etc.), as well as false descriptions, composite species or artefacts (skins fabricated from

² Oberholser (1918) did not indicate the etymology of *epia*, but it is clearly the Latinized Greek adjective ἠπιος (-α, -ου) [gentle, kind] in its feminine form. Therefore, as the genus *Leucotreron* is masculine, the original combination *Leucotreron epia* requires a mandatory correction to *Leucotreron epius*.

³ Verreaux first visited South Africa when he was only 11, accompanying Delalande's expedition for the Paris museum and staying three years. After returning to France, he soon went back to the Cape in 1825, where he stayed for 13 years, thereby gaining vast first-hand knowledge of the southern African avifauna (Stresemann 1975: 162).

parts of more than one species), fictitious birds and some doubtful cases⁴. In his paper, he gave details of each case. His conclusion on 'Le Colombi-Caille' was that the bird was entirely fictitious.

After this landmark publication, Sundevall's careful and considered conclusions appear to have been universally accepted, and thereafter any references to Levaillant's dove have invariably described it as fictitious (e.g. Layard 1867: 264, Gray 1870: 240, Salvadori 1893: 644–645, Oberholser 1918: 48).

Application of the Code

Several articles of the *International code of zoological nomenclature* (hereafter the Code; ICZN 1999) are particularly relevant to this case and require comment.

Exclusions and availability.—The names *Columba hottentotta* Temminck, 1811, and *C. gularis* Wagler, 1827, were coined for a fictitious species. As a result, they are not regulated by the Code (see Art. 1.3.1, and Glossary: concept, hypothetical), and are not available (see Glossary: unavailable name). They are expressly excluded by the Code and have no standing in zoological nomenclature. Effectively, as scientific names they have never existed.

When Oberholser (1918) supplied a new replacement name for *Columba gularis* Quoy & Gaimard, 1832, he did so stating that their name was preoccupied by *Columba gularis* Wagler, 1827. But Wagler's name is unavailable, as it was based on a non-existent bird, a point noted by Oberholser himself⁵. Therefore, Oberholser's replacement name was completely unnecessary because *Columba gularis* Quoy & Gaimard, 1832, was perfectly valid and not preoccupied: it was at all times the correct name for the Sulawesi bird. The fact that Oberholser's new name was not needed does not make it unavailable; it was validly introduced but is a junior objective synonym of *gularis* Quoy & Gaimard⁶.

Had *Columba gularis* Wagler, 1827, been an available name, *Columba gularis* Quoy & Gaimard, 1832, would have been a primary homonym, and thus permanently invalid (Art. 57.2). But, because for the purposes of the Code Wagler's name has effectively never existed, Quoy and Gaimard's name has always been valid: there is no case of homonymy here⁷.

Usage—Having established that *gularis* Quoy & Gaimard, 1832, is available and has priority over *epia* Oberholser, 1918, it is worth checking to establish if this is a case where reversal of precedence (Art. 23.9) might be applicable. This article is the one place where the Code gives a reasonably precise and workable definition of 'prevailing usage', as can be seen here.

⁴ Sundevall remarked that confusion of the origins of skins was not unusual at the time, with many species being attributed to southern Africa because vessels from the East typically stopped off at the Cape, and often transferred their cargoes to other Europe-bound ships, with the result that a European collector on purchasing an undocumented series of birds might easily be erroneously led to believe that they had originated in the Cape. However, while most European collectors might not be expected to discover these errors, what was unforgivable in Levaillant's case was that he invariably stated that he had seen the species in southern Africa, providing a series of bogus details concerning the circumstances, as well as notes on their behaviour and even their nests and eggs.

⁵ Subsequent to its original introduction by Wagler (1827), it was never used as a valid name.

⁶ Oberholser's (1918) introduction of *epia* could well be considered insufficient for making the name available under Art. 11.5, as he cited the name but did not actually use it in his species heading (*Leucotreron gularis*); indeed, it might even be argued that he introduced the name conditionally, as he stated '...it may be called *Leucotreron epia*, nom. nov.'. However, the name would nonetheless have been made available (Art.11.6.1) through subsequent use, for example by Riley (1924); names proposed conditionally before 1961 are not automatically to be excluded (Art. 11.5.1).

⁷ It is worth noting, in passing, that Art. 59.3 talks of names that were replaced before 1961 becoming permanently invalid, but this article explicitly relates to secondary homonyms, which is not the case here.

'23.9.1. prevailing usage must be maintained when the following conditions are both met:

23.9.1.1. the senior synonym or homonym has not been used as a valid name after 1899, and

23.9.1.2. the junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years.'

It is important to note the requirement that *both* conditions be met. In this case, if both are met, the junior objective synonym *epia* would overthrow the priority of the senior *gularis*, so we must examine the facts for each condition in turn.

For Art. 23.9.1.1 to be met, *gularis* Quoy & Gaimard *must not* have been used as a valid name after 1899. We found seven (arguably eight) publications post-1899 in which *gularis* was used as the valid name of this species: Forbes & Robinson (1900: 121), Dubois (1902: 736), Hose (1903: 81), Lampe (1905: 200), Mathews (1910: 100), Hartert (1927: 4), Stresemann (1936: 365), and perhaps arguably (see footnote 6) Oberholser (1918: 48). One such use would technically be sufficient, but there is evidence of at least seven or eight. The required condition is not met.

For Art. 23.9.1.2 to be met, *epia* Oberholser needs to have been used as the valid name for this dove in at least 25 works from the immediately preceding 50 years (i.e. 1971–2020). We undertook an exhaustive search but managed to find no more than 21 such uses: Wolters (1975: 53), Goodwin (1977: 341, 1983: 277), Howard & Moore (1980: 149, 1991: 92), White & Bruce (1986: 199), Rösler (1996: 271), Baptista *et al.* (1997: 207), Coates & Bishop (1997: 321), Clements (2000: 125, 2007: 124), Gibbs *et al.* (2001: 228), Dickinson (2003: 174), Rheindt *et al.* (2011: 429–440), Dickinson & Remsen (2013: 76), del Hoyo & Collar (2014: 206), Eaton *et al.* (2016: 52), Bahr (2016: 130), Martin *et al.* (2017: 75), Arlott (2018: 128), and del Hoyo (2020: 110). Indeed, six of these (Goodwin, Howard & Moore and Clements, each twice) might more appropriately be considered to amount to three cases of duplication, as in each case the second date listed above refers simply to an updated version of the same work, with the same authors, same combinations, and precisely the same information; it seems difficult to justify counting each member of these pairings as different 'works'⁸. Either way, again the required condition of the article is not met.

A few mentions of the name from this period are clearly excluded from the 'uses' stipulated in Art. 23.9 (see, especially, 23.9.6). For example, Martens & Bahr (2016: 218) is a serious scientific paper but, in line with the overall purpose of its series, it simply reports usage elsewhere (del Hoyo & Collar 2014) of a new combination, *Ramphiculus epius*. It is perfectly clear that the authors of this paper were not themselves using this as the correct name for the taxon.

Given the remarkably few uses of *epia* detected within the required timescale⁹, for interest we decided to extend our search back to the introduction of this name by Oberholser in 1918, although any earlier uses would have no bearing on Art. 23.9. In addition to Oberholser's paper, we found only seven other uses: Riley (1924: 12), Mathews (1927: 28), Peters (1937: 26), Stresemann (1941: 53), Kuroda (1953: 108) and Goodwin (1967:

⁸ In this vein, we have excluded the numerous reprints, translations and editions (sometimes 'revised' or 'annotated') of Wallace's (1869) classic *The Malay Archipelago* that have appeared regularly over the last 150 years or so; the original text (and presumably all others) uses the name *gularis* for this species on p. 431.

⁹ The minimal use of the name *epia* may well be related to the fact that for most of the last 100 years or so the taxon has been lumped with Banggai Fruit Dove *Ramphiculus subgularis* (Meyer & Wigglesworth 1896), which has priority over the name *epia* (but not *gularis*). As a result, unless referring to it at subspecific level, most ornithologists would have known the Sulawesi birds as *Ptilinopus subgularis*.

341, 1970: 341). This figure compares very unfavourably with at least 41 uses of *gularis* Quoy & Gaimard that we located from before the cut-off date for Art. 23.9.1.1 of 1899 (see Appendix).

Note that Goodwin (1967) is the first edition and Goodwin (1970) the second of the same work that is cited twice in the 1971–2020 list, above. Differences between the 1967 and 1970 versions appear minimal, and mostly related to details of life histories, while the ‘edition’ of 1977 is apparently simply a reprint with a different cover page, as already reported by Bock (1979: 646). The 1983 edition is much the same but with a different layout. The species account for *Ptilinopus subgularis* (including *epia* [sic]) is absolutely identical word-for-word and space-for-space across the four editions, apart from the two-column layout used in 1983, which appears to have had the unfortunate side effect of introducing two (very minor) typographical errors¹⁰. As such, it would seem against the spirit of the Code (see, e.g., Art. 23.9.6) to count four versions of the same book as four uses (only two are potentially relevant to Art. 23.9). In truth, for the purposes of Art. 23.9, it might be argued that perhaps the first (1967) edition should be considered the only valid use, and this falls outwith the relevant period of Art. 23.9.1.2.

Conclusions

The name *Columba gularis* Quoy & Gaimard, 1832, is valid and available. It is not, and never has been, preoccupied. The proposed replacement name *Leucotreron epia* Oberholser, 1918, is a valid and available name, but is an objective junior synonym of *Columba gularis* Quoy & Gaimard, 1832.

To qualify for reversal of precedence due to possible prevailing usage, both conditions of Art. 23.9 must be met. Having studied uses of both epithets as the valid name for the taxon, we find that the case for promoting *epia* over *gularis* fails on both counts, as neither of the required conditions is met.

Nowadays, this taxon is normally placed in either *Ptilinopus* or *Ramphiculus*, traditionally in a polytypic species but increasingly as a separate, monotypic species. Irrespective of its treatment, the correct name for this taxon is *gularis* Quoy & Gaimard, 1832.

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¹⁰ The word ‘tail’ is misspelt ‘tall’, and an en-dash is mistakenly replaced with a hyphen.

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Appendix

List of works using *gularis* Quoy & Gaimard, 1832 (1832–99; and after 1899), and list of works using *epia/epius* Oberholser, 1918 (1918–70; and 1971–2020). The lists present combinations used by the authors with indications of publication date and page. All cited authors are listed in the References.

Uses of *gularis* Quoy & Gaimard, 1832 (1832–1899)

- | | |
|---------------------------------|---------------------------------|
| <i>Columba gularis</i> | <i>Ptilonopus gularis</i> |
| Quoy & Gaimard (1832: 247) | Wallace (1860: 141) |
| Lesson (1837: 39) | Wallace (1861: 348) |
| Prévost (1838: 21) | Wallace (1865: 377) |
| <i>Carpophaga gularis</i> | Finsch (1865: 176) |
| Gray (1844: [469]) | Wallace (1866: 278) |
| <i>Leucotreron gularis</i> | Wallace (1869: 431) |
| Bonaparte (1854: 876) | <i>Laryngogramma gularis</i> |
| Bonaparte (1855a: 216) | Reichenbach (1861: 102) |
| Bonaparte (1857: 15) | Heine & Reichenow (1890: 282) |
| Verreaux & Des Murs (1862: 343) | <i>Ptilopus gularis</i> |
| Walden (1872: 83) | Schlegel (1863: 59) |
| Salvadori (1875: 670) | Schlegel (1873: 37) |
| Walden (1877: 214) | Giebel (1877: 364) |
| Meyer (1879: 135) | Elliot (1878: 570) |
| Blasius (1883: 138) | Rosenberg (1878: 275) |
| Blasius (1886a: 131) | Wallace (1880: 440) |
| Blasius (1886b: 207) | Jentink (1883: 141) |
| de Elera (1895: 301) | Salvadori (1893: 78) |
| Blasius (1897: 363) | Meyer & Wiglesworth (1895: 15) |
| Sharpe (1899: 56) | Meyer & Wiglesworth (1896: 19) |
| <i>Trerolaema gularis</i> | Meyer & Wiglesworth (1898: 605) |
| Bonaparte (1855b: 247) | <i>Ptilinopus gularis</i> |
| Gray (1870: 230) | Brüggemann (1876: 82) |
| | Hartert (1897: 165) |

Uses of *gularis* Quoy & Gaimard, 1832 (after 1899)

- | | |
|---------------------------------------|--|
| <i>Ptilinopus gularis</i> | <i>Ptilopus gularis</i> |
| Forbes & Robinson (1900: 211) | Hose (1903: 81) |
| Stresemann (1936: 365) | <i>Leucotreron gularis</i> |
| <i>Ptilopus (Leucotreron) gularis</i> | Mathews (1910: 100) |
| Dubois (1902: 736) | †Oberholser (1918: 48) |
| Lampe (1905: 200) | <i>Ptilinopus gularis mangoliensis</i> |
| | Hartert (1927: 4) |

Uses of *epia* Oberholser, 1918 (1918–70)

- | | |
|------------------------------------|-----------------------------------|
| <i>Leucotreron epia</i> | <i>Ptilinopus subgularis epia</i> |
| †Oberholser (1918: 48) | Stresemann (1941: 53) |
| Riley (1924:12) | Kuroda (1953: 108) |
| <i>Leucotreron subgularis epia</i> | # Goodwin (1967: 341) |
| Mathews (1927: 28) | # Goodwin (1970: 341) |
| Peters (1937: 26) | |

Uses of *epia/epius* Oberholser, 1918 (1971–2020)

- | | |
|--|------------------------------------|
| <i>Megaloprepia (Trerolaema) subgularis epia</i> | White & Bruce (1986: 199) |
| Wolters (1975: 53) | # Howard & Moore (1991: 92) |
| <i>Ptilinopus subgularis epia</i> | Rösler (1996: 271) |
| # Goodwin (1977: 341) | Baptista <i>et al.</i> (1997: 207) |
| # Howard & Moore (1980: 149) | Coates & Bishop (1997: 321) |
| # Goodwin (1983: 277) | # Clements (2000: 125) |

Gibbs *et al.* (2001: 228)
Dickinson (2003: 174)
Clements (2007: 124)
Ptilinopus epia
Rheindt *et al.* (2011: 437)
Ptilinopus subgularis epius
Dickinson & Remsen (2013: 76)
Ramphiculus epius

del Hoyo & Collar (2014: 206)
Bahr (2016: 130)
Martin *et al.* (2017: 75)
del Hoyo (2020: 110)
Ptilinopus epius
Eaton *et al.* (2016: 52)
Arlott (2018: 128)

†Note that Oberholser (1918) introduced the new name *epia*, but the heading for his species account used only the name *gularis*. In the main text, we have treated this primarily as a use for *epia*, but recognise that it is at the very least arguable that he actually used the name *gularis* for the species (see footnote 6). Accordingly, in this Appendix the reference is listed under both names.

The listed references Goodwin (1967, 1970, 1977, 1983), Howard & Moore (1980, 1991) and Clements (2000, 2007) might more appropriately be reduced to a single mention for each, as in each case the different dates refer to different editions of the same work (see main text and footnote 8; also Art. 23.9.1.2 of the Code).

Non-breeding season records of the Alpine Leaf Warbler *Phylloscopus occisinensis*

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SUMMARY.—We present non-breeding season records of the recently named Alpine Leaf Warbler *Phylloscopus occisinensis* from Bangladesh (four individuals) and northern Thailand (one). Identification was based on mitochondrial DNA assay of feathers or blood from birds handled during ringing. Tickell's Leaf Warbler *P. affinis* (*sensu lato*) was abundant in scrub and scattered trees at the margins of wetlands in north-east Bangladesh, whilst the record from Thailand represents a significant eastwards extension of the previously recorded wintering range. Further sampling in South and South-East Asia will be necessary to resolve the winter ranges of the taxa *affinis* and *occisinensis*.

Within the 'Tickell's Leaf Warbler *Phylloscopus affinis* species complex', breeding around the margins of the Tibetan Plateau (which also encompasses the Sulphur-bellied Leaf Warbler *P. griseolus*), eastern populations of *P. affinis* were shown to constitute a distinct mitochondrial lineage that has been named Alpine Leaf Warbler *P. occisinensis* (Martens *et al.* 2008). Following this treatment, *P. affinis* breeds in the Himalayas, eastwards to Xizang, China, whereas *P. occisinensis* is distributed further east, beyond the Himalayan chain, in Yunnan, Sichuan, Qinghai and Kansu (China). Despite their deep mitochondrial divergence (15.8–16.0% in *cytb*, Martens *et al.* 2008; c.7.8% for the complete mitochondrial genome, Zhang *et al.* 2019) the two taxa are scarcely distinguishable using morphology and nuclear DNA, whilst any difference in song appears to be clinal, with 'bioacoustic intermediacy' over a narrow contact zone in eastern Xizang (Zhang *et al.* 2019). The deep mitochondrial divergence has been attributed to 'ghost introgression' as an easterly distributed ancestor expanded west and interbred with another, unknown, and presumably extinct *Phylloscopus* species (Zhang *et al.* 2019). Treatment as two species is not universally followed, however (BirdLife International 2020).

Irrespective of whether *P. affinis* and *P. occisinensis* are treated as one or two species, it is of both faunal and possible future conservation interest that the winter (non-breeding) ranges of the two lineages are identified. The winter range of *P. affinis* (*sensu lato*) extends from northern and peninsular India (in the south-west Ghats) to Bangladesh and Myanmar (Rasmussen & Anderton 2005, Dickinson & Christidis 2014). Here we present records of overwintering birds sampled in north-east Bangladesh and northern Thailand.

Methods

Field collection.—Prior to their release, we collected feathers of three *P. affinis* (*sensu lato*) from a total of 28 individuals, mist-netted and ringed in low trees and scrub around two wetland sites in north-east Bangladesh during 2012–14 (Round *et al.* 2014), and from one additional individual of another 11 ringed at a third site during 2015 (Fig. 1).

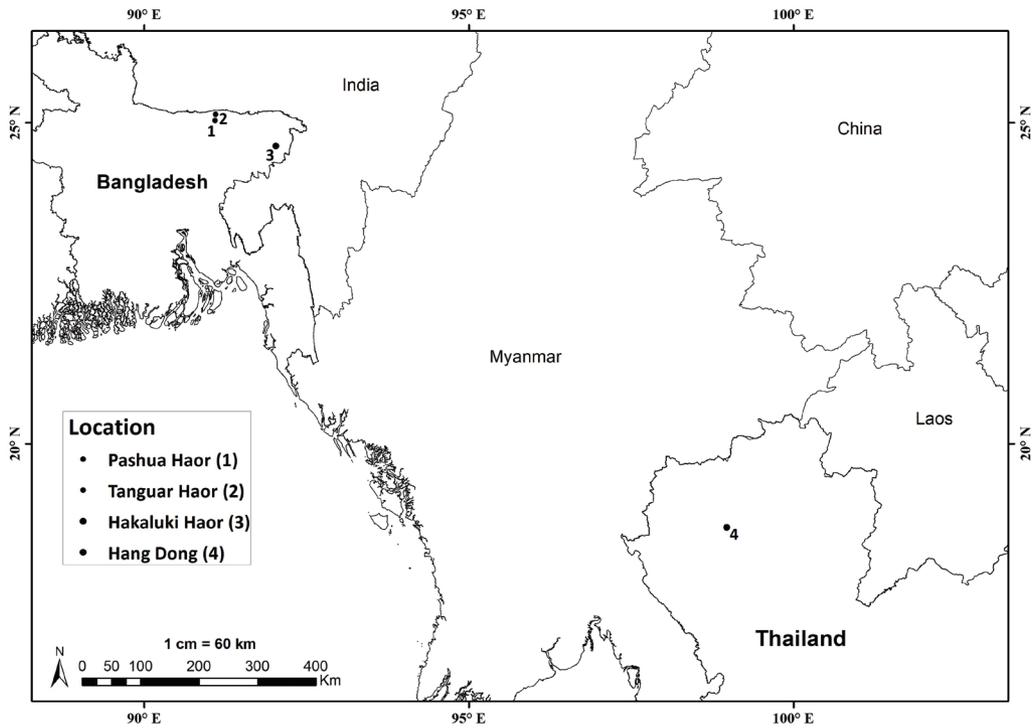


Figure 1. Sampling localities of *Phylloscopus affinis* (*sensu lato*) in Bangladesh and Thailand.



Figure 2. Alpine Leaf Warbler *Phylloscopus occisinensis*, before release, Hang Dong District, Chiang Mai Province, Thailand, 24 January 2020 (Sontaya Manawattana)

Additionally, a single *Phylloscopus* with yellowish underparts and supercilium, lacking wingbars, in Hang Dong District, Chiang Mai province, northern Thailand (Fig. 1), first found on 17 January 2020 by Thammarat Kaosombat, was tentatively identified from digital photographs as either Tickell's or Alpine Leaf Warbler by Wich'yanan Limparungpatthanakij

TABLE 1
Biometrics (mm) and mass (g) of five wintering Alpine Leaf Warblers *Phylloscopus occisinensis* sampled.
The first four individuals were trapped in Bangladesh, the fifth in Thailand.

Ring no.	Date	Location	Wing	Tail	Bill	Tarsus	Mass
AAA140	14 Feb 2012	Pashua Haor, Sylhet Division, 25°03'00"N, 91°06'00"E	53	40	12.9	19.6	5.9
AAA504	23 Feb 2014	Tanguar Haor, Sylhet Division, 25°04'59"N, 91°07'01"E	56	44	12.8	17.8	6.2
AAA509	23 Feb 2014	Tanguar Haor	54	43	12.5	17.5	6.0
AAA631	19 Feb 2015	Hakaluki Haor, Sylhet Division, 24°38'13"N, 92°01'34"E	56	44	12.8	20.4	6.7
A35121	24 Jan 2020	Hang Dong, Chiang Mai, 18°41'39"N, 98°58'34"E	55	43	12.6	18.9	5.9

a day or two after its discovery. This individual attracted particular interest as there were no previous records of *P. affinis* or *P. occisinensis* in Thailand or Indochina. On 24 January 2020, it was caught in a mist-net, ringed, measured, photographed in the hand (Fig. 2), and a blood sample taken on filter paper before release. The same bird remained at the site and was repeatedly observed until 9 February 2020. It was not heard to call during this period.

All individuals were caught in scrub in open marshy areas fringing wetlands on the plains, and mass and basic biometric data recorded (Table 1). The feathers were stored in labelled paper envelopes in a freezer at 0°C and the blood samples at -20°C.

Laboratory protocols.—Genomic DNA was extracted from feathers (the four Bangladesh individuals) and blood (the Thai bird) using NucleoSpin tissue kit (Macherey-Nagel), with 0.1% Dithiothreitol (DTT) added to increase the DNA yield (Olsson *et al.* 2005). Partial mitochondrial genes were amplified using primers: Bird F1 (5'-TTCTCCAACCACAAAGACATTGGCAC-3') and Bird R1 (5'-ACGTGGGAGATAATTCCAAATCCTG-3') for Cytochrome C oxidase subunit 1 (COI; Saitoh *et al.* 2015) and L14841 (5'-AAAAAGCTTCCATCCAACATCTCAGCATGATGAAA-3') and H15547 (5'-AATAGGAAGTATCATTCCGGGTTTGATG-3') for cytochrome *b* (*Cytb*; Helbig *et al.* 1995). Polymerase chain reaction (PCR) was performed using AccuStart II GelTrack PCR SuperMix (Quanta BioSciences) following the concentration of ingredients suggested by the manufacturer. The reactions for both genes were performed with the following steps: 94°C for three minutes followed by five cycles at 94°C for 30 seconds, 48°C for 30 seconds, 72°C for one minute, then 30 cycles at 94°C for 30 seconds, 51°C for 30 seconds, 72°C for one minute, and a final 72°C for five minutes (Saitoh *et al.* 2015) using an Eppendorf Mastercycler gradient thermocycler. PCR products were visualised with 1.5% agarose gel electrophoresis. The products successfully amplified were purified using NucleoSpin Gel and PCR Clean-up (Macherey-Nagel) and sent for sequence analyses using the Applied Biosystems BigDye Terminator v3.1 Cycle Sequencing Kit protocol.

Genetic analyses.—Sequences of collected samples were deposited in GenBank. These sequences and those of other species downloaded from GenBank (Table 2) were aligned using ClustalW in MEGA7 v.7.0.21 (Kumar *et al.* 2016) and used to conduct Maximum Likelihood (ML) and Bayesian Inference (BI) phylogenetic analyses, with Yellow-streaked Warbler *P. armandii* serving as the outgroup. Phylogenetic trees for *cytb* and COI were constructed separately because the sequences of both genes were not available for concatenative analyses. Kakusan4 (Tanabe 2007) was used to select the best-fit evolutionary model under Akaike information criterion (AIC; Akaike 1974) and Bayesian information criterion (BIC; Schwarz 1978) for ML and BI, respectively. The selected models for the ML

TABLE 2
Ring numbers, localities and accession numbers for collected samples, and the samples in GenBank used in this study.

Ring no.	Region	Accession no.	
		COI	Cytb
Collected samples			
AAA140	Bangladesh	MT921110	MT921114
AAA504	Bangladesh	MT921109	MT921113
AAA509	Bangladesh	MT921108	MT921112
AAA631	Bangladesh	MT921107	MT921111
A35121	Thailand	-	MT921115
Sequences downloaded from GenBank			
<i>P. occisinensis</i>	China	HQ608869	-
<i>P. occisinensis</i>	China	MK360490	-
<i>P. occisinensis</i>	China	-	HQ608829
<i>P. occisinensis</i>	China	-	MK360315
<i>P. occisinensis</i>	Tibet	-	EU815089
<i>P. affinis</i>	China	MK360452	-
<i>P. affinis</i>	China	MK360460	-
<i>P. affinis</i>	China	-	FJ155878
<i>P. affinis</i>	Nepal	-	EU851090
<i>P. affinis</i>	India	-	L77128
<i>P. griseolus</i>	Russia	GQ482433	-
<i>P. griseolus</i>	China	MK360478	-
<i>P. griseolus</i>	China	-	MK360295
<i>P. griseolus</i>	Russia	-	FJ155894
<i>P. griseolus</i>	Russia	-	EU851091
<i>P. armandii</i>	China	HQ608871	-
<i>P. armandii</i>	China	-	EU851092

trees were GTR Gamma (both COI and *cytb*) and for the BI trees HYK85 Gamma (both COI and *cytb*). The ML trees were constructed using RAxML v8.2.12 (Stamatakis 2014) on CIPRES Science Gateway V3.3 (Miller *et al.* 2010) with 1,000 bootstrapping iterations. A bootstrap value of 70% or higher was considered significant support. The BI trees were performed in MrBayes v3.2.6 (Huelsenbeck & Ronquist 2001) under a Metropolis-coupled, Markov chain Monte Carlo (MC-MCMC) approach, started from a random tree, run twice in parallel with a four-chain analysis for five million generations. The trees were sampled every 100 generations and 25% of these were discarded as 'burn-in'. We ran Tracer v1.7.1 (Rambaut *et al.* 2018) to evaluate stationarity, and Effective Sample Size (ESS) values >200 were obtained for all outputs. Consensus topology, branch length, and bipartition posterior probability were estimated from the remaining trees, with posterior probabilities of 95% or higher considered as significant support. The trees for both ML and BI approaches were visualised and edited in FigTree v1.4.3 (Rambaut 2009).

Results

The samples from all four Bangladesh-caught birds were successfully amplified for both COI and *cytb* genes, whereas only *cytb* was successfully amplified in the blood sample from the single northern Thai bird (Table 2). The alignments revealed 668 bp for

COI (104 variable sites, 77 parsimony informative sites) and 673 bp for *cytb* (115 variable sites, 84 parsimony informative sites). As the phylogenetic analyses based on ML and BI approaches provided similar results, only the BI trees are shown (Fig. 3). Phylogenetic trees for COI and *cytb* were largely concordant in topology, and revealed the monophyly of all collected samples (AAA140, AAA504, AAA509, AAA631 and A35121) with *P. occisinensis*, with strong statistical support (COI: 91/100% and *cytb*: 100/100% for bootstrap values and posterior probabilities, respectively). The *P. occisinensis* clade was distinct from both *affinis* and *griseolus*. However, whilst the *P. occisinensis* clade was resolved as sister to *P. affinis* in the COI tree, *occisinensis* appeared as sister to *P. griseolus* in the *cytb* tree (Fig. 3). In the *cytb* tree indicated by Martens *et al.* (2008) *affinis* was sister to *griseolus*, while in a concatenated tree of *tRNA*, *rRNA* and *cytb* it was *occisinensis* and *griseolus* that appeared as sisters. Incongruities in mtDNA topologies among these taxa were discussed by Alström *et al.* (2018) and are not surprising as the mitochondrial divergence is almost identical among all three lineages (Zhang *et al.* 2019).

Discussion

Four wintering *P. affinis* (*sensu lato*) caught and ringed at wetlands in north-east Bangladesh, and another individual, a presumed vagrant, in northern Thailand, the easternmost South-East Asian wintering record known (Clement 2020), proved to lie in the recently distinguished Alpine Leaf Warbler *P. occisinensis* lineage.

Even considering the greater proximity of Bangladesh to the Himalayan breeding areas of the more westerly distributed *P. affinis* (*sensu stricto*), the discovery of *P. occisinensis* there was not especially surprising considering that north-east India and Bangladesh also harbour wintering populations of other species that breed in south-west China such as Firethroat *Calliope pectardens* (Rasmussen & Anderton 2005, Round *et al.* 2014). Given the abundance of *P. affinis* (*sensu lato*) in trees and scrub around the margins of northern Bangladesh wetlands in winter, and considering that so few individuals were sampled, the question arises whether *P. affinis* (*sensu stricto*) and *P. occisinensis* might winter alongside each other in the same areas as yet undetected. Clearly more sampling is needed to improve understanding of the winter distribution of these taxa across South Asia. Because *P. affinis* (*sensu lato*) winters as far south as the Western Ghats (Rasmussen & Anderton 2005) it might be productive to first sample individuals there to discover whether there is any major disparity in the wintering ranges of the two, the more southerly and westerly distributed birds perhaps being exclusively *P. affinis* (*sensu stricto*). It also remains to be investigated whether names applied to specimens currently synonymized with *P. affinis* (e.g., *Abrornis xanthogaster* Hodgson, 1844, *Phyllopneuste flaveolus* G. R. Gray, 1846) might in fact be applicable to the newly described taxon.

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The conundrum of an overlooked skeleton referable to Imperial Woodpecker *Campephilus imperialis* in the collection of the Natural History Museum at Tring

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SUMMARY.—The discovery of an overlooked skeleton of Imperial Woodpecker *Campephilus imperialis* in the bird collection of the Natural History Museum at Tring (NHMUK) is documented, one of very few known to exist worldwide of this almost certainly extinct species. We present evidence that, on balance of probabilities, it is one of two collected by Alphonse Forrer in 1882 near the settlement of La Ciudad in the Sierra Madre Occidental, Durango, western Mexico; the whereabouts of the other, which did not come to NHMUK, appears currently unknown. During research into the NHMUK specimen, we demonstrated that the supposed Imperial Woodpecker skull held in the collection of the Russian Academy of Sciences, St. Petersburg, must in fact be that of an Ivory-billed Woodpecker *C. principalis*.

The recent discovery in the bird research collections of the Natural History Museum (NHMUK) at Tring of a very large woodpecker skeleton identified in its box merely as a '*Picus* sp.' appeared potentially noteworthy. In fact, it is clearly not a *Picus* sp., instead appearing comparable to the largest and probably extinct species, the Imperial Woodpecker *Campephilus imperialis*. Below, prior to reaching a definitive identification, we refer to it as the unidentified NHMUK skeleton.

The unidentified NHMUK skeleton exhibits several morphological characters diagnostic of the closely related (e.g. Fuchs *et al.* 2013) woodpecker genera *Campephilus*, *Chrysocolaptes* and *Reinwardtipicus*. Following the terminology of Baumel & Witmer (1993), these include an elongated proc. postorbitalis, which almost reaches the lateromedially broad and rostrally bifurcated proc. zygomaticus (pers. obs.; compare Donatelli 1996, fig. 13, and Donatelli 2014, figs. 7–8), medially converging cristae iliacae dorsales delimiting deep fossae iliacae dorsales (see Webb 2002, character 48), and a proximodistally elongated trochlea metatarsi IV (Webb 2002, character 55). However, the specimen in question is far larger than any species of *Chrysocolaptes* or *Reinwardtipicus*. Another large woodpecker, Great Slaty Woodpecker *Mulleripicus pulverulentus*, is also eliminated as it lacks the morphological characters of the new specimen described above and the craniofacial flexion zone (Donatelli 2012); moreover whilst the premaxilla is similar in length it is significantly narrower. Therefore we initially compared measurements of the length and width of the skull of the unidentified NHMUK skeleton with analogous measurements derived from NHMUK skins of the largest potentially relevant species, i.e. Imperial Woodpecker, Ivory-billed Woodpecker *Campephilus principalis* and Magellanic Woodpecker *C. magellanicus*.

In making this comparison, it is important to bear in mind that, besides the skin specimen measurements including skin / feather thickness, the skull of the unidentified NHMUK skeleton not only has a slightly damaged bill tip but, more importantly, lacks a rhamphotheca (Fig. 1). Therefore, we first took X-rays of a male and a female skin in the NHMUK collection of both *C. imperialis* and *C. principalis*, enabling us to derive estimates of their skull length both with and without the rhamphotheca. This revealed that the



Figure 1. Skull of the unidentified NHMUK skeleton in dorsal and lateral views. ZFC: craniofacial flexion zone; PrPO: proc. postorbitalis; PrZ: proc. zygomaticus (Harry Taylor, © Natural History Museum, London)

presence of a rhamphotheca increases skull length by on average 17.28% (range 16.2–18.0%, $n = 4$). As the skull without rhamphotheca of the unidentified NHMUK skeleton measured 105.3 mm, this indicated that with its rhamphotheca it would have had a total skull length of *c.*123.5 mm. Using these results, a plot of maximum skull width against skull length with rhamphotheca clearly indicated that the unidentified NHMUK skeleton must be either a small individual of *C. imperialis* or a large *C. principalis* (Fig. 2).

Skeletons of Imperial and Ivory-billed Woodpeckers are very rare in natural history collections. According to the *World inventory of avian skeletal specimens* (Wood *et al.* 1982, Wood & Schnell 1986) only three complete skeletons of *C. imperialis* and five of *C. principalis* were potentially available, all at institutions in the USA other than one supposed *C. imperialis* at the Russian Academy of Sciences, Institute of Zoology, St. Petersburg (ZISP). We therefore requested and received a standard set of measurements for each complete skeleton of *C. imperialis* and *C. principalis* from curators in the relevant museums: the

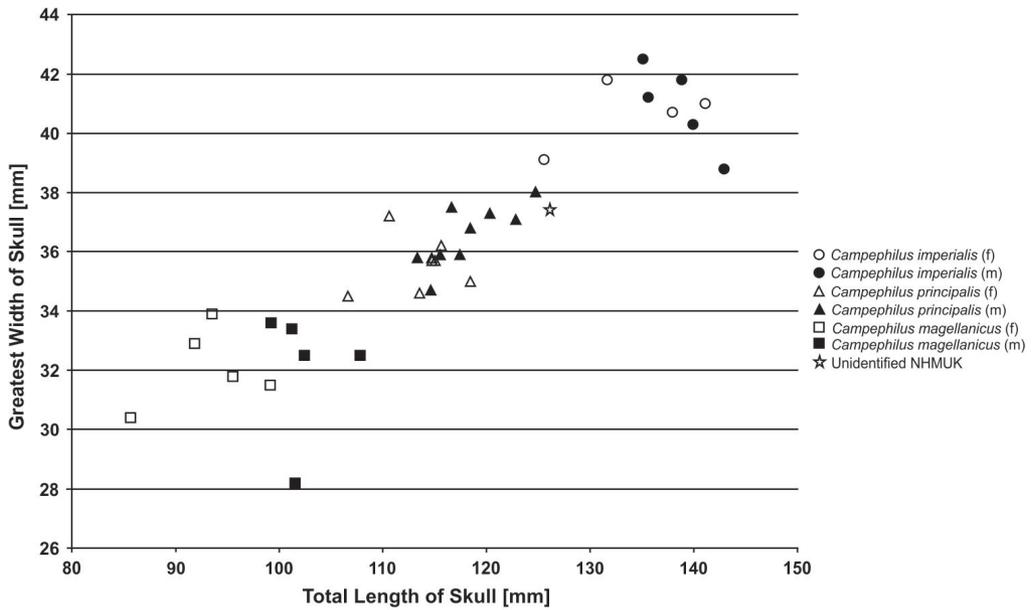


Figure 2. Graph plotting skull max. width against total length (bill tip to rear of skull) for skins of three species of *Campephilus* woodpecker in the NHMUK collection. Also shown are analogous measurements from the unidentified NHMUK skeleton, for which a correction factor upwards of 17.28% has been made to total skull length, to account for its missing rhamphotheca (see text for explanation), thereby making its measurements directly comparable with the others.



Figure 3. The ZISP skull (ZISP 1791), supposedly of Imperial Woodpecker *Campephilus imperialis* but actually Ivory-billed Woodpecker *C. principalis*, in dorsal view (Judith White, courtesy of Russian Academy of Sciences, St. Petersburg)

American Museum of Natural History, New York (AMNH), United States National Museum, Smithsonian Institution, Washington DC (USNM), Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ), and ZISP. All responded, and MCZ

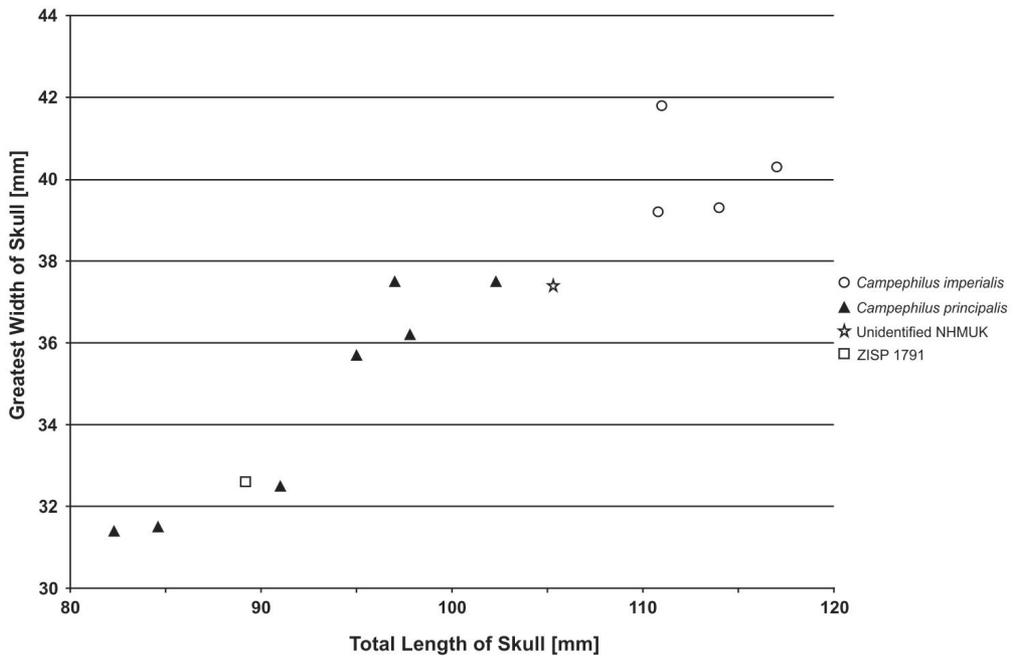


Figure 4. Graph plotting skull max. width against skull total length without rhamphotheca for Imperial Woodpecker *Campephilus imperialis* and Ivory-billed Woodpecker *C. principalis*, using data from Table 1.

kindly also supplied length and width measurements for an additional *C. principalis* skull in their collection.

During this process we learned that the ZISP specimen comprises only a skull, including a detachable rhamphotheca (Fig. 3), and subsequently JW & RPP-J were able to visit ZISP to study it further. The skull length of this specimen with its rhamphotheca was 17.7% longer than when measured without, adding confidence to the correction factor derived from X-raying NHMUK skins. The skull length measurements provided for the two AMNH skeletons alone included the rhamphotheca, so a correction based on the NHMUK skin X-ray results outlined above was made to these to derive estimates for skull length without rhamphotheca, comparable to the rest. Finally, in order to enhance the still limited sample for skull measurements, we further made use of the X-ray results from the four NHMUK skins.

Table 1 compares an array of cranial and post-cranial skeletal measurements derived from the unidentified NHMUK skeleton, from the available identified skeletons and skulls, and from X-rays of the four NHMUK skins. The post-cranial elements from the unidentified NHMUK skeleton are uniformly comparable in size to those of *C. imperialis* and unambiguously larger than those of *C. principalis*. The skull measurements are less clear-cut (Table 1, Fig. 4), with skull width approximating that of the largest *C. principalis* and total skull length falling between the ranges of the two species. Overall, given the post-cranial findings, the evidence strongly supports identification of the unidentified NHMUK skeleton as a relatively small, possibly female, *C. imperialis*. Henceforth, we therefore refer to it as the NHMUK *C. imperialis* skeleton.

A further striking conclusion from Fig. 4 is that both the length and width of the skull ZISP 1791, which lacks any associated data, are firmly embedded with those of our skeletal sample of *C. principalis* and indicate that it must be this species and not *C. imperialis*.

TABLE 1

Measurements (in mm) of specimens of Imperial Woodpecker *Campophilus imperialis* and Ivory-billed Woodpecker *C. principalis* in the collections of NHMUK, AMNH, MCZ, USNM and ZISP, compared to the unidentified NHMUK skeleton. Abbreviations: Cmc, carpometacarpus; Fe, femur; GW, max. width; Hu, humerus; Sk, skull; Skr, skull with ramphotheca; Tbt, tibiotarsus; TL, total length; Tmt, tarsometatarsus; Ul, ulna. Bracketed measurements were derived measurements using a conversion factor obtained from X-rays (see text for details).

Registration	Unidentified	<i>C. imperialis</i>				<i>C. principalis</i>							
		NHMUK 1898.3.10.2487	NHMUK 1898.3.10.2486	USNM 34441	AMNH 1081	ZISP 1791	NHMUK 1898.3.14.875	NHMUK 1898.3.14.876	USNM 291358	AMNH 4708	MCZ 342302	MCZ 347308	MCZ 342397
Sex	unsexed	female	male	male	unsexed	unsexed	female	male	male	male	unsexed	unsexed	unsexed
Preparation	skeleton	skin ^a	skin ^a	skeleton	skeleton	skeleton	skin ^a	skin ^a	skeleton	skeleton	skeleton	skeleton	skull
Skr TL	[123.5]	129	137.3	-	130 ^b	105	114	114	114	-	-	-	-
Sk TL	105.3 ^b	111	117	114	[110.8]	89.2 ^d	95	97	97.8	[102.3]	91	84.6	82.3 ^b
Sk GW	37.4	41.8	40.3	39.3	39.2	32.6	35.7	37.5	36.2	37.5	32.5	31.5	31.4
Hu TL	69.4	-	-	72.5	72.9	-	-	-	60.1	58	56.7	56.3	-
Ul TL	85.7	-	90	88.3	88.1	-	-	75	71.9	70.9	68.5	69.6	-
Cmc TL	42.6	44	45	42.6	43.2	-	35	36	36.1	34.3	35.2	33.8	-
Fe TL	55.3	-	-	56.3	57.2	-	-	-	47.4	47	46.3	44.4	-
Tbt TL	71.5	-	76	74.6	74.8	-	62	65	63.2	60.8	60.4	60.4	-
Tmt TL	48.4	50	50	50.8	50.7	-	44	46	45.7	43.5	42.7	41.3	-

^ameasurements taken from X-ray of study skin.

^bslight damage to bill tip.





Figure 5. Pelvis of the unidentified NHMUK skeleton, illustrating the two different registration numbers inscribed on the same part (Harry Taylor, © Natural History Museum, London)

Although it was noted during examination of the specimen that its bill tip had some minor damage, even with the rhamphotheca in place its total skull length (105 mm) indicates it cannot be a *C. imperialis* (Table 1).

Labelling, not original, in the box of the NHMUK *C. imperialis* skeleton states that receipt was from Henry Seebohm but, most unusually, two different NHMUK registration numbers are inked on an overlapping selection of the skeleton's elements. Whereas the skull is labelled as 1896.2.16.12, the mandible is inscribed 1888.2.20.1 (Fig. 1), and the pelvis has both of these numbers written on different parts of it (Fig. 5)! The skull and mandible, despite bearing different numbers, clearly belong to the same specimen, as is the rest of the skeleton, of which parts remain articulated. This apparent double registration of one specimen clearly required further investigation.

The relevant register reveals that specimen 1896.2.16.12 is indeed recorded as a skeleton of *Picus* sp., contained in a batch of avian osteological specimens (1896.2.16.1–230) bequeathed to NHMUK¹ by Henry Seebohm (1832–95) and received following his death in November 1895 (Sharpe 1906: 472). By contrast, 1888.2.20.1 is a number whose use was

¹ NHMUK has changed its name and acronym several times over its history, but for convenience is referred to by its current official acronym throughout this paper. A synopsis of the relevant name and acronym changes was presented by Prŷs-Jones *et al.* (2014).

erroneously duplicated in different NHMUK registers for two specimens: one is a skin specimen of '*Sylvia cinerea*' (= Common Whitethroat *Sylvia communis*), received as part of a series of 971 turdid and sylviid skins (1888.2.20.1–971) in the Tweeddale collection (Sharpe 1906: 446); the other refers to a skeleton of a '*Tiga* sp.' woodpecker (= Common Flameback *Dinopium javanense*), which is alone in its series and lacks details regarding from whom it was acquired. The woodpecker skeleton would *prima facie* appear more likely to be relevant here, but still makes little sense. Firstly, *Dinopium* are distinctly smaller than *Campephilus*, so confusion is unlikely; furthermore, the hallux is either reduced in size or completely lacking in *Dinopium*, but not in *Campephilus*. Secondly, in the comprehensive specimen listing by Hargitt (1890), only a single '*Tiga*' skeleton is noted (on p. 416) as being present at NHMUK, and this is accounted for by the still extant specimen 1850.8.15.76 of what is now *Dinopium javanense* purchased from the dealer Warwick. Neither a skeleton of a '*Picus* sp.' with registration number 1896.2.16.12 nor one of a '*Tiga* sp.' with registration number 1888.2.20.1 is currently present in the NHMUK collection, and we have found no other evidence relating to either of them.

Hargitt (1890: 466), however, did indicate that a single skeleton of a female *C. imperialis*, collected at La Ciudad, Durango (see Salvin & Godman 1888–1904: 445, for clarification of locality) and purchased from A. Forrer, was received by NHMUK in or before 1890. Unfortunately, this catalogue does not include specimen registration numbers, but a search of relevant registers revealed that a *C. imperialis* skeleton with these data was registered in September 1886, but with a number, 1886.9.9.1, different from either inscribed on the NHMUK *C. imperialis* skeleton! However, there is no indication of any skeleton of this species being recognised as present in the more recent NHMUK catalogues of Blandamer & Burton (1979) and Knox & Walters (1994).

Reference to the NHMUK archives revealed correspondence showing that in 1882 Alphonse Forrer had indeed collected two *C. imperialis* specimens near the village of Ciudad in the sierra of Durango, Mexico, that he made into skeletons, and which he then offered in early 1886 to NHMUK at £5 each (A. Forrer *in litt.* 19 January 1886; DF200/29/118-119). A subsequent letter confirms that one of these was purchased by NHMUK in the same year (A. Forrer *in litt.* 19 April 1886; DF200/29/121). There is therefore no reasonable doubt that NHMUK formerly held a Forrer *C. imperialis* skeleton.

Alphonse Forrer (1836–99) was born in London and studied languages in Switzerland before his emigration to the USA, where he participated in the American Civil War, siding with the North. After the war, he earned his living as a naturalist and collector, visiting at least western North America in 1880, the Tres Marias Islands in 1881, and mainland western Mexico in 1882 (Breninger 1899, Salvin & Godman 1888–1904, Sharpe 1906). Thus, after decades of political turmoil there lasting from the 1840s until about 1880 (Brown & Clark 2009), Forrer was among the first collectors to visit Mexico and obtain specimens of *C. imperialis* since the 1830s (Sharpe 1906: 368, Prÿs-Jones 2011).

According to Sharpe (1906: 353), the first series of Forrer's Mexican bird collections was obtained by F. D. Godman; this included a pair of *C. imperialis* skins collected in January (no year on label), passed to Godman in 1882 and which subsequently formed part of the great Godman and Salvin donation of Neotropical birds to NHMUK from 1885 (Sharpe 1906: 366). However, Edward Hargitt, who specialised in the study of the Picidae, also acquired a pair of Forrer's *C. imperialis* skins collected on 15 February (no year on label) that NHMUK purchased along with more than 1,800 of his other woodpeckers in 1897 following his death (Sharpe 1906: 380). Moreover, two additional skins of *C. imperialis* collected by Forrer are in the collections of the Natural History Museum, Vienna (Snyder *et al.* 2009; H.-M. Berg *in litt.* 2020), and the Senckenberg Museum Frankfurt am Main holds yet another (SMF 32083) that

was also collected by Forrer at La Ciudad, in Durango, on 15 February (year missing) and acquired from him by Count Berlepsch in December 1882 (G. Mayr *in litt.* 2020). However, no information appears to be available concerning the fate of Forrer's second *C. imperialis* skeleton mentioned in his 1886 correspondence with NHMUK; in this context, USNM and AMNH acquired their skeletons from other sources (Snyder *et al.* 2009, AMNH 2020). As a naturalist who made his living from collecting, very probably Forrer sold this valuable specimen during his lifetime, although on his death in California on 15 March 1899 he retained a substantial residual collection that was shortly thereafter put up for sale by his wife (Barlow 1900, Forrer 1900).

What then can we conclude regarding the identity and provenance of the hitherto unidentified NHMUK skeleton under discussion? First, we are confident that it is a skeleton of *C. imperialis*, one of only three currently known of a now extinct species. Second, we believe that on balance of probability it is extremely likely to be the otherwise missing Forrer skeleton 1886.9.9.1. The multiple documentation confusions that clearly occurred historically concerning this important specimen are quantitatively particularly egregious, especially in light of its rarity, but in our experience qualitatively by no means unique.

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Avifauna of the Adelbert Mountains, New Guinea: why is Fire-maned Bowerbird *Sericulus bakeri* the mountains' only endemic bird species?

by Jared Diamond & K. David Bishop

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SUMMARY.—The Adelbert Mountains, one of ten outlying ranges along New Guinea's north and north-west coasts, surprised ornithologists when their first exploration by Western scientists yielded the striking endemic Fire-maned Bowerbird *Sericulus bakeri*. It was then another surprise when further exploration revealed no other distinctive endemic. We summarise previous Adelbert studies and our four explorations including a survey of the highest summit. A total of 71 upland species has been recorded from the Adelberts, all of them also present as the same species or (in the case of *S. bakeri*) same superspecies on other outliers. The Adelberts are exceptional among low-elevation outliers in harbouring populations of seven upland species shared only with much higher outliers. The Adelberts are unique in supporting populations of ten upland species compressed at the highest elevations into a narrow elevational band below the summit. The elevational floors of those species lie a much shorter distance below the summit than for any species on any other outlier. In explanation, we propose the hypothesis that, among outliers, the Adelberts are especially accessible to colonisation by upland species from other upland areas, with two consequences: endemism is almost non-existent in the Adelberts except *S. bakeri*; and high-elevation populations of the Adelberts may be subsidised by colonists from other upland areas. The highest-elevation populations may have disappeared during the mid-Holocene hypsithermal and subsequently recolonised, further contributing to the lack of endemism. The Adelbert upland avifauna is more closely related, in presence / absence and taxonomic relationships, to that of the nearby Huon Mts. to the east than to the avifauna of the more distant North Coastal Range to the west. That suggests why the Adelberts support *S. bakeri* as such a distinctive endemic but the rest of their avifauna is undifferentiated: *Sericulus* is the only upland superspecies of north New Guinea that reaches its eastern distributional limit in the Adelberts; and its low elevational floor permitted it, but not higher-elevation species, to survive upwards shifts in range during the hypsithermal. An appendix summarises all 235 species recorded from the Adelberts, our observations of their elevational range and abundance, and their names in two local mountain languages of the Adelberts.

Along the north and north-west coasts of New Guinea lie ten isolated mountain ranges rising from the lowlands, lower in elevation and poorer in species than New Guinea's Central Range that forms the island's west / east axis (Fig. 1). In previous papers we described the avifaunas, especially the upland avifaunas, of three of those ranges (Foja, Fakfak and Kumawa: Beehler *et al.* 2012, Diamond & Bishop 2015), and of one former outlier that is now an island (Yapen: Diamond & Bishop 2020). The present paper describes the avifauna of the fourth lowest and nearly the least isolated of the outliers, the Adelbert Mts.



Male (left) and female Fire-maned Bowerbird *Sericulus bakeri*, the endemic bowerbird of the Adelbert Mountains (William Cooper, reproduced from Cooper & Forshaw 1977, with the kind permission of Dr Wendy Cooper)

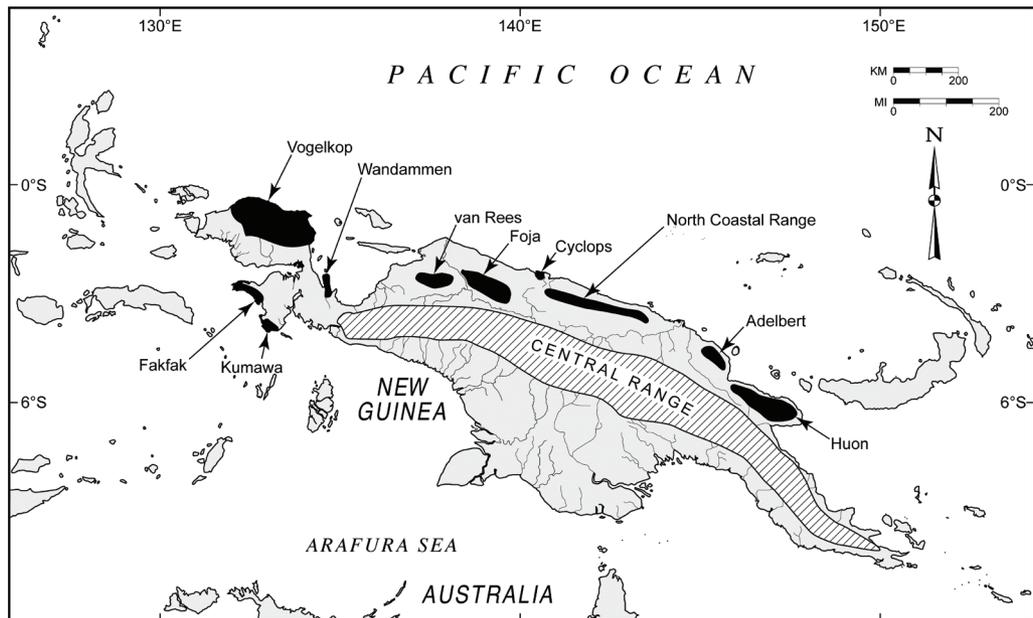


Figure 1. New Guinea's principal mountain ranges: the Central Range forming New Guinea's backbone; and the ten outlying ranges along the north and north-west coasts, from Huon and Adelbert in the east, to Fakfak and Kumawa in the west.

Four features make the Adelberts of particular interest. First, the Adelberts are home to one of the most spectacular, surprising, distinctive and beautiful discoveries of modern New Guinea ornithology: the Fire-maned Bowerbird *Sericulus bakeri* (Gilliard 1969, Frith & Frith 2004; see painting). When its discovery was first recorded, its home range was erroneously recorded by its collector Rollo Beck as Madang. But Madang was one of New Guinea's largest towns, and was the ornithologically already well-explored former capital of German New Guinea (Chapin 1929). Ever since Gilliard proved in 1959 that the bowerbird's range is actually the Adelberts, the question has remained: why is such a distinctive species endemic to such an unlikely location, a low mountain range close to a much higher and larger mountain range (the Huon Mts.; Fig. 2)?

Second, the search for *S. bakeri* was motivated partly by the hope that the home of such a distinctive endemic would also prove to harbour other distinctive undiscovered endemics. Indeed, until LeCroy & Diamond (2017) rediscovered Beck's diary and specimen register, and found that Beck had labelled the bowerbird's collecting site as Madang for banal reasons, it was believed that Beck had intentionally mislabelled the locality in order to preserve for himself the option of returning and discovering other new species (Gilliard 1969, Frith & Frith 2004). In fact, subsequent explorations of the Adelberts yielded not only no further distinctive endemic species but just two endemic subspecies, both of them barely worth recognising (Gilliard & LeCroy 1967, Pratt 1982, Beehler & Pratt 2016). How could no other distinctive taxon have evolved in a mountain range that generated one endemic that is so distinctive?

Third, subsequent explorations did reveal that the Adelberts are home to non-endemic populations of some upland species that are otherwise restricted to much higher mountain ranges of New Guinea, such as Superb Bird of Paradise *Lophorina superba* and the Papuan Lorikeet superspecies *Charmosyna [papou]*. (Here and elsewhere, we adopt the usual

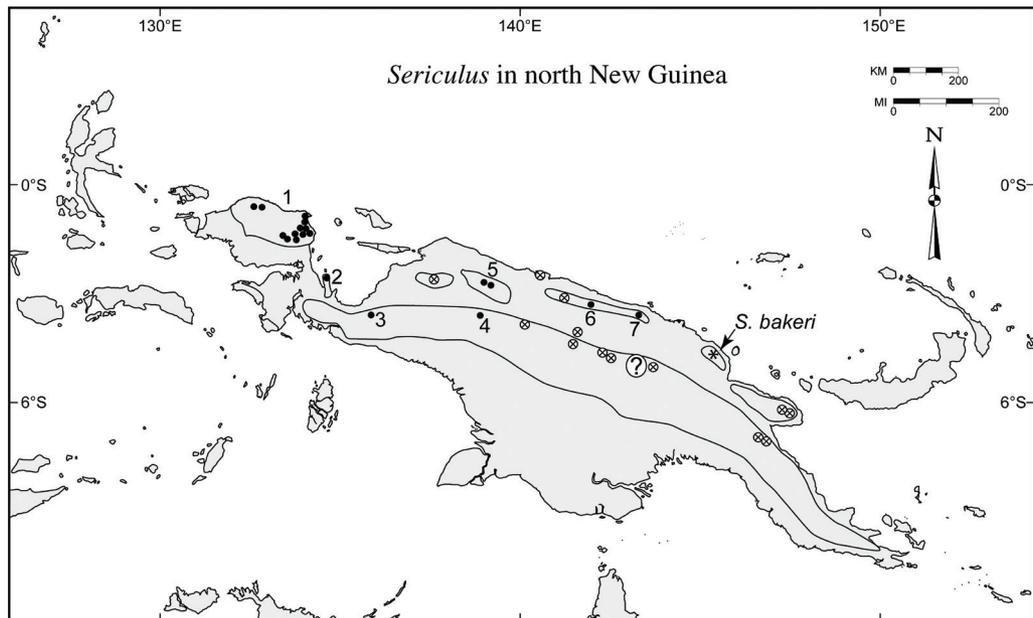


Figure 2. Presence and absence of *Sericulus* bowerbirds on New Guinea's northern watershed, modified from Diamond (1969). Each filled dot represents records by one observer. There are only seven documented areas of occurrence of the allospecies Masked Bowerbird *S. aureus*, numbered from west to east, with observer names in parentheses: 1 = Tamrau Mts. (E. T. Gilliard and B. M. Beehler) and Arfak Mts. (many observers) of the Vogelkop. 2 = Wandammen Mts. (E. Mayr). 3 = Weyland Mts. (F. Shaw-Mayer). 4 = Bernhard Camp (A. Rand). 5 = Foja Mts. (B. M. Beehler and J. Diamond). 6 = Mt. Nibo (J. Diamond). 7 = Mt. Turu (J. Diamond). The asterisk depicts the range of the allospecies Fire-maned Bowerbird *S. bakeri* in the Adelberts. X = areas surveyed intensively without finding any *Sericulus*. ? = an undocumented report of *S. aureus* from the Jimi River. Except for the latter, *S. aureus* is known mainly from outlying ranges (locations 1, 2, 5, 6 and 7). There are only two documented localities for it in the Central Range (3–4), and there is a large gap between the easternmost record of *S. aureus* (7) and the range of *S. bakeri*. The remaining *Sericulus* allospecies in New Guinea is Flame Bowerbird *S. ardens* of the southern watershed.

convention of denoting a superspecies by square brackets.) How can the Adelberts support those populations despite the Adelberts' modest elevation?

Finally, ten species are confined in the Adelberts to a narrow altitudinal band extending only *c.* 100 m below the highest summit. In all other well-explored New Guinea outliers, the highest-elevation populations extend at least 265 m, in some cases even 1,500 m, below the summit. How can those Adelbert populations survive when crammed into such a narrow altitudinal band, presumably supporting only a small population doubtfully sustainable in isolation?

We shall address these and other questions in light of our four explorations of the Adelberts, including their summit, in the years 2001, 2002, 2004 and 2006. We review and summarise records of other observers in a table listing all species known to have been recorded in the Adelberts.

Background

Environment and people.—The environment and people of the Adelberts are important for understanding the origins of the Adelbert avifauna, and the history of its ornithological exploration. The Adelbert Mts. rise from the lowlands of New Guinea's north-east coast (Fig. 1). The nearest mountains are those of the Huon Peninsula to the south-east, separated

from the south-eastern Adelberts by the narrow Gogol River valley. The narrow Ramu River valley in turn separates the Huon Mts. to the north from the Central Range to the south, but broadens to the west to constitute a wider lowland gap between the south slopes of the Adelberts and the north slopes of the Central Range. A much broader gap, formed by the Sepik River and its marshy lowland basin, separates the Adelberts from the nearest outlying range to the west, the North Coastal Range. Hence upland habitats in the Adelberts are closest to those of the Huon Mts., then to those of the Central Range, and further from those of the North Coastal Range (Fig. 3).

The chain of the Adelberts lies along a south-east / north-west axis, rising towards the north-west. The highest peak is Mt. Mengam near the chain's north-west end, whose elevation we determined as 1,675 m by ascending it and measuring the elevation repeatedly with our altimeters. Because Mt. Mengam is at the end of the chain furthest from the coastal town of Madang and was recognised only in the 1970s to be the tallest Adelbert peak (T. K. Pratt pers. comm.), it was not explored ornithologically until 1974 by Pratt and colleagues and in 2004 by us. Earlier explorations of the Adelberts by Beck, Gilliard and Ziegler were of lower but more accessible mountains to the south-east.

Rainfall in the Adelberts is highest in December–March and lowest in August–October (Brookfield & Hart 1966, McAlpine *et al.* 1975, Tupper 2012). However, seasonality is modest, and rainfall in the wettest months is barely double that in the driest months. Annual rainfall at the two recording stations closest to our field sites, Wanuma and Saruga, is 320–340 cm.

The Adelbert terrain is sandstone formed into steep, narrow, razorback ridges separated by deep narrow valleys. Even by the standards of montane New Guinea's generally rugged terrain with which we are familiar, the Adelberts rank as especially difficult for travel. In our helicopter flights over the Adelberts, we saw no large level-ground area.

That terrain has several consequences relevant to ornithologists. First, there is no motor vehicle road at higher elevations within the Adelberts, and only one landing strip for small fixed-wing aircraft (at Wanuma, 22 and 29 km south-east of our two study sites). Second, that lack of transport impedes commercial logging, and the terrain's steepness compels villagers to seek small favourable patches for their gardens, so that the Adelberts are still largely covered by rainforest. Third, the terrain's difficulty, and the chronic warfare and fierce reputation of its inhabitants, explain why the Adelberts remained unknown to Europeans for so long, despite their proximity to the German colonial capital of Madang (Friedrich-Wilhelmshafen)—and why the discovery of *Sericulus bakeri* at 'Madang' (see below) occurred so late and caused such astonishment. Only one additional bowerbird species (Archbold's Bowerbird *Archboldia papuensis*) and one bird of paradise (Ribbon-tailed *Astrapia Astrapia mayeri*) were discovered after *S. bakeri*, both of them in remote areas of the Central Range.

Information about European contact in our two study sites comes from our conversations with older villagers, and from the linguist Ian Tupper (2012). Stone tools were abandoned, and steel tools began to be acquired by trade from the coast, only in the 1940s. There was never any contact with a foreign patrol during German colonial times, which ended in 1914. Australian patrols did not visit the Adelberts until 1944. The first missionary visit to our study site of Kangaragate was in 1959, and the first mention (by a missionary linguist) of the Pamosu language spoken at our other study site of Munggur was in 1975. Chronic warfare was late in disappearing: our Kangaragate hosts told us that warfare compelled them to abandon their homeland in 1949, and that they could not make peace and return until 1982. That chronic warfare, plus the rugged Adelbert terrain, contribute to explaining why Beck and Gilliard collected only up to 760 m and about 1,220 m, respectively, and depended on native collectors to go further: because it would have been too dangerous for

a European to do so. Even at the time of our 2004 and 2006 visits, few of the villagers at our two study sites had travelled, worked or lived outside their language area.

As mentioned above, arable land occurs in only small patches, and gardens are small and scattered. For example, we encountered an isolated garden c.1 km from the summit of Mt. Mengam, more than an hour's walk from Munggur village even for the briskly trotting villagers. Hence people traditionally spent most of their time in garden houses and scattered hamlets. While Australian patrols and then the Papua New Guinea government tried to induce people to gather in villages, Australian patrol reports mention finding few people in the villages, because they were instead mostly in their garden houses. In such small-scale societies there were no hereditary chiefs.

Subsistence traditionally depended on gardens producing yams as the major crop, plus taro, bananas, sago, *Pandanus*, and the introduced crop cassava. The only domestic food animals, pigs and chickens, yield little meat: pigs are saved to be slaughtered at a big feast held every year or two. Instead, protein is obtained mainly by hunting wild mammals.

Languages.—While New Guinea is famous for having the world's highest language diversity, the Adelberts are diverse even by New Guinea standards. Approximately 60 languages, all of them confined to the Adelberts, are spoken in an area of about 7,000 km² (Lewis 2009). Hence the area occupied by the average language is c.120 km², and the average cross-section of a language area is only about 11 km. (These numbers refer to mutually unintelligible languages, not mere dialects.)

That diversity is a consequence of New Guinea's and the Adelberts' rugged terrain, chronic warfare impeding travel, long history of human occupation (c.60,000 years) and lack of political unification until colonial times (Foley 1986). With one exception, New Guinea languages fall into dozens of language families that are strictly or almost entirely confined to New Guinea, and that have no demonstrable relationship to each other or to any other language family in the world. Most Adelbert languages belong to the largest of those families, the Trans-New Guinea family, whose extent is attributed to population expansions associated with New Guinea's independent development of agriculture within the last 10,000 years. The sole exception is the Austronesian language family that spread from Taiwan to Polynesia, reaching New Guinea about 3,500 years ago, and that is represented mainly in the lowlands of northern New Guinea. Five Austronesian languages, presumed to have arrived with recent invaders, are spoken in small Adelbert coastal enclaves and south of the Gogol River near the Adelberts.

The languages at both of our study sites belong to the so-called Madang subgroup of the Trans-New Guinea family. The Pamosu language, with about 1,500 speakers, is that spoken at Munggur and four nearby mountain villages. The Aiti language, with about 3,300 speakers, is spoken at Kangaragate and some neighbouring villages. (Kangaragate villagers insisted to us that Aiti is the name of their language, although it appears to be referred to as Mum or Katiati in Lewis 2009.) These are the two languages whose names for bird species we used in our conversations with villagers, and which we provide in Appendix 1 for the convenience of future ornithologists wishing to find *Sericulus bakeri* and other Adelbert bird species. It will be apparent from Appendix 1 that the two sets of names are almost entirely different, illustrating the mutual unintelligibility of those two related languages spoken only 9 km apart.

Previous ornithological studies.—Although numerous collectors obtained bird specimens near the German colony coastal capital of Madang from the 1880s onwards, the first collection in the Adelberts just inland of Madang was not made until 1928–29, by the professional collector Rollo Beck. On Beck's return from eight years as leader of the American Museum of Natural History's (AMNH) Whitney South Sea Expedition, the

museum paid Beck to conduct further collecting in New Guinea, thereby helping Beck deal with personal financial difficulties (LeCroy & Diamond 2017). Beck evidently received no specific instructions about where in New Guinea to collect, and he had no opportunity to familiarise himself in advance with its birds. Instead, it seems likely that, after Beck landed in Madang, he selected the nearby Adelberts as his first field site merely because missionaries could arrange for him to stay at their stations there.

Beck's Adelbert itinerary, including his collecting locality for *Sericulus bakeri*, remained unknown for many decades, because Beck initially labelled the sites of all of his Adelbert specimens simply as 'Madang'. He adopted this practice because he had previously been collecting on smaller Pacific islands where differences between sites on the same island were unimportant. Only recently did Mary LeCroy (*in* LeCroy & Diamond 2017) reconstruct Beck's itinerary from his diary and specimen registers. LeCroy showed that Beck collected at four sites in and near the Adelberts between August 1928 and January 1929: Madang itself, on the coast; Nobonob, a lowland mission station near Madang at the foot of the Adelberts; Maban, at an elevation of a few hundred feet (Beck's estimates are in feet, not metres) on the Gogol River in the Adelberts' southern foothills; and Meganum only c.9 km from Maban at an elevation of 1,200 feet. From Meganum, Beck himself collected up to approximately 2,500 feet, and his local collectors spent three days further inland and probably at somewhat higher elevations. Beck himself could go no further, because the Adelberts were still lethally dangerous for a European at that time. (Another of Beck's sites, Keku, was in the western foothills of the Huon Mts., not in the Adelberts, and is not to be confused with Keki Lodge now frequented by birdwatchers in the Adelbert foothills.)

Beck's Adelbert collections, housed at AMNH, comprised 502 specimens of 129 species (Table 1 of LeCroy & Diamond 2017). Only 11 of those species were upland taxa (records listed in Appendix 1), almost all of them obtained while Beck was based at Meganum—including *Sericulus bakeri*, probably taken by Beck's local collector. All of those species are ones that we and other observers have found at elevations below 1,000 m, supporting the evidence from Beck's itinerary that he and his collector remained at modest elevations.

The next collection was made in 1959 by E. Thomas Gilliard, who was searching specifically for *Sericulus bakeri*. In the course of two months Gilliard and his New Guinean hunters reached elevations of c.1,220 m on Mt. Memenga in the south-eastern Adelberts and collected 385 specimens of 130 species, thereby adding 26 species to the list of Adelbert upland species (Gilliard & LeCroy 1967). That collection is also at AMNH.

In 1967 Alan Ziegler collected up to 1,100 m at Atitau and obtained 32 species, including 11 upland species, two of them (Black-bellied Cicadabird *Edolisoma montanum* and Russet-tailed Thrush *Zoothera heinei*) new records for the Adelbert upland avifauna. His collection, also housed at AMNH, was examined by one of us (JD) and by Pratt (1982).

In 1974 an expedition of the Wau Ecology Institute including Thane Pratt collected for two months and became the first collectors to reach the highest summit (Mt. Mengam, not to be confused with the lower Mt. Memenga reached by Gilliard). They added 25 upland species (Pratt 1982) including all but one of the high-elevation populations now known from the Adelberts. Those specimens are mostly housed at the Bishop Museum, Honolulu.

In 1985 C. B. Frith, D. W. Frith and Roy Mackay visited Mt. Mengam to seek *Sericulus bakeri* and to photograph MacGregor's Bowerbird *Amblyornis macgregoriae* at its bowers. Frith & Frith (1988) described the courtship display of Superb Bird of Paradise *Lophorina superba*. From 1985 to 1988 Mackay and others made five additional Adelbert visits, from which Mackay (1991) reported eight species not found by any previous or subsequent visitor to the Adelberts: Wattled Brushturkey *Aepyodius arfakanus*, Mountain Kingfisher *Syma megarhyncha*, Dimorphic Fantail *Rhipidura brachyrhyncha*, Friendly Fantail

R. albolimbata, Brown-backed Whistler *Pachycephala modesta*, Papuan Sittella *Daphoenositta papuensis*, Elfin Myzomela *Myzomela adolphinae* and Varied Honeyeater *Gavicalis versicolor*. Those records were queried or not accepted by Beehler & Pratt (2016). While an Adelbert population of *Aepyodius arfakianus* appears to us quite possible, and *Daphoenositta papuensis* and *Myzomela adolphinae* unlikely but not impossible, the other five records are in our opinion improbable. The two *Rhipidura* species and *Pachycephala modesta* are behaviourally or vocally conspicuous, are unlikely to have escaped Pratt and us if they had been present on Mt. Mengam's summit as claimed, and probably involved misidentified sightings of congeners that are common there. Especially unlikely is the report of *Gavicalis versicolor*, a strictly coastal species, reported at 700 m in the interior of the Adelberts. Out of caution we have not included these records in the Appendix but mention them here for the consideration of future observers.

In May 1999 Bruce Beehler and Kevin Vang observed 90 species at elevations of 500–900 m, including 17 upland species. Two of those (Red-fronted Lorikeet *Charmosyna rubronotata* and Banded Yellow Robin *Gennaodryas placens*) had not been previously reported for the Adelberts but were subsequently observed by us. In 2010 Beehler observed the rare Obscure Berrypecker *Melanocharis arfakiana* at Keki Lodge in the Adelberts (Beehler & Pratt 2016: 345).

We are aware of two other Adelbert collections that we cannot discuss because they have not been published and we have not examined them: that by William Peckover in 1969 (mentioned by Pratt 1982), housed at Yale's Peabody Museum; and the other by Brett Benz in 2007, housed at the Univ. of Kansas. A list of Benz's specimens that he kindly sent us reports one specimen of an upland species not otherwise known from the Adelberts, New Guinea White-eye *Zosterops novaeguineae*. That identification awaits confirmation because of the close resemblance in north-east New Guinea between that species and the abundant Black-fronted White-eye *Z. atrifrons* of the Adelberts.

Our study

We observed (but did not collect) Adelbert birds in 2001, 2002, 2004 and 2006. Our principal study was from 26 July to 15 August 2004 at two Adelbert sites that KDB selected during a previous helicopter visit: Munggur village (04°41.38'S, 145°14.64'E) at an elevation of 1,223 m, directly below the Adelberts' highest peak, Mt. Mengam; and Kangaragate village (04°39.34'S, 145°10.24'E) at 875 m, and c.8 km west-northwest of Munggur. The habitat around both villages consisted largely of forest, interrupted by scattered or regenerating gardens.

We arrived at Munggur by helicopter from Madang on the morning of 26 July and divided our time between two campsites: the village itself, and a mountain camp at 1,655 m on Mt. Mengam's summit ridge (04°42.13'S, 145°13.70'E), near Mt. Mengam's summit of 1,675 m (04°42.20'S, 145°13.83'E). We occupied the mountain camp on 30 July–2 August, and devoted those days plus 27–28 July to surveying the ridge for c.1 km west and east of the camp. From Munggur we descended the Ululu trail to 1,150 m, surveyed a trail west from and at the same altitude as the village, and ascended steeply to our mountain camp.

On the morning of 4 August 2004 we transferred by helicopter from Munggur to Kangaragate, where we again divided our time between two campsites: the village itself, and a mountain camp at 1,191 m (04°38.63'S, 145°94.67'E). From the mountain camp we surveyed up to 1,294 m above Musiamunat village. From Kangaragate we surveyed down to a pond at 835 m and a river at 639 m, and steeply up to Makokapi hamlet on

a ridge crest at 994 m, and up to the 1,260-m crest of the trail from Kangarangate to the coast. On the morning of 15 August we returned by helicopter to Madang.

In 2006 we again travelled by helicopter on 2 May from Madang to Munggur, and then on 4 May from Munggur to Kangarangate, before returning to Madang on 7 May. During those visits we remained within 1 km of each village. We observed five lowland species and one upland species that we had not observed in 2004.

On 12 August and 1 September 2001 and 27 July 2002 KDB made single-day trips by car to Keki Lodge (700–1,080 m, 04°41.49'S, 145°24.22'E). He observed 90 species, including nine lowland species and two migrant visitors that we did not subsequently see in 2004 or 2006.

Methods.—Our methods were similar to those that we described for our studies elsewhere in New Guinea (Diamond & Bishop 2015, 2020). Briefly, except KDB's visits in 2001 and 2002, all of our observations were made on foot trails, mostly within forest, in areas with no motor vehicle roads. We devoted much effort to recording vocalizations with Sony TCM 5000 EV tape recorders, playing back unidentified vocalisations in the field to attract and identify the singers, and re-listening to recordings in camp each day because our directional microphones often captured vocalisations that we had not noticed in the field. We stopped at fruiting and flowering trees where birds gathered. We began observing by 05.00 h to detect nocturnal birds. Elevations of all significant observations were measured using Thommen altimeters or a Garmin GPS. We did no collecting.

We were constantly accompanied by Munggur or Kangarangate villagers, who pointed out and identified birds seen and heard, informed us about their experience of each species, and described to us other species that lived in the area of their village, but which we did not encounter together. These conversations were undertaken in the language Tok Pisin, and the bird names used were in the local Pamosu or Aiti languages spoken at Munggur or Kangarangate. As we routinely do elsewhere in New Guinea, we went to much effort to identify these names, for several reasons: local people thereby helped us to identify birds seen or heard; they guided us to find species that we particularly wished to observe; they shared with us their lifelong knowledge of bird species in their environment; and they provided clear identifiable descriptions of 11 species that we did not encounter. Those 11 are denoted by square brackets in Appendix 1; all have been recorded by other European visitors to the Adelberts except the Palearctic winter visitor Grey Wagtail *Motacilla cinerea*, for which there is no other local record, but it is widespread in New Guinea's mountains during the boreal winter.

We elicited most of those names when we and our guide saw or heard a bird together. If there was any doubt as to which individual bird in the vicinity was being referred to, we confirmed the identity by asking our guide to describe the species named. Once we had accumulated many such names securely identified in the field, we elicited more by asking our guides to name and describe for us additional species that we and they had not yet encountered together, e.g., we asked them to describe nocturnal species, or ground-dwelling species, or species found near water, or species similar to ('brata bilong') species that we and our guide had already encountered. For example, after we and our Munggur guides had found several species of lorries that they named ('kirikirik' = Dusky Lory *Pseudeos fuscata*, 'ororovion' = Black-capped Lory *Lorius lory*), we asked them to name and describe other very similar birds that proved to be other species of lorries, then other somewhat similar birds with similar bills that proved to be other parrots. The Appendix gives the Pamosu and Aiti names that we identified in this way, so that future visitors to these villages can use the names in order to find particular species.

Results and Discussion

Species number.—The total number of species recorded from the Adelberts is 235 (Appendix). Of those, we observed 197 ourselves. Other visitors observed 37 species that we did not record. As already mentioned, one additional species (*Motacilla cinerea*) was reported to us by Adelbert residents, but not observed by us or by other visiting ornithologists.

Our focus here is on upland species, defined as those largely confined to sloping elevated terrain, and absent from the flat lowlands at or near sea level. We have found this definition more useful and less arbitrary than defining ‘montane species’ as species largely confined to elevations above some arbitrary specified elevation, such as 1,000 m or 1,700 m. We have discussed in more detail elsewhere (Diamond & Bishop 2015, 2020) the advantages of this definition, and the ambiguities and practical issues in applying it. By this definition, we recognise 71 Adelbert species as upland species (abbreviated S_{up}), denoted by an asterisk in the Appendix.

Let us place this number in context by comparing it with S_{up} values for New Guinea’s nine other outlying mountain ranges. One of those ranges (Van Rees) is much lower (1,262 m) and much poorer in upland species ($S_{up} = 37$) than the Adelberts. Two of them (Vogelkop and Huon) are much higher (2,954 and 4,121 m respectively) and richer in upland species ($S_{up} = 129$ and 127 respectively) than the Adelberts. The remaining six are more comparable to the Adelberts, with elevations of 1,400–2,218 m, and S_{up} values from 44 to 95 species.

Table 1 summarises, for all ten mountain ranges, their elevations, S_{up} values, and numbers of upland species shared with the Adelberts. The following conclusions emerge from Table 1.

First, the number of upland species in a mountain range increases with the range’s elevation, from 37 to 129 species. That is, as one expects, in accordance with experience gained from mountains elsewhere in the world: greater elevation translates into more

TABLE 1
Upland avifaunas of the Adelberts and the other outliers.

Outlier	Elevation (m)	S_{up} (species)	S_{up} shared with Adelberts	% Shared
Van Rees	1,262	37	30	42%
Fakfak	1,400	65	42	59%
Kumawa	1,654	72	48	68%
Adelbert	1,675	71		
NCR	1,886	78	50	70%
Wandammen	2,075	77	50	70%
Cyclops	2,160	44	29	41%
Foja	2,218	95	56	79%
Vogelkop	2,954	129	65	92%
Huon	4,121	127	64	90%

Column 1. NCR = North Coastal Range.

Column 3: the number of upland species on that outlier.

Column 4: the number of upland species shared between that outlier and the Adelberts.

Column 5: Column 4, as a percentage of the Adelberts’ S_{up} value of 71.

Note that an outlier’s S_{up} , and the percentage of Adelbert species shared with the outlier, tend to increase with outlier elevation, but that the Cyclops fall below this trend.

TABLE 2
Upland species distributions on the Adelberts and other outliers.

No. of outliers occupied	No. of upland species occupying that no. of outliers	No. of Adelbert upland species
0	35	0
1	28	0
2	19	4
3	17	4
4	14	7
5	14	9
6	10	1
7	10	9
8	20	12
9	17	16
10	9	9
Total	193 species	71 species

Columns 1 and 2 are from Table 3 in Diamond & Bishop (2020). For each of New Guinea's 193 upland species, we tabulated how many of New Guinea's ten outliers that species occupies. That number (column 1) ranges from zero (no outlier occupied) to ten (all ten outliers occupied).

Column 3: number of Adelbert upland species falling within that species class. For example, the next-to-last row indicates that there are 17 upland species occupying nine outliers, and that 16 of those 17 occur in the Adelberts.

'niches', i.e. more opportunities for elevationally specialised species. The same trend is more weakly evident for the seven comparable ranges (the Adelberts and the other six), partly because their span of elevations is modest (only 1,400–2,218 m). The other disturbance of the trend arises from the flagrantly low S_{up} value of only 44 species in the Cyclops, although they are second-highest of the seven comparable ranges. Evidently, elevation is not the only factor influencing S_{up} values. Some others include area of upland habitats, and extensive flat lowlands isolating a mountain range from other ranges. The Cyclops, although they are high, are small in area.

Second, although New Guinea has approximately 193 upland species or superspecies (Diamond & Bishop 2020), the Adelberts share most of their upland species (59–79%) with five of the other six comparable ranges. (The outlier is again the species-poor Cyclops.) The percentage of Adelbert species shared increases with the S_{up} value of the range compared, from 41–42% for the most species-poor (Van Rees and Cyclops) to 92% for the most species-rich (Vogelkop). That is as one would expect if richer ranges tended to contain those of poorer ranges plus additional species.

If each range contained a random sample of New Guinea's 193 upland species, one would not expect such high sharing among seven samples of only 44–95 species each. That outcome suggests that some species are disproportionately good colonists and succeed in establishing themselves on many isolated mountain ranges. The next section explores this interpretation systematically.

Species identity.—Table 2 provides a systematic test of the suggestion that some upland species are disproportionately able colonists of outlying ranges, and that the upland avifauna of the Adelberts (as well as of the other outliers) is enriched in such species. For each of New Guinea's approximately 193 upland species or superspecies, we calculated

TABLE 3
Number of 'restricted' upland species on each outlier.

Outlier	Elevation (m)	No. of one-range species	No. of two-range species	No. of three-range species	Total restricted species
Huon	4,121	18	16	12	46
Vogelkop	2,954	10	15	14	39
Foja	2,218	--	1	7	8
Cyclops	2,160	--	--	--	0
Wandammen	2,075	--	--	1	1
NCR	1,886	--	2	4	6
Adelberts	1,675	--	4	3	7
Kumawa	1,654	--	--	4	4
Fakfak	1,400	--	--	2	2
Van Rees	1,262	--	--	1	1

'Restricted' upland species are those restricted to just one, two or three of the ten outliers. Columns 1–2 are from Table 1, but in reverse order.

Column 3: of the 28 upland species restricted to just one outlier, how many occur on each outlier?

Column 4: of the 19 species restricted to just two outliers, and column 5: of the 17 species restricted to just three outliers, how many occur on each outlier? For example, the 19 species restricted to two outliers have $19 \times 2 = 38$ outlier populations, of which most are on Huon (16 populations) or Vogelkop (15 populations), the two highest outliers.

Column 6: total number of restricted populations on each outlier: the sum of columns 3–5.

Note that the number of restricted populations tends to increase with outlier elevation, but the high but small Cyclops and Wandammen have fewer than expected, and Adelberts have more than expected. See text for discussion.

on how many of the ten outliers that species occurs. Those calculations are summarised in columns 1–2 of Table 2. That number ranges from zero for species of the Central Ranges present on no outlier (e.g., Sooty Honeyeater *Melionyx fuscus*), to one for species present on just a single outlier (e.g., Papuan Treecreeper *Cormobates placens*, present only on the Vogelkop), to ten for species present on all ten outliers (e.g., White-eared Bronze Cuckoo *Chalcites meyerii*).

As we noted previously (Diamond & Bishop 2020: Table 3), many upland species occur on no outlier (35 species) or on only a few outliers (e.g., 28 species confined to a single range). Few species (14, ten and ten) occur on an intermediate number of outliers (five, six or seven outliers, respectively), but somewhat more species (20, 17 or nine) occur on most or all outliers (eight, nine or ten outliers, respectively). That is, New Guinea upland species are not randomly distributed in colonising ability: there is instead a large excess of unsuccessful colonists, and a smaller excess of very successful ones.

Consider the Adelberts from this perspective (column 3 of Table 2). Inevitably, all nine species that occur on all ten of the outliers occur on the Adelberts. Unsurprisingly, most species present on the majority but not all outliers also occur on the Adelberts (e.g., 16 of the 17 species on nine outliers). Also inevitably, the 35 species absent on outliers do not occur on the Adelberts. Most of those 35 are high-elevation species of the tall (5,000 m) Central Range, for which the outliers provide no or little high-elevation habitat. The 28 species confined to a single outlier are also mostly confined to elevations above 1,500 m, with the result that all of them are confined either to the highest (Huon, 4,121 m) or second-highest outliers (Vogelkop, 2,954 m) (Table 3, column 3).

A surprising result involves species present on just two or three outliers (Table 3, columns 4–5). Because species restricted to a single outlier prove to be confined to either of the two highest outliers, one might guess by extrapolation that, for species restricted to 2–3 outliers, the number of populations would just increase with outlier elevation: the highest outliers would have the most such ‘restricted’ populations, and the next highest would have the next most. In partial accord with this expectation, the two outliers that are by far the highest (Huon and Vogelkop) far exceed all other outliers in their numbers of restricted populations (46 and 39 species, respectively), while the next highest outlier (Foja) has the third-largest number (eight species). But the next two-highest outliers, Cyclops and Wandammen, have zero and one restricted populations, respectively. Instead, the next-highest number of restricted populations, seven, is on the Adelberts, despite their being fourth from last in elevation among the ten outliers!

Those seven Adelbert populations (Table 4) are shared only with the much higher Vogelkop or Huon (five shared populations each). For three of those seven restricted species in Table 4, we should not attribute significance to their absence from low outliers other than the Adelberts, because two of the species (*Melanocharis arfakiana* and Papuan Parrotfinch *Erythrura papuana*) are very rare and cryptic, and the third (Dimorphic Jewel-babbler *Ptilorhoa geislerorum*) is almost confined to New Guinea’s north-east corner. But three others of those seven Adelbert species absent from other low outliers (Stella’s Lorikeet *Charmosyna [papou] stellae*, Marbled Honeyeater *Pycnopygius cinereus* and Ornate Melidectes *Melidectes torquatus*) are common vocal species confined in the Adelberts to the highest elevations. Why do those high-elevation species succeed in maintaining small populations at the top of the Adelberts, but not on the other low outliers, four of which are higher than the Adelberts?

Table 5 lists all ten species for which we have sufficient observations to suggest that their Adelbert populations were confined during our study to within 150 vertical metres of the Adelbert summit (1,675 m). Among the outliers, the Adelberts are unique in this respect. For the seven other outliers for which we have sufficient information concerning elevational ranges, Table 6 summarises how far below the summit is the highest elevational floor of any species. For example, in Kumawa, whose summit is at 1,654 m, the highest floors are of a

TABLE 4
Adelbert populations of ‘restricted’ upland species. This table names the ‘restricted’ upland species that occur in the Adelberts, and that constitute the seven entries for the Adelberts in the right-hand column and row 7 of Table 3.

	Species	No. of outliers	Other outliers	
	Stella’s Lorikeet	<i>Charmosyna [papou] stellae</i>	3	Huon, V
	Marbled Honeyeater	<i>Pycnopygius cinereus</i>	3	Huon, V
	Ornate Melidectes	<i>Melidectes torquatus</i>	3	Huon, V
	Obscure Berrypecker	<i>Melanocharis arfakiana</i>	2	V
	Slaty-headed Longbill	<i>Toxorhamphus poliopterus</i>	2	Huon
	Dimorphic Jewel-babbler	<i>Ptilorhoa geislerorum</i>	2	Huon
	Papuan Parrotfinch	<i>Erythrura papuana</i>	2	V

Column 3: the number of outliers to which each species is restricted.

Column 4: the outliers other than the Adelberts on which the species occurs (V = Vogelkop). The Adelberts are unusual among the four lowest outliers in having many populations of restricted species: the two other outliers listed in column 4 as sharing these restricted species are much higher than the Adelberts.

TABLE 5
Adelbert species with high elevational floors.

	Species	Floor (m)	Other outliers
Forbes's Forest Rail	<i>Rallicula [leucospila] forbesi</i>	1,525	Huon, V, Cyclops, Wand, Foja, NCR, Kum
MacGregor's Bowerbird	<i>Amblyornis [inornata] macgregoriae</i>	1,525	Huon, V, Wand, Foja, Kum, Fak
Marbled Honeyeater	<i>Pycnopygius cinereus</i>	1,580	Huon, V
Large Scrubwren	<i>Sericornis nouhuysi</i>	1,535	Huon, V, Foja, Kum
Buff-faced Scrubwren	<i>Sericornis [rufescens] perspicillatus</i>	1,590	Huon, V, Foja, NCR, Kum
Brown-breasted Gerygone	<i>Gerygone ruficollis</i>	1,590	Huon, V, Wand, Foja, Kum, Fak
Rufous-naped Bellbird	<i>Alcedryas rufinucha</i>	1,545	Huon, V, Wand, Foja, NCR, Kum, Fak
Slater's Whistler	<i>Pachycephala soror</i>	1,570	Huon, V, Kum, Fak
Superb Bird of Paradise	<i>Lophorina superba</i>	1,570	Huon, V, Wand
Black-capped Robin	<i>Heteromyias [albispecularis] armiti</i>	1,570	Huon, V, Foja, Kum

These ten species have the highest Adelbert elevational floors that we measured. Last column: the other outliers on which each species occurs. Abbreviations: V = Vogelkop, Wand = Wandammen, Kum = Kumawa, Fak = Fakfak, NCR = North Coastal Range. Note that these species mostly occupy outliers higher than the Adelberts: all ten occur on both of the highest outliers (Huon and Vogelkop), only four are present on the second-lowest outlier (Fakfak), and none is on the lowest (Van Rees).

smoky honeyeater *Melipotēs* sp. and Regent Whistler *Pachycephala schlegelii*, both at 1,389 m. That is, those species are compressed into an elevational band extending 265 m below the summit. That minimum elevational range of high-elevation populations is between 265 and 299 m for the four lowest mountains of Table 6 other than the Adelberts, and 541, 954 and 1,521 m for the three highest mountains in order of elevation. As an explanation for that increase in minimum elevational range on the highest mountains, we note that ambient temperature, hence productivity, decreases with elevation. Therefore, populations confined to the summits of the highest mountains require a larger area of habitat, and so a greater elevational range, to sustain some minimum population size than those confined to the summits of lower mountains.

Thus, Table 5 suggests that in the Adelberts the highest-elevation populations are compressed into a narrower elevational band, and presumably have smaller populations, than on other outliers of similar elevation. But there is a caveat; of the ten species listed in Table 5, Pratt (1982; pers. comm.) reported nine as extending to lower elevations than we do. Probable contributory factors for this difference include the following. (1) Pratt *et al.* spent more time (22 days) at elevations of 1,400–1,600 m than did we (six days), potentially allowing them to pick up more low-elevation records. (2) We recorded precise elevations for every significant observation (e.g., 1,545 m), while Pratt's reported elevation ranges are general (e.g., '1,400–1,600 m', or 'down to 1,400 m'). (3) Pratt collected not only on Mt. Mengam at or somewhere near our highest camp, but also at another site, Kowat, that provided lower elevations of 1,200–1,400 m. Hence the three of the ten species in Table 5 that Pratt recorded at Kowat certainly reached elevations lower—during Pratt's study—than the floors of 1,525 m or higher that we found on Mt. Mengam in Table 5. However, for the other seven species in Table 5, Pratt's generalised elevation ranges are compatible with the precise apparent floors of 1,525 m or higher that we measured. (4) Pratt's study was in 1974, but ours was in 2004. In the intervening three decades, global warming caused bird elevational ranges to shift upwards on New Guinea's mountains (Freeman & Class Freeman

TABLE 6
Summit elevations and highest elevational floors.

Outlier	Summit (m)	Highest floor (m)	Extent (m)
Van Rees	1,262	965	297
Yapen	1,430	1,160	270
Kumawa	1,654	1,389	265
Adelbert	1,675	1,590	85
North Coastal Range	1,886	1,587	299
Foja	2,218	1,677	541
Vogelkop	2,954	2,000	954
Huon	4,121	2,800	1,521

The third column is the elevational floor of the species with the highest floor on that mountain. Sources: our published observations for Yapen (Diamond & Bishop 2020), Kumawa (Diamond & Bishop 2015), Foja (Beehler *et al.* 2012) and Adelbert (this paper); our unpublished observations for Van Rees, North Coastal Range and Vogelkop; and Mayr (1931) for Huon.

The fourth column ('extent') is the second column minus the third column: i.e., the potential elevational range, on that outlier, of that species with the highest floor, if it could occupy the entire elevational span from its floor to the summit. Note that extent is lowest for the Adelberts, and that for other outliers it is greater for higher outliers.

2014) and on tropical mountains elsewhere in the world. On p. 91 we shall discuss further consequences of those shifts for the Adelbert avifauna.

Why are the Adelberts unusual among New Guinea's outliers (perhaps more so in 2004 than in 1974) in the high floors, narrow elevational bands, and small populations of their highest-elevation populations? We suggest two contributing factors: proximity to much higher and larger mountain ranges, permitting immigration from the latter to augment small Adelbert populations that would otherwise not be viable; and climate fluctuations.

Proximity of the Adelberts to higher and larger mountain ranges.—Examination of a map and of contours reveals that the Adelberts are the least isolated, or one of the least isolated, of New Guinea's ten outliers. Only *c.*15 km of low-elevation forest in the narrow Gogol River valley separates the southern foothills of the Adelberts from the western foothills of the mountains of the Huon Peninsula, which in turn are separated from the foothills of the Central Range by the even narrower upper Ramu River valley (Fig. 3). The distance between the Adelbert Mts. and the Huon Mts. across the Gogol River is 18 km or 12 km at the 500-m or 300-m contours, respectively. The corresponding distance between the Huon Mts. and the Central Range across the Ramu River is only 5 km at the 500-m contour; and these ranges are connected at the 300-m contour. (We are grateful to I. Woxvold for these measurements and for Fig. 3.) In contrast, the North Coastal Range is separated along most of its length from the Central Range by the broad Sepik Basin, *c.*100 km wide; the Foja and Van Rees Mts. are separated from the Central Range by the Lake Plains, *c.*50 km wide; the Kumawa and Fakfak Mts. are both isolated by 70–100 km of flat lowlands; and the Cyclops Mts. are isolated by undulating but low terrain. Perhaps the Adelberts are sufficiently accessible to the Huon and the Central Range that the small populations of the Adelberts' ten high-elevation species listed in Table 5 are not truly isolated, but are augmented by immigrants from high elevations in the Huon and Central Range. Seemingly *contra* this admittedly speculative interpretation stands the feature for which the Adelbert avifauna is famous: its distinctive endemic bowerbird allospecies *Sericulus bakeri*.

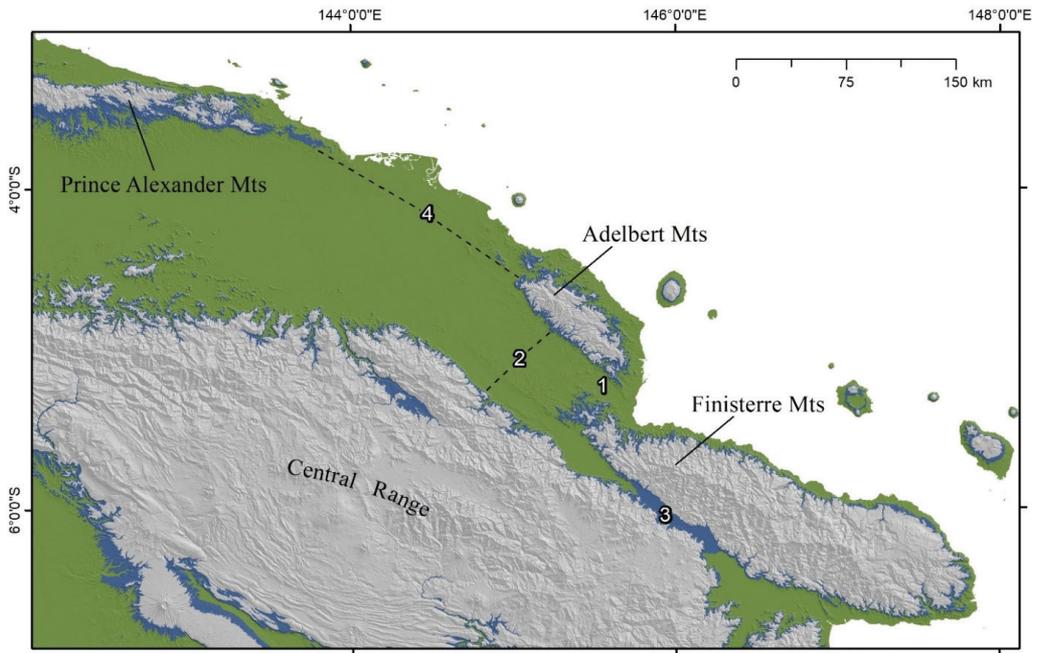


Figure 3. Terrain map of north-east New Guinea. Areas above 500 m are coloured grey; areas between 300 and 500 m blue; and areas below 300 m green. 1 = the Gogol River valley, between the Adelbert Mts. to the north and the Finisterre Mts. of the Huon Peninsula to the south. 2 = the Ramu River valley, between the Adelberts to the north-east and the Central Range to the south-west. 3 = the upper Ramu River valley and its headwaters, between the Finisterre Mts. of the Huon Peninsula to the north and the Central Range to the south. 4 = the Sepik River basin, between the Adelbert Mts. to the east and Prince Alexander Mts. of the North Coastal Range to the west. Map kindly produced by Iain Woxvold.

Adelbert endemism and climate fluctuations.—Other than *Sericulus bakeri*, the Adelbert avifauna is very poor in endemics. Beehler & Pratt (2016) recognised just two endemic subspecies, both of which are weakly defined: Forbes's Forest Rail *Rallicula forbesi parva* and Large Scrubwren *Sericornis nouhuysi adelberti* (described by Pratt 1982). Just two other endemic subspecies have been proposed for the Adelberts—Trumpet Manucode *Phonygammus keraudrenii adelberti* and MacGregor's Bowerbird *Amblyornis macgregoriae amati* described by Gilliard & LeCroy (1967) and Pratt (1982), respectively—but Beehler & Pratt (2016) considered both too undistinctive to recognise. All other Adelbert populations belong to the same subspecies as their conspecifics on the Huon or Central Range or both, or in one or more cases as their conspecifics on the North Coastal Range (Pratt 1982, Beehler & Pratt 2016).

That Adelbert upland populations are near-identical to those on the nearest other mountains is expected given two factors. One is the already discussed narrowness of the lowland barriers separating the Adelberts from those sources (Fig. 3). That prompted our speculation that the high elevational floors, narrow elevational ranges, and small population sizes of the Adelberts' highest upland populations (Table 5) might be due in part to their being augmented by immigrants, and not completely isolated.

The other factor is natural climate fluctuations of the mid-Holocene. During the so-called hypsithermal period from about 8,000–4,000 years ago, global temperatures were warmer than at present, with peaks *c.*1°C higher than present around 7,000 and again 4,000 years ago. But even the more modest temperature increases of the last half-

century have produced measurable upward shifts in avian elevational ranges on tropical mountains worldwide. On two New Guinea peaks, Mt. Karimui and Karkar, Freeman & Class Freeman (2014) found that elevational floors shifted upslope by an average of 100 m between 1965 or 1969 and 2012 or 2013, respectively, associated with a 0.4°C rise in annual mean temperature over that period. Assuming that these floor shifts are linearly related to temperature changes, then the recent 0.4°C rise that shifted floors 100 m upslope suggests that the 1°C increase at the peak of the hypsithermal would have shifted floors upwards by c.250 m. But today's Adelbert floors of the ten species in Table 5 are already just 85–150 m below the Adelbert summit, so if during the hypsithermal the floors of these species had risen 250 m they would have effectively disappeared. Consequently, today's populations probably became established or re-established only within the last 4,000 years. That inferred young age of the Adelbert high-elevation avifauna is a second reason for its non-existent or weak endemism.

We have suggested two factors—weak isolation and young age—contributing both to the lack of endemism in almost all Adelbert upland birds, and to the small population sizes and high floors of the highest-elevation populations. But how should one then interpret the distinctness of *Sericulus bakeri*, which seemingly implies strong isolation and considerable age? Read on!

The three easternmost outliers.—Of the ten outlying mountain ranges along New Guinea's north and north-west coasts, the three easternmost are the North Coastal Range (NCR), Adelberts and Huon (Figs. 1 and 3). The lowland gap between the eastern foothills of the NCR (the Prince Alexander Mts.) and the western foothills of the Adelberts is c.200 km wide at the 500-m contour (I. Woxvold pers. comm.). But the lowland gap between the Adelberts' southern foothills and the Huon's western foothills is only c.15 km wide (as mentioned above). Hence the NCR / Adelbert gap is a barrier for bird distributions more than ten times wider than the Adelbert / Huon gap.

Table 7 compares the effects of those two gaps on upland bird distributions at the species or allospecies level. At the broad gap between the NCR and Adelberts, five species reach their eastern limit (present in the NCR and further west, absent in the Adelberts): Claret-breasted Fruit Dove *Ptilinopus viridis*, Josephine's Lorikeet *Charmosyna josefinae*, Tropical Scrubwren *Sericornis beccarii*, Piping Bellbird *Ornorettes cristatus* and Capped White-eye *Zosterops fuscicapilla*. No species reaches its western limit there, i.e. is present in the Adelberts and further east, but absent in the NCR and further west. (*Ptilorrhoea geislerorum*, formerly believed to reach its western limit there, was recently discovered far to the west on Yapen Island: Verhelst & Pottier 2020.) Three superspecies are represented by different allospecies on opposite sides of the NCR / Adelbert gap: the *Rallicula* [*leucospila*] forest rail superspecies, the *Sericulus* [*aureus*] bowerbird superspecies, and the *Zosterops* [*atrifrons*] white-eye superspecies.

In contrast, at the narrow gap between the Adelberts and Huon, the only species-level limits are that *Charmosyna rubronotata* and the *Sericulus* superspecies reach their eastern limit there, and that the *Amblyornis* [*inornata*] bowerbird superspecies and perhaps the *Ailuroedus* [*crassirostris*] catbird superspecies may be represented by different allospecies either side of the gap. Even that limit in the *Amblyornis* superspecies can be questioned, because the distinctiveness of the two *Amblyornis* populations is based on a very slight size difference, different bower form and display, and an unpublished molecular analysis (summarised in Frith & Frith 2004: 278, and Beehler & Pratt 2016: 278). But bower design is in part culturally transmitted, as shown by the drastic differences in bower form and decorations between *A. inornata* populations only 8 km apart, although the populations constructing those bowers are near-identical morphologically and exhibit only slight molecular differences (Diamond

TABLE 7
Species-level differences between the Adelberts and neighbouring upland avifaunas

Species or superspecies		NCR	Adelberts	Huon
Forbes's Forest Rail	<i>Ralllicula [leucospila]</i>	<i>R. [l.] mayri</i>	<i>R [l.] forbesi</i>	<i>R [l.] forbesi</i>
Claret-breasted Fruit Dove	<i>Ptilinopus viridis</i>	✓	--	--
Josephine's Lorikeet	<i>Charmosyna josefinae</i>	✓	--	--
Red-fronted Lorikeet	<i>Charmosyna rubronotata</i>	✓	✓	--
MacGregor's Bowerbird	<i>Amblyornis [inornata]</i>	--	<i>A. [i.] macgregoriae</i>	<i>A. [i.] germana</i>
Fire-maned Bowerbird	<i>Sericulus [aureus]</i>	<i>S. [a.] aureus</i>	<i>S. [a.] bakeri</i>	--
Tropical Scrubwren	<i>Sericornis beccarii</i>	✓	--	--
Dimorphic Jewel-babbler	<i>Ptilorhoa geislerorum</i>	--	✓	✓
Piping Bellbird	<i>Ornorettes cristatus</i>	✓	--	--
Black-fronted White-eye	<i>Zosterops [atrifrons]</i>	<i>Z. [a.] minor</i>	<i>Z. [a.] atrifrons</i>	<i>Z. [a.] atrifrons</i>
Capped White-eye	<i>Zosterops fuscicapilla</i>	✓	--	--

This table compares the upland avifaunas of the Adelberts and the two nearest outliers (North Coastal Range = NCR to the west, Huon to the east) with respect to two features: presence (✓) vs. absence (--); and which allospecies represents that superspecies on that outlier, if the superspecies (designated by a square bracket) involves different allospecies on different outliers. For example, the *Ralllicula [leucospila]* superspecies is represented by the allospecies *mayri* on NCR, but by *forbesi* on Adelbert and Huon. Note that, under both criteria, the Adelbert upland avifauna is more similar to that of the Huon to the east than to that of the NCR to the west.

& Bishop 2015: 314–315). Four other upland species present in the Adelberts are absent from the Huon, but do not reach an eastern limit between the Adelberts and Huon, because they reappear immediately east and south of the Huon (Blue-collared Parrot *Geoffroyus simplex*, Yellow-legged Flyrobin *Kempiella griseiceps*, Papuan Scrub Robin *Drymodes beccarii* and *Phonygammus keraudrenii*).

Thus, the distinctiveness of *Sericulus [aureus] bakeri* may be partly due to the fact that it is unique in being absent east of the Adelberts, and in being separated by a broad geographic barrier from the nearest allospecies to the west, Masked Bowerbird *S. [a.] aureus* (Fig. 2). All other Adelbert upland populations are identical or similar to upland populations nearby on the Huon and the Central Range. We acknowledge that Mackay reported two sightings of *S. aureus* from the Jimi River at 144°25'E on the northern slopes of the Central Range (Frith & Frith 2004: 334). However, there is no other record of *S. aureus* from the Central Range east of the Third Archbold Expedition's Bernhard Camp at 129°22'E, which is 1,600 km west of the Jimi River. KDB now discounts his own possible sighting in the Jimi Valley reported by Coates (1990: 400), and made at a time when KDB had only recently arrived in New Guinea. Five experienced collectors and observers undertook extensive studies of the Central Range's northern watershed in Papua New Guinea, three of them within 25 km of the Jimi River, without encountering *S. aureus*: E. T. Gilliard at Telefolmin (141°63'E), J. Bürgers on four mountains south of the upper Sepik River (Mäanderberg, Hunsteinspitze, Lordberg, Schraderberg: 141°68'E, 142°82'E, 143 00'E and 144°22'E, respectively), Gilliard in the Schrader Mts. (144°40'E), and I. Majnep and R. Bulmer in the Kaironk Valley (144°47'E). The easternmost record of *S. aureus* of which we are confident is not from the Central Range but from Mt. Turu at 143°34'E in the NCR (Diamond 1969). The range map of *S. aureus* in Pratt & Beehler (2015: 172) shows it as distributed continuously along the north slopes of the Central Range, from the Weyland Mts., in the far west, east to the Jimi River. However, the only firm records known to us on those slopes are from the Weyland Mts. and

Bernhard Camp. Instead, in northern New Guinea the *S. [aureus]* superspecies, like Barred Cuckooshrike *Coracina lineata*, is much more frequently recorded on the outlying mountains than on the north slopes of the Central Range itself (Fig. 2, p. 78).

The other likely reason for the far greater distinctiveness of *Sericulus bakeri* than of other Adelbert upland populations is its low elevational floor: only 700 m. Upwards shifts of 250 m in elevational floors during the hypsithermal, potentially sufficient to eliminate Adelbert high-altitude populations, would have left *S. bakeri* secure in an elevational range from 950 m to the summit at 1,675 m. Thus, the floor of *Sericulus* has been sufficiently low to protect it against the risk of extinction during mid-Holocene warm climates, but sufficiently high to impede its dispersal via the Sepik lowlands between the North Coastal Range and the Adelberts during Pleistocene cold climates.

Outlook

What additions to the Adelbert upland avifauna are possible? Beck's initial exploration at low elevations in 1928–29 recorded 11 upland species. Gilliard in 1959 and Ziegler in 1967 reached middle elevations and added 26 and two species, respectively. Pratt was the first to reach the Adelberts' summit in 1974, adding 25 upland species. Beehler in 1999 and 2010 added three species at low elevations. Finally, our visit in 2004 reached the summit and added four more species.

For three other species there are uncertain reports: *Aepyodius arfakianus*, Black-billed Sicklebill *Drepanornis albertisi* and *Zosterops novaeguineae*. We consider it likely that the first two of those will be found. Other possibilities are Meyer's Goshawk *Accipiter meyerianus*, *Charmosyna josefinae*, Wallace's Owlet-nightjar *Aegotheles wallacii*, Grey Thornbill *Acanthiza cinerea* and Obscure Honeyeater *Caligavis obscura*. Unlikely but not impossible are Bronze Ground Dove *Alopecoenas beccarii*, Rusty Whistler *Pachycephala hyperythra* and *Daphoenositta papuensis*.

Selected species accounts

We provide brief details of significant observations and species for which there were few or no previous Adelbert records.

SALVADORI'S TEAL *Salvadorina waigiensis*

This duck was our most surprising addition to the Adelberts' upland avifauna. It was previously known only from the Central Range, plus three outliers (Huon, Vogelkop and Foja) all much higher than the Adelberts. Our sole sighting was on 6 August 2004, when JD saw a pair on a river at 640 m below Kangaragate. The river at that point was 6 m wide, rushing, dropping, and with many large boulders. As soon as JD reached the river at 09.18 h, one *Salvadorina* that was perched beside the river flushed and flew off downstream. At 09.25 h a presumably different individual appeared 9 m upstream, perched on a stone 15 cm high next to the river, and occasionally slid its tail rapidly sideways. It swam upstream and reappeared on another boulder mid-river. Occasionally it raised the forebody and shook its wings, which appeared short. At 09:41 h it flew off upstream with quick ponderous flaps. Neither individual made any sound during the observation, which afforded a close prolonged view. The bill was dull yellow-orange, the speculum in flight green edged white anteriorly and posteriorly. Kangaragate villagers, who refer to this duck by the Aiti-language name 'asavi', state that it is common but shy and prone to flee on seeing people, and that it lays many eggs on a rock with much grass near the river.

RED-LEGGED BRUSHTURKEY *Talegalla jobiensis*

Heard at Kangarangate once in 2004, and twice in 2006. Local names 'mibu' (Kangarangate), 'sawa' (Munggur). Villagers described by call and habits only one other mound-building species, evidently New Guinea Scrubfowl *Megapodius decollatus*, as 'niako' (Kangarangate) or 'burukate' (Munggur). They denied knowledge of any additional mound-building species that would have been *Aepyodius arfakianus*, for which the only Adelbert report was by Mackay. As explained under Methods, we hesitate to accept that report without confirmation, especially as none of Beck, Gilliard, Pratt and ourselves observed the species and its distinctive mounds. Villagers could hardly have been unaware of *Aepyodius* if it had been present. Yet its absence from the Adelberts would be surprising, because it has been recorded in all nine other outliers.

FORBES'S FOREST RAIL *Rallicula forbesi*

Seen, heard and taped only at 1,525–1,600 m above Munggur, and recorded previously for the Adelberts solely by Pratt. Known and named by villagers at both Munggur and Kangarangate. The very long call is a buzzy note repeated *ad nauseam* three times per second.

MOUNTAIN OWLET-NIGHTJAR *Aegotheles albertisi*

We tape-recorded its call at night at 1,655 m above Munggur: a squeaky short upslurred note repeated at a rate of six notes per five seconds, with a quality similar to the bark of a small dog. Our recording is identical to those of *A. albertisi* from the Kumawa Mts. and Hela Province. We also taped the similar-sized Barred Owlet-nightjar *A. bennettii* at lower elevations. Both species are first records for the Adelberts. In the Adelberts, Pratt (1982) collected their larger congener Feline Owlet-nightjar *A. insignis*, double their mass, at an elevation (1,500 m) similar to *A. albertisi*. Munggur villagers are familiar, using the local name 'dalek', with the distinctive three-note angry-cat call of *A. insignis*. Hence *A. albertisi* and *A. insignis* are now known to co-exist at similar elevations on at least seven of New Guinea's outlying ranges, as well as the Central Range. Their ability to co-exist may be due to ecological consequences of their size difference.

RED-BREASTED PARADISE KINGFISHER *Tanysiptera nympha*

Noisy, commonly heard and seen at Kangarangate but not at our higher elevation site of Munggur. Two calls are frequently given: a very fast descending trill, similar to the first part of the call of Yellow-billed Kingfisher *Syma torotoro*, but with a spitted unmusical quality; and a very faint, long, medium-high pitch, single ascending note. Segregated ecologically from Common Paradise Kingfisher *T. galatea* by inhabiting higher elevations, and by perching higher in forest (at 6–15 m) rather than in the lower storey. We encountered *T. galatea* just once, at low elevation (815 m), at Kangarangate.

RED-FRONTED LORIKEET *Charmosyna rubronotata*

Heard and seen at both Munggur and Kangarangate, whereas its low-altitude sibling Red-flanked Lorikeet *C. placentis* was found only at Kangarangate. The two species can be distinguished by voice: *C. rubronotata* has a louder call.

STELLA'S LORIKEET *Charmosyna stellae*

Another high-elevation species recorded previously only by Pratt, which we encountered daily at 1,470–1,655 m. As did Pratt, we encountered only red-morph birds; the black morph from other parts of the species' range has not been observed in the Adelberts.

MACGREGOR'S BOWERBIRD *Amblyornis macgregoriae*

We heard calls and saw two bowers at 1,525 and 1,565 m: one on the ridge crest, the other on a broad slope considerably below the crest. The bowers comprised a circular moss platform 1.07 or 1.22 m in diameter, with a raised rim 15 or 23 cm wide and 15 cm tall, built around a central sapling. Sticks up to 25 cm long were piled around the sapling to a height of 0.6 or 1.5 m. The platform's floor consisted of soft brown earth or moss. Decorations at one bower involved dozens of small (3 mm) straw-coloured seeds, pieces of black charcoal on the rim, and two piles of black charcoal outside the rim and on opposite sides of the bower from each other. Decorations at the other consisted of several dozen pieces of black charcoal on the rim; sprigs of 4-mm blue berries hung from seven thin saplings; an 8-cm piece of blue cloth on the rim; and, outside the rim, several dozen 8-mm dull olive-brown fruits, and one bright green beetle skeleton. The charcoal and cloth had presumably been brought from a considerable distance.

FIRE-MANED BOWERBIRD *Sericulus bakeri*

Present at both of our sites, in small numbers from 1,150 to 1,385 m, giving diverse harsh calls, most of them soft, a few loud. Several female-plumaged birds and multiple adult males gathered in one fruiting tree. We found one bower at 1,150 m, on the shaded sloping forest floor. Its shape was rectangular, 38 × 20 cm, and it comprised several dozen dark brown sticks 13 cm long lying flat on the ground or inserted diagonally in two rows. Decorations consisted of 128 white fruits 1 cm in diameter. Munggur name: 'mororáng'. KDB also observed males and female-plumaged individuals at Keki Lodge.

RED-COLLARED MYZOMELA *Myzomela rosenbergii*

Abundant in flowering trees, and singly in the canopy, from 1,430 m upwards.

MARBLED HONEYEATER *Pycnopygius cinereus*

Calls: a snapped disyllabic note repeated once per second (Mountain Meliphaga *Meliphaga orientalis* does not repeat its snapped disyllable), and a musical note. Once we learned those calls, we recognised this species as abundant from 1,580 m upwards. Approaches in response to playback.

MOUNTAIN MELIPHAGA *Meliphaga orientalis*

Identified vocally by its short, bright, distinctively snapped disyllabic note; its staccato *tp* note is shared with other *Meliphaga*. The Adelbert population is identified visually by its small yellow ear patch, medium-small body size, and inconspicuous mottling on the underparts. Common or abundant at 930–1,570 m.

WHITE-EARED MELIPHAGA *Meliphaga montana*

Identified vocally by its distinctive upslurred *whEEP* note, and visually by its white ear, dull dark almost brownish upperparts, and heavier bill than *M. orientalis* of the same elevations. Noisy wingbeats, unusual for a small passerine. In small numbers from 1,020 to 1,255 m.

YELLOW-GAPED MELIPHAGA *Meliphaga flavirictus*

One, seen well by KDB in the lower canopy at 1,220 m, was identified by the long rictal streak, long narrow yellow ear patch, and moderately long slender bill. KDB taped its distinctive call, a squeaky downslur. First Adelbert record of this, the rarest *Meliphaga* species.

ORNATE MELIDECTES *Melidectes torquatus*

Abundant and often vocal, in the canopy, from 1,385 m upwards.

LARGE SCRUBWREN *Sericornis nouhuysi*

Common along with Buff-faced Scrubwren *S. perspicillatus* at high elevations, singing its characteristic gerygone-like song. Collected by Gilliard and by Pratt, and described by Pratt (1982) as an endemic subspecies. The taxonomic relationship between *S. nouhuysi* and its low-elevation sibling Tropical Scrubwren *S. beccarii* has been much debated because of the confusing geographic variation in plumage of *S. beccarii* (Diamond 1969, 1985, Beehler & Pratt 2016). However, their ecological relationship is simple and clear: they segregate by elevation at c.1,400 m wherever they co-exist (e.g., Kumawa, Foja, north slopes of western New Guinea's Central Range). Each species is confined to approximately that same elevational range in the absence of the other (e.g., *S. beccarii* in the North Coastal Range and Wandammen, *S. nouhuysi* in Huon and the northern watershed of the eastern Central Range). The Adelbert population of *S. nouhuysi* fits this pattern: it is confined to elevations above 1,535 m despite the absence of *S. beccarii*, which reaches its eastern distributional limit in the northern watershed of the North Coastal Range 160 km west of the Adelberts.

BUFF-FACED SCRUBWREN *Sericornis perspicillatus*

Common above 1,590 m, singing mainly at dawn. We once identified Grey-green Scrubwren *S. arfakianus* at 1,650 m, but it may also have accounted for sightings of *Sericornis* unidentified to species.

BROWN-BREASTED GERYGONE *Gerygone ruficollis*

Confined to elevations above 1,590 m, and easily located by its unmistakable long song, but surprisingly uncommon. The first record for the Adelberts.

CHESTNUT-BACKED JEWEL-BABBLER *Ptilorrhoa castanonota* and **DIMORPHIC JEWEL-BABBLER** *P. geislerorum*

Jewel-babblers were common and vocal at both of our sites, especially Kangaragate. At our higher elevation site, Munggur, where we heard and saw jewel-babblers from 1,170 to 1,655 m, all sightings were of the bicoloured (deep blue and rich chestnut) *P. castanonota*. At Kangaragate, most of our sightings were also of *P. castanonota* down to 1,000 m. However, we saw the duller, uniformly coloured *P. geislerorum* three times, at 1,070, 1,110 and 1,265 m: dull slate-blue individuals that were presumed males, and dull brown individuals presumed to be females. Calls of the two species seemed similar: paired notes, *tsp-tsp*, the second of each pair louder; and a series of notes on the same high pitch, the first notes short, then a long note, and finally the loud *tsp-tsp*. Gilliard collected both species in the Adelberts at different sites but similar elevations (Gilliard & LeCroy 1967: 66), as did Stevens in the Herzog Mts. (Greenway 1935: 55). Coates (1990: 66) found both species co-existing in the Adelberts, even on adjacent territories, at 800–1,220 m. The ecological relations between these species remain mysterious to us, because the other four co-existing species of *Ptilorrhoa* (*P. castanonota*, Spotted *P. leucosticta*, Blue *P. caerulescens* and Black-vented Jewel-babblers *P. nigricrissus*) segregate cleanly by elevation (Diamond *et al.* 2019: 455–456). *P. geislerorum* was believed to be confined to the northern watershed of south-east New Guinea west to the Adelberts, until Verhelst & Pottier (2020) surprisingly discovered *P. geislerorum* or a similar taxon sharing Yapen Island with *P. castanonota*.

BLACK-BREASTED BOATBILL *Machaerirhynchus nigripectus*

Common and calling from 1,225 m upwards, usually alone, occasionally in pairs or in mixed-species flocks. Previously recorded from the Adelberts only by Pratt (1982).

BARRED CUCKOOSHRIKE *Coracina lineata*

Heard and seen three times, both at Kangaragate and at Munggur. Like *Sericulus [aureus]*, this species is encountered much less often on the Central Range than on the outlying mountains, where it is known from eight ranges.

SCLATER'S WHISTLER *Pachycephala soror*

Modestly common above 1,570 m, from the understorey to the canopy. Sings mainly at dawn. All songs are a simple pattern of a half-dozen whistled notes and slurs, but each rendition differs from the previous one. Despite the absence in the Adelberts of its usual hill-forest congener Rusty Whistler *P. hyperythra*, the Adelbert population of *P. soror* does not expand its elevational range downslope.

BLACK FANTAIL *Rhipidura atra*

Common above 1,475 m, singing, often in pairs. Previously recorded for the Adelberts only by Pratt (1982).

WAHNE'S PAROTIA *Parotia wahnesi*

Uncommon: heard five times between 1,495 and 1,660 m. Its vocalisations are a medley of staccato clucks; short harsh notes are repeated at half-second intervals, like the sound made by striking a hollow log; other unusual sounds; and clear notes. Well known to Munggur villagers and named 'kakopelima'. We found no display courts, probably because villagers reported that these are sited in gullies rather than on the ridge. Previously reported by Pratt (1982).

SUPERB BIRD OF PARADISE *Lophorina superba*

Common above 1,570 m, with calling males spaced along the ridge. We saw adult males but no female-plumaged birds. As true of other New Guinea mountaineers, Munggur villagers gave different names to males ('menemenemburúm') and females ('soboromúnga').

TORRENTLARK *Grallina bruijnii*

We observed this species just once, along a river at 615 m, but it is so distinctive in behaviour that it is well known to villagers (named 'manini' and 'asliklik' at Munggur and Kangaragate, respectively). Previously reported by Pratt (1982).

YELLOW-LEGGED FLYROBIN *Kempiella griseiceps*

We observed this inconspicuous flycatcher twice (once at each study site), sallying in the canopy, at 1,165 and 1,260 m. First Adelbert records.

TORRENT FLYCATCHER *Monachella muelleriana*

We observed this specialist of rushing mountain streams only at a river at 650 m. The sole previous Adelbert record was a specimen obtained by Beck.

BLACK-CAPPED ROBIN *Heteromyias armiti*

Abundant above 1,570 m, where the species was heard far more often than it was seen. There are two different high-pitched whistled long songs, one slow and the other fast, both consisting of a repeated four-note or five-note series on two closely spaced pitches. The call is a single short clear whistle. Previously collected in the Adelberts by Pratt (1982).

BLUE-GREY ROBIN *Peneothello cyanus*

Very uncommon (just four records) at 1,500–1,570 m. Like elsewhere in New Guinea, there are two quite different songs: a soft, very fast, rising, musical series of notes; and a loud

unmusical outburst comprising a repeated three-note pattern. Previously collected by Pratt (1982).

BANDED YELLOW ROBIN *Gennaedryas placens*

We observed one pair at 1,000 m near Kangaragate. KDB heard and saw several at 850 m (Keki Lodge). Previously observed in the Adelberts by Beehler.

BLACK-FRONTED WHITE-EYE *Zosterops atrifrons*

Common at Kangaragate down to 905 m, and abundant at Munggur up to 1,645 m. The Adelbert song is the 'wheel song' characteristic of the species elsewhere in New Guinea: a descending series of notes like the sound of a wheel turning, terminating in a flourish. Because two or three *Zosterops* species co-exist by elevational segregation on all other outliers except Van Rees, and because one *Zosterops* specimen collected in the Adelberts by W. Peckover was catalogued as *Z. novaeguineae* (very similar in plumage to *Z. atrifrons*, but very different in song) before being prepared as a skeleton, we paid particular attention to Adelbert white-eyes and their songs. All singing *Zosterops* that we encountered gave the 'wheel song' of *Z. atrifrons*. Because we found *Z. atrifrons* abundant up to the highest elevations in the Adelberts, it seems unlikely that *Z. novaeguineae* or any other *Zosterops* species could be present at high elevations along with *Z. atrifrons*.

STREAK-HEADED MANNIKIN *Lonchura tristissima*

We saw no mannikins in the Adelberts, but Kangaragate villagers described birds that were clearly mannikins as 'kugursarsar'. The only mannikin known to occur in the Adelberts is the forest-edge species *L. tristissima*, collected by Beck and by Gilliard. Evidently, the garden and grassland patches of the Adelberts are too small and recent to have attracted any of New Guinea's open grassland *Lonchura* species yet. In contrast, many areas of the Central Range and three other outliers, where dense human farming populations and open grassland have existed for centuries or millennia, each support one or two of six specialised grassland *Lonchura* species. We mention this to alert future visitors to look for colonisation of the Adelberts by some grassland *Lonchura*.

Mixed-species flocks.—Elsewhere in New Guinea (Diamond 1987) one encounters two types of mixed-species foraging flocks: a 'brown-black' flock of medium-sized omnivores, most of them with brown and / or black plumage, and consisting especially of pitohuis, birds of paradise, drongos and cuckoo-shrikes; and a flock of small insectivores. In our Adelbert studies at elevations above 640 m we encountered only the latter type. We met no brown-black flocks despite the abundant presence of two *Pitohui* species, and we encountered no mixed-species flocks of either type at the highest elevations above 1,500 m. Between 1,050 and 1,415 m at both Munggur and Kangaragate, the noisiest and most regularly encountered members of small insectivore flocks were Chestnut-bellied Fantail *Rhipidura hyperythra*, Black-winged Monarch *Monarcha frater* and Fairy Gerygone *Gerygone palpebrosa*, plus the pseudo-drongo Drongo Fantail *Chaetorhynchus papuensis* that is now considered a fantail (Beehler & Pratt 2016) and usually accompanies brown-black flocks. Other frequent members of these flocks were Ochre-collared *Arses insularis* and Fantailed Monarchs *Symposiachrus axillaris*, and three brown species that elsewhere accompany brown-black flocks (female King Bird of Paradise *Cicinnurus magnificus*, Tawny-breasted Honeyeater *Xanthotis flaviventer* and Little Shrikethrush *Colluricincla megarrhyncha*).

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Appendix: Adelbert bird species

Listed in column 2 are all bird species recorded from the Adelbert Mts. by the observers named in column 3.

Column 1: * = upland species, as defined in the text.

Column 3: observers who recorded the species. To the left of the dot are our records; to the right those by other observers. Our records: M = Munggur, K = Kangaragate, D = KDB's observations near Keki Lodge; [] =

named and described to us by Munggur or Kangarangate villagers, but not observed by us. Records of other observers: R = R. Beck, G = E. T. Gilliard, P = T. K. Pratt *et al.*, Z = A. Ziegler, B = B. M. Beehler.

Column 4 ('ab'): our estimates of abundance at Munggur and Kangarangate in 2004 (left and right of slash respectively). 1 = just 1–2 records. 2 = three or more records, but uncommon. 3 = common. 4 = the most abundant species.

Column 5 (L): elevational range, in metres, within which we observed the species.

Column 6 (no. of outliers): on how many of New Guinea's ten outlying mountains, including the Adelberts, does this upland species occur?

Column 7 (other mts.): on which of the six outliers most similar in elevation to the Adelberts does this upland species occur? F = Fakfak, K = Kumawa, N = North Coastal Range, W = Wandammen, C = Cyclops, J = Foja.

Column 8: local name in the Pamosu language spoken at Munggur.

Column 9: local name in the Aiti language spoken at Kangarangate. Spellings are those used by our Kangarangate informants. In their spelling system the letter r often functions as a semi-vowel that sounds to us like the English syllable 'ru' or 'ri', and several consonants are nasalised. What Kangarangate villagers write as b, d, g, j, k, s and y sounds to our ears like mb, nd, ng, nj, ng, nj or ny and ny, respectively.

Upland species?	Scientific and English names	Records	ab	L (m)	No. of mts.	Other mts.	Pamosu name	Aiti name
	cassowaries <i>Casuarius</i> sp.						oyor	marshung
	Northern Cassowary <i>Casuarius unappendiculatus</i>	[M][K]•G					olimes, sovove	kovár, tapungóvi
*	Dwarf Cassowary <i>Casuarius bennetti</i>	MK•P		815–1,450	7	NWJ	kurumbum-ate	
	Red-legged Brushturkey <i>Talegalla jobiensis</i>	[M]KD•RG	-/1	800–1,050			sawa	mibu
	New Guinea Scrubfowl <i>Megapodius decollatus</i>	[M][K]•RG					burukate	niáko
	Spotted Whistling Duck <i>Dendrocygna guttata</i>	•RG						
*	Salvadori's Teal <i>Salvadorina waigiuiensis</i>	[M]K•	-/1	640	4	J		as-avi
	Great Cuckoo-Dove <i>Reinwardtoena reinwardtii</i>	MKD•RGB	2/2	640–1,600			elevana	itgi
*	Black-billed Cuckoo-Dove <i>Macropygia nigrirostris</i>	MKD•RPZ	3/2	1,100–1,655	10	FKNWCJ	nangilinom	otgot
	Brown Cuckoo-Dove <i>Macropygia amboinensis</i>	MKD•RGPB	4/3	800–1,655			funate	otgot
	New Guinea Bronzewing <i>Henicophaps albifrons</i>	M•	1/-	1,000			enaemaeng- uru?	kbathithí
	Cinnamon Ground Dove <i>Gallinula rufiflora</i>	MK•	1/2	740–1,495			bururovov	primumu
	White-bibbed Ground Dove <i>Alopecoenas jobiensis</i>	•RGP						
*	Pheasant Pigeon <i>Otidiphaps nobilis</i>	MK•GP	3/1	1,195–1,585	9	FKNWX	gavogavo, marirumbe, mavok	aonagári
	Victoria Crowned Pigeon <i>Goura victoria</i>	[K]•RG					muvo	kobi
	Pacific Emerald Dove <i>C. longirostris</i>	•P						
	Stephan's Emerald Dove <i>Chalcophaps stephani</i>	[K]D•RGP		700–800			bururovov-uru	prthithí
	Wompoo Fruit Dove <i>Megaloprepia magnifica</i>	KD•RGPB	-/2	800–1,125			ileli-etat	yaki
	Dwarf Fruit Dove <i>Ptilinopus nainus</i>	D•		700–800				

Upland species?	Scientific and English names	Records	ab	L (m)	No. of mts.	Other mts.	Pamosu name	Aiti name
	Superb Fruit Dove <i>Ptilinopus superbus</i>	MKD•RGPB	4/4	800–1,640			ilahil	tgrv
*	Mountain Fruit Dove <i>Ptilinopus bellus</i>	MK•P	4/2	1,190–1,655	10	FKNWCJ	mafua	
	Pink-spotted Fruit Dove <i>Ptilinopus perlatus</i>	MKD•RB	2/3	815–1,235				
*	Ornate Fruit Dove <i>Ptilinopus ornatus</i>	MD•R	3/-	1,590–1,655	9	FKNWCJ	mapoko	
	Orange-bellied Fruit Dove <i>Ptilinopus iozonus</i>	KD•RGP	-/2	835–980				
	Beautiful Fruit Dove <i>Ptilinopus pulchellus</i>	MKD•RGPB	2/3	730–1,215			gaugau	saganai
	Purple-tailed Imperial Pigeon <i>Ducula rufigaster</i>	•RGB						
	Pinon's Imperial Pigeon <i>Ducula pinon</i>	M[K]•RGP	1/-	700–1,515			imbienum	iwog
	Zoe's Imperial Pigeon <i>Ducula zoeae</i>	MKD•RGPB	2/2	640–1,520			pepisekuri	mkósvi
*	Papuan Mountain Pigeon <i>Gymnophaps albertisii</i>	MKD•GP	2/2	700–1,650	10	FKNWCJ	kurupa	ivugu-wugu
	Yellow Bittern <i>Ixobrychus sinensis</i>	•R						
	Little Pied Cormorant <i>Microcarbo melanoleucos</i>	•R						
	Australasian Darter <i>Anhinga novaehollandiae</i>	•R						
*	Forbes's Forest Rail <i>Rallidula forbesi</i>	M[K]•P	2/-	1,525–1,600	8	KNWCJ	elekora	musupia
	White-browed Crane <i>Amaurornis cinerea</i>	•R						
	Rufous-tailed Bush-hen <i>Amaurornis moluccana</i>	[K]•G						uniakawa
	Greater Black Coucal <i>Centropus menbeki</i>	MKD•RGPB	2/2	875–1,445			timbu	tugát
	Lesser Black Coucal <i>Centropus bernsteini</i>	D•		700–800				
	Dwarf Koel <i>Microdynamis parva</i>	MKD•RB	3/4	700–1,505			kuwang-kuwang	niohám
	Eastern Koel <i>Eudynamis orientalis</i>	MK•	2/3	640–1,585				niohám
	Channel-billed Cuckoo <i>Scythrops novaehollandiae</i>	[K]D•R						manmigras
*	White-eared Bronze Cuckoo <i>Chalcites meyerii</i>	MK•G	2/3	875–1,250	10	FKNWCJ		Imákava?
	Little Bronze Cuckoo <i>Chalcites minutillus</i>	K•	-/1	835				
	White-crowned Cuckoo <i>Caliechthrus leucolophus</i>	MKD•B	2/2	840–1,445			pepisekoko	niakaka
	Chestnut-breasted Cuckoo <i>Cacomantis castaneiventris</i>	MKD•PB	3/3	700–1,655			pukakiri	inakosiri
	Brush Cuckoo <i>Cacomantis variolosus</i>	KD•RPZ	-/3	700–1,295			pukakiri	inakosiri
	Marbled Frogmouth <i>Podargus ocellatus</i>	MK•RGZ	2/2	875–1,655			kumbevi	krovikná

Upland species?	Scientific and English names	Records	ab	L (m)	No. of mts.	Other mts.	Pamosu name	Aiti name
	Papuan Frogmouth <i>Podargus papuensis</i>	K•RGZ	-/2	875			mum	mumugéw
	Large-tailed Nightjar <i>Caprimulgus macrurus</i>	D•		700–800				
*	Feline Owlet-nightjar <i>Aegotheles insignis</i>	M•P			7	KNWJ	dalek	
*	Mountain Owlet-nightjar <i>Aegotheles albertisi</i>	M•		1,655	6	KWJ	sipipolov	
	Barred Owlet-nightjar <i>Aegotheles bennettii</i>	MK•	-/1	875, 1,225				
	Moustached Treeswift <i>Hemiprocne mystacea</i>	[M]KD•RG	-/1	640–800			busiang	pogit
	Glossy Swiftlet <i>Collocalia esculenta</i>	MKD•B	1/2	700–1,220				
	Aerodramus sp.	MKD•PB	2/2	640–1,220			mai	niaba-mari-mari
*	Mountain Swiftlet <i>Aerodramus hirundinaceus</i>	•R			8	FKNWJ		
	Papuan Spinetailed Swift <i>Mearnsia novaeguineae</i>	K•	-/2	875				
	Little Ringed Plover <i>Charadrius dubius</i>	•P						
	Comb-crested Jacana <i>Irediparra gallinacea</i>	•R						
	Marsh Sandpiper <i>Tringa stagnatilis</i>	K•	-/1	875				
	Common Sandpiper <i>Actitis hypoleucos</i>	D•		700–800				
	Pacific Baza <i>Aviceda subcristata</i>	KD•	-/1	815				
	Long-tailed Buzzard <i>Henicoperis longicauda</i>	MK•GB	1/1	835–1,600			mambukom-mosu	pogi-as
	New Guinea Harpy-Eagle <i>Harpyopsis novaeguineae</i>	MK•RP	1/1	700–1,225			mambukom	pogi-tuguáya
*	Pygmy Eagle <i>Hieraetus tweiskei</i>	•G			6	CJ		
	Gurney's Eagle <i>Aquila gurneyi</i>	K•	-/1	830				
	Black Kite <i>Milvus migrans</i>	K•R	-/1	700–875				
	Whistling Kite <i>Haliastur sphenurus</i>	D•		700–800				
	Brahminy Kite <i>Haliastur indus</i>	MKD•G	1/2	835–1,225			siruwarum	pogi-mnáho-gnáha
	Variable Goshawk <i>Accipiter hiogaster</i>	K•GP	1/1	625–830			sikikin	pogi-soi
	Grey-headed Goshawk <i>Accipiter poliocephalus</i>	KD•B	1/1	700–1,060				
	Collared Sparrowhawk <i>Accipiter cirrocephalus</i>	MD•PB	1/-	700–1,400				
*	Chestnut-shouldered Goshawk <i>Erythrotriorchis buergeri</i>	•P			4	NJ		
	Sooty Owl <i>Tyto tenebricosa</i>	MK•B	-/1	1,190			yan	kius
	Papuan Boobook <i>Ninox theomacha</i>	KD•B	-/2	700–875			kol	tagogo
	Papuan Hawk-Owl <i>Uroglaux dimorpha</i>	•R						

Upland species?	Scientific and English names	Records	ab	L (m)	No. of mts.	Other mts.	Pamosu name	Aiti name
	Blyth's Hornbill <i>Rhyticeros plicatus</i>	MKD•RGB	2/2	640–1,400			kumbarom	sabkór
	Rainbow Bee-eater <i>Merops ornatus</i>	KD•GB	-/2	700–1,070			malimunga	sopirpir
	Oriental Dollarbird <i>Eurystomus orientalis</i>	KD•GPB	-/2	700–875				prakiki
	Common Paradise Kingfisher <i>Tanysepta galatea</i>	K•RGPZ		700–815				sambai-mká-mká
	Red-breasted Paradise Kingfisher <i>Tanysepta nympa</i>	K•GP	-/3	835–1,085			morumunga	konjeriki
	Hook-billed Kingfisher <i>Melidora macrorrhina</i>	MKD•RB	2/2	700–1,225			yayan-orov	kiykiyakna
	Shovel-billed Kookaburra <i>Clytoceyx rex</i>	•R						
	Rufous-bellied Kookaburra <i>Dacelo gaudichaud</i>	KD•RGB	-/2	640–975				katkro
	Blue-black Kingfisher <i>Todiramphus nigrocyaneus</i>	•RG						
	Forest Kingfisher <i>Todiramphus macleayii</i>	D•		700–800				
	Sacred Kingfisher <i>Todiramphus sanctus</i>	KD•R		700–875				kóko-wóra-wóra
	Yellow-billed Kingfisher <i>Syma torotoro</i>	KD•GZB	-/3	730–1,120				kóngakawa
	Common Kingfisher <i>Alcedo atthis</i>	•P						
	Papuan Dwarf Kingfisher <i>Ceyx solitarius</i>	MKD•GPB	2/3	700–1,295			epihiafemu	yobir
	Azure Kingfisher <i>Ceyx azureus</i>	K•RP	-/1	835				yobir
	Little Kingfisher <i>Ceyx pusillus</i>	•R						
	Oriental Hobby <i>Falco severus</i>	M•GP	1/-	830				
	Peregrine Falcon <i>Falco peregrinus</i>	M•G	1/-	1,225				
	Palm Cockatoo <i>Probosciger aterrimus</i>	MKD•RGB	1/2	700–1,295			kokovai	okyáki
	Sulphur-crested Cockatoo <i>Cacatua galerita</i>	MKD•RGPB	2/2	700–1,445			engev	motgáya
*	New Guinea Vulturine Parrot <i>Psitttrichas fulgidus</i>	KD•GPB	-/2	700–1,195	7	NWJ	tepal	manabu
*	Red-fronted Lorikeet <i>Charmosyna rubronotata</i>	MK•B	1/2	640–1,590	5	NC		
	Red-flanked Lorikeet <i>Charmosyna placentis</i>	KD•GP		700–1,100				
*	Stella's Lorikeet <i>Charmosyna stellae</i>	M•P	2/-	1,470–1,655	3		siovov	
*	Fairy Lorikeet <i>Charmosyna pulchella</i>	M•P		1,445–1,600	9	FKNWCJ	ikokik	
	Black-capped Lory <i>Lorius lory</i>	MKD•RPB	2/3	640–1,380			ororovion	úyouyó
	Rainbow Lorikeet <i>Trichoglossus haematodus</i>	MKD•RGPB	1/3	700–1,295			tiken	
	Dusky Lory <i>Pseudeos fuscata</i>	MKD•GPZB	2/3	700–1,600			kirikirik	kgggrs
	Edward's Fig Parrot <i>Psittaculirostris edwardsii</i>	•R						

Upland species?	Scientific and English names	Records	ab	L (m)	No. of mts.	Other mts.	Pamosu name	Aiti name
	Orange-breasted Fig Parrot <i>Cyclopsitta gulielmitertii</i>	•B						
	Double-eyed Fig Parrot <i>Cyclopsitta diophthalma</i>	D•		700–800				
	Papuan King Parrot <i>Alisterus chloropterus</i>	•P						
	Eclectus Parrot <i>Eclectus roratus</i>	MKD•RGPB	1/2	640–1,220			gelevan	apra (male), muko (female)
	Red-cheeked Parrot <i>Geoffroyus geoffroyi</i>	KD•RGB	-/2	700–875				kikimiya
*	Blue-collared Parrot <i>Geoffroyus simplex</i>	MK•P	2/1	1,190–1,655	9	FKNWCJ	enaenaeng-munga	kri-ró
	Buff-faced Pygmy Parrot <i>Micropsitta pusio</i>	K•RGB	-/3	700–875			opeliriruv	kam-tskin-tskín
*	Red-breasted Pygmy Parrot <i>Micropsitta bruijnii</i>	M•P	2/-	1,220–1,620	9	FKNWCJ	nangikiroton	
	Red-bellied Pitta <i>Erythropitta erythrogaster</i>	[K]•GPZB					maneme-savu	korakam
	Hooded Pitta <i>Pitta sordida</i>	•RGZ						
	White-eared Catbird <i>Ailuroedus buccoides</i>	[K]•RGB					senovov	pkhújo
*	Black-eared Catbird <i>Ailuroedus melanotis</i>	K•GP	-/2	1,150–1,265	9	FKNWCJ	melanong	mimikuráw
*	MacGregor's Bowerbird <i>Amblyornis macgregoriae</i>	M•P	2/-	1,525–1,565	7	FKW	nomu	
*	Fire-maned Bowerbird <i>Sericulus akeri</i>	MKD•RGPB	2/2	700–1,385	5	NWJ	mororang	sinené
	White-shouldered Fairywren <i>Malurus alboscapulatus</i>	MKD•G	2/2	700–1,225				
*	Red-collared Myzomela <i>Myzomela rosenbergii</i>	M•P	4/-	1,430–1,645	9	FKNWCJ	meruru	
	Ruby-throated Myzomela <i>Myzomela eques</i>	•RG						
*	Red Myzomela <i>Myzomela cruentata</i>	MKD•GPZ	4/3	700–1,570	8	FKNCJ	ituetat	kawa-yágu
	Papuan Black Myzomela <i>Myzomela nigrita</i>	M•G	1/-	1,225				
	Tawny-breasted Honeyeater <i>Xanthis flaviventer</i>	MKD•RGPZB	3/4	700–1,400			ekup	porowóro
*	Spotted Honeyeater <i>Xanthis polygrammus</i>	K•GPZ	-/1	1,000	9	FNWCJ	sikurakuron-pope	kbrsíh
	Meyer's Friarbird <i>Philemon meyeri</i>	KD•RGB	-/3	700–1,140				koko-poro-woro
	Helmeted Friarbird <i>Philemon buceroides</i>	MKD•RGB	3/3	700–1,225			kawohok	poro-áya
	Green-backed Honeyeater <i>Glycichaera fallax</i>	K•RGPB		750				
	Plain Honeyeater <i>Pycnopygius ixoides</i>	KD•RGB	-/2	700–1,055				
	Streak-headed Honeyeater <i>Pycnopygius stictocephalus</i>	K•R	-/2	835–875				
*	Marbled Honeyeater <i>Pycnopygius cinereus</i>	M•P	4/-	1,580–1,620	3		momol	

Upland species?	Scientific and English names	Records	ab	L (m)	No. of mts.	Other mts.	Pamosu name	Aiti name
	Long-billed Honeyeater <i>Melilestes megarhynchus</i>	MK•RGPZB	3/3	700–1,655			etel	padiobre
	Puff-backed Meliphaga <i>Meliphaga aruensis</i>	•G						
	Mimic Meliphaga <i>Meliphaga analoga</i>	•RGZ						kbrták
*	Mountain Meliphaga <i>Meliphaga orientalis</i>	MK•GP	4/3	930–1,570	9	FKNWJ	kikimo	
*	White-eared Meliphaga <i>Meliphaga montana</i>	MKD•P	2/2	700–1,255	9	FKNCJ	kikimo	kbrták
	Yellow-gaped Meliphaga <i>Meliphaga flavivictus</i>	M•	1/-	1,220				
*	Ornate Melidectes <i>Melidectes torquatus</i>	M•P	4/-	1,385–1,665	3		sikura-kuron	
	Rusty Mouse-Warbler <i>Crateroscelis murina</i>	MKD•RGPZB	3/4	640–1,555			mil	kindgo
	Pale-billed Scrubwren <i>Sericornis spilodera</i>	MK•GPB	1/2	735–1,400				kindgo-mstám
*	Large Scrubwren <i>Sericornis nouhuysi</i>	M•GP	3/-	1,535–1,645	5	KJ	kuasisieva	
*	Buff-faced Scrubwren <i>Sericornis perspicillatus</i>	M•P	3/-	1,590–1,655	6	KNJ	kuasisieva-unend	
*	Grey-green Scrubwren <i>Sericornis arfakianus</i>	M•GPZ	1/-	1,650	8	NWCJ		
	Yellow-bellied Gerygone <i>Gerygone chrysogaster</i>	K•RGB	-/3	650–1,000			sepelak-munga	akoríma-kawa
	Green-backed Gerygone <i>Gerygone chloronota</i>	MKD•B	2/3	700–1,225				
	Fairy Gerygone <i>Gerygone palpebrosa</i>	MKD•GPB	4/4	700–1,430			itumemal	akoríma-kawa
	Large-billed Gerygone <i>Gerygone magnirostris</i>	•RGP						
*	Brown-breasted Gerygone <i>Gerygone ruficollis</i>	M•	2/-	1,590–1,645	7	FKWJ		
	Papuan Babbler <i>Garritornis isidorei</i>	[K]•RG						ua
*	Obscure Berrypecker <i>Melanocharis arfakiana</i>	•B			2			
	Black Berrypecker <i>Melanocharis nigra</i>	MKD•RGPZB	3/3	700–1,550			itu-uru?	pijruke-ruke
	Spectacled Longbill <i>Oedistoma iliolophus</i>	K•RGPB	-/2	875–1,295				
	Pygmy Longbill <i>Oedistoma pygmaeum</i>	MKD•GB	2/2	700–1,350			pelepele-kovov?	
	Yellow-bellied Longbill <i>Toxorhamphus novaeguineae</i>	KD•RGPZB	-/3	700–1,190				paniaták
*	Slaty-headed Longbill <i>Toxorhamphus poliopterus</i>	MK•GPZ	4/-	1,225–1,650	2		otemasik	paniaták
	Blue Jewel-babbler <i>Ptilorrhoa caerulescens</i>	D•RPB		700–800				
*	Dimorphic Jewel-babbler <i>Ptilorrhoa geislerorum</i>	K•G	-/3	1,070–1,265	2			
*	Chestnut-backed Jewel-babbler <i>Ptilorrhoa castanonota</i>	MK•GPB	3/3	1,000–1,655	9	FKNWJ	sasan	sojók wáw

Upland species?	Scientific and English names	Records	ab	L (m)	No. of mts.	Other mts.	Pamosu name	Aiti name
	Yellow-breasted Boatbill <i>Machaerirhynchus flaviventer</i>	D•PB		700–800				
*	Black-breasted Boatbill <i>Machaerirhynchus nigripectus</i>	M•P	3/-	1,225–1,655	7	FKWJ		
	Lowland Peltops <i>Peltops blainvillii</i>	•G						
*	Mountain Peltops <i>Peltops montanus</i>	MK•GP	2/3	700–1,590	9	FKNWJ	gamililik	opri-sbiá-sbiá
	Black Butcherbird <i>Cracticus quoyi</i>	K•RGB	-/1	640				kukarúbu
	Hooded Butcherbird <i>Cracticus cassicus</i>	KD•RG	-/2	700–875			kupakup	madoró
*	Great Woodswallow <i>Artamus maximus</i>	MKD•RGPZB	2/2	700–1,655	8	FKNWJ	arik	siksik
*	Stout-billed Cuckooshrike <i>Coracina caeruleoigrisea</i>	MKD•RGPB	3/2	700–1,580	10	FKNWCJ	seveve	sinené
*	Barred Cuckooshrike <i>Coracina lineata</i>	MKD•RGPB	2/2	700–1,340	8	KNWC		
	Boyer's Cuckooshrike <i>Coracina boyeri</i>	KD•RPB		700–875				
	White-bellied Cuckooshrike <i>Coracina papuensis</i>	D•RP		700–800				
	Black-browed Triller <i>Lalage atrovirens</i>	MKD•G	1/2	700–1,225			alík-ote	mdut-ba-kri-kri
*	Black-bellied Cicadabird <i>Edolisoma montanum</i>	MK•PZ	3/3	1,190–1,595	9	FKNWCJ	sakunane	uasíyí
*	Papuan Cicadabird <i>Edolisoma incertum</i>	MKD•RGPB	4/4	700–1,300	10	FKNWCJ	sapik	kr-nyá-kr-nya
	Common Cicadabird <i>Edolisoma tenuirostre</i>	•R						
	Black Cicadabird <i>Edolisoma melas</i>	KD•RGB	-/2	635–830				
*	Rufous-naped Bellbird <i>Alcedryas rufinucha</i>	M•P	3/-	1,545–1,660	8	FKNWJ		
	Little Shrikethrush <i>Colluricincla megarhyncha</i>	MKD•RGPZB	4/4	640–1,585			kukuvelu	kwidak
	Rusty Shrikethrush <i>Pseudorectes ferrugineus</i>	[K]•RG						yokaya
*	Sclater's Whistler <i>Pachycephala soror</i>	M•GP	3/-	1,570–1,655	5	FK	kikimo-aniv	
	Grey Whistler <i>Pachycephala simplex</i>	MKD•RGB	2/3	700–1,350				orkiakía
	Northern Variable Pitohui <i>Pitohui kirhocephalus</i>	K•RGP	-/4	640–1,085				sohé
*	Hooded Pitohui <i>Pitohui dichrous</i>	MKD•RGPB	4/4	930–1,500	10	FKNWCJ	kiakovov	sripopo
	Brown Oriole <i>Oriolus szalayi</i>	KD•RG	-/3	700–875			uruhar	káko-póro-áuga
*	Drongo Fantail <i>Chaetorhynchus papuensis</i>	MK•GPB	3/3	640–1,515	9	FKNWJ	mungawahak	tind
	Willie Wagtail <i>Rhipidura leucophrys</i>	MD•P		700–1,225				
	White-bellied Thicket Fantail <i>Rhipidura leucothorax</i>	KD•GZ	-/1	835			sigogogil	saggná

Upland species?	Scientific and English names	Records	ab	L (m)	No. of mts.	Other mts.	Pamosu name	Aiti name
	Sooty Thicket Fantail <i>Rhipidura threnothorax</i>	K•RGPZB	-/2	730–1,070			sigogogil	pigusése
	Rufous-backed Fantail <i>Rhipidura rufidorsa</i>	K•	-/1	800–835				pho-sokrí-sokrí
*	Black Fantail <i>Rhipidura atra</i>	M•P	4/-	1,475–1,640	9	FKNWCJ	pingege	
	Chestnut-bellied Fantail <i>Rhipidura hyperythra</i>	MKD•GPZB	4/3	700–1,590			siongigi	kora-sokrí-sokrí
	Northern Fantail <i>Rhipidura rufiventris</i>	MK•RGPB	3/1	835–1,235				Pho-sokrí-sokrí
	Spangled Drongo <i>Dicrurus bracteatus</i>	MKD•RG	1/2	640–1,220			fikafika	krs-kiyá-kiyá
*	Trumpet Manucode <i>Phonygammus keraudrenii</i>	MK•GP	3/3	1,005–1,660	8	FKNWJ	uru	korasatu
	Crinkle-collared Manucode <i>Manucodia chalybatus</i>	MKD•RGP	2/3	880–1,600			uru	satu
	Jobi Manucode <i>Manucodia jobiensis</i>	D•		700–800				
	Glossy Manucode <i>Manucodia ater</i>	•R						
*	Wahnes's Parotia <i>Parotia wahnesi</i>	M•P	2/-	1,495–1,660	5	WJ	kakopelema	
	Growling Riflebird <i>Ptiloris intercedens</i>	K•RGP	-/3	1,050–1,265				karaba uruwe
*	Superb Bird of Paradise <i>Lophorina superba</i>	M•P	3/-	1,570–1,655	4	W	mene-mene-mburúm (male), soboro-múnga (female)	
	King Bird of Paradise <i>Cicinnurus regius</i>	[K]•G					seva-etat	manara
*	Magnificent Bird of Paradise <i>Cicinnurus magnificus</i>	MKD•RGPB	2/3	640–1550	10	FKNWCJ	seva	pisáw
	Lesser Bird of Paradise <i>Paradisaea minor</i>	MKD•RGPZB	3/3	700–1,295			koyavi	kogíw
*	Torrentlark <i>Grallina bruijnii</i>	[M]K•P	-/1	615	5	NJ	yer	asliklik
	Ochre-collared Monarch <i>Arses insularis</i>	MK•RGP	2/3	640–1,350				manbue
	Shining Flycatcher <i>Myiagra alecto</i>	MK•RGPZ	-/1	875				
*	Fantailed Monarch <i>Symposiachrus axillaris</i>	MK•GP	2/2	870–1,550	9	FKNWJ	mungawahak-mengelena-fua	
	Rufous Monarch <i>Symposiachrus rubiensis</i>	•P						
	Hooded Monarch <i>Symposiachrus manadensis</i>	•RP						
	Spot-winged Monarch <i>Symposiachrus guttula</i>	•RGPB						
	Golden Monarch <i>Carterornis chrysomela</i>	•RGB						
*	Black-winged Monarch <i>Monarcha frater</i>	MK•GPZB	4/4	700–1,415	8	FKNWJ	fovaihua	manbue
	Grey Crow <i>Corvus tristis</i>	MKD•RGPB	2/2	640–1,550			mekand	tagapa
	Torresian Crow <i>Corvus orru</i>	D•P		700–800				

Upland species?	Scientific and English names	Records	ab	L (m)	No. of mts.	Other mts.	Pamosu name	Aiti name
*	White-eyed Robin <i>Pachycephalopsis poliosoma</i>	MK•GPZ	4/4	1035–1600	7	NWJ	singovulu	yokyok
*	Yellow-legged Flyrobin <i>Kempiella griseiceps</i>	MK•	1/1	1,165–1,260	8	FKNWC		
	Olive Flyrobin <i>Kempiella flavovirescens</i>	K•R	-/1	835				
*	Torrent Flycatcher <i>Monachella muelleriana</i>	K•R	-/2	650	6	NJ	manini	mnáki-pokipó
*	Papuan Scrub Robin <i>Drymodes beccarii</i>	MK•P	2/2	875–1,320	7	NWCJ	jin	kindgo-sapasapa
*	Black-capped Robin <i>Heteromyias armiti</i>	M•P	4/-	1,570–1,660	5	KJ	namenovi	
	Black-sided Robin <i>Poecilodryas hypoleuca</i>	MK•GPZB	3/4	665–1,225			motondo	tó-se
*	White-rumped Robin <i>Peneothello bimaculata</i>	MD•GB		700–1225	5	J		
*	Blue-grey Robin <i>Peneothello cyanus</i>	M•P	2/-	1,500–1,570	8	FKNWCJ	ulafamu-ngeva?	
*	Banded Yellow Robin <i>Gennaodryas placens</i>	KD•B	-/1	700–1,000	5	FKW	golugolulovov?	omtóndo
*	White-faced Robin <i>Tregellasia leucops</i>	MK•GPZ	3/2	735–1,655	9	FKNWCJ	natuemil?	Aoádkáwa
	Pacific Swallow <i>Hirundo tahitica</i>	D•G		700–800				
*	Island Leaf Warbler <i>Seicercus poliocephalus</i>	MK•P	4/1	1,260–1,655	9	FKNWCJ		
*	Black-fronted White-eye <i>Zosterops atrifrons</i>	MKD•GPB	4/3	700–1,645	10	FKNWCJ	malilovov	kima-oróró
	Golden-headed Cisticola <i>Cisticola exilis</i>	•G						
	Metallic Starling <i>Aplonis metallica</i>	[K]D•RG		700–800			kuseng	snha
	Yellow-faced Myna <i>Mino dumontii</i>	MKD•RGPB	2/3	640–1,350			evakurok	awgura
	Golden Myna <i>Mino anais</i>	K•RG	-/2	830–845				kriro
*	Russet-tailed Thrush <i>Zoothera heinei</i>	•Z			5	KJ		
	Red-capped Flowerpecker <i>Dicaeum geelvinkianum</i>	MKD•RGPB	3/4	640–1,515			titieva	psták
	Black Sunbird <i>Leptocoma aspasia</i>	MKD•RGB	1/-	700–1,200				
	Olive-backed Sunbird <i>Cinnyris jugularis</i>	D•G		700–800				
*	Blue-faced Parrotfinch <i>Erythrura trichroa</i>	MKD•PB	3/-	875–1,570	8	FKNWJ		
*	Papuan Parrotfinch <i>Erythrura papuana</i>	•P			2			
	Streak-headed Mannikin <i>Lonchura tristissima</i>	•RG						kungur-sargar
	Grey Wagtail <i>Motacilla cinerea</i>	[K]•						

Neotypification of *Catharus ustulatus* (Nuttall)

by Matthew R. Halley

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SUMMARY.—In a recent paper, I demonstrated that the original description of *Turdus ustulatus* Nuttall, 1840, was likely based on a specimen of *Catharus guttatus* (Pallas, 1811). Herein, I resolve this anomaly by designating a neotype that stabilises traditional nomenclature. Formal review by the International Commission of Zoological Nomenclature determined that intervention was not necessary because neither syntype from the original description is extant or traceable. This is the third in a series of papers concerning historical aspects of *Catharus* taxonomy and nomenclature.

Few genera of American birds have endured as much taxonomic confusion and disagreement as *Catharus* (Turdidae), known commonly as nightingale-thrushes or simply thrushes. The controversy traces to the late 18th century and a taxonomic amalgamation (*Turdus minor* J. F. Gmelin, 1789), which Wilson (1812) split into two species: *T. solitarius*, itself an amalgamation (!); and *T. mustelinus* (= *T. fuscescens* Stephens, 1817), which was long considered to be the first description of Veery *C. fuscescens* (Stephens), but was in fact yet another amalgamation and required a neotype to stabilise (Halley 2018). This was the confused state of taxonomy in 1836, when the first specimens of thrushes from western North America, collected by John Kirk Townsend (1809–51) in coastal Washington, USA, arrived at the Academy of Natural Sciences of Philadelphia (ANSP), where they were examined by Thomas Nuttall (1786–1859) and John James Audubon (1785–1851).

In a recent paper, I scrutinised the original description of *T. ustulatus* Nuttall, 1840, which was based on two specimens in this collection (Halley 2019). I reviewed non-print primary sources and the published literature, and prepared a series of fresh study skins of both *Catharus* species from coastal Washington—*C. guttatus* (Pallas, 1811) and *C. ustulatus* (Nuttall, 1840)—and directly compared them to two of Townsend's extant skins at ANSP. I published compelling evidence that Nuttall's (1840: 401) original description of *T. ustulatus* was based on a specimen of *C. guttatus*, a different species to prevailing usage (Halley 2019).

Neither study skin promoted as 'the only specimen' of *T. ustulatus* described by Nuttall (1840)—USNM 2040 (Baird *et al.* 1860: VII, Deignan 1961) and ANSP 23644 (Stone 1899: 19)—has a legitimate claim to type status (Halley 2019). *T. ustulatus* was based on two syntypes: (1) a female collected on the '10th of June' (1834 or 1835) that was the subject of Nuttall's (1840: 401) morphological diagnosis, and (2) a female collected on 'the 19th June [1835]' that was mentioned in a note by Audubon (1839: 203–204) and cited among the synonyms of *T. ustulatus* by Nuttall (1840: 400, 'in a note'). However, these purported types have collection dates and sex data that conflict with the accounts of Nuttall (1840) and Audubon (1839) (see Halley 2019: Figs. 3 and 6), and neither matches Nuttall's (1840) description of the dorsal plumage of *T. ustulatus*, which presents a closer match to *C. guttatus* than to *C. ustulatus* (Halley 2019: Figs. 7–8). Two extant *C. guttatus* specimens from Townsend's collection—MCZ 16298 and ANSP 16091—can also be eliminated as potential types for the same reason: original data that conflict with Nuttall's (1840) and Audubon's (1839) accounts (Halley 2019: 248).

The name *Catharus ustulatus* (Nuttall) has been in use for more than 180 years, referring to the 'russet-backed' taxon that breeds in coastal forests of western North America and migrates along the Pacific coast to non-breeding grounds in Middle America. The nomenclatural instability exposed by Halley (2019) requires nomenclatural action to resolve, irrespective of whether *C. ustulatus* and its sister taxon *C. swainsoni* (Cabanis in Tschudi, 1845), which has a transcontinental breeding distribution in the boreal zone of North America and migrates to non-breeding grounds in Central and South America, are classified as species (e.g., del Hoyo & Collar 2016, Halley 2019) or subspecies (e.g., Chesser *et al.* 2018).

Following independent review by a member of the Working Group on Avian Nomenclature of the International Ornithologists' Union, I applied to the International Commission of Zoological Nomenclature, a case number was assigned (Case 3817), and a notice was published in the *Bulletin of Zoological Nomenclature* (December 2019). However, two additional reviewers concluded that, although the issues raised in my application were substantive, and would require nomenclatural action to resolve, intervention by the Commission was not necessary. Therefore, neotypification of *T. ustulatus* Nuttall, 1840, may proceed according to the normal revisionary process.

Neotypification of *T. ustulatus* Nuttall, 1840

The name *T. ustulatus* Nuttall, 1840, is not unambiguously identifiable because none of its syntypes are extant and the morphological diagnosis was probably based on a specimen of a different species, *C. guttatus* (Pallas, 1811). To fix its taxonomic identity, an adult male (UWBM 79993) in the collection of the University of Washington Burke Museum of Natural History and Culture (UWBM), Seattle, WA, is hereby designated as its neotype (Fig. 1). This action stabilises traditional nomenclature and prevents confusion arising from alternative identifications. It fulfills the requirements for neotype designation in the Code (ICZN 1999) by clarifying the taxonomic application (status) of the name, as explained above (Art. 75.3.1) and at length by Halley (2019), describing, illustrating and referencing the defining characters of *C. ustulatus* and its neotype (Art. 75.3.2), providing data sufficient to ensure recognition of the specimen designated (Art. 75.3.3), providing grounds for believing that all original type material has been lost and is untraceable (Art. 75.3.4), showing that traits of the neotype are included in the original description (Art. 75.3.5), choosing a neotype collected during the breeding season in coastal Washington, where Nuttall's (1840) syntypes originated (Art. 75.3.6), and recording that the neotype is preserved in a recognised scientific institution (Art. 75.3.7). The choice of a specimen from its breeding grounds provides more stability than selecting a migrant individual with an unknown breeding locality.

UWBM 79993 is an adult female (study skin and spread wing) that was killed by a cat and salvaged on 27 June 2002 by staff of the Island Wildlife Shelter on Bainbridge Island, Kitsap County, Washington (47°38'34.35"N, 122°32'32.49"W). The study skin and spread wing were prepared by S. M. Vigallon (prep. = 23), who measured the wingspan (291 mm) and wing chord (95 mm) of the fresh (pliable) specimen before removing the skin. The bird weighed 26 g with no fat, enlarged ovaries (7 × 3 mm and smooth) and an oedematous brood patch. The skull was 100% pneumatized. No bursa was observed. Two flight feathers were missing (s9 on the right wing and rectrix 4), suggesting moult, although they may have been lost during the altercation with the cat. The stomach contained seeds. The left wing was pinned and dried in an open position with a perpendicular angle relative to the body and a straight leading edge. The outer primaries of the spread wing are worn and the tip of p7 is broken.



UWBM 79993

Catharus ustulatus

Figure 1. UWBM 79993, the neotype of *Turdus ustulatus* Nuttall, 1840; see text for detail of the specimen's provenance (Matthew R. Halley)

UWBM 79993 was examined by the author in 2019 at the Academy of Natural Sciences of Drexel University, Philadelphia, PA, where it was received on loan from UWBM as a candidate for neotypification. Like the fresh series of *C. ustulatus* specimens described by Halley (2019), the colour of the dorsal plumage of UWBM 79993 is browner and more rufescent than *C. swainsoni*, which is more olivaceous (see Pyle 1997: 398), and the specimen does not exhibit an obvious contrast between the back and tail, unlike *C. guttatus* and the original description of *T. ustulatus* ('Above olive-brown ... the tail strongly tinged with rufous' (Nuttall 1840: 401, Halley 2019).

Diagnosis. — *C. ustulatus* is distinguished from other *Catharus* species by the combination of a buffy eye-ring, which is bold and spectacle-like, and uniform olive-brown dorsal plumage and tail. In contrast to the similar *C. fuscescens salicicola* (Ridgway, 1882), which also has olive-brown upperparts and tail, the eye-ring of *C. ustulatus* is 'full and distinct,' the breast spots are 'larger and less distinct' and there is a 'lack of emargination on p6' (Pyle 1997: 397).

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The provenance of an exceptionally early specimen of Cape Verde Barn Owl *Tyto alba detorta* E. Hartert, 1913

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In the account for *Strix flammea*, i.e. modern *Tyto alba*, in his exhaustive catalogue of the owl specimens then held in the British Museum (BM) and now in the Natural History Museum (NHMUK), Sharpe (1875: 300) listed specimen *p*' as 'Male ad. sk. Porto Praya, Santiago, Cape-Verd Islands, Jan 25, 1822. Charles Darwin, Esq. [C.]'. Something is clearly wrong here, as Charles Darwin would have been less than 13 years old at the time and certainly not yet collecting in the Cape Verde Islands!

The most obvious possibility of error is that the year could actually have been 1832, not 1822: Charles Darwin did indeed visit the Cape Verde Islands twice during his voyage on H.M.S. *Beagle*, on the first occasion arriving on 16 January 1832 and staying for 21 days, i.e. including 25 January 1832. However, there is no evidence that Darwin did collect such a specimen, which is not mentioned by Gould & Darwin (1838–41), and Steinheimer (2004) did not include it in the comprehensive appendix to his Darwin bird specimen paper. Moreover, the specimen survives (Fig. 1) and what is clearly its original label reads merely 'Strix male Port Praya Jan. 25. 1822', i.e. the date is unambiguously 1822, but there is no mention of a collector (Fig. 2). Moreover, the label is totally unlike those of Darwin, who used a twist of paper with merely a number on it that cross-referenced data he recorded in his notebook (Steinheimer 2004).

This all tends to indicate that Sharpe's ascription of the specimen to Darwin was incorrect. Another suggestion was later made by Hazevoet (1995: 75) who, in mentioning a few early Cape Verde specimens with uncertain collector(s) in NHMUK, commented



Figure 1. The early Barn Owl *Tyto alba detorta* specimen from Santiago, Cape Verde Islands (Hein van Grouw, © Natural History Museum, London)



Figure 2. Detail of seemingly original label from the early *Tyto alba detorta* specimen from Santiago, Cape Verde Islands (Hein van Grouw, © Natural History Museum, London)

that 'The oldest of these is a male *Tyto detorta* collected at Praia, Santiago, 25 January 1822, presumably by the French *Coquille* expedition.' However, the *Coquille* expedition, commanded by L.-I. Duperrey, did not sail from Toulon in France until August 1822 (Duperrey 1826), so this again appears improbable.

In an attempt to disentangle this conundrum, I used an approach that started from the locality information given on the specimen label (Fig. 2). Many (somewhat more than 6,000), but by no means all, bird specimens that had both arrived in the BM bird skin collection before the mid 1830s and were still extant were included in the 44 volumes of the manuscript 'Vellum Catalogues' (Thomas 2012). These were begun around the middle of 1835 and continued to receive at least some entries until 1843, when curatorial attention switched to producing published catalogues. Although many specimens therein are incompletely identified, often with just an archaic generic name, and the catalogues were never comprehensive, they remain an extremely valuable early source of information.

The *Tyto alba* specimen under consideration is unfortunately not included in the Vellum Catalogues and, for unclear reasons, neither does it appear in the subsequent relevant published catalogues by Gray (1844, 1848). However, my search of the Vellum Catalogues for the locality 'Port(o) Praya' did yield two other specimens, both donated by Captain Sabine, undated and recorded merely as *Fringilla* (Vell. Cat. 19: 113a,b). These specimens proved to be examples of the endemic Cape Verde Sparrow *Passer iagoensis*, which both unfortunately lack original labels, each having only a late 19th-century BM one (Fig. 3). They were listed by Sharpe (1888: 324) as specimens *g* and *h*, both with the data 'Male ad. sk. Cape Verde Islands Sir E. Sabine [P.]'. The species was first described only in 1838, by Gould, based on a specimen collected in Cape Verde in January 1832 by Darwin.

A further search in the Vellum Catalogues for 'Sabine' turned up an array of other early specimens from West Africa donated by Capt. Edward Sabine, with a few localised to Sierra Leone, but no more listed as from the Cape Verdes. This ties in with a comment made by Sharpe (1906: 460) to the effect that 'Sir Edward Sabine gave many [bird] specimens from West Africa in the early part of the nineteenth century, but no register of the donations appears to have been kept.' The latter indeed appears to be the case, as my search of the Book of Presents, which recorded specimen donations to the BM (see Thomas 2012), failed to find his name mentioned. Exactly when in the early 19th century Sabine's material



Figure 3. Two Cape Verde Sparrow *Passer iagoensis* specimens collected by Edward Sabine in January 1822 on Santiago, Cape Verde Islands. Note that neither has an original label, but only a BM one dating from the late 1800s, and that '117b' on one of them is an error for '113b', its correct Vellum Catalogue number (Hein van Grouw, © Natural History Museum, London)

arrived in the museum therefore is unclear, although it was almost certainly prior to 1837, when modern registration of incoming specimens commenced (Thomas 2012).

Captain (later Sir) Edward Sabine (1788–1883) was an army officer (Royal Artillery) and physicist, who was assigned to serve as astronomer on John Ross's search for the North-West passage in 1818 and sailed to the Arctic again with William Edward Parry in 1819–20, conducting magnetic observations (Good 2011). He took a considerable interest in wider natural history, including ornithology, to which he had been introduced by his older brother Joseph Sabine, for example publishing on Greenland birds following his return from his first Arctic trip (Sabine 1819). On 17 November 1821, he joined H.M.S. *Iphigenia* in Portsmouth bound for West Africa, although the ship did not finally depart Britain until 4 January 1822, was approaching Cape Verde on 23 January (Rennell 1832: 284), and finally arrived in Freetown, Sierra Leone, on 18 February 1822. Here Sabine remained until 18 April 1822, when he embarked on H.M.S. *Pheasant* for a programme of geodesical studies in the tropical seas between Africa and the Americas, finally arriving in Britain on 2 February 1823 (Challenger 1973).

Edward Sabine was asked by Joseph Sabine, then Secretary of the Horticultural Society, to enlist a plant collector, George Don, to make botanical collections for the society in West Africa, South America and the West Indies during his voyage (Challenger 1973). Don most helpfully kept a detailed journal of the trip, now held in five volumes by the Lindley Library, Royal Horticultural Society, London. Vol. 1 (RHS/Col/2/1/1) records that the Atlantic island ports of call by H.M.S. *Iphigenia* en route to West Africa comprised Madeira, Tenerife and the Cape Verdes, with the ship coming in sight of the latter on 24 January, anchoring at 'Porto Prayii, St. Jago' on 26 January and sailing again for West Africa on 28 January (Don ms.). In his entry for 26 January, Don noted that he, Edward Sabine and John Smith, Sabine's assistant, landed, and that John Smith was shooting birds, specifically

including ‘a curious owl’. He further noted that on 27 January ‘this day Captain Sabine had several birds brought to him by the officers, among which was a very strange kingfisher’.

In conclusion, there is therefore no reasonable doubt that the *Tyto alba detorta* specimen under consideration was collected on Santiago, Cape Verdes, by John Smith, on behalf of Edward Sabine, in January 1822, although Don (ms.) indicated this occurred on 26 January rather than the 25 January noted on the label (Fig. 1). During his two days on Santiago, Sabine clearly also acquired several other bird specimens, although only the two *Passer iagoensis* can be documented to have reached the BM. The kingfisher was undoubtedly Grey-headed Kingfisher *Halcyon leucocephala*, a common resident on Santiago (Hazevoet 1995). This early collecting visit was not noted by Hazevoet (1995) in his chapter on History of Ornithological Exploration on the Cape Verdes, and seems to have escaped the attention of ornithologists until now.

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