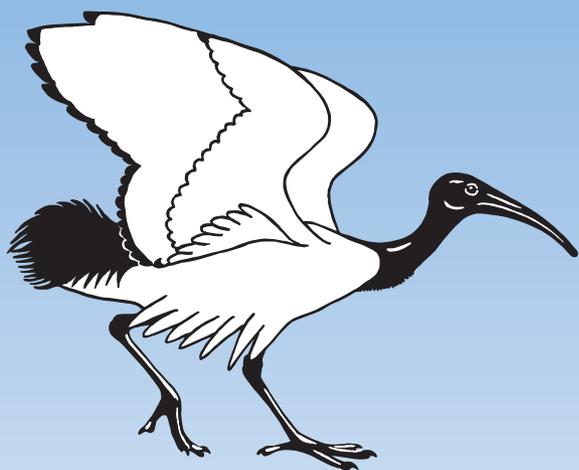


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CLUB ANNOUNCEMENTS

British Ornithologists' Club meetings in 2020

As previously announced and owing to the Corvid-19 pandemic, the 2020 meetings programme has had to be substantially adjusted. The current situation is that Prof. Diamond's talk, in conjunction with the Linnean Society has been deferred, subject to his availability, until a date in 2021. It is also looking distinctly uncertain as to whether the 21 September meeting, including the Annual Review, will be able to proceed. Should it do so, Dr Beth Okamura has most kindly provisionally agreed to give her previously planned talk on *How birds shape freshwater biodiversity* on that date. The talk scheduled for 16 November, which again had been planned in conjunction with the Linnean Society at their premises, is intended to be by Professor Jon Fjeldså, Univ. of Copenhagen, on the subject of the evolution of passerine birds. This talk had been designed to celebrate the 1,000th evening meeting of the BOC but, should it go ahead, will now be slightly ahead of the anniversary given the forced cancellation of prior 2020 meetings! At present, we remain very hopeful that this event will occur on schedule, but it is clearly too early to be definitive on this point, so please keep checking the website <https://boc-online.org/> for updates.

Robert Prŷs-Jones

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://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
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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. 132–139 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).

First record of Rufous-thighed Kite *Harpagus diodon* in Colombia

by Orlando Acevedo-Charry, William Daza-Díaz & Zuania Colón-Piñeiro

Received 8 January 2020; revised 25 March 2020; published 22 June 2020

<http://zoobank.org/urn:lsid:zoobank.org:pub:7D696246-E30F-47FD-B8B0-E89306470798>

SUMMARY.—We report the first record of Rufous-thighed Kite *Harpagus diodon* in Colombia, the north-westernmost documented record of this species during its non-breeding season. In addition, we conducted a spatiotemporal analysis of the species' distribution based on a compilation of available records. Documented records evidence that this raptor either moves further north-west than was previously assumed, or that vagrants reach north-western Amazonia, suggesting that further ornithological research into austral and intra-tropical migrants in southern Colombia is needed. Differences between patterns of documented and undocumented records of this species suggest the need for multimedia evidence to substantiate data generated by citizen science initiatives.

One of the most remarkable global phenomena in nature is bird migration. Migration, the regular seasonal movement of individuals between breeding and non-breeding ranges, can be over short to long distances, even in the same species (Monti *et al.* 2018, Gómez-Bahamón *et al.* 2020). Neotropical birds exhibit different types of migrations—latitudinal, longitudinal or altitudinal. Latitudinal migration includes Nearctic–Neotropical (boreal), i.e. species that breed in North America, and austral–Neotropical (austral), i.e. those that nest in southern South America, both of which migrate to the tropics. Longitudinal and altitudinal, or intra-tropical migrations, include movements across elevational gradients and between forest types, to over-winter within the tropics (Hayes 1995, Jahn *et al.* 2004, Ocampo-Peñuela 2010). Nearctic–Neotropical migration is by far the best-studied migration system, with more than 40 years of extensive investigation (Faaborg *et al.* 2010, Gómez *et al.* 2012). In contrast, austral and intra-tropical migration systems are still relatively poorly known (Ocampo-Peñuela 2010, Gómez *et al.* 2012). To ensure successful conservation of Neotropical birds, a complete and updated baseline of distribution, habitat use, spatial abundance, spatiotemporal analysis of pattern movements, and long-term abundance change is needed.

The inclusion of semi-structured data from citizen science initiatives (Sullivan *et al.* 2009, La Sorte *et al.* 2018) is important to the development of research focused on austral and intra-tropical migrations (Johnston *et al.* in review). For example, the distribution and migratory status of Rufous-thighed Kite *Harpagus diodon* were recently analysed using citizen science data (Lees & Martin 2015). Although its status as a migrant was known (Cabanne & Seipke 2005), the species' breeding distribution has only recently been clarified and systematic long-term monitoring to assess the extent of its migratory behaviour is still lacking. Originally considered to be a near-endemic breeder to the Atlantic Forest (Lees & Martin 2015), Rufous-thighed Kite is now known to nest also in the Austral Yungas of Bolivia and Argentina (Areta & Juhant 2019). Nevertheless, during the presumed non-breeding season (May–August) the species extends its range north into Amazonia (Lees & Martin 2015, Areta & Juhant 2019). We report here the first documented record of *H. diodon* in Colombia, in north-western Amazonia. We also analysed records between the

expected breeding and non-breeding seasons and the spatiotemporal distribution of this poorly known raptor using documented (museum specimens, photo, audio) records and undocumented observations (citizen science and published sightings).

Methods

On 12 June 2019, we observed a Rufous-thighed Kite on a 9-km trail (03°77.5'N, 70°33.9'W) between Puerto Nariño and San Martín de Amacayacu, dpto. Amazonas, in southern Colombian Amazonia between the Amazon and Amacayacu Rivers. This trail has been used for environmental outreach and for training local communities in tourism and monitoring activities.

To place this record in context, we compiled all available breeding, non-breeding and migratory records of the species and conducted a spatiotemporal analysis. Distributional records (both documented and undocumented) were accessed via two previously published studies of the species' breeding range (Lees & Martin 2015, Areta & Juhant 2019), WikiAves (<https://www.wikiaves.com.br>), Bierregaard *et al.* (2019), the Macaulay Library at the Cornell Lab of Ornithology (<https://www.macaulaylibrary.org>), and Global Biodiversity Information Facility (GBIF), which include specimens and citizen science data (i.e. eBird). Via the Kaggle platform, we downloaded the dataset 'Brazilian bird observation metadata from Wikiaves' which includes all observations of Rufous-thighed Kite prior to 8 December 2019 (Lessa-Bernardineli 2019). To avoid duplication, we deleted WikiAves data from the Lees & Martin (2015) dataset and selected one record per day from each locality in WikiAves. To access GBIF data, we used the 'dismo' package as of 20 June 2019 (Hijmans *et al.* 2017). Multimedia data in the Macaulay Library at the Cornell Lab of Ornithology were manually extracted using dates and coordinates for photo and audio records made on the same day. We categorised a record as documented if it involves a specimen in a museum, photo or audio, and all others as undocumented, even for those published in peer-reviewed journals (e.g. Ridgely 1980).

We assigned each record to one of the five life-cycle categories representing six temporal periods designated by Areta & Juhant (2019): breeding season (16 October–14 March), breeding / migration overlap (15–31 March and 1–15 October), northbound migration (1–30 April), non-breeding season (1 May–31 August), and southbound migration (1–30 September). To display spatiotemporal relationships, we used a Loess-smoothing algorithm with the `geom_smooth` in the 'ggplot2' package (Wickham 2016) for the documented and the undocumented datasets separately. Assessment and data analysis were performed in the R program, creating figures using 'ggplot2' and QGIS.

Results and Discussion

We report for the first time a documented record of Rufous-thighed Kite in the Colombian Amazon (Fig. 1). Rufous-thighed Kite can be confused with Bicoloured Hawk *Accipiter bicolor*, probably due to Batesian mimicry (Willis 1976) or interspecific social dominance mimicry (Prum 2014, but see Leighton *et al.* 2018). We eliminated *A. bicolor* based on the diagnostic combination of the obvious rufous thighs and two notches in the maxilla (Fig. 1b).

We assessed a total of 4,164 records collected between 1884 and 2019, from which we excluded 63 records due to incomplete date information (i.e. month and day) and 510 due to their being duplicates (Appendix, see Supplementary Information). Overall 3,591 records were utilised in the analyses, 2,030 documented and 1,561 undocumented (Fig. 2). Citizen science data contributed 90% of these (WikiAves 1,743 and eBird 1,515). Of the total,



Figure 1. First documented record of Rufous-thighed Kite *Harpagus diodon*, dpto. Amazonas, Colombia, June 2019, showing (a) predation of a lizard, and (b) the two notches in the maxilla (William Daza-Díaz).

2,607 records were from the breeding season (Fig. 2a), 56 during northbound migration (Fig. 2b), 260 during the non-breeding season, including our own record (Fig. 2c), and 209 during southbound migration (Fig. 2d). Additionally, the first breeding / migration overlap category in March accounted for 90 records, and the second breeding / migration overlap category in October for 369 (Fig. 2).

Our record is not the northernmost but is the westernmost of the species to be documented, more than 600 km from the nearest record supported by verifiable evidence (at San Carlos de Rio Negro, Amazonas, Brazil; Fig. 2a–e). There is an undocumented but probably correct record from the Ecuadorian Amazon during the non-breeding season (Ridgely 1980), 800 km west of Puerto Nariño (Fig. 2c). Our record in Colombia is from the non-breeding season of this raptor, but it might represent only a vagrant occurrence in north-west Amazonia, although ornithological field work in this region is comparatively low, and raptor surveys, especially standardised migration surveys, basically non-existent (e.g. Juhant 2012).

Spatiotemporal Loess fits revealed a consistent pattern of seasonality in latitude (Fig. 2f) but less clear in longitude (Fig. 2g). Changes in latitude supported by documented data during migration were more evident than undocumented data (Fig. 2f), which pattern was also highlighted by Lees & Martin (2015). The difference between documented and undocumented patterns could be explained by two possibilities. First, some individuals remain in the southern breeding range year-round. As already noted, there is a lack of long-term systematic monitoring of the species' migratory behaviour, with just two sites where active migration has been recorded, one in south-east Brazil (Cabanne & Seipke 2005) and the other in eastern Bolivia (Juhant 2012). Secondly, misidentification of Rufous-thighed Kite via confusion with the very similar Bicoloured Hawk, Double-toothed Kite *Harpagus bidentatus* and / or Sharp-shinned Hawk *Accipiter striatus*. To assess Wallacean shortfalls— incomplete knowledge of a species' distribution—Areta & Juhant (2019) recommended (a) to integrate bibliographic searches and specimen data with citizen science, and (b) critically determine life-cycle categories, as was attempted here. Nevertheless, multimedia evidence

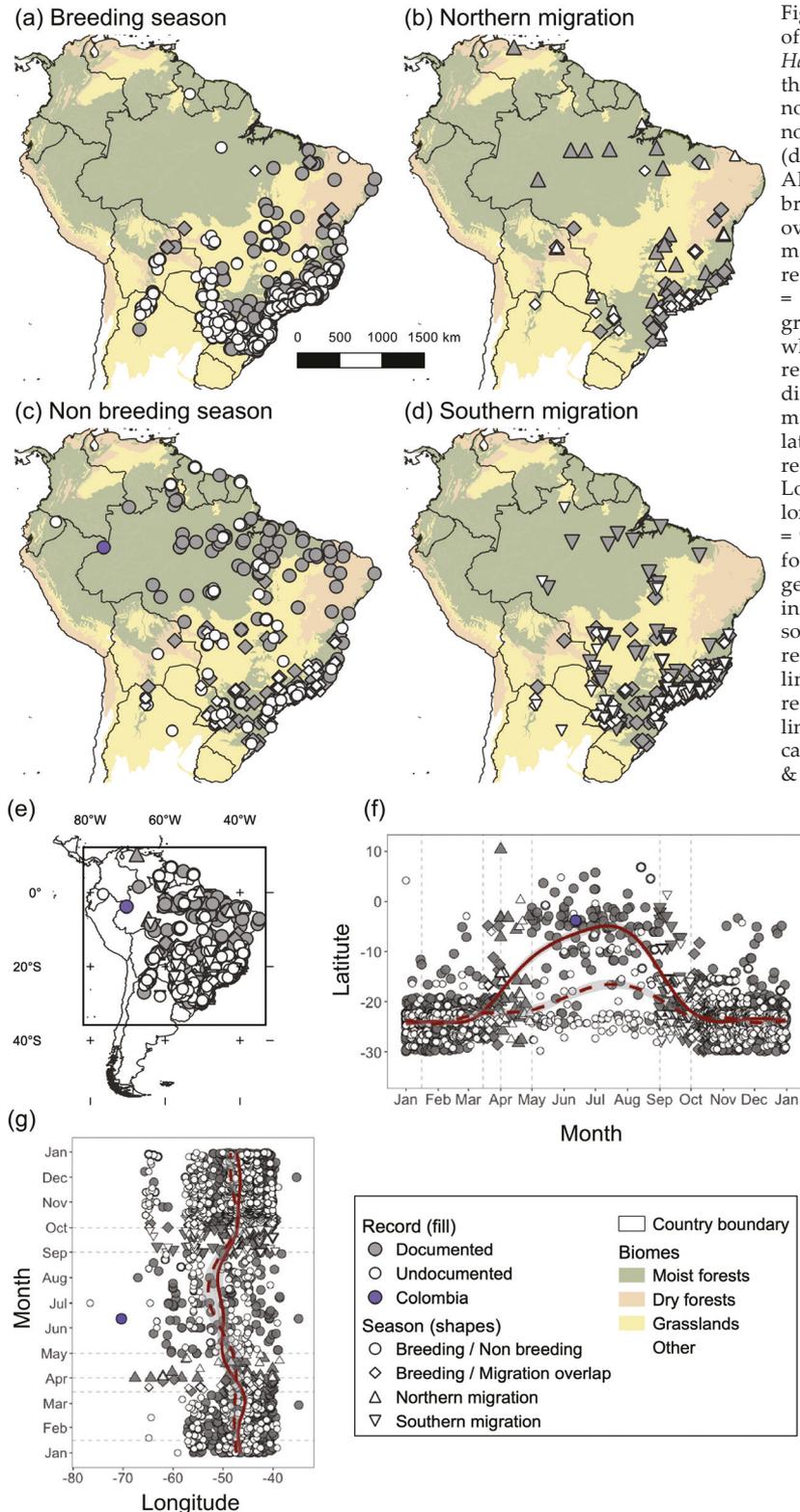


Figure 2. Map of records of Rufous-thighed Kite *Harpagus diodon* during (a) the breeding season, (b) northerly migration, (c) non-breeding season, and (d) southerly migration. All four panels show breeding / migration overlap, with (e) an inset map combining all of the records; the purple dot = the Colombian record; grey = documented and white = undocumented records. Spatiotemporal distribution of records is mapped in relation to (f) latitude and (g) longitude; red lines in (f–g) show Loess fits for latitude / longitude, the shaded area = 95% confidence interval for each fit following geom_smooth function in ggplot2 R package, solid line = documented records and dashed line = undocumented records; dashed vertical lines separate life-cycle categories following Areta & Juhant (2019).

(photo and audio recordings) is crucial, especially during the non-breeding season, to confirm the migration and overwintering ranges of the species.

Our updated spatiotemporal analysis could suggest that misidentification of Rufous-thighed Kite is more frequent than previously believed (Fig. 2f). Moreover, we added the species to the Colombian avifaunal list (Avendaño *et al.* 2017), from north-west Amazonia (see Ridgely 1980), a region in need of urgent conservation focus and monitoring because of recent increases in deforestation (Armenteras & Defler 2019, Clerici *et al.* 2019). Nonetheless, the Colombian portion of this part of Amazonia has also yielded several recent novelties in avian distribution (Carantón Ayala *et al.* 2016, Peña Alzate *et al.* 2020), highlighting the need for further surveys and field work. Additional work with Rufous-thighed Kite could include the use of satellite tags or solar geolocators to analyse the movements of this austral migrant across Amazonia (Lees & Martin 2015, Winkler *et al.* 2017), techniques which have proven efficient at tracking raptor movements elsewhere in the world (Phipps *et al.* 2019). Such studies should include birds breeding in the Atlantic Forest of Brazil (Lees & Martin 2015), the Cerrado in eastern Bolivia, and Austral Yungas in Bolivia and Argentina (Areta & Juhant 2019). Another priority is to conduct systematic migration counts of this (and other migratory raptors) throughout South America (M. A. Juhant pers. comm.).

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Appendix (Supplementary Information): Records of Rufous-thighed Kite *Harpagus diodon* used in the spatiotemporal analyses (see Fig. 2). .xls file available online at <https://10.25226/bboc.v140i2.2020.a2>.

Audubon's Bird of Washington: unravelling the fraud that launched *The birds of America*

by Matthew R. Halley

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SUMMARY.—The Bird of Washington *Falco washingtonii* Audubon, 1827, was a new species of eagle published in the opening plates of John James Audubon's influential work, *The birds of America* (1827–38). It was the first plate engraved by Robert Havell Jr. and the first new species Audubon described in his career. However, the Bird of Washington was published without specimen evidence and, to this day, no specimen with the anatomical characters in Audubon's descriptions and plate has ever been found. To shed light on the case, I conducted an exhaustive search for primary (non-print) sources in multiple archives in the USA and transcripts in the literature. Here, I demonstrate beyond reasonable doubt that Audubon's painting of the Bird of Washington was not 'faithfully figured from a fresh-killed specimen', as he claimed, but was the product of both plagiarism and invention. The preponderance of evidence suggests that the Bird of Washington was an elaborate lie that Audubon concocted to convince members of the English nobility who were sympathetic to American affairs, to subscribe to and promote his work. Audubon rode his Bird of Washington to widespread fame and then actively maintained the ruse for more than 20 years, until his death, fuelling decades of confusion among scientists and the general public. The broad implications for Audubon-related scholarship and ornithology are discussed.

'...my motto is: *'Le temps decouvrira la vérité.'* [Time will uncover the truth.]'—Audubon (1897: 271)

Art and science are both creative and intellectual activities, but their products are judged by different (almost opposite) standards. Works of art are primarily evaluated based on their impacts on the subjective (emotional) experience of the observer. There is no penalty for infusing art with imaginative scenes and objects that resemble reality but do not (and are not intended to) accurately represent it. In contrast, the standard by which a body of scientific work is judged (its reliability) depends in large part on the author's integrity. Rasmussen & Prÿs-Jones (2003), who investigated the now infamous specimen fraud perpetrated by the British ornithologist, Richard Meinertzhagen (1878–1967), remarked: 'how slow and difficult the path may be from well-founded suspicion to a reasonable level of proof [of fraud] and ... in the intervening period, most researchers ... may remain entirely ignorant of the doubts surrounding the data ... with negative effects on ornithology.' In the case of 'natural history artists', who produced mixed works of visual art and scientific text, the different standards by which artists and scientists are judged may result in conflicting assessments of quality. 'Few men can transcendently excel in more than one branch' (Stroud 2000: 119).

John James Audubon (1785–1851) is regarded as one of the most influential and prolific natural history artists of all time. In the USA, the name Audubon is widely known and has become synonymous with everything related to birds. There are hundreds of local and

regional Audubon Societies and dozens of towns, neighbourhoods and streets bear his name. Audubon's work is considered by historians to signal a new era in American ornithology (Allen 1951). According to the standards by which artists are judged, Audubon's legacy is beyond dispute. His images are creative, demonstrate technical mastery and have broad aesthetic appeal. However, Audubon's writings must be judged by the rigorous standards of science (i.e., agnostic to the emotional appeal of his artwork). Remarkably, a thorough assessment of this kind is still pending because, to date, few professional ornithologists have immersed themselves in the primary record of Audubon's life. With the exception of Herrick (1917), who conducted early field research on the Bald Eagle *Haliaeetus leucocephalus* (Linnaeus, 1766), Audubon's biographers have not been professional ornithologists (e.g., St. John 1856, Peirce 1863, Arthur 1937, Ford 1964, Rhodes 2004, Souder 2014, Nobles 2017). This bias apparently contributed to several misconceptions concerning his scientific accomplishments (e.g., Halley 2018a,b).

By the time Audubon began publishing, in the late 1820s, the institutionalisation of the natural sciences in America and Europe was well underway. National and regional governments were funding scientific expeditions (e.g., James 1823) and universities and academic societies were offering classes in ornithology and other disciplines. Philadelphia, c.28 km from Audubon's teenage home (Mill Grove), was the hub of scientific activity in America. However, despite this proximity, Audubon was not formally trained in science. Like many other 'ordinary Americans' who dabbled in natural history observation, he apparently felt some contempt for wealthy elites and their scholarly institutions (Lewis 2011). This feeling was reinforced in 1824, when Audubon was rejected for membership at the Academy of Natural Sciences of Philadelphia (Halley 2018c: 63). Two years later, he would leave his wife and children in the USA and travel to Europe to seek subscribers and an engraver for the work that would become *The birds of America* (1827–38). In the months prior to his departure, Audubon corresponded with Reuben Haines III (1786–1831), the Corresponding Secretary who had nominated him for (the rejected) Academy membership, and his letters were filled with anxiety about an uncertain future:

'I must touch the only thing that ever vibrated sorrow to my heart.—I must leave America. ... With an allmost despairing heart I shall leave America early this ensuing spring, and now bid you my farewell.—Yes it is my farewell indeed for unless a success scarce expected should take place, I never will review this happy continent, will have to abandon my long acquired habits of watching nature at work and will droop moreso amongst the dreg of the world as it is called.' (Audubon to Haines, 25 December 1825; Haverford College Library, Quaker and Special Collections (HCL), reproduced in Halley 2015)

To say that Audubon's journey to Europe was a success would be a gross understatement. The publication of *The birds of America* was initiated within one year of his arrival in England, with the critical financial support of the British crown and European nobility (Fries 2006). The pivotal point in Audubon's fortune coincided with his publication of a new species of North American eagle that he called the Bird of Washington *Falco washingtonii* (Audubon, 1827, Pl. 11). It was the first new species described by Audubon and the first species engraved by Robert Havell Jr. (1793–1878). It was published when Audubon's financial prospects were at their bleakest, and helped to instigate a dramatic reversal in his career. Soon after publication of Pl. 11, on 3 December 1827, Audubon wrote triumphantly to Reuben Haines: 'I am engaged in the publication of my work at last' (HCL, see Halley 2015).

However, Audubon never produced a specimen with the anatomical characters of the Bird of Washington, as shown in Plate 11 (1827) and described in multiple text accounts (e.g., Audubon 1828, 1831, 1839). After nearly two centuries, the species is still known only from Audubon's anecdotes and plate, and secondary (anecdotal) sightings by his friends. Professional ornithologists have generally assumed that Audubon (innocently, most argue) misidentified an immature *H. leucocephalus*. On this basis, Audubon's scientific name *Falco washingtonii* and its variants (e.g., *F. washingtoniensis*) have occasionally been used for the northern subspecies of *H. leucocephalus*, depending on the extent to which different committees of ornithologists trusted Audubon's anecdotes (e.g., AOU 1944: 445, Mengel 1953). The name *washingtonii* has not been used in recent years, but 25 of Audubon's species names are currently in use by the American Ornithological Society (Chesser *et al.* 2018) and many more continue to be used for subspecies (e.g., Harris's Hawk *Parabuteo unicinctus harrisi* (Audubon); see Halley 2020a).

Methods

I conducted a multi-year (2015–19) investigation of primary (non-print) materials in the Academy of Natural Sciences of Drexel University Archives (ANSP), American Philosophical Society Library (APS), Historical Society of Pennsylvania (HSP), New-York Historical Society (N-YHS) and Yale University Archives (Yale). Whenever possible, I reconstructed the timeline of events exclusively via independent and / or contemporaneous primary sources (letters, memoranda, meeting minutes, etc.) because Audubon tended to distort the timelines in his published writings (e.g., Dallett 1960: 90–91, Halley 2018a). This approach differs from most previous authors, who treated *Ornithological biography* (1831–39) as a 'primary' historical source, despite many of Audubon's statements in that work being contradicted by independent primary sources. For example, contemporaneous sources confirm that Audubon was not in Pennsylvania when he claimed to have re-sighted ringed Eastern Phoebes *Sayornis phoebe* (Latham, 1790) there in 1805, and the original source of his (probably apocryphal) ringing experiment was Audubon's (1834: 126) own anecdotal account, published 30 years after the purported events took place (Halley 2018a). For this reason, unlike previous authors, I did not assume *a priori* that any published statement of Audubon was true. Only by reconstructing the timeline from independent sources were Audubon's manipulations (some inadvertent, some likely deliberate) able to be exposed. My semi-chronological approach thus enables the reader to assess the critical events of the Bird of Washington case as they developed in proper sequence.

With the exceptions of Herrick (1917) and Souder (2014), most biographers of Audubon barely mentioned the Bird of Washington. Thus, many of the sources quoted here are taken from my transcriptions of materials that have not appeared in print previously, to my knowledge. In such cases, I cite the appropriate archives and collections where the primary materials are stored. Where possible, I verified published transcriptions of primary sources by personally examining the original materials and, when necessary, translated from French and provided the original text for comparison. The remainder of the paper contains the results of this research, presented as a mixture of historical narrative and contemporary analysis. The narrative begins in 1826, when Audubon arrived in Europe and first displayed the Bird of Washington to the British public.

Unveiling the Bird of Washington

In late July 1826, Audubon arrived in England with his large portfolio of original paintings, hoping to find a publisher for his planned work, *The birds of America*. Within



Figure 1. Audubon's original painting of 'Falco ossifragus / Sea Eagle' (N-YHS 1863.17.11), reproduced courtesy of the New-York Historical Society. Digital image created by Oppenheimer Editions.

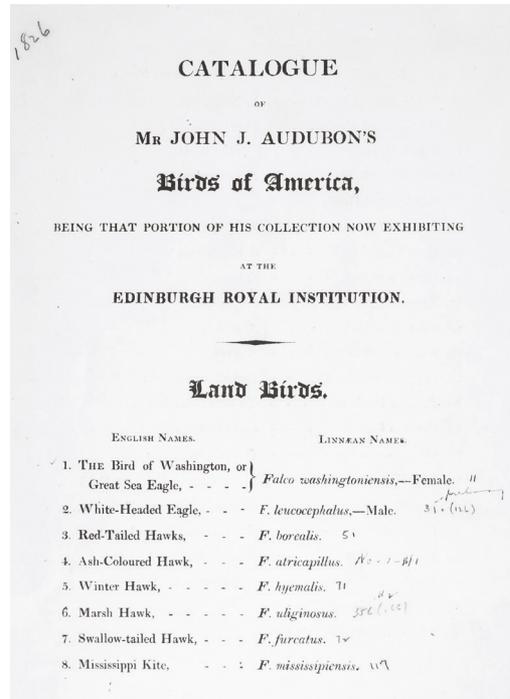


Figure 2. Title page of a 'Catalogue of Mr John J. Audubon's *Birds of America*, being that portion of his collection now exhibiting at the Edinburgh Royal Institution,' printed for attendees of his 1826 exhibition. Reproduced courtesy of the Division of Rare and Manuscript Collections, Cornell Univ. Library (coll. 3427).

two weeks, via the generosity of William Roscoe (1753–1831) and the Rathbone family, his paintings were enthusiastically received by more than 400 attendees at the Liverpool Royal Institution (Fries 2006: 5). Three months later, a similar exhibition was held in Edinburgh, where 'success was immediate [and Audubon] became the talk of the town' (Herrick 1917, 1: 359). There, Audubon was introduced to William Home Lizars (1788–1859), who would engrave the first ten plates of *The birds of America* in 1827.

The subject of Audubon's opening number—the first 'painting' (graphite, pastel, black ink and watercolour) on display in his exhibition of 209 original works—was a massive eagle perched on a bare rock (Fig. 1). Audubon's claim was extraordinary: it was a new species, not yet described by naturalists, and Alexander Wilson (1766–1813), late author of *American ornithology* (1808–14), had overlooked the largest eagle in North America despite travelling extensively within its range. Audubon's new species was most like *H. leucocephalus*, but differed in several anatomical details including the scutellation pattern on the feet, the shape of the bill, its much larger size, and (assuming it was an adult) the lack of white on the head and tail. Audubon prominently listed the 'Bird of Washington, or Great Sea Eagle / *Falco washingtoniensis*' in a pamphlet printed for exhibition attendees (Fig. 2). It was evidently sometime after he arrived in Europe that Audubon decided to name the new species after the celebrated American patriot and statesman, George Washington (1732–99),



Figure 3. Annotations on the original ‘painting’ of the Bird of Washington (N-YHS 1863.17.11): (left) ‘Sea Eagle / *Falco Ossifragus*.’ (centre) ‘Drawn from Nature / by / John J. Audubon / New Orleans 1822.’ (right) ‘Male ... Total Length 3 feet 6 ½ / 12 ... Breadth – 10 [feet] 1 / 12 ... Weight – 14 [pounds] 12 / 16.’ Images reproduced courtesy of the New-York Historical Society. Digital image created by Oppenheimer Editions.

because the names ‘Sea Eagle’ and ‘*Falco ossifragus*’, a synonym of *H. leucocephalus* (Ord in Wilson 1814: 129, Bonaparte 1824: 344), were (and still are) painted on the rock surface in Audubon’s original painting (Fig. 3, N-YHS 1863.17.11).

By the 1820s, there was a general expectation among zoologists on both continents that new species descriptions should be accompanied by specimen evidence (Lewis 2011). In America, ornithologists had been depositing their new discoveries at the Philadelphia (Peale) Museum for more than two decades (e.g., Wilson 1813, Say in James 1823, Miller 1988). Audubon did not have a specimen of the Bird of Washington when he displayed his painting in Liverpool and Edinburgh, but the following year he claimed that his painting was based on a (non-extant) specimen that he had collected in Kentucky several years earlier (Audubon 1828). Curiously, Audubon’s painting was annotated with the word ‘Male’ (Fig. 3) although the 1826 catalogue stated ‘Female’ (Fig. 2); in his 1828 paper and subsequent publications, Audubon maintained that his massive specimen had been a male. Females are the larger sex in *Haliaeetus* ‘sea eagles’, so it would stand to reason that if the dimensions Audubon wrote (in black ink) on his painting were indeed taken from a male specimen, a female Bird of Washington would be even larger (Fig. 3). These mensural data, and the fact that he signed and dated his painting with Wilson’s usual tagline, ‘Drawn from Nature’, also implied that Audubon once had a specimen—evidence to support his extraordinary claim.

Evidence of plagiarism

In the late 20th century, Partridge (1996) noticed a striking resemblance between Audubon’s painting of the Bird of Washington and an older image labelled ‘Golden Eagle’, ostensibly depicting *Aquila chrysaetos* (Linnaeus, 1758), published in an edited serial work *The Cyclopædia* (Rees 1802–19):

‘Evidence points to the published plate [from *The Cyclopædia*] as [Audubon’s] direct source. The golden eagle is perched on its out-cropping precisely as is Audubon’s bird, with the same curve to the wings and wingtip overlapping tailfeathers [*sic*], the same angle of stance, contour of the head and beak, furrowed brow line, and even an identical highlight in the eye ... [Audubon] clearly shows ten tail-feathers in the drawing, where he specifies twelve in his text; but there are ten, though asymmetrically arranged, in the Rees print.’ (Partridge 1996: 300)

Partridge (1996) and Olson (2012: 104) assumed that the 'Golden Eagle' image in the American edition of *The Cyclopædia* (1806–20) published by S. F. Bradford was Audubon's source and that it had been based on a specimen in the Peale Museum in Philadelphia. However, the 'Golden Eagle' in this edition was based on an earlier image that first appeared in January 1802, in the original British edition of *The Cyclopædia* published by Longman *et al.* (1802–19). The original image was produced in Europe, presumably to accompany the entry for 'Accipitres', following Linnaean taxonomy, and had no connection to a specimen in any American museum. Differences between the British and American editions merit consideration because many of the plates were re-engraved in Philadelphia. Indeed, the 'Golden Eagle' was re-engraved by George Murray (1766–1822) and published by Bradford in May 1806. Coincidentally, Alexander Wilson began working for Bradford as assistant editor in April 1806, one month earlier, so Wilson was probably familiar with the image (Hunter 1983: 79).

Murray's engraving differs subtly from the original and it is not clear which edition was Audubon's source (Fig. 4). A notch on the lower edge of the maxilla in Audubon's image, known to ornithologists as a 'tomial tooth', is more prominent in the British edition image than the American, but present in both. Neither *H. leucocephalus* nor *A. chrysaetos* in fact has a prominent tomial tooth, a character more typical of falcons (family Falconidae) than of Accipitriformes (del Hoyo *et al.* 1994). Another anatomical discrepancy, the scutellation pattern on the foot of the Bird of Washington, was evidently copied from a different line drawing in *The Cyclopædia*: the disembodied foot of a raptorial bird (labelled 'Falco' but anatomically ambiguous) first published in 1812, ten years before Audubon purportedly painted his Bird of Washington from a 'fresh-killed specimen' (Fig. 4). Also, neither *H. leucocephalus* nor *A. chrysaetos* has a scutellation pattern like the one shared by Audubon's image and the 'Falco' foot in *The Cyclopædia* (Cassin 1856). By the time he displayed his painting in Europe in 1826, the men most likely to have noticed Audubon's deception were dead, or nearly so: Sydenham Edwards (1768–1819), the English artist who drew the original images that Audubon copied; Thomas Milton (1743–1827), who engraved them for the British edition; George Murray (1766–1822), who re-engraved the 'Golden Eagle' image for the American edition; and Alexander Wilson, who had died in 1813.

As noted by Partridge (1996), Audubon had access to *The Cyclopædia* during his year-long residency (1819–20) in Cincinnati, Ohio, just prior to the date written on his Bird of Washington painting (1822). The Circulating Library Society of Cincinnati (CLSC) was housed in one of the lower rooms of the newly constructed Cincinnati College building, where Audubon was employed as a taxidermist preparing mounted specimens for the new 'Western Museum', which opened to the public the following year (Kellogg 1945, Hendrickson 1946). A rare pamphlet contains the following notice: 'a deposit of five dollars shall be made with the librarian by every shareholder on receiving a volume of the 'Cyclopædia' (Rees), 'Wilson's Ornithology', or the 'English and Classical Dictionary' (CLSC 1816). The copy of the American edition of *The Cyclopædia* owned by the CLSC was sold in 1824 to the University of Miami, where it is still present (McSurely 1908: 2).

Audubon probably had an opportunity to study the British edition too. One of the few American subscribers was John W. Francis (1789–1861), who was an undergraduate student in 1806–09 at Columbia College in New York (Duyckinck & Duyckinck 1856: 122). Francis was enrolled in class with Samuel L. Mitchill (1764–1831), professor of natural history, when Mitchill hired Audubon to prepare mounted specimens for his classroom during the winter of 1806–07 (Ford 1964: 66). Audubon was working in pastels during this period, and many of his drawings are now preserved in the Houghton Library at Harvard University



Figure 4. (1A–1C) Three images of Audubon’s original painting of the Bird of Washington (N-YHS 1863.17.11), reproduced courtesy of the New-York Historical Society. Digital image created by Oppenheimer Editions. The close-up image at bottom left (1C) has been flipped horizontally for comparison to Audubon’s sources. (2A, 2B) ‘Golden Eagle’ drawn by Sydenham Edwards, engraved by Thomas Milton and published in 1802 in the British edition of *The Cyclopædia* (Longman, Hurst, Rees, Orme & Brown), reproduced courtesy of the Univ. of Michigan (<https://catalog.hathitrust.org/Record/001464694>, accessed 9 October 2019). (2C) ‘Falco’ foot, published in 1812 in the British edition (Plate IV) of Rees (1802–19), reproduced courtesy of the Univ. of Michigan (<https://catalog.hathitrust.org/Record/001464694>, accessed 9 October 2019). (3A, 3B) ‘Golden Eagle’ re-engraved by William Murray and published in 1806 in the American edition of Rees (1806–20); reproduced courtesy of the Academy of Natural Sciences of Drexel Univ. (ANSP) Library (QH13.R32). (3C) ‘Falco’ foot, re-engraved by H. S. Tanner (Philadelphia) and published in the American edition (Plate IV, date uncertain), reproduced courtesy of the ANSP Library (QH13.R32).

(MS Am 21, MS Am 21.5, MCZ 118). Partridge (1996: 298) speculated that the Bird of Washington painting ‘may be a copy of an earlier pastel’, in part because of its similarity to Audubon’s early pastel-dominated images. She remarked that the ‘design and handling of some [of Audubon’s later] drawings ... are more relaxed and assured than in the stilted ‘Bird of Washington’; its archaic quality is odd even in light of his reliance on illustrational

conventions' (Partridge 1996: 298). This may be because the original 'painting' (pastel and pencil) of the Bird of Washington was executed in 1806–07, with both images from *The Cyclopædia* being used as source material (i.e., 'Golden Eagle' and 'Falco'); then, prior to Audubon's European exhibitions, he touched it up and embellished it with watercolour and black ink. At some point, Audubon also cut out the bird (and rock) and adhered it to a large piece of paper. The timing of these developments is not known.

Regardless of which edition of *The Cyclopædia* was Audubon's source, the most parsimonious explanation for the evidence presented here is that the Bird of Washington was not drawn from a specimen as he claimed. Rather, it was an amalgamation of two apparently imaginary images (i.e., not based on specimens themselves, as evidenced by multiple anatomical errors), copied by Audubon without attribution, to which he added colour and fine artistic details that rendered his painting more life-like and obscured the plagiarism. The fraudulent origin of the Bird of Washington painting is critical to understanding the subsequent developments in the story, including how and why Audubon concealed the truth from his readers, friends and family.

Publication of the Bird of Washington

By early June 1827, with fewer than ten of the plates for *The birds of America* completed, problems arose in Edinburgh and the production schedule of the book fell behind. 'I received a letter from Mr. Lizars that was far from allaying my troubles,' Audubon wrote in his journal, 'I was so struck with the tenure [*sic*] of it that I cannot help thinking now that he does not wish to continue my work' (Audubon 1897: 257)¹. However, the bad news was soon tempered by a new opportunity. The following day, Charles Lucien Bonaparte (1803–57), who was passing through London on his way back to America, introduced Audubon to influential members of the Royal Society:

'My portfolios were opened before this set of learned men, and they saw many birds they had not dreamed of [including the Bird of Washington]. Charles offered to name them for me, and I felt happy that he should; and with a pencil he actually christened upwards of fifty, urging me to publish them at once in manuscript at the Zoological Society.' (Audubon 1897: 257)

A few days after that meeting, Bonaparte boarded a ship to America with the first ten (Lizars) plates of *The birds of America* in his possession (Stroud 2000: 90). Audubon then 'removed the publication of [his] work from Edinburgh to London, from the hands of Mr. Lizars into those of Robert Havell ... because the difficulty of finding colourers made it come too slowly, and also because [he had] it done better and cheaper in London' (Audubon 1897: 258). The Bird of Washington was the first of Audubon's paintings to be engraved by

¹ Audubon's journals did not contain a contemporaneous account of events as they truly occurred. Rather, they contained a curated version that he prepared for his wife and sons, who were apparently ignorant of his plagiarism and did not know that the Bird of Washington painting was fraudulent. Almost every entry in Audubon's journals 'begins and ends with a morning greeting, and an affectionate good-night' to his family (Audubon 1897: 247). The questionable veracity of the accounts in Audubon's journals may have been one reason that his granddaughter Maria destroyed (burned) them, after publishing bowdlerised excerpts that showed 'what [she believed] he was and not what others *thought* he was' (Arthur 1937: 14). Thus, not only was the 'primary' record manipulated by Audubon himself; after his death, it was edited by his descendants so that he would be portrayed in the most favourable light. 'I burned it myself in 1895', wrote Maria Audubon in 1904, 'I had copied from it all I ever meant to give to the public' (Arthur 1937: 243). For this reason, journal extracts published by Lucy Audubon (Buchanan 1869) and Maria Audubon (1897) cannot now be verified.

Havell, and it served as the large plate in Audubon's third 'number' (set)². Each set included five double-elephant folio prints: one large species, followed by four relatively smaller species. This scheme served to attract subscribers while minimising costs (i.e., conserving paint and labour) during the early stages of *The birds of America*, when its pecuniary success was uncertain (Fries 2006). Of all the large, charismatic bird species that Audubon could have chosen at this critical juncture, for his third large plate, he chose to publish a (plagiarised) painting of a 'new' species of which (the evidence presented here suggests) he had no physical evidence (Fig. 5).

Audubon followed through on the suggestion of his new acquaintances at the Royal Society to publish an account of the Bird of Washington (Herrick 1917, 1: 400). In April 1828, at the insistence of John C. Loudon, editor of *The Magazine of Natural History*, Audubon submitted a manuscript entitled 'Notes on the Bird of Washington (*Falco Washingtoniæna*), or Great American Sea Eagle' for publication in the inaugural issue (Audubon 1828)³. In that article, which was distributed in July 1828, Audubon stated unambiguously that 'the bird here described [was] faithfully figured from a fresh-killed specimen', a statement he knew was not true. However, his readers seemingly were distracted by the political symbolism of the name, Bird of Washington, and Audubon's derisive (and ironic, in retrospect) criticism of his predecessor: 'Mr. Wilson's figure [of Sea Eagle *Falco ossifragus* Wilson, 1813, Pl. 55] is not so well done; it seems to be taken from a stuffed specimen' (Audubon 1828).

William Swainson (1789–1855), one of England's leading ornithologists, was convinced of the Bird of Washington's authenticity and, 'for a copy of the work at its cost price', published a glowing review of *The birds of America* in the same issue as Audubon's article (Herrick 1917, 1: 400). 'I have long aimed at that perfection, which M. Audubon has so fully attained', Swainson (1828) wrote, promoting Audubon as a 'genius' and imploring those individuals with the means to subscribe to Audubon's book to do so. Swainson (1828) did not comment on the Bird of Washington's unique anatomy or the remarkable circumstances of Audubon's discovery. Rather, he framed the species as Audubon



Figure 5. The Bird of Washington in *The birds of America* (1827, Pl. 11), engraved by Robert Havell Jr. and hand-coloured by Havell's team. Reproduced courtesy of the John James Audubon Center at Mill Grove, Audubon, PA, and Montgomery County Audubon Collection (<https://www.audubon.org/birds-of-america>, accessed 9 October 2019).

² The copper plate with Havell's engraving of the Bird of Washington is preserved in the collection of the Metropolitan Museum of Art, New York, NY (Fries 2006: 395).

³ For unknown reasons, Audubon changed the scientific name of the Bird of Washington three times in rapid succession: *Falco washingtoniensis* (1826, Fig. 2) became *Falco Washingtonii* in Pl. 11 (Audubon, 1827) and then *Falco Washingtoniæna* in Audubon (1828).

intended—a patriotic symbol—an idea he knew would appeal to wealthy English nobility who were sympathetic to American causes: ‘This noble figure is an upright, and occupies the full size of the paper ... if the passions of the brute creation can be traced in their physiology, (and no doubt they can,) we can discern as much of the mild dignity of the great American patriot [Washington], in this his emblem, as can well be expressed in the head of a bird.’ Furthermore, not only did Swainson give *The birds of America* his scientific endorsement; he made a direct appeal and sowed guilt among the English nobility who had not yet subscribed:

‘It will depend on the powerful and the wealthy, whether Britain shall have the honour of fostering such a magnificent undertaking [as *The birds of America*]. It will be a lasting monument, not only to the memory of its author, but to those who employ their wealth in patronising genius ... It is surely this; in as much as it exhibits a perfection in the higher attributes of zoological painting, never before attempted. To represent the passions and the feelings of birds, might, until now, have been well deemed chimerical [more irony] ... on casting my eyes over the list of subscribers, it is with gratified feelings that I see His Most Gracious Majesty at the head. From the fine and original taste which our king seems intuitively to possess, I question whether any of his subjects are better qualified to appreciate the merits of M. Audubon. The number of nobility who have followed the example of our sovereign, as yet, are few.’ (Swainson 1828)

Audubon added parts of Swainson’s review to a new issue of his prospectus for *The birds of America*, which helped him garner the subscribers needed to continue the work (Fries 2006: 30, 388). Swainson, however, eventually came to regret his full-throated endorsement. Two years later, in 1830, he conceded to Bonaparte that ‘many [species in Audubon’s book] are too obscure to be admitted on the mere authority of drawings which do not point out their specific characters ... I thought he would have been an authority, but few men can transcendently excel in more than one branch’ (Stroud 2000: 119). After the publication of Audubon (1831), Swainson remarked frankly that, ‘so far as technical science is concerned, it is, in short, a complete failure’ (Stroud 2000: 120).

Origins of the Bird of Washington

Plagiarism aside, did Audubon really think there were two species of ‘Sea Eagle’ in North America? His journal from late 1820, after he left his position in Cincinnati, was fortunately not burned by his granddaughter. It confirms that Audubon was aware that *Falco ossifragus* Wilson, 1813, the name on his Bird of Washington painting (Fig. 3), had been identified as an immature Bald Eagle by Wilson himself (Ord in Wilson 1814: 129)⁴. On 5 November 1820, while travelling south by boat on the Ohio River, Audubon ‘Saw about the same time a fine Brown Eagle—[and] Shot at it without effect.’ On 13 November, he wrote: ‘M^r Aumack saw an Eagle with a White head and Brown Body & Tail, [and] this Corroborates with the Idea of Willson of its being the same Bird with the Brown Eagle’, and the next day, he ‘Saw several Eagles, Brown & White headed.’ On 15 November Audubon wrote: ‘Saw

⁴ In fact, even before Wilson, the plumage maturation of the Bald Eagle was determined by Charles Willson Peale (1741–1827), proprietor of the Peale Museum in Philadelphia. Peale wrote in a letter to Etienne Geoffroy Saint-Hilaire on 30 April, 1797: ‘this [specimen] sent is young. they change the colour of the Bill to a light yellow, in 2 yrs become light coloured, the head & Tail feathers become quite white, and the other feathers change from that russet brown to a fine dark brown almost black. [About when] they attain the fifth year of their age. At least such has been the case with one that I have, which was taken from the nest 12 years past...’ (Miller 1988: 198).

more than a Dozen of Eagles and one I had a good view of had a White Tail & a Brown head, Again [Yet] I remark^d that the *Brown Eagles In Ohio* Esp. [i.e., not in Kentucky where he later claimed to have collected a specimen] were at Least $\frac{1}{4}$ Larger than the White headed ones' (Corning 1929: 15–28). One week later, after shooting an adult Bald Eagle on 23 November, Audubon was 'Convinced that the *Bald Eagle* and the *Brown Eagle* [were] Two Diferent [*sic*] Species', though he had still not collected a specimen of a brown eagle for comparison (Corning 1929: 38).

This is the earliest evidence that Audubon thought there was a second species that was larger than, but closely related to the Bald Eagle. Critically, his conjecture that the brown eagles in Ohio were larger than the 'White headed ones' was not based on specimen evidence, but on a field observation. It was only after he had an opportunity to see many eagles together in different plumages that Audubon concluded that (1) Wilson was right: Bald Eagles are brown in their immature plumage, and (2) there might also be another species, still unknown, that is larger than the Bald Eagle and brown in both immature and adult plumages. Nevertheless, the journal confirms that he did not have physical evidence of that putative species as of November 1820, only an unconfirmed speculation that they 'were at Least $\frac{1}{4}$ Larger'.

This is important because, eight years later, in his published account, Audubon (1828) claimed that this was his *last* sighting of the species, *after* he had already secured a specimen. 'My last opportunity of seeing the sea eagle,' Audubon (1828) wrote, 'was on the 15th of November, 1821, a few miles above the mouth of the Ohio; two passed over our boat, moving down in easy flappings.' Audubon did not travel 'a few miles above the mouth of the Ohio' river in 1821, and the 15 November entry of his 1820 journal contains his last sighting of 'brown eagles' of that year, so Audubon was presumably referring to that passage in his published account. However, based on his published timeline, the specimen Audubon claimed to have collected in Kentucky could not have been acquired later than 1819–20, despite his insistence that his painting inscribed 'New Orleans 1822' (N-YHS 1863.17.11) was 'faithfully figured from a fresh-killed specimen' (Audubon 1828).

Audubon (1828: 115) retroactively claimed to have first seen the species in February 1814, 'on a trading voyage, ascending the Upper Mississippi'. His next observations were 'a few years afterwards ... in Kentucky, near its junction with the Ohio' (c.1817–18), when he reportedly saw an adult Bird of Washington at the nest. Finally, 'after two years had gone by, since the discovery of the nest', Audubon (1828: 118) claimed that he collected a specimen of the Bird of Washington in Kentucky (c.1819–20). And yet, in his 1820 journal entries, Audubon was still uncertain whether his hunch about the larger eagle was correct: 'Again I remarkd that the Brown Eagles In Ohio Esp. were at Least $\frac{1}{4}$ Larger than the White headed ones' (Corning 1929: 15–28). Audubon's (1828) distortion of the timeline makes the story seem plausible, but it is not supported by his own journal.

Considering the evidence that the Bird of Washington was in part copied (without attribution) from line drawings (Fig. 4), the most parsimonious explanation for the myriad inconsistencies in Audubon's published anecdotes is that they were also invented. This includes his purported discovery of a nest of the Bird of Washington on a rocky cliff (vs. the Bald Eagle, which nests in trees) and his extraordinary claim that he observed copulations between members of both species, 'but on no occasion did they mix' (Audubon 1828: 116). Audubon's dramatic story of collecting a specimen, the purported subject of his painting, was also most likely fictional, but passed off as authentic:

'I come at last to the day I had so often and so ardently desired. Two years had gone by, since the discovery of the nest, in fruitless excursions; but my wishes were no longer to remain ungratified. In returning from the little village of Henderson [Kentucky] to the house of Doctor Rankin, about a mile distant, I saw [a Bird of Washington] rise from a small enclosure not a hundred yards before me, where the doctor had a few days before slaughtered some hogs, and alight upon a low tree branching over the road. I prepared my double-barrelled piece, which I constantly carry, and went slowly and cautiously towards him; quite fearless he awaited my approach, looking upon me with an undaunted eye. I fired and he fell; before I reached him he was dead. With what delight I surveyed this magnificent bird! Had the finest salmon ever pleased him as he did me? – Never. I ran and presented him to my friend, with a pride which those can only feel, who, like me, have devoted their earliest childhood to such pursuits; to others, I must seem 'to prattle out of fashion.' The doctor who was an experienced hunter, examined the bird with much satisfaction, and frankly acknowledged he had never before seen or heard of it' (Audubon 1828: 118)⁵.

Mc'Aren's Eagle and the Brano specimen

By 1830, two years after Audubon's (1828) account of the Bird of Washington was published, some European ornithologists, including Swainson, had begun privately to express doubts as to the authenticity of the species (Stroud 2000: 119). It was around this time that a rumour began about a specimen of the Bird of Washington in Philadelphia, which temporarily allayed these concerns. Audubon was passing through Philadelphia in March 1830, on his way to London via New York, when he met with an old acquaintance, the zoologist Richard Harlan (1796–1843). Harlan, like Audubon, had a mixed reputation among the intelligentsia of Philadelphia. According to the charismatic ornithologist George Ord (1781–1866), who completed the final two volumes of *American ornithology* after his mentor Wilson's untimely death, Harlan's 'moral character [was] so infamous ... that he [was] excluded from the society of gentlemen' (APS, Mss.B.Or2).

Two influential events that bear on the history of the Bird of Washington occurred during the meeting of Audubon and Harlan in March 1830. (1) They visited 'Mc'Aren's Garden' in (what was then considered) the Philadelphia suburbs⁶, where they saw a captive eagle that Harlan thought was a Bird of Washington. Audubon identified the captive bird as a Bald Eagle and correctly predicted that the bird would eventually moult into the normal adult plumage. However, Harlan was insistent that it was a Bird of Washington and they made a friendly (pretend) wager over it, which Audubon (unsurprisingly) won. (2) They visited the taxidermy shop of Joseph Brano (listed in Putnam 1866: 37), where they found a stuffed specimen of a large, immature Bald Eagle in its brown plumage. This time, Audubon took the opposite approach and convinced Harlan that it was indeed a specimen of the

⁵ To 'prattle out of fashion' is a quote from Shakespeare's *Othello* (Act 2, Scene 1). The interjection of this phrase into his narrative about killing a Bird of Washington is more evidence that Audubon had a target audience in mind when he wrote the manuscript: well-educated and affluent English citizens who might become subscribers. Othello said 'I prattle out of fashion, and I dote in mine own comforts' to save face with his wife (Desdemona) after talking too much about himself. Audubon's flirtatious, self-deprecating humour was probably not overlooked by his female readers in England.

⁶ The spelling of this location varies in literary sources. A catalogue published in Philadelphia for 'strangers' (tourists) in 1830 gives a brief description: 'M'Arens Garden / This beautiful garden lies between West Filbert street and Courtland street, and Schuylkill Fifth and Sixth streets. It is handsomely laid out, and the proprietor has collected a great variety of plants. It is an agreeable place of resort in the summer season' (Anon. 1830: 148). The historic garden was located only 300 m from the modern site of the ANSP, in the lot where the (now historic) Arch Street Presbyterian Church was built in 1855. The city block is now dominated by the Comcast Center skyscraper.

Bird of Washington. Thus began the widespread rumour that the Bird of Washington was supported by a specimen in Philadelphia.

Shortly after returning to London, on 14 July 1830, Audubon nonchalantly mentioned in a letter to Bonaparte, who doubted the validity of the species, that '[he] saw in Philadelphia a fine specimen of the Bird of Washington' (Yale 4, f. 172). Audubon had little reason to believe that Bonaparte, who had ceased all contact with Ord and had bitter feelings about the ANSP, would ever return to Philadelphia and see the purported specimen himself. 'Do not speak to me of the [Academy]. I think it is [damned]', Bonaparte had written in 1826, 'The death blow has been inflicted! ... my feelings are those of a foreigner [étrangé]' (Stroud 2000: 80). Bonaparte responded to Audubon on 6 December 1830:

'Vous me dites avoir vu a Philadelphia un bel individu de votre aigle Washington; etait-il mort ou vivant, et a que [...]? J'admire votre courage et vos beaux projects.' [You tell me that you have seen in Philadelphia a fine individual of your Washington eagle; was he dead or alive, and of what [...]? I admire your courage and your beautiful projects.] (APS, Mss.B.642)

Meanwhile, in Philadelphia, apparently without Audubon's knowledge, Harlan returned to Brano's shop and made a deal for the specimen, which he then deposited in the ANSP museum⁷. Curiously, the specimen did not appear in the list of donations during 1830 that was printed in the *Journal of the Academy of Natural Sciences of Philadelphia* (6: 323), although an anonymously written article published in January 1831 claimed that 'The Eagle of Washington (*Falco Washingtonianus*) recently described for the first time by Mr. Audubon' was in the ANSP bird collection (Anon. 1831: 93). Audubon, who was living in London, received a letter from Harlan dated 19 August 1830, which read:

'... that fine specimen of *Washington Eagle*, which you noticed in Brano's Museum is at present in my possession...I lent him some money on it as a pledge, and I believe he means to cheat me, I have deposited it in the Academy, where it will most likely remain ... the large Eagle you seen [sic] at MacArens Garden, does not wear a *white head* yet, though it must be 5 or 6 years old.' (Yale 4, f. 172)

Harlan's confidence in Audubon was strengthened when he lost the wager. Audubon (1834: 163) quoted from a letter from Harlan dated 26 April 1831: 'I wish I could walk with you this moment in M'Arran's [sic] garden, to shew you how *white* the head of the eagle, which we talked of betting about, has at last become, as well as his tail; but he must have been at least nine or ten years old first.' Meanwhile, although the deposit of the Brano specimen at the ANSP was potentially problematic for Audubon, he made the best of the situation and used it for leverage in Europe. He responded to Bonaparte on 2 January 1831: 'The bird of Washington is actually in the Society of Natural History of Philadelphia [i.e., ANSP, remainder of page illegible]' (Yale 4, f. 172). Audubon also quoted Harlan's 1830 letter in his (second) text account of the Bird of Washington, which was printed and ready for distribution by the end of March (Corning 1969, 1: 132):

⁷ My efforts to relocate this specimen at the ANSP have been unsuccessful. Only one contemporaneous record of the specimen at ANSP has been located, a notice inexplicably penned in a ledger of library (book) loans, which reads: 'Rec^d May 1st 1832, from curators, the Washington Eagle deposited by ... R. Harlan.' (ANSP, coll. 291)

'Whilst in Philadelphia, about twelve months ago, I had the gratification of seeing a fine specimen of this Eagle at Mr. Brano's Museum⁸. It was a male in fine plumage, and beautifully preserved. I wished to purchase it with a view of carrying it to Europe, but the price put upon it was above my means.'

'My excellent friend, Richard Harlan, M.D. of that city, speaking of this bird, in a letter, dated 'Philadelphia, August 19, 1830,' says, 'That fine specimen of Washington eagle, which you noticed in Brano's Museum, is at present in my possession. I have deposited it in the Academy, where it will most likely remain.' I saw the specimen alluded to, which, in as far as I could observe, agreed in size and markings exactly with my drawing [of the Bird of Washington], to which, however, I could not at the time refer ...' (Audubon 1831: 61–62)

Bonaparte replied to Audubon's letter on 10 April 1831: 'I should be very glad to see & examine the Washington eagle you mention, in order to persuade myself of its' specific existence of which I must confess I still strongly doubt. What I am certain of is that all those I examined were young Bald Eagles' (APS, Mss.B.B642). Bonaparte's doubt was not widely shared among European naturalists, however, as praise for Audubon's discovery continued to pour in. Rennie (1831) quoted long passages from Audubon's (1828) account and, though he found it peculiar that Audubon described a nest on the 'shelves of rocks' (i.e., on cliffs), was otherwise impressed by his 'very animated and interesting narrative of his discovery of this magnificent eagle, with a portion of which we shall enrich our pages.' The noted English botanist, Thomas Nuttall (1786–1859), who, like Audubon, published large commercial books about American birds that contained many errors (Brewster 1906: 79–80, Halley 2019), put his full support behind the Bird of Washington (Nuttall 1833). 'According to the magnificent plate of Audubon, it appears to be wholly of an almost uniform dark brown', wrote Nuttall (1833: 92), 'If this be the color of the adult bird, it is unquestionably a new species, and an additional piscatory kind to those already known.' Nuttall further remarked that 'a specimen from the vicinity of Egg-Harbor in new Jersey, is now in Brannau's [sic] Museum, in Market Street, Philadelphia; but in this there are some white spots, indicating the incomplete character of the plumage.' Nuttall (1833: 106) penned his article in April 1831, when he was living in Boston, and evidently did not realise that the specimen was no longer in Brano's Museum. As mentioned earlier, Harlan claimed in a letter to Audubon on 19 August 1830, that the specimen was 'at present in [his] possession' (Yale 4, f. 172).

Resistance in Philadelphia

Audubon's claims about the Brano specimen aroused the interest of ornithologists in Philadelphia, including Ord and Titian R. Peale (1799–1885), who went to ANSP to examine the specimen for themselves. After doing so, both men were convinced that Audubon was lying, but were hesitant to speak out because of his growing fame. In a letter dated 23 April 1832, to the English naturalist Charles Waterton (1782–1865), Ord wrote exasperatedly: 'I am confident that I should have a swarm of hornets about my ears, were I to proclaim to the world all that I know of this impudent pretender, and his stupid book' (Fig. 6).

⁸ A pencilled annotation inserted here in Sir William Jardine's (1800–74) copy of *Ornithological biography* (1831), reads: '[Brano's] Museum burned in 1839 or 40.' Jardine's copy later passed to Charles Darwin (1809–82), who consulted it while preparing *On the origin of species* (1859). It is now preserved in the Natural History Museum Library (London).

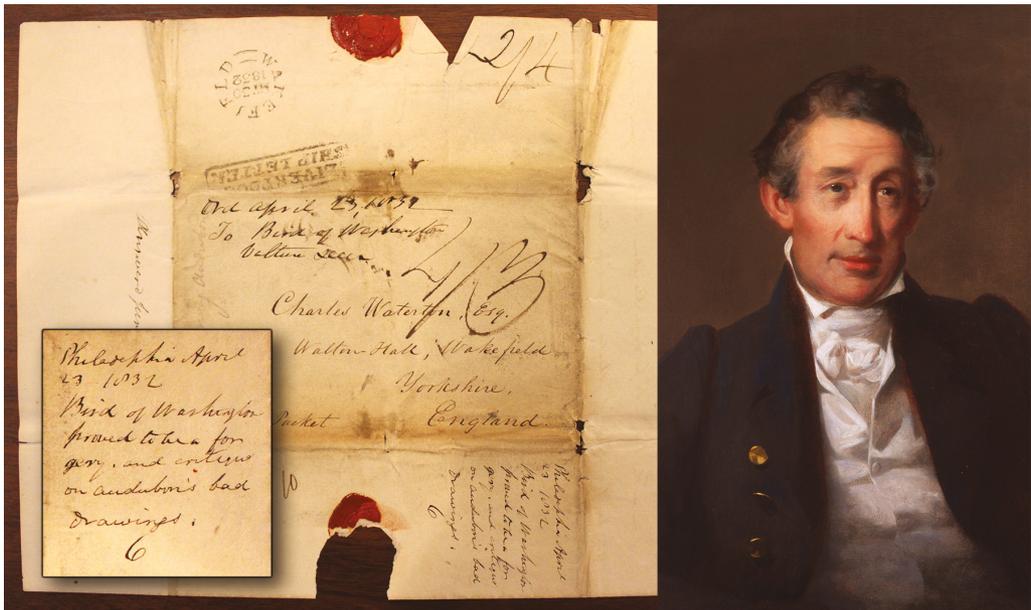


Figure 6. (Left) Address-bearing face of a letter from George Ord (1781–1866) to Charles Waterton (1782–1865) with the following inscription: ‘Philadelphia April 23, 1832 / Bird of Washington proved to be a forgery, and critique on Audubon’s bad drawings’ (lower left inset); reproduced courtesy of the American Philosophical Society Library, Philadelphia, PA (Ms.B.Or2). (Right) Oil portrait of George Ord executed in 1829 by John Neagle (1796–1865), reproduced courtesy of the ANSP Archives (coll. 286).

Biographers have almost universally cast Ord as a petty antagonist, while minimising (or underestimating) his ornithological knowledge and prowess (e.g., Ford 1964, Souder 2014: 13). Rhodes (2004: 394) introduced Ord as a ‘long-faced quarrelsome, wealthy English dilettante ... [who] marked [Audubon] down for destruction’ because he was ‘competition’. By all accounts, Ord was indeed cantankerous, but his antipathy for Audubon was not merely a personal grudge between men with incompatible personalities as implied or stated by recent biographers (e.g., Rhodes 2004, Souder 2014). Rather, the antipathy was Ord’s reaction to the gradual uncovering of Audubon’s extensive record of dishonesty and plagiarism (see Ord 1840). Substantial evidence has emerged in modern times that lends credence to Ord’s suspicions (e.g., Dallett 1960, Partridge 1996, Markle 1997, Pick 2004, Woodman 2016, Halley 2016, 2018a, this study).

Ord and the other ornithologists in Philadelphia were evidently ignorant of Audubon’s plagiarism in the Bird of Washington, but they rejected the species nonetheless because they were unable to verify his extravagant claims without specimen evidence. They followed the same standard of scientific evidence used by professional ornithologists today, a precedent that had been established by Audubon’s predecessors in Philadelphia (e.g., Wilson 1812b, Say in James 1823). Audubon failed to meet that standard. In his letter to Waterton on 23 April 1832, Ord further wrote (author’s comments in brackets):

‘Patience, my dear, and you shall know all. Learn, then, that the boasted Bird of Washington must be eliminated, as Charles Bonaparte would say, for it is no other than the Bald Eagle, in an immature state of plumage. A specimen of this supposed new species is in the cabinet of our Academy. This is the identical specimen which belonged to a bird-stuffer named Brano (mentioned by A. in his book) and which has since been acknowledged by A. himself as the real Washingtonianus [Audubon 1831: 61–62].

I have diligently examined this bird, and compared it with two fine specimens of the acknowledged Bald Eagle, and can find no difference whatever in their characters: they are precisely the same; and you are at liberty to make use of my name, provided you esteem me of sufficient authority, for this decision.'

'This examination was made at the [insistence] of Titian Peale, who had previously announced to me his opinion that the birds were identical. Audubon's figure of the bird is greatly defective; he has represented the lower mandible of the bill much larger than it is in reality, and the tooth-like process of the upper mandible is falsely given; the head is also unnaturally flattened [see Fig. 4]. These circumstances are calculated to mislead those who have not an opportunity of comparing specimens. His dimensions are false, as can be proved by analogy. By his statement, his bird was 3 feet 7 inches long [1.1 m], and ten feet 2 inches broad [3.1 m]. Now this difference does not obtain in any known Eagle, or Hawk of similar conformation. The following table will enable us to form a pretty good idea of proportion.' (Table 1)

'Now, supposing Audubon's Eagle to have been 3 feet 7 inches long [1.1 m], it ought to have measured in breadth, or from wing-tip to wing-tip, 8 feet, 4 inches [2.5 m], instead of 10 feet 2 inches [3.1 m], as he says, which is an evident error. But his whole statement of its size is to be doubted, as well as its weight, which he says was 14 ½ lbs [6.6 kg]. [According to Audubon's 1820 journal, the adult male Bald Eagle that was the model for Pl. 31 weighed '8½ lb.' [3.9 kg], see N-YHS 1863.18.40 and Corning 1929: 40]. Wilson says that the Bald Eagle weighs 11 lbs [5.0 kg], and I think that it is seldom heavier. A male shot by Mr. Peale in Florida weighed only 7 lbs [3.2 kg]. In Audubon's Book it is said that Brano's specimen is of the size of the individual figured by the former. Now this very specimen is of the same size as our Bald Eagle: we hence see what reliance can be placed in Audubon's correctness.'

TABLE 1

George Ord's table of measurements, compiled from the writings of Alexander Wilson (1766–1813) and Thomas Bewick (1753–1828), comparing the distance from the tip of the bill to the tip of the longest rectrix (length) and wingspan (breadth) of freshly killed specimens of North American and European birds of prey. The top rows contain the measurements from Audubon's annotation on the original painting of the Bird of Washington (N-YHS 1863.17.11), his published text accounts (Audubon 1828, 1831), and the minimum expected values of an eagle 'at least ¼ larger' than the Bald Eagle, as per Audubon's 1820 journal (Corning 1929). Common names are given as Ord knew them, and scientific names reflect currently accepted nomenclature (Chesser *et al.* 2018). All measurements are reported in inches, as in Ord's original table.

English name	Scientific name	Length	Breadth	Source
Bird of Washington	<i>Falco washingtoniensis</i>	42.5	121	N-YHS 1863.17.11
'	'	43	122	Audubon (1828, 1831)
'	'	45	105	Corning (1829)
Bald Eagle	<i>Haliaeetus leucocephalus</i>	36	84	Wilson (1811b)
Sea Eagle	<i>Haliaeetus leucogaster</i>	42	84	Bewick (1797)
Osprey	<i>Pandion haliaetus</i>	24	60	Bewick (1797)
'	'	22	63	Wilson (1812a)
Red-tailed Hawk	<i>Buteo jamaicensis</i>	20	45	Wilson (1812b)
Broad-winged Hawk	<i>Buteo platypterus</i>	14	33	Wilson (1812b)
Black Hawk	<i>Buteo lagopus</i>	21	50	Wilson (1812b)
Marsh Hawk	<i>Circus cyaneus</i>	21	47	Wilson (1812b)
Peregrine Falcon	<i>Falco peregrinus</i>	20	44	Wilson (1814)

'In [Table 1] it will be observed, that the greatest difference obtains in the Osprey [*Pandion haliaetus*], which is a long-winged bird, the wings, when folded, extending about an inch beyond the tail, according to Wilson, and more than two inches according to Temminck. Now Audubon's Eagle's tail is said to be of ordinary length, extending considerably beyond the tips of the wings; he gives the same description of that of the Bald Eagle. Thus, from analogy, we are enabled to prove the falsity of the statement with respect to the size of this supposititious species.'

'One observation more, and then I am done. The wings of Brano's specimen measure, when folded, 26 inches [66.0 cm] from the shoulder to the tip. Audubon says that the length of his bird's wing, when folded, is 32 inches [81.3 cm]; now if this was the fact, then wouldn't the wings extend considerably beyond the tail, whereas it is asserted that the tail 'extends considerably beyond the tips of the wings.' The tail of Brano's specimen is 15 inches [38.1 cm] long, precisely the length of Audubon's.'

'When I commenced this epistle little did I suppose that I should fill two entire sheets; but the sin is committed, and I must run the risk of your displeasure. When I get on the subject of that individual [Audubon], who has afforded me so much space for remark, matter crowds so fast upon me, that I find it difficult to extricate myself.' (APS, Mss.B.Or2)

The Bird of Washington takes flight

Fuelling Ord's anxiety, the Bird of Washington was a marketing success on both continents and helped propel Audubon to widespread fame. In 1832, the first American edition of *Ornithological biography*, vol. 1, was published in Philadelphia, and the Bird of Washington was also featured in a popular book for youth by Goodrich (1832: 184), who wrote 'The following account of this noble bird, is from a description by the celebrated Audubon.'

In London, Jardine (1832: 92) was convinced by Audubon's claim about the Brano specimen and included the Bird of Washington in his expanded version of Wilson's *American ornithology*, perpetuating the Brano specimen fallacy: 'It has been first beautifully figured and described by [Audubon], and a specimen of it exists in the Academy of Philadelphia. Its immense size, and some other differences, seem to keep it distinct from any species we are acquainted with, and it is most probably before this time proved to be new.'

Likewise, Stanley (1835) included the Bird of Washington in *A familiar history of birds* (1835), with a woodcut image of an adult eagle feeding at a nest (Fig. 7). He further embellished Audubon's (1828, 1831) untrustworthy anecdotes and presented them as pure fact, including that Audubon (who he did not name, referring only to 'a naturalist') 'was fortunate enough to shoot [a Bird of Washington] dead on the spot ... the bird in this case seemed to be perfectly fearless, not only allowing the sportsman to approach within easy gun-shot distance, but looking at him all the time with an undaunted eye.' The clergyman Edward Stanley (1779–1849) served as the Bishop of Norwich and President of the Linnaean Society (both during 1837–49) and *A familiar history of birds* became so popular that six editions were printed by 1854, each repeating the Bird of Washington myth unchanged and adding to Audubon's fame⁹. In Philadelphia, Ord marvelled and lamented at these circumstances in a letter to Waterton dated 15 April 1835:

⁹ Stanley's (1835) text about the Bird of Washington even remained intact in the 'new edition' of *A familiar history of birds* (1890), despite the publisher's note that it had been 'revised by a practical ornithologist of much experience.'

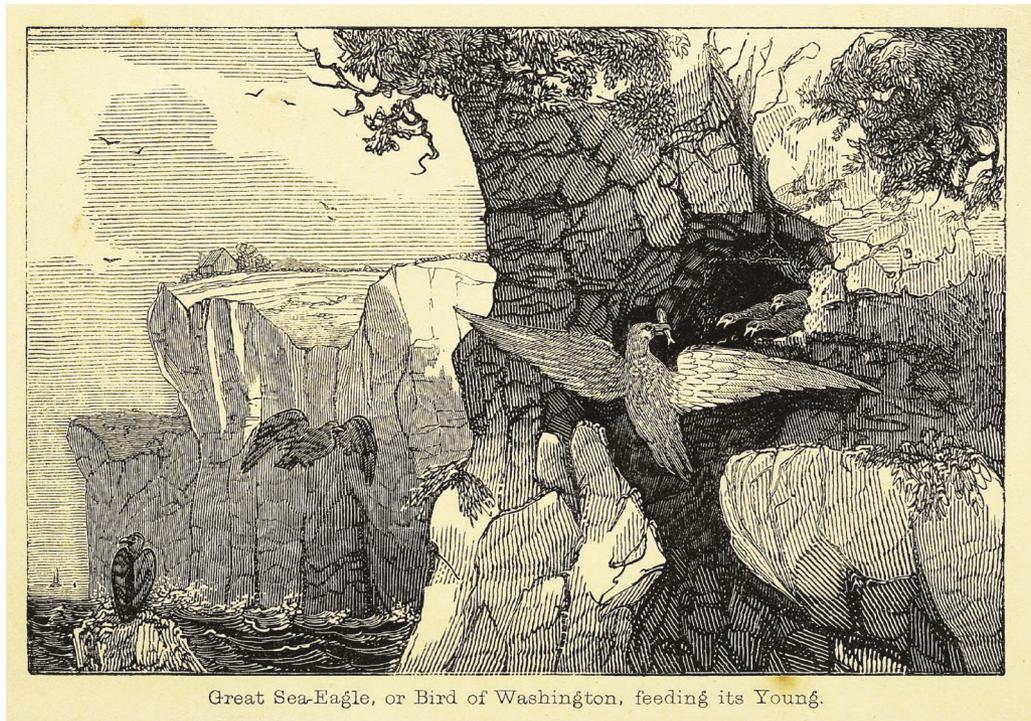


Figure 7. Woodcut print of the Bird of Washington feeding young at the nest, reproduced from Stanley (1835). The original caption reads, 'Great Sea-Eagle, or Bird of Washington, feeding its Young.'

'With respect to the Bird of Washington, [Titian Peale] says, positively, that he has no doubt of it being the Bald Eagle; and his opinion is of more weight, in my mind, in matter of this kind, than that of any person in existence. His [brother Rembrandt's] picture of [George] Washington, about which you request information, was purchased by our Congress, to adorn the capitol at Washington. What has possessed the self-called friends of Audubon? Are they determined to make him a great man in defiance of truth and common sense?'

'Mr. Audubon is certainly a prodigy, he hears what no other mortal hears, he sees what no other mortal sees ... [he has been] specially selected for the great purpose of writing the history of our birds, by the Deity himself, extraordinary powers must have been given, as to the Seers of old the divine [message] was communicated for the enlightening of the human race. Lest Mr. Audubon's singular assumption should be doubted, I quote his own words [Audubon 1834: 2]: 'and now, kind reader, let me resume my descriptions, and proceed towards the completion of a task, which, with reverence would I say it, seems to have been imposed upon me by Him who called me into existence!' Search the whole annals of egotism, from the creation of man, for an instance of presumptuous vanity to be paralleled with this: I should doubt whether one can be found.' (APS, Mss.B.Or2)

William MacGillivray (1796–1852), the often-acknowledged ghost-writer of large sections of Audubon's *Ornithological biography* (see Fries 2006: 48), expressed some doubt about the Bird of Washington. '[It] seems to be a distinct species of this genus; but although superior in size, it is too nearly allied to [White-tailed Eagle *Haliaeetus albicilla* (Linnaeus, 1758)], to be

generally admitted as such, until living individuals or skins of it can be shewn' (MacGillivray 1836: 52). Regardless, the opinions of sceptical ornithologists made little difference once the Bird of Washington myth made its way into popular press. For example, the following year, an article about the Bird of Washington appeared in *The Family Magazine* (Anon. 1837), a cheap and widely distributed periodical printed in New York under the editorship of an 'Association of Gentlemen'. It recycled details from Audubon's (1828, 1831) anecdotes and reproduced the woodcut print from Stanley (1835). Such publications likely had more of an impact on the opinions of the general public than MacGillivray's expensive volumes.

Inexplicably, Bonaparte (1838: 3) briefly recognised the Bird of Washington as a valid species: '*Haliaeetus Washingtoni*, Nob. / (*Falco Washingtoni*, Aud.) / Aud. pl. 11. Northern parts'. Notwithstanding, in the preface to this book, Bonaparte (1838) wrote 'the merit of M. Audubon's work yields only to the size of his book; whilst Mr. Gould's work on the Birds of Europe, inferior in size to that of M. Audubon's, is the most beautiful work on Ornithology that has ever appeared in this or any other country.' Audubon's vanity was wounded, and animosity flourished between him and Bonaparte (Stroud 2000: 138). In a letter dated 20 December 1837, Audubon announced to his American colleague, Revd. John Bachman (1790–1874), who believed in the Bird of Washington, that 'Bonap. has at last acknowledged the Bird of Washington as a good species having accidentally seen one of my specimen [*sic*]' (Corning 1969, 2: 193). However, unbeknownst to Bachman, no specimen that matched Audubon's painting existed in Europe, although there were many rumours. Bonaparte soon corrected the error by pulling the Bird of Washington from subsequent works without comment (e.g., Bonaparte 1850: 15).

On 19 December 1838, Audubon wrote about the Bird of Washington to Edward Harris (1799–1863), one of his closest allies and benefactors in the USA. Harris had been one of his earliest American subscribers and provided the funds for Audubon to purchase duplicates from John K. Townsend's (1809–51) collections of birds from western North America (Mearns & Mearns 2007). As a member of the Ornithological Committee at ANSP, Harris was probably aware of the controversy over the Brano specimen, but he remained loyal to Audubon and was a steadfast believer in the Bird of Washington, though he too had never seen a specimen. Audubon maintained the illusion and reassured Harris, who had reported to him an unconfirmed sighting:

'I am glad that you should have seen what you conceive to be the great *rara avis F. Washingtonii*. I am sorry you could not have pocketed it, but who knows if it is not left yet in store for you and I to shoot a pair of these noble birds at The West, and that, after having satisfactorily examined its habits, its eggs, or its young! Bonaparte, between you and I, is exceedingly ignorant as regards our birds, as I found to my cost when he was in London, and where he pumped me sadly too much, but it is now over and I forgive him as I do all others who have or who may try to injure me.' (Rhoads 1903: 382)

Audubon (1839: 10) stubbornly repeated the most controversial details of the Bird of Washington. He wrote that 'the specimen figured [had been] procured in Kentucky' and that the tarsometatarsus and toes of this 'exceedingly rare' species were 'uniformly scutellate in their whole length'. Then he doubled down, publishing the Bird of Washington image a second time in *The birds of America* Royal Octavo edition (1840–44), as a reduced-size lithograph (Steiner 2003: 188). Meanwhile, although Ord and his colleagues berated Audubon in private, they did not go public with their evidence that the Bird of Washington was a lie. 'The time for fully displaying [Audubon's] incompetency and mendacity to the world is not yet come', Ord wrote to Waterton on 30 April 1849:

'Both Charles Bonaparte and Titian Peale told me that in looking over [Audubon's] drawings of birds they saw several that they were convinced were fictitious representations. Depend upon it, he who will deliberately lie in words, will not hesitate to invent a representation. I have challenged all his admirers to produce a specimen of his boasted Washington Eagle; Bonaparte did the same. When last in Paris two of his friends assured me that they had found it in a private collection, the specimen would not be questioned, and I should be convinced of it by [regular] evidence. However, when they found that I was not willing to rely upon their authority, they had to admit that they themselves had some doubts on the subject. So the bird I did not see.' (APS, Mss.B.Or2)

Audubon's death and its aftermath

The symbolic power of the patriotic name Bird of Washington was as effective in the USA as in Europe. In 1842, an anonymously penned article defending the Bird of Washington posed the question: 'Is not John James Audubon, as we said in the outset, an admirable specimen of the Hero as a man of science? ... 'Learned societies, to which the likes of Cuvier belonged, [bowed] down to welcome his presence' (Anon. 1842). One year before his death, Audubon was included in *The gallery of illustrious Americans* (Lester 1850), published in New York, which profiled 12 of the most influential American citizens since the death of Washington. The editor proclaimed that Audubon was, like Washington, 'an imperishable name — a name that is not in the keeping of history alone. From every deep grove the birds of America will sing his name ... and the bird of Washington, from his craggy home far up the rocky mountains, will scream it to the tempests and the stars' (Fries 2006: 128).

After his death in 1851, an obituary in the *Illustrated London News* praised Audubon not only for his scientific contributions, but for his 'pecuniary sacrifices' and 'indefatigable exertions'. It was claimed that, 'as a delineator of birds, Audubon never had an equal', and that his paintings were 'remarkable for the accuracy and imitation of the feathering, and in those parts most essential to the naturalist, namely the beaks and feet, [which] are drawn with matchless skill and beauty' (Fries 2006: 127–129). However, in Philadelphia, at least in intellectual circles, reactions to Audubon's death were more measured. At the ANSP, his perseverance and skill with the paintbrush were not disputed, but many members openly questioned Audubon's scientific merits. At a meeting on 4 February 1851, in a carefully worded statement, it was 'Resolved, That by the demise of this truly great man, Science has lost one of her most zealous and gifted disciples of the Arts, a master in the branch he cultivated' (ANSP, coll. 502). However, some ANSP members (notably the ornithologists) were unable to appreciate the art for its own sake because they were aware of pervasive dishonesty in Audubon's written accounts and 'fictitious representations' in *The birds of America*. A shadow of doubt was cast across his entire body of work. On 8 October 1852, Ord wrote frankly of Audubon's death to Waterton:

'Looking in the Proceedings of the Linnaean Society of London, I find a notice of Audubon's death. He is there said to be 'deservedly celebrated' as one of the finest ornithological painters.' The principal events of his life are taken from an autobiography, published some years ago. Born near New Orleans, went young to France, and studied the elements of design under David; presented by his father with a plantation in Pennsylvania, &c., all of which is a fable. Audubon is fairly entitled to the merit of perseverance and industry. His elephant folio is a proof of this. [However] As a naturalist and a traveller, but little reliance can be placed on his narratives, in

consequence of an inveterate habit of mendacity, which should seem to have been the *premium mobile* [prime mover] of his intellect.’ (APS, Mss.B.Or2)

Ord was not alone in his opinion that Audubon’s works could not be relied on as sources of scientific knowledge. As Audubon’s reputation soared in other American cities and in Europe, it was not Ord but the ANSP curator of birds, John Cassin (1813–69), who publicly rebuked the Bird of Washington and its creator in a popular column in the *United States Magazine*: ‘This eagle is stated by Mr. Audubon to have been discovered by him in the state of Kentucky, and noticed also elsewhere, but there has always been an air of doubt and mystery involving both the discovery and the existence of the species. Most unfortunately, many statements made by this author have proved to be erroneous, which fact, and the egotistical and pretentious style of all his writings, have rendered it quite impossible for him to be regarded with entire confidence by naturalists¹⁰, or entitled to high popular regard.’

‘No specimen possessing all the characters of this bird, as given by Mr. Audubon, has ever come under the notice of any other naturalist¹¹; and late European ornithologists have regarded it generally as the young of the Bald Eagle, but in some instances as a pure invention ... As a naturalist [Audubon’s] works are very doubtful authority, and contain more errors and misstatements than those of any other modern author ... [the Bald Eagle] has not the large scales in front of the tarsus continued without interruption to the toes, as represented in the plate to which we allude. That character we have never seen in any species of Eagle, and [it] is unknown to naturalists.’ (Cassin 1856: 205)

Nevertheless, despite the objections of the Philadelphians, the Bird of Washington myth continued to spread, propelled by its symbolic name. Ross (2017) wrote that ‘Audubon’s status as a celebrated naturalist and accomplished artist pushed the eagle into the realm of controversy’ when in fact it was the other way around: Audubon rode the Bird of Washington to stardom. His apparently fabricated anecdotes were repackaged and elaborated in St. John (1856), one of the first popular biographies to appear after his death. The manuscript was derived from ‘Audubon’s works, from the recollections of his friends, and from fragments published in the United States’. The book was so popular that more than 30 editions were printed between 1856 and 2000 (WorldCat.org, accessed 12 January 2020). The Bird of Washington also found its way into musical culture. In Boston, a songwriter named James G. Clark published a song called ‘Bird of Washington’, which clearly demonstrates that it was no longer merely a bird, but a symbol of American independence and pride:

‘When Liberty looks on the woes of the world,
Thro’ clouds of oppression and crime
When tyrants and knaves from their high thrones are hurled
And men burst the fetters of Time,

¹⁰ For example, Hoy (1853) claimed that he kept a living specimen of the Bird of Washington in captivity, though he conceded that ‘before its death it underwent changes plumage which led [him] to believe that, had it lived, it would have proved to be the white-headed species.’ Haymond (1856) was also misled by Audubon’s apocryphal anecdotes (and comparisons to the Osprey, e.g., Audubon 1831: 60) and placed the Bird of Washington in the genus *Pandion*: ‘I have myself observed one or more [Birds of Washington] almost every winter for more than twenty years. Their habits being almost identical with those of the Osprey, I have placed them, without any other authority, in the same genus.’ These observations were not supported by specimen evidence.

¹¹ Cassin, a colleague of Ord and Peale, undoubtedly knew the Brano specimen had been identified as an immature Bald Eagle. Whether Cassin ever examined the specimen himself is unknown.

'Tis then that I rise on the death rolling night
And strike for the brave in the battle of Right,
I laugh as the legions of tyranny flee
And they call me the bird of the free.' (Clark 1857)

Trade books continued to repeat the fallacious claim that the Bird of Washington was supported by specimen evidence, lending it legitimacy. 'But one specimen as yet exists in the American collections', wrote LeMoine (1866: 14), 'that in the museum of the Natural History Society of Philadelphia.' By this time, the resistance to Audubon was waning. The deaths of Ord (1866) and Cassin (1869) began a period of 20 years when the collection was 'almost untouched by ornithologists' (Stone 1899: 176). By the time activity resumed, in early 1888, the controversy about the Bird of Washington had been forgotten, and many in the new generation of ornithologists naïvely assumed that Audubon had simply misidentified an immature Bald Eagle (e.g., Allen 1870, but see Coues 1876). Still, the symbolic power endured, and the myth persisted among the general public for decades after Audubon's death. The ornithologist-historian Elliott Coues (1842–99), who was ignorant of the plagiarism in the Bird of Washington, nevertheless remarked: 'I wonder how many more times the 'Washington Eagle' must be put down before it will stay down!' (Gilpin 1873).

Cryptozoology and the Bird of Washington

The Bird of Washington did not stay down. The controversy was reinvigorated by Maruna (2006), who overlooked and / or neglected to cite the evidence of plagiarism uncovered by Partridge (1996). Under the assumption that Audubon was an honest narrator, Maruna (2006) argued that the Bird of Washington was in fact a real species and that Audubon was one of the last witnesses of a now-extinct member of the Pleistocene megafauna. Maruna (2006) cited the unique scutellation pattern on the feet of the Bird of Washington (see Fig. 4) and many details from Audubon's (unreliable) published anecdotes in support of his hypothesis. Souder (2014: 160) added that the dimensions of the bird in the original painting and Audubon's description of a 'mated pair with their young' made the story plausible. This thin evidence was enough to convince the owners of Donald H. Heald Rare Books (New York, NY) to use Maruna's (2006) paper in advertisements for one of the double-elephant folio prints of Pl. 11, which was on sale for \$25,000:

'...it has now been convincingly argued by Scott Maruna in an article entitled 'Substantiating Audubon's Washington Eagle' that the Bird of Washington was indeed a third species of North American eagle, larger than both the Bald and Golden Eagles, that became extinct or confined to very remote regions.' (<http://www.donaldheald.com>, accessed 11 March 2019)

To his credit, Maruna (2006) effectively demonstrated that 'the [Bird of Washington's] distribution, morphology, and ethology lay outside the accepted range of variation for the bald eagle, especially those of its juvenal stages.' However, every piece of evidence cited in support of his cryptozoological hypothesis stemmed from unreliable anecdotes published by Audubon (1828, 1831) and second-hand field observations reported by his friends (like Edward Harris) who, like Maruna (2006) and Souder (2014), assumed *a priori* that Audubon's accounts were truthful, including the claim that his painting was 'faithfully drawn from a fresh-killed specimen' (Audubon 1828). Maruna (2006) sympathetically wrote that Audubon was 'attacked' and suffered 'abuse' from his

'detractors', but the truth is that Audubon did not meet the standard of evidence required by systematic zoologists.

Maruna (2006: 141) mischaracterised Cassin's position by implying that the ANSP curator thought the Bird of Washington was a 'good species'. In fact, as quoted above, Cassin (1856: 205) fiercely rebuked the Bird of Washington in a paper Maruna (2006) did not cite. To this day, no reliable documentation of a species that matches the details in Audubon's painting and descriptions has ever been produced. In contrast, there is compelling evidence of plagiarism (Fig. 4). With respect to cryptozoological theories about the Bird of Washington, it is probably worth revisiting the sage advice of Elliott Coues:

'While we have gray eagles, and black eagles, and eagles without tint, [take] my word for it, reader, this eagle business is about done to death. Let me beg you not to publish the next eagle you kill. Eagle-stories are almost always 'fishy.' As to the number of different kinds of eagles in this country, believe me when I assure you that there never have been but two species discovered in all the length and breadth of this country. That famous 'bird of Washington' was a myth. Either Audubon was mistaken, or else, as some do not hesitate to affirm roundly, he lied about it. The two species are, the golden eagle (*Aquila chrysaetos*), and the bald eagle (*Haliaeetus leucocephalus*).' (Coues 1876)

Separating man from myth

There are now at least six cases of alleged plagiarism in Audubon's works, in addition to several 'mystery birds' in *The birds of America* that have never been seen by any other naturalist (Holt 2005). William Dunlap (1766–1839), the American playwright and art historian, reported an anecdote about Audubon from Alexander Lawson (1773–1846), engraver of most of Wilson's plates. Lawson told Dunlap that, in 1824, Audubon showed him a painting of Great Horned Owl *Bubo virginianus* (J. F. Gmelin, 1788): 'On examining it closely he thought, notwithstanding its size, that it had a remarkable resemblance to his friend Wilson's original picture of the same bird. 'Come here, my dear,' said [Lawson] to his daughter, 'bring down the Horned Owl.' It was brought, and Audubon's proved to be a copy from Wilson's, reversed and magnified' (Dunlap 1834: 203–204). An anonymous author defended Audubon from Dunlap's claim and several other accusations of misconduct: '[Mr. Dunlap] has the presumption to suppose, that on his bare assertion, his readers will believe that Mr. Audubon's figures, in his great work, are occasionally copies from Wilson, 'reversed and magnified!' (Anon. 1835: 58). Audubon's plate of Great Horned Owl (Pl. 61, 1829) indeed does not closely resemble Wilson's, but possibly he painted a new image after his encounter with Lawson.

Ord investigated further and found undeniable proof that Lawson's (*vide* Dunlap 1834) charge of plagiarism was valid (Ord 1840: 272). Two birds in Audubon's image (Pl. 67) of Red-winged Blackbird *Agelaius phoeniceus* (Linnaeus, 1766) were evidently copied from Wilson (1811a, Pl. 30) and subsequently embellished (Fig. 8). One of these birds, Wilson's adult female, was printed by Audubon at reduced size and claimed by him to be a juvenile. Also, one of the Mississippi Kites *Ictinia mississippiensis* (Wilson, 1811) in Pl. 117 of *The birds of America* is indeed a mirror image of Wilson's illustration (1811b, Pl. 25), as Lawson claimed Audubon had done with the Great Horned Owl. When one image is flipped horizontally, the outlines of the birds overlap perfectly (except a toe which was sliced off in Audubon's plate) (Fig. 9; Ord 1840).

Audubon falsely claimed that the Mississippi Kite in his plate was a female; the illustration he plagiarised was of a male (Wilson 1811b: 82). 'I first saw the Mississippi Kite: ascending in the Steamboat Paragon in June 1819,' Audubon wrote in his 1820 journal,



Figure 8. Comparison of two images of Red-winged Blackbird *Agelaius phoeniceus* (Linnaeus, 1766) in (right) Pl. 67 of *The birds of America* (Audubon 1829) and (left) Pl. 30 of *American ornithology* (Wilson 1811b). Reproduced courtesy of the John James Audubon Center at Mill Grove in Audubon, PA, the Montgomery County Audubon Collection (<https://www.audubon.org/birds-of-america>, accessed 9 October 2019) and Smithsonian Libraries (QL674.W73).

several months after the events; 'having At that time no Crayons or Paper, [I] did not Draw one, and determined Never to Draw from a Stuffed Specimen, [and] Carried No Skins' (Corning 1929). Ironically, when the time came to produce his plate of Mississippi Kite in 1831, Audubon plagiarised Wilson's image that had been drawn from a stuffed specimen! This represents yet more evidence that Audubon's journal entries were not a contemporaneous record of events as they happened, but a manicured version prepared for his family, who were apparently ignorant of the plagiarism and fictional species in *The birds of America*. Yet another accusation was levied by Hunter (1983), who stated that one of the birds in Audubon's plate 117, which depicts the Northern Flicker *Colaptes auratus* (Linnaeus, 1758) is extremely similar in profile to Wilson's Pl. 25 (1811). The images are indeed similar, but the match is not conclusive.

Two of Audubon's original paintings of an adult Bald Eagle, the first clutching a Canada Goose *Branta canadensis* (Linnaeus, 1758) with its right foot (N-YHS 1863.18.40) and the second with a large catfish swapped for the goose (N-YHS 1863.17.31), which served as the basis of Pl. 31 (1828), are extremely similar in pose and composition to Wilson (1811a, Pl. 36; Fig. 10). The similarity of the plates led Rhodes (2004: 93) to suggest that Audubon's painting was, like Wilson's, based on the mounted Bald Eagle in the Peale Museum and not a freshly killed specimen as the passages in his 1820 journal imply. Nevertheless, the painting with the goose bears the inscription, 'Drawn from Nature by



Figure 9. Comparison of Mississippi Kite *Ictinia mississippiensis* (Wilson, 1811) in (left) Pl. 25 of *American ornithology* (Wilson 1811a) and (right) Pl. 117 of *The birds of America* (Audubon 1831). Reproduced courtesy of the John James Audubon Center at Mill Grove in Audubon, PA, the Montgomery County Audubon Collection (<https://www.audubon.org/birds-of-america>, accessed 9 October 2019) and Smithsonian Libraries (QL674.W73).

J. J. Audubon / Little Prairie Mississipi [sic] November 24, 182[...]', and is corroborated by passages in Audubon's journal (Corning 1929). 'I shot a Beautiful White headed Eagle *Falco Leucocephalus*—probably 150 yards off,' Audubon wrote on 23 November 1820, 'My Ball Went through its body' (Corning 1929: 37). The probability of killing an adult Bald Eagle with an early 19th century muzzle-loaded gun at 150 yards [137 m] is extremely low, so the distance of his shot seems to be exaggerated. Nevertheless, on the following day, Audubon wrote that he 'spent the greater part of the day drawing,' and on 25 November, 'spent the whole day drawing the *White headed Eagle*.' On 27 November, Audubon 'finished [his] drawing of the *White headed Eagle*, having been 4 days at it.' Despite these apparently contemporaneous sources, it is difficult to believe that Audubon was not influenced by Wilson's image (Fig. 10), especially when he had easy access to *American ornithology* in Cincinnati during the months preceding this trip (CLSC 1816).

In addition to these alleged instances of plagiarism, Audubon scholars have revealed a case of probable specimen theft (Fries 2006: 189–90, Halley 2020a), fraudulent drawings and data given to Rafinesque (Markle 1997, Woodman 2016), complete or partial fabrication of his famous ringing experiment (Halley 2018a), the seemingly deliberate distortion of the timeline in his published writings (Halley 2015, 2018a, this study) and a case of suspected backdating of a painting (Pick 2004). There is also an interesting case of self-plagiarism; the



Figure 10. Comparison of (top) White-headed Eagle (Pl. 36) in *American ornithology* (Wilson 1811b) and (bottom) White-headed Eagle (Pl. 31) in *The birds of America* (Audubon 1828). Reproduced courtesy of the John James Audubon Center at Mill Grove in Audubon, PA, the Montgomery County Audubon Collection (<https://www.audubon.org/birds-of-america>, accessed 9 October 2019) and Smithsonian Libraries (QL674. W73).

image that accompanied the original description of Western Meadowlark *Sturnella neglecta* Audubon, 1844, was copied and modified from an image of a juvenile Eastern Meadowlark *S. magna* (Linnaeus, 1758) in the double-elephant folio (Pl. 136), though the plate bears

the false caption ‘drawn from nature by J. J. Audubon’ (Halley 2016, based on a drawing reproduced in Tyler 1993: 100).

‘I cannot help mentioning another anecdote as to his veracity,’ Bonaparte wrote to the naturalist William Cooper (1798–1864) in July 1831, after perusing *Ornithological biography* vol. 1 (1831) for the first time. ‘Audubon has strenuously maintained to me that *Strix noevia* & *Strix Asio* [i.e., colour morphs of the Eastern Screech-Owl *Megascops asio* (Linnaeus, 1758)] were two species, that he had bred them, found their nests & had every proof’ (Stroud 2000: 118). However, Audubon (1831: 486) treated them as one species and claimed that the idea ‘was first publicly maintained by my friend Charles Lucien Bonaparte, although the fact was long before known to many individuals with whom I am acquainted, as well as to myself.’ Bonaparte mused, ‘What must we suppose by such misrepresentation?’ (Stroud 2000: 119). A few years later, a similar case was discussed by Ord in a letter to Waterton dated 29 September 1835:

‘I should wish the English reader to compare Wilson’s account of the Cow Bunting [*Molothrus ater* (Boddaert, 1783)] with Audubon’s: he would find that, notwithstanding the boasted knowledge of the ornithologist par excellence, the latter has pilfered the whole of Wilson’s supposed facts; and palmed them upon the reader, as the result of his own researches.’ (APS, Mss.B.Or2)

Audubon’s claim to have studied under the French painter David was also a lie, exposed by Bonaparte, whose sister-in-law Charlotte was actually David’s student in Brussels (Ford 1964: 374, Stroud 2000: 56). As Ord intimated, even basic information in Audubon’s autobiographical writings cannot be trusted. It took more than a century after Audubon’s death to confirm that he was actually born on the island of Hispaniola (Dallett 1960), not in France, as he claimed to Bonaparte and others, or the USA, as he implied in *Ornithological biography* (1831: v–x) and claimed outright in his autobiographical essay, ‘Myself’ (Audubon 1897: 7). There is no doubt that Audubon knew his true origin. In his naturalisation papers, filed in Philadelphia on 3 July 1812, he claimed to be ‘a native of the Island of St. Domingo aged about Twenty Six years’ (Dallett 1960: 91). ‘What in fact must we think of a man who prints he is born an American,’ Bonaparte wrote to Cooper, ‘after he has for years repeated to every body he was a Frenchman by birth though an American by heart’ (Stroud 2000: 118).

What was Audubon’s motivation?

When Audubon (1828) published his description and chose the Bird of Washington as the large plate for the third set of *The birds of America*—his first plate with Havell—he was gambling that his audience (potential subscribers) would believe in its authenticity. Audubon disingenuously stated in his 1827 prospectus that his paintings were the result of ‘attentive examination of the objects portrayed during a long series of years’ (Fries 2006: 385), when his leading painting was plagiarised and invented (Fig. 4). Irrespective of whether or not he believed that the Bird of Washington was, in fact, a real and distinct biological entity, (1) Audubon’s painting was not based on a specimen and he knew it, (2) he fabricated data to make the painting more convincing (e.g., Fig. 3) and (3) published the fraudulent species with boisterous claims of discovery:

‘Not even Herschell when he discovered the famous planet which bears his name [now Uranus] could have experienced more happy feelings. To have something new to relate,

to become yourself a contributor to science, must excite the proudest emotions of the human heart.' (Audubon 1828: 115)

We can only assume that Audubon's motive to lie was economic, as evidenced by the fact that, with the help of the Bird of Washington, he succeeded in his attempts to attract the wealthy patrons needed to launch *The birds of America*. However, after he published, backed by the investments of the British nobility and the King himself, Audubon could not afford to jeopardise his new success by admitting the truth to anyone. It was probably for this reason alone that, 'In spite of the opinions of others, Audubon, to the day of his death, stubbornly maintained his *Haliaetus Washingtoni* was separate and distinct from the emblematic bird of his adopted land' (Arthur 1937: 245). How could Audubon admit the truth, when his closest friends and family were believers in the Bird of Washington and had thrown their own resources behind his project? At Beech Woods plantation, where Audubon's wife Lucy worked as governess, a portrait of her husband and a print of the Bird of Washington were juxtaposed on the parlour wall:

'In the hospitable mansion of [William Garret Johnson], in the parish of West Feliciana [Louisiana], if one will look into the parlor, they will see over the piano a cabinet-sized portrait [of the ornithologist], remarkable for a bright eye and intellectual look ... Opposite hangs 'a proof impression' of 'the bird of Washington,' a tribute of a grateful heart to an old friend ... in the family holding these pleasing mementos, the 'Audubons' lived for many years ... Here it was that the wife of the great naturalist bid him go forward with his work, and not only cheered him on, but threw the acquirements of her own industry into the glory of the future.' (Thorpe 1851)

Conclusions and implications

The Bird of Washington fraud was not perpetrated with a chimerical specimen like the 'Piltdown Man' (Russell 2012), but with a fictional painting that Audubon claimed was based on a specimen that never existed. It was the first of Audubon's plates to be engraved by Havell and the first new species Audubon published. He described the Bird of Washington in a scientific journal, in the very place where the 'new science' of specimen-based ornithology began more than a century before (Birkhead 2018, Halley 2020b). Audubon led with the Bird of Washington after his arrangement with Lizars fell through and the financial success of *The birds of America* seemed most unlikely. He attached to his fictional species the venerated name 'Washington', an established symbol of American patriotism that was likely to appeal to his target subscriber base (i.e., affluent members of English society who were sympathetic to American affairs). The Bird of Washington was more than a hoax. It was the cornerstone of a highly successful (and fraudulent) marketing strategy and a lie that Audubon took to the grave.

Some insight can be gained through comparison to other fraudsters, the most notable being Richard Meinertzhagen. Garfield (2007) called the life of Meinertzhagen 'an eye-popping case study in narcissistic pathology', to which Olson (2008) responded, 'it provides powerful testimony in support of the fact that we cannot believe a word that Richard Meinertzhagen ever wrote or said about anything.' By the time his 'colossal fraud' was exposed (e.g., Knox 1993, Rasmussen & Prÿs-Jones 2003, Garfield 2007), Meinertzhagen's works had been widely cited in biological literature and popular books including the epoch-making *Evolution: the modern synthesis* (Huxley 1942). Olson (2008) summarised the situation:

'[Meinertzhagen] stole specimens of birds from museum collections, fabricated label data for them, and published deliberately falsified information about birds in scientific journals—facts that have only been brought to light in recent years through painstaking research and scientific investigation. Many of us in the museum community who had long been aware of Meinertzhagen's ornithological perfidies had come to wonder if the rest of his history might prove to be just as grand a prevarication.'

The above 'ornithological perfidies' (and more) were also committed by Audubon, but historians and ornithologists have routinely given him a free pass. 'If one were to believe the claim that [Audubon] backdated a portrayal of a grouse to compete with [Wilson], he would be not just an occasional teller of tall tales, but rather a cut-throat participant in a bid to dominate the American ornithological landscape' (Olson & Mazzitelli 2017). Audubon's biographers have instead depicted his 'romantic imagination which defeats verification' (Arthur 1937: 14) as a positive and charming characteristic, shrugging it off as merely reflective of his 'frontier sense of humor' (Rhodes 2004: 134). Audubon has been given the benefit of the doubt perpetually, no matter how much doubt accumulates. As in the case of Meinertzhagen, a 'cover-up appears still [to] be in effect' (Olson 2008).

Audubon's untrustworthy anecdotes were cited by Darwin (1859) without critical scrutiny and many of his fabrications are still believed by biologists and the general public (see Halley 2018a). Audubon fabricated data (see Fig. 3) and 'published deliberately falsified information about birds in scientific journals' (e.g., Audubon 1828) and commercial books (e.g., Audubon 1831, 1839). He also gave falsified data to other naturalists, who published them unknowingly (e.g., Markle 1997, Woodman 2016). There is strong evidence that he stole the type specimen of Harris's Hawk *Parabuteo unicinctus harrisi* (Audubon, 1837) and then pretended not to know its collector, one of his subscribers (!), who intended to name the species 'Morton's Hawk' after Dr Samuel Morton (Fries 2006: 189–90; Halley 2020a).

Ord warned that a thorough review of 'The misrepresentations and lies of five enormous octavo volumes would severely tax the patience of him who should undertake to expose them, as well as of him who should listen to the detail' (APS, Mss.B.Or2). The 'Audubon collection' includes more than 435 life-size paintings (N-YHS collection), the Havell and Royal Octavo editions of *The birds of America* and more than five volumes of anecdotal accounts of American birds (*Ornithological biography*) and various other writings (e.g., Audubon 1828, 1839, 1897). Dozens of scientific names authored by Audubon are currently in use and many are based on his plates alone, because they were published prior to the text descriptions (Stone 1906, Chesser *et al.* 2018).

More than a century of Audubon-related scholarship needs to be revisited because most of the 'primary' sources used by biographers (e.g., *Ornithological biography* and Audubon's journals) are replete with deliberate distortions of the truth, perpetrated by Audubon himself and / or bowdlerised by his descendants (Arthur 1937: 243). Olson's (2008) lament, 'we cannot believe a word that Richard Meinertzhagen ever wrote or said about anything', applies as well to Audubon, but the rise of birding as a hobby in America and abroad has created a voracious appetite for Audubon-related books, which publishing houses are eager to satiate with little regard for historical accuracy. Few ornithologists today are sufficiently acquainted with historical primary sources, and therefore are unable to identify Audubon's timeline distortions and false narratives. Biographers writing for a general audience seem not to notice or care about the extent of his deception. Notwithstanding these difficulties, 'Time will uncover the truth' (Audubon 1897: 271).

Final thoughts

'Your remarks on the subject of Audubon's Biography of Birds are just', George Ord wrote to Waterton in February 1844, 'but should you seriously engage in a criticism of that voluminous romance, where will it end?' (APS, Mss.B.Or2). Ord's question remains unanswered, but a critical review is now underway, as he envisioned, and a more accurate history of Audubon and his ornithology will inevitably emerge as fact is separated from fiction. Audubon's works are indeed voluminous, but the fruits of careful scholarship are cumulative.

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Clarifying the morphology of the enigmatic Kiritimati Sandpiper *Prosobonia cancellata* (J. F. Gmelin, 1785), based on a review of the contemporary data

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SUMMARY.—The extinct Kiritimati Sandpiper *Prosobonia cancellata* is known from a single contemporaneous illustration by William Wade Ellis and a description by William Anderson. We reproduce Ellis' illustration for the first time, and we consider the illustration as almost in line with Anderson's description. Further, using both Anderson's work and Ellis' illustration, we prepared a description of the bird to replace Latham's interpretation of the depiction. Finally, we show that Kiritimati Sandpiper possessed several unique morphological characters.

Only two of the five species of Polynesian sandpipers (*Prosobonia* sp.), have available skins and mounts: the extant Tuamotu Sandpiper *Prosobonia parvirostris*, and a unique skin of Tahiti Sandpiper *P. leucoptera*. The extinct Moorea Sandpiper *P. ellisi* and Kiritimati Sandpiper *P. cancellata* are each known from a single illustration executed on the third circumnavigation commanded by Captain James Cook (Walters 1991, 1993). The fifth species, endemic to Henderson Island, is known only from bones and is undescribed (Wragg 1995, De Pietri *et al.* submitted). *Prosobonia* sandpipers were once widespread in the Pacific (Thibault & Cibois 2017).

Kiritimati Sandpiper was confined to Kiritimati (or Christmas) Island, now in the Republic of Kiribati, and geographically part of the Line Islands. It was illustrated by William Wade Ellis, surgeon's mate on board HMS *Discovery* during the third circumnavigation commanded by Captain James Cook (1776–80). Part of his crew visited the island between 24 December 1777 and 2 January 1778. There, or soon afterwards, an illustration was made by Ellis. He also illustrated, from the same island, Kiritimati Reed Warbler *Acrocephalus aequinoctialis* and Pacific Golden Plover *Pluvialis fulva* (Lysaght 1959: 334, 338). In 1785, John Latham initially described the sandpiper based on the drawing (see also Latham 1824: 9). However, it was formally described by Johann Friedrich Gmelin in 1789 (Gmelin 1789) from Latham's 1785 description. The illustration is now at the Natural History Museum, London (NHMUK), having originally formed part of the collection of Sir Joseph Banks.

As our entire knowledge of this species apparently derives from a single illustration, we located a description provided by William Anderson, the expedition's surgeon, which was mentioned but not presented by Lysaght (1959: 332–333). However, the identity of Kiritimati Sandpiper was challenged, for example by R. B. Sharpe, who identified it as a Wood Sandpiper *Tringa glareola* (Lysaght 1959: 332–333). Here, we present all of the known details concerning this enigmatic bird and publish the illustration for the first time, as well as discussing the trustworthiness of Ellis's drawing.

Extant descriptions

In Anderson MS (c.1780: 12):

23. *Tringa aequinoctialis*. Magnitudo *Alauda paula majora*. Longitudo uncio 7.

Corpus superne fuscum albido variegatum. Inferne albidum pectore hypochondrusque fusco pari[ll]is. Pileum fuscum linea alba supra oculos a basi Rostri fere a i [ad] nucham. Remiges fusca. Cauda rotundata reatricibus faucis albo fasciatim. Rostrum rectum nigrum. Habitat insula Diei Christi. Solitaria. Affinis Tringarum alpina helveticaque.

[Our translation]

23. **Tringa aquinoctialis**. Slightly taller than a lark. Length 7 inches.

Upper body brown with various white markings. Underside, white breast and flanks similarly brown. Brown cap, white line from top of eye to base of beak, almost reaching nape. Remiges brown. Tail rounded by rectrices (= round tail), white throat streaked. Beak straight and black. Lives on Christmas Island. Solitary. Affiliated with *Tringa [Calidris] alpina* and *Tringa helvetica [Pluvialis squatarola]*.

Although the species were probably not present on Kiribati, these are the names the author referred to (i.e. species he was familiar with and that he used for comparison).

In Latham (1785: 274) we find the following description:

Barred Phalarope Length seven inches and a half. Bill one inch, black: the feathers on the upper parts of the bird brown, edged with white transversely barred with dusky: quills dusky, with the ends brown, and the margins and tips very pale: tail the same, spotted on both webs with white: legs dusky.

Inhabits Christmas Island. In the collection of Sir Joseph Banks.

In Gmelin (1789: 675) there is the following description:

cancellata 34. Tr. Pennis superioribus fulcis, margine albis, inferioribus albis transversim obscure lineatis, pedibus pinnatis obscuris.

Barred Phalarope, Lath. Syn. III. I. p. 274. N. 5.

Habitat in insula nativitatis Cristi, 7 ½ polices longa.

Rostrum nigrum; remiges restrictesque obscurae, margine et apice pallidiori.

[Our translation]

cancellata 34. Tr[inga], plumage dark brown above, with white edges, underside white transversely barred with dark lines, pinnate dark feet.

Barred Phalarope, Lath[am]. Syn. III. I. p. 274. N. 5.

Lives on Christmas Island, 7 ½ inches long.

Bill black; remiges and rectrices dark, with paler margins and tips.

The use by Gmelin of ‘pedibus pinnatis’, literally ‘winged’ or ‘feathered’ feet, is odd. The feet are not feathered, so we believe that this adjective refers to the shape of the feet and should be translated as ‘pinnate’, i.e. having branches, tentacles, etc., either side of an axis, like the vanes of a feather.

In Latham (1824: 9) is the following description:

Barred Phalarope Length seven inches and a half. Bill one inch, black: shape uncertain, feathers on the upper parts of the body brown, edged with white, transversely barred with dusky: quills dusky, with brown ends, the margins and tips very pale: tail the same, spotted on both webs with white: legs dusky.

Inhabits Christmas Island. - Sir Joseph Banks.



Figure 1. William Wade Ellis's painting of Kiritimati Sandpiper *Prosobonia cancellata*, held by the Natural History Museum, London, UK.

The illustration

One of our main aims was to confirm the accuracy of Ellis's illustration. Therefore, we analysed ten random illustrations made by Ellis during the third expedition, and checked the reliability of the artist: Blue-crowned Lorikeet *Vini australis* (Ellis no. 13), Hawaii Oo *Moho nobilis* (Ellis no. 26), Hawaii Mamo *Drepanis pacifica* (Ellis no. 27), Lesser Akialoa *Hemignathus obscurus* (Ellis no. 28), Iwi *Drepanis coccinea* (Ellis no. 29), Hawaii Amakihi *Chlorodrepanis virens* (Ellis no. 31), South Island Saddleback *Philesturnus carunculatus* (Ellis no. 73), Tahiti Reed Warbler *Acrocephalus caffer* (Ellis no. 76), Ou *Psittirostra psittacea* (Ellis no. 79) and Akepa *Loxops coccineus* (Ellis no. 85). In general, most of these drawings are accurate, albeit with some incorrect details in several illustrations, but all of the species illustrated are recognisable beyond doubt. For example: there should be no red on the

forehead of Blue-crowned Lorikeet *Vini australis* (Ellis no. 13); the Hawaii Mamo *Drepanis pacifica* (Ellis no. 27) lacks pale wingtips and the yellow undertail-coverts are too short; the South Island Saddleback *Philesturnus carunculatus* (Ellis no. 73) should have reddish-brown (not black) undertail-coverts, a reddish (not yellow) wattle and the bill is proportionately slightly too large in the illustration; and the adult Ou *Psittirostra psittacea* (Ellis no. 79) has yellow reaching too far down the neck, should show whitish yellow undertail-coverts, has incorrect bill and nostril shapes, and the legs should be pinkish (not greyish, as depicted). On the illustration of the sandpiper (Lysaght 1959, no. 64) is written: 'W. W. Ellis ad viv: delint: et pinxt: 1778. Christmas Isle' (Fig. 1).

Conclusion

As Ellis's drawing in combination with Anderson's description are trustworthy (for some differences see below), the following combination should be used for the species description, rather than Latham's interpretation of the illustration.

Size and structure.—Kiritimati Sandpiper was of similar size to Tuamotu Sandpiper (15–17 cm; van Gils *et al.* 2020) according to Anderson (7 inches = 17.8 cm), or slightly larger according to Latham (7.5 inches = 19 cm). The shape appears unnatural, which may be a result of the artist's interpretation. The small head and short wings are clearly similar to Tuamotu Sandpiper.

Head.—Short white supercilium (not extending behind eye in the illustration, unlike in Anderson's text), and nape dark. Forehead, crown and hindneck darker brownish, remainder of the head paler brownish. Streaks of brown on throat, background paler brown.

Upperparts.—Brownish with paler feather fringes on the wing-coverts and primaries. Mantle as coverts.

Underparts.—Pale brownish / white underparts, undertail-coverts paler, with darker brown chevron-shaped feathers on the underparts.

Tail.—Rounded, with uniform-coloured feathers. Brownish background with dark streaks. Longer than the tips of the wings when folded.

Bare parts.—Bill black, straight, legs dusky-coloured, part of tibia feathered, tarsus long. Four toes.

Behaviour.—Solitary, loosely associated with other shorebirds.

Differs from Tuamotu Sandpiper in tail pattern, size and whitish throat.

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Picus Rafflesii Vigors, 1830¹, re-assigned to *Chloropicoides* Malherbe, 1849

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SUMMARY.—A recent comprehensive molecular phylogeny of the Picidae recovered the genus *Dinopium* as paraphyletic, with Olive-backed Woodpecker *D. rafflesii* sister to Pale-headed Woodpecker *Gecinulus grantia*. Of the available taxonomic responses, we favour assigning *D. rafflesii* to its own genus, in line with the modern trend to recognise more and smaller genera. Several genus names were used for *rafflesii* between the mid-19th and early 20th centuries, of which *Chloropicoides* Malherbe, 1849, is the oldest. Available information suggests, however, that it was not Malherbe's intention to designate *rafflesii* as the type of his new genus, but that in near-simultaneously publishing two works on the Picidae he inadvertently introduced *Chloropicoides* first in combination solely with *rafflesii*, making it the type species by monotypy. Should it be proven that his other, more detailed paper was in fact published first, then another Malherbe genus, *Gauropicoides*, could be used by those who seek to recognise the distinctiveness of *rafflesii*.

Olive-backed Woodpecker *Dinopium rafflesii* occurs from southern Myanmar and peninsular Thailand south to Sumatra, with a separate subspecies on Borneo (del Hoyo & Collar 2014). It is one of 4–6 species (taxonomy-dependent) assigned to the genus *Dinopium* Rafinesque, 1814 (Dickinson & Remsen 2013, del Hoyo & Collar 2014, Fernando *et al.* 2016). However, in a comprehensive molecular review of the Picidae, sampling 203 of the 217 well-recognised species across six loci, Shakya *et al.* (2017: 187) found that

'*Dinopium* is paraphyletic because *D. rafflesii* is sister to [Pale-headed Woodpecker] *Gecinulus grantia*. Morphologically, *D. rafflesii* resembles other *Dinopium* woodpeckers, except that it has plain brownish rather than black-and-white striped underparts, and its females do not have spotted crests as in *Dinopium*. In respect to these characters, and also wing coloring and red crests, *D. rafflesii* is most similar to *Gecinulus* species.'

The implications of this are that either (1) *Gecinulus* should be merged in *Dinopium*, (2) *D. rafflesii* should be reassigned to *Gecinulus* or (3) *D. rafflesii* should be transferred to another genus. The general trend in modern taxonomy is to split genera rather than lump them (2,161 genera in Dickinson 2003, increased to 2,340 genera in Dickinson & Remsen 2013, Dickinson & Christidis 2014). Given this, plus the fact that option 1 would obscure the distinctiveness of the two species in *Gecinulus* and option 2 would negate that of *D. rafflesii*, we here propose that *D. rafflesii* be moved to another genus. This is not, however, to pretend that anomalies might not result as a consequence: in the phylogenetic trees generated by Shakya *et al.* (2017) a number of pairs of congeners are indicated as being separated for longer than *D. rafflesii* has been from *Gecinulus*, including Eurasian Wryneck *Jynx torquilla* and Rufous-necked Wryneck *J. ruficollis*, Rufous Piculet *Sasia abnormis* and White-browed Piculet *S. ochracea*, Heart-spotted Woodpecker *Hemicircus canente* and Red-

¹ Bruce (2003) demonstrated that Vigors alone, not Vigors & Horsfield, should be considered the authority.

crested Woodpecker *H. concretus*, Maroon Woodpecker *Blythipicus rubiginosus* and Bay Woodpecker *B. pyrrhotis*, and Orange-backed Woodpecker *Chrysocolaptes validus* and all other *Chrysocolaptes* sampled; but genus limits in some of these cases may indeed merit review.

Unfortunately, the second species of *Gecinulus*, Blyth, 1845, *G. viridis* (Bamboo Woodpecker) was not sampled by Shakya *et al.* (2017), but a close relationship between these congeners has long been assumed, with conspecificity sometimes proposed (Short 1982, Dickinson 2003), in part doubtless because a narrow hybrid zone between them exists in northern Thailand and, presumably, northern Laos (Round *et al.* 2012). The risk that the absence of molecular data for *G. viridis* might complicate the scenario recovered by Shakya *et al.* (2017) therefore appears remote.

Similarities between *D. rafflesii* and both species of *Gecinulus* are the unspotted throat and otherwise concolorous underparts; *D. rafflesii* and *G. viridis* further share concolorous upperparts (both with olive rump) and blackish tail. Differences between *D. rafflesii* and both species of *Gecinulus* are the former's (i) bold *Dinopium*-like black-and-white vs. plain olive-yellow facial pattern; (ii) more extensive and crested red on crown in the male; (iii) black vs. yellowish-olive crown in the female; (iv) sparse whitish spots on the flanks and lower belly; (v) large blackish vs. stubby yellowish bill; and (vi) browner-olive underparts. Differences between *D. rafflesii* and other *Dinopium* species are its: (i) lack of white spotting or streaking on the black crown in the female; (ii) lack of yellow, flame-yellow or red on the dorsal area; (iii) continuous olive-green vs. either bright red or black rump; (iv) lack of markings on the pale throat; and (v) dull plain sooty brownish-olive vs. black-on-whitish underparts. Moreover, Stresemann (1921) indicated that the nostrils of *rafflesii* are covered by feathers, but those of other *Dinopium* species are not, and in Natural History Museum (Tring) material we find that this distinction is supported (albeit with some exceptions, presumably caused by abrasion).

All the above lends support to the proposition that the most appropriate course of action based on current evidence would be to remove *rafflesii* to its own genus. The synonymy in Peters (1948: 143) indicates the availability of several names, of which two, *Chloropicoides*, Malherbe, 1849, and *Gauropicoides*, Malherbe, 1861, are seen to have as their type species by monotypy *Picus rafflesii*. Clearly, the former would have priority, and during the first half of the 20th century it was used multiple times for this species, e.g., by Stresemann (1921), Baker (1927) and Chasen (1935). Baker (1927: 75), who had earlier used *Gauropicoides* (Baker 1919), following among others Hargitt (1890: 132) and Hesse (1912: 233), noted that the latter genus is antedated by *Chloropicoides*, and went on to define how *Chloropicoides* can be distinguished from *Brachypternus* (the genus invoked by Baker for Black-rumped Flameback *Dinopium benghalense*).

Nevertheless, this evidence of priority is considerably muddled because Malherbe published two different works in 1849. One was a brief note reporting the description (elsewhere) of some new species of Picidae, including a clarification of the taxon *Picus rafflesii* Vigors, 1830, which he assigned to *Chloropicoides* (Malherbe 1849a). The second, offering a new classification of the Picidae (Malherbe 1849b), is a longer paper which he evidently regarded as a direct foretaste of his monograph (both 1849 publications, and Strickland 1845: 197, indicate that that work was already well advanced). In his new classification, Malherbe again mentioned *Chloropicoides*, but this time considered it to form three parts, the first of which comprised multiple species and the others single species each, one of them *rafflesii*. Certainly by the time his monograph eventually appeared, Malherbe (1861: 53) had settled on the Himalayan Flameback *Dinopium shorii* (which he had mentioned in his first group in Malherbe 1849b: 346) to represent the type of his genus *Chloropicoides*.

It is clear that the author himself generally considered the new classification paper (Malherbe 1849b) to have primacy—perhaps he even expected it to appear first—and there is evidence that contemporaries (Strickland 1850²) and subsequent commentators (Hargitt 1890: 132, Sherborn 1925: 1246) also did so, and although of itself this confers no evidence of priority, it bears mention that Malherbe (1862: 102) in the synonymy of *rafflesii* listed the new classification after his *Bull. Soc. Hist. Nat. Dept. Moselle* note. Irrespective of any of this, there appears to be no unequivocal internal evidence that either paper was published first. Crucial, therefore, is Stresemann (1921: 89), who (i) noted that on p. 520 of the same volume in which Malherbe's new classification was published it was reported that the relevant part of the *Bull. Soc. Hist. Nat. Dept. Moselle* in which Malherbe (1849a) appeared had already been received at the Metz Academy, and (ii) offered testimony that volume 30 of *Mém. Acad. Natl. Metz* was published as a single part, meaning therefore that the new classification must have appeared later. This clearly establishes priority for Malherbe (1849a) and thus *rafflesii* as the type species of *Chloropicoides*, notwithstanding that Malherbe's intention was almost certainly not to confer this status upon the taxon.

Nevertheless, one of our referees (A. Elliott *in litt.* 2020) notes that Stresemann's (1921) assertion (ii, above) could conceivably be challenged. Consequently, should evidence come to light establishing the priority of Malherbe (1849b), then Malherbe's (1861) own subsequent designation of *Dinopium shorii* as the type species of *Chloropicoides* would render the latter genus unavailable for *rafflesii* alone, and instead necessitate the use of *Gauropicoides* Malherbe, 1861³, by those who wish to recognise the distinctiveness of *rafflesii*.

The frequency with which *rafflesii* has been afforded its own genus is notable, with *Mesospilus* Sundevall, 1866, also introduced to accommodate it. However, the treatment by Peters (1948: 143) and commentary by Goodwin (1968) served to stymie a separate generic assignment for *rafflesii* until the study by Shakya *et al.* (2017). As far as we can establish, while acknowledging that Stresemann's (1921) testimony might ideally be subject to independent confirmation, the earliest available generic name for *rafflesii* is *Chloropicoides* and, in the light of the genetic evidence (Shakya *et al.* 2017) and the morphological data provided above, we propose that *Chloropicoides* be resurrected to accommodate *rafflesii* henceforth.

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² It is abundantly clear that Strickland considered Malherbe something of a nomenclatural anarchist, with a complete disregard for priority; Strickland rejected all of the new replacement names in the new classification (Malherbe 1849b).

³ Nevertheless, it must be noted that there is considerable doubt and confusion as to the precise years in which the four volumes of Malherbe's magnum opus appeared. Although generally considered to have been published in 1861 and 1862, as indicated by the imprints, there is evidence that early parts of the work appeared sometime in 1859 (Dickinson *et al.* 2011, wherein it is concluded that the dating of new names in this work remains a matter for clarification).

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Two new but threatened subspecies of Rufous Grasswren *Amytornis whitei* (Maluridae)

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SUMMARY.—Rufous Grasswren *Amytornis whitei* is the most widely distributed of three species formerly included within the Striated Grasswren *A. striatus* complex. Included among four phenotypically, geographically and ecologically distinct populations are *A. w. whitei* of the Pilbara ironstone ranges of Western Australia and *A. w. oweni* of inland sandy deserts. The other two are the little-known small-billed isolate of the limestone plateau of the Cape Range, North West Cape Peninsula, Western Australia, and a larger form present in the mallee of the Eyre Peninsula, South Australia. We present morphometric and other data and describe these two populations as new subspecies; both are of conservation concern.

Until recently, 11 species of Australian grasswrens (genus *Amytornis*) were recognised (Black *et al.* 2010, Garnett *et al.* 2011, Black & Gower 2017, Gill & Donsker 2019, BirdLife Australia 2019, BirdLife International 2019). The most widely distributed, albeit with a broken distribution, was known as Striated Grasswren *A. striatus* (Gould, 1840) but its infraspecific taxonomy and taxonomic ranking were unsettled (Schodde & Mason 1999, Christidis *et al.* 2010, 2013, Black & Gower 2017, Black *et al.* 2019). In a phylogenetic and phenotypic analysis of the Striated Grasswren complex, Black *et al.* (in press) assessed plumage and morphometry of 161 specimens from across its range and sequenced mitochondrial DNA (ND2) from most populations. From the mtDNA data, two clades were recovered, separated across the Eyrean Barrier, a Plio-Pleistocene agency of vicariance in southern Australian birds (Ford 1974, 1987a, Schodde & Mason 1999, Dolman & Joseph 2015). An eastern clade comprised two highly divergent subclades of south-eastern Australian and central Queensland populations, respectively. The western clade included all other sampled populations. Nucleotide divergences between each of the three clades of between $3.01 \pm 0.87\%$ and $4.56 \pm 1.39\%$ are levels typical of species-rank distinction in birds (Avice & Walker 1998, Joseph & Omland 2009, Hung *et al.* 2016, Joseph 2018). Accordingly, and with statistically validated phenotypic correlation among larger groups, three species and seven distinct populations were identified within the complex, thus:

1. Striated Grasswren *A. striatus sensu stricto* (south-eastern subclade) in south-eastern Australian mallee (a semi-arid low woodland of multi-stemmed *Eucalyptus* spp. trees, themselves also called mallees), with allopatric subspecies *A. s. striatus* in central New South Wales and *A. s. howei* (Mathews, 1911) in the Murray Mallee region of Victoria, South Australia and south-west New South Wales;
2. Opalton Grasswren *A. rowleyi* Schodde & Mason, 1999 (north-eastern subclade) in central Queensland, in a varied open woodland on lateritic gravel; and
3. Rufous Grasswren *A. whitei* Mathews, 1910 (western clade) in the west of the continent, comprising four distinct phenotypes. Two were recognised as subspecies, nominate *A. w. whitei* of the Pilbara ironstone ranges of Western Australia, and *A. w. oweni* Mathews, 1911 of central and western sandy deserts, including the Great Victoria Desert (Fig. 1).

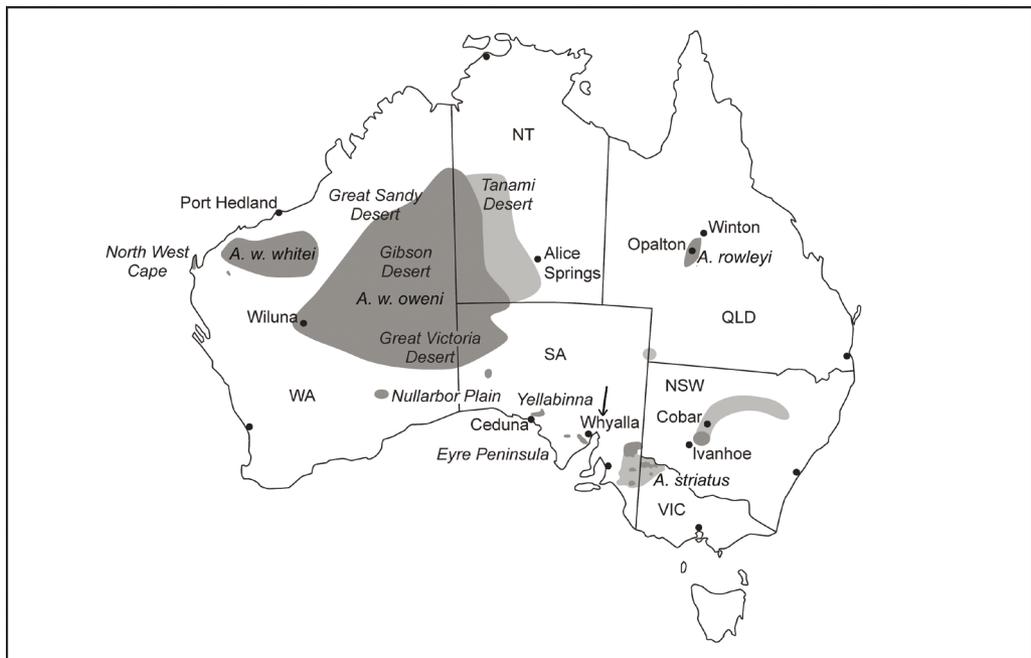


Figure 1. Distribution of the Striated Grasswren *Amytornis striatus*–Rufous Grasswren *A. whitei* complex; from west to east, North West Cape Peninsula, the Pilbara (*A. w. whitei*), western deserts (*A. w. oweni*), western (Yellabinna) and eastern Eyre Peninsula and, east of the Eyrean Barrier (arrow at Spencer Gulf, South Australia), central Queensland (*A. rowleyi*) and the south-eastern mallee of South Australia, Victoria and New South Wales (*A. striatus*). Pale shading indicates former distribution (B. Cale, modified by B. Blaylock)

Two additional phenotypes were identified within Rufous Grasswren from populations of the Cape Range, North West Cape Peninsula, Western Australia, and the Eyre Peninsula, South Australia respectively. The last comprises two disjunct subpopulations, in the southern Yellabinna, a south-eastern extension of the Great Victoria Desert, and in the eastern Eyre Peninsula. We count geographically partitioned intraspecific differentiation as a measure of biodiversity best identified through the naming of subspecies (Patten 2015, Patten & Remsen 2017) and here describe the Cape Range and Eyre Peninsula populations accordingly.

Methods

One of us (ABB) examined all adult specimens of *A. whitei* in the following institutions: Western Australian Museum, Perth; South Australian Museum, Adelaide; Australian National Wildlife Collection, Canberra; Museum Victoria, Melbourne; and American Museum of Natural History, New York: 13 male and 12 female *A. w. whitei*, 37 male and 22 female *A. w. oweni*, eight male and five female Eyre Peninsula, South Australia specimens, and the only adult male and adult female specimens from the Cape Range, Western Australia. Specimens were collected between 1894 and 2007; 40 before 1965, 42 between 1965 and 1984, and 17 since 1997.

The underlying plumage tone of crown, upperparts and underparts was assessed using selected individual colours in Smithe (1975) suitable for comparison among populations of the species complex, also the nature of the dorsal streaking, the breadth of the white shaft-streaks, the breadth and tone of their dark edges, and the colour of the bill, legs and feet.

Standard measurements were taken as follows: bill length from skull attachment to tip, bill depth at the point of the frontal feathering, wing length (max. flattened chord) and tail length (central rectrix from point of emergence to tip).

As described by Black *et al.* (in press) (R Core Team 2018), all morphometric data were compared using type-II two-way ANOVA. Subsequent post-hoc analyses were conducted using pairwise comparison of least-square means and Welch two-sample t-tests. Principal component analysis (PCA) of morphometric data was calculated and a PCA biplot drawn, using the ‘factoextra’ package for R. Sample means, standard deviations, standard errors of the mean and 95% confidence intervals for the mean were calculated for all parameters in each sex and all groups. Two-way ANOVA showed the significant effects of group assignments and of sex. Post-hoc least-square comparison of the ANOVA model showed where groups differed with respect to individual parameters in each sex at 95% confidence. Welch two-sample t-tests were applied to those metrics shown to differ between groups by the post-hoc analysis.

Results

Plumage.—Dorsal tone varies individually within all populations of *A. whitei* but ranges from the darkest and dullest in Eyre Peninsula populations through brighter (more saturated) tones of *A. w. oweni* to the darkest rufous in *A. w. whitei* and palest



Figure 2. Dorsal view of specimens of the Striated Grasswren *Amytornis striatus*–Rufous Grasswren *A. whitei* complex; from left: *A. w. whitei* male, SAMA B646, Fortescue River, Western Australia, 9 February 1915; *A. w. oweni* female, SAMA B37659, 165 km north of Cook, South Australia, 31 August 1983; *A. whitei* (Yellabinna) male, ANWC 52262, 96 km north of Ceduna, South Australia, 12 August 2007; *A. whitei* (Yellabinna) male, SAMA B37658, 50 km north of Ceduna, South Australia, 21 August 1983; *A. whitei* (eastern Eyre Peninsula) female, SAMA B55486 Secret Rocks, South Australia, 3 September 2000; *A. s. howei* male, SAMA B55502, Gluepot Reserve, South Australia, 8 November 2006; *A. s. striatus* female, ANWC 31651, Yathong Nature Reserve, New South Wales, 31 August 1999; *A. rowleyi* female, ANWC 48514, 80 km south-southwest of Winton, Queensland, 26 September 1996; note the comparative size of *A. w. whitei* and *A. w. oweni*, and the variation in plumage tone between Yellabinna specimens (P. Horton)



Figure 3. Ventral view of the same specimens in the same order, as in Fig. 2. Note the more evenly distributed cinnamon underparts of *A. w. whitei* (P. Horton)

cinnamon-rufous in *A. w. oweni*. Generally, Eyre Peninsula specimens are predominantly rufous-russet to rufous, although two western (Yellabinna) specimens more closely resembled *A. w. oweni* and *A. w. whitei* in tone, being rufous to cinnamon-rufous. White dorsal feather streaking is narrower in *A. w. oweni* and less distinctly edged paler brown in both *A. w. oweni* and *A. w. whitei* (Fig. 2). Underparts also vary in all populations, generally pale buff or off-white, darker towards the flanks. In *A. w. whitei* and some *A. w. oweni* the tone is more evenly distributed on the underparts and is closer to cinnamon (Fig. 3). Bare parts are dark in Eyre Peninsula specimens, generally paler in *A. w. oweni* and *A. w. whitei*.

Morphometrics.—The results of all measurements are summarised in Table 1. Analysis of variance (ANOVA) for each parameter revealed discrete morphometric clusters. PCA provided separation of *A. w. whitei* from both *A. w. oweni* and Eyre Peninsula birds on bill dimensions, and the latter two on wing and tail lengths (Fig. 4). A t-test pairwise comparison of parameters identified by ANOVA as distinct revealed statistically significant differences among samples of *A. w. whitei*, *A. w. oweni* and Eyre Peninsula (Table 1).

The bills of *A. w. whitei* are both longer and deeper than in other populations and their wings and the wings of birds on the Eyre Peninsula are longer than those of *A. w. oweni*. The bill of birds on the Eyre Peninsula is relatively long and slender compared to *A. w. oweni* whose bills are statistically deeper, and their tails are longer than those of *A. w. oweni* in males (Table 1, Fig. 4).

The two small Cape Range specimens have shorter bills than any specimen of *A. w. whitei*. Most measurements fall within the range for *A. w. oweni*, but their wings are longer than all but two of 37 male specimens and one of 22 females of *A. w. oweni* (Table 1).

TABLE 1

Morphometrics (mm) of populations within Rufous Grasswren *A. whitei*, showing (except for Cape Range) sample number, mean and standard deviation for each parameter. Superscripts indicate metrics that show differences among Eyre Peninsula, Cape Range, and named populations.

MALES				
Population	Wing	Tail	Bill length	Bill depth
<i>A. w. whitei</i> (n = 13)	61.5 ± 2.1 ¹	85.4 ± 4.1	13.8 ± 1.0 ^{3 5}	5.1 ± 0.3 ³
<i>A. w. oweni</i> (n = 37)	56.4 ± 2.2 ^{1 4}	84.2 ± 5.0 ²	12.1 ± 0.7 ³	4.7 ± 0.3 ³
Eyre Peninsula (n = 8)	61.6 ± 2.6 ¹	88.1 ± 3.4 ²	12.5 ± 0.4 ³	4.5 ± 0.2 ³
Cape Range (n = 1)	60 ⁴	82.7	12.1 ⁵	

¹ Wings of *A. w. whitei* > *A. w. oweni* $p < 0.0001$, Eyre Peninsula > *A. w. oweni*, $p = 0.00047$.
² Tails of Eyre Peninsula > *A. w. oweni*, $p = 0.018$.
³ Bill length and depth of *A. w. whitei* > Eyre Peninsula, *A. w. oweni* $p < 0.0001$, bill depth of *A. w. oweni* > Eyre Peninsula, $p = 0.036$.
⁴ Wing of Cape Range ≥ *A. w. oweni*.
⁵ Bill length of Cape Range << *A. w. whitei*.

FEMALES				
Population	Wing	Tail	Bill length	Bill depth
<i>A. w. whitei</i> (n = 12)	57.9 ± 2.1 ¹	82.1 ± 4.2	13.7 ± 0.8 ^{2 4}	5.1 ± 0.3 ²
<i>A. w. oweni</i> (n = 22)	55.0 ± 1.4 ^{1 3}	82.5 ± 4.8	11.9 ± 0.5 ²	4.6 ± 0.3 ²
Eyre Peninsula (n = 5)	59.0 ± 2.6 ¹	80.5 ± 3.2	12.2 ± 0.3 ²	4.3 ± 0.1 ²
Cape Range (n = 1)	57 ³	82.1	12.1 ⁴	

¹ Wings of *A. w. whitei* > *A. w. oweni* $p = 0.00051$, Eyre Peninsula > *A. w. oweni*, $p = 0.023$.
² Bill length and depth of *A. w. whitei* > Eyre Peninsula, length of *A. w. whitei* > *A. w. oweni* $p < 0.0001$, depth of *A. w. whitei* > *A. w. oweni* $p = 0.00093$, depth of *A. w. oweni* > Eyre Peninsula, $p = 0.0036$.
³ Wing of Cape Range ≥ *A. w. oweni*.
⁴ Bill length of Cape Range << *A. w. whitei*.

Discussion

In the mtDNA data of Black *et al.* (in press) *A. w. oweni* and Yellabinna samples were genetically close in a polytomy with *A. w. whitei*, but Cape Range and eastern Eyre Peninsula populations were not sequenced. More extensive sampling is therefore needed to clarify phylogenetic relationships within the species.

Plumages are similar across all populations of *A. whitei* and vary within groups, so are relatively uninformative. Grasswren plumage tone is not known to change throughout the annual cycle and variation was not found to correlate with season of collection or specimen age. Eyre Peninsula populations are mostly darker and more distinctly streaked but two western (Yellabinna) specimens approach the brighter tones of *A. w. oweni*. The underparts of *A. w. whitei* are more extensively and evenly cinnamon-coloured. Upperparts streaking is narrower in *A. w. oweni*.

While neither plumage diversity nor available genetic data identify clear subspecific boundaries within *A. whitei*, four morphometrically distinct phenotypes occur (Black *et al.* in press; this study). *A. w. whitei* has longer wings than *A. w. oweni* and its bill is larger than all others. Eyre Peninsula specimens have longer wings than *A. w. oweni*, in both sexes and longer tails in males, but relatively finer bills. While the two Eyre Peninsula populations, separated by more than 250 km, are provisionally placed in the same taxon, it is plausible

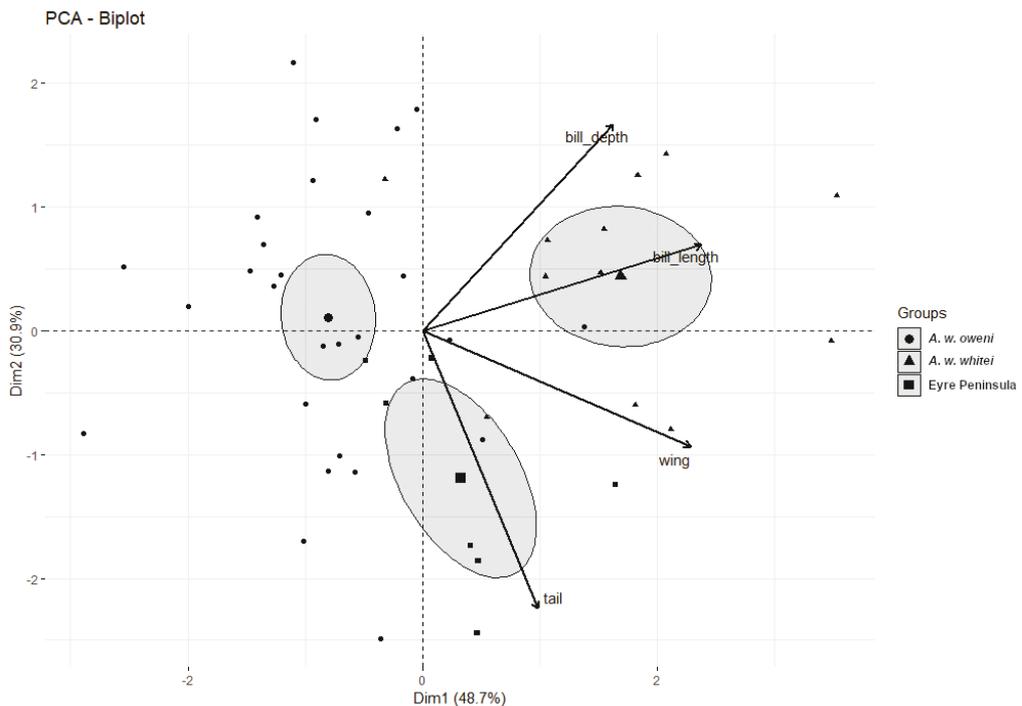


Figure 4. Principal Component Analysis of the morphometrics, showing standard 95% confidence ellipses of centroids for males of three populations, *A. w. whitei*, *A. w. oweni* and the Eyre Peninsula.

that DNA sequencing of eastern Eyre Peninsula samples might expose further diversity. The Cape Range population has been included implicitly (Higgins *et al.* 2001) or explicitly (Johnstone & Storr 2004, Johnstone *et al.* 2013) in *A. striatus whitei*, now *A. whitei*, both occupying stony uplands and distinct ecologically from *A. w. oweni* of sandy deserts. The two specimens are smaller than Pilbara *A. w. whitei* but have wings and tails of similar length yet much smaller bills (Figs. 5–6). The Cape Range is an area of endemism for fauna, including birds (Ford 1987b, Kendrick 1989, Frith & Frith 1997, Chakrabarty 2010, Taylor *et al.* 2015, Doughty *et al.* 2016).

Two new subspecies of Rufous Grasswren Amytornis whitei

Cape Range Rufous Grasswren

Hartert (1905: 226) commented in relation to a grasswren specimen collected near Marble Bar in the northern Pilbara by J. T. Tunney on 5 May 1901 that it ‘closely resembles specimens called *A. striatus* and collected near Point Cloates [North West Cape Peninsula], Western Australia by Mr Tom Carter, but the bill is very much larger, measuring 15 mm? The dimensions also are generally a little larger but not much. It would be interesting to know if such size differences exist in this species, or whether there are different races.’

The Cape Range grasswrens collected by Carter were, as above, accepted simply as examples of *A. striatus* (Carter 1903, North 1901–04) but the population is presently included in the Pilbara taxon *A. s. whitei* (Johnstone & Storr 2004, Johnstone *et al.* 2013).

When Tunney’s specimen (AMNH 598127) and Carter’s (AMNH 598125 male, AMNH 59126 female) were examined together on 10 April 2013, the size difference was obvious (Fig. 5), and an earlier observer had written ‘oweni?’ (the smaller desert form) on a label



Figure 5. Ventral view of specimens of Rufous Grasswren *A. whitei*, from left: *A. w. oweni* male, AMNH 598115, Bore Well, Western Australia, 5 August 1909; *A. whitei* (Cape Range) male, AMNH 598125, 21 May 1900; *A. whitei* (Cape Range) female, AMNH 598126, 21 May 1900; *A. w. whitei* female, AMNH 598127, Marble Bar, Western Australia, 5 May 1901; note the small and barely streaked Cape Range specimens (B. Bird)

of the female. Measurements did not reveal a marked disparity in wing and tail lengths but confirmed Hartert's remark concerning the striking difference in bill size, 15.8 mm in Tunney's specimen, vs. 12.1 mm in the others (Fig. 6). The above Cape Range specimens are the only two adult skins known from this population and are here described as holotype and paratype of a new subspecies.

Amytornis whitei parvus Black, *subsp. nov.*

Holotype.—Adult male, AMNH 598125, collected by Thomas Carter at 'a rocky kopje [= hill, hillock, mound] on the table-land country' (Carter 1903: 37) of the Cape Range, North West Cape Peninsula, Western Australia, on 21 May 1900. Wing (max. flattened chord) 60 mm, tail (central rectrix from emergence to tip) 82.7 mm, bill length (skull attachment to tip of maxilla) 12.1 mm, bill depth not measured because of damage to the mandible, tail/wing ratio 1.38.

Paratype.—Adult female, AMNH 598126, collected by Thomas Carter with the holotype and a juvenile (AMNH 598124) on the Cape Range tableland, as above on 21 May 1900. Wing 57 mm, tail 82.1 mm, bill length 12.1 mm, bill depth not measured because of damage to the mandible, tail/wing ratio 1.44.

Description.—The holotype and paratype are similar in tone to most *A. w. whitei* and *A. w. oweni*, being rufous above, moderately streaked on the forehead, crown, back and rump, striations formed as brown-edged, whitish central feather shaft-streaks. In contrast, streaking below is almost lacking and restricted to the lower throat and upper breast. The

underparts are cinnamon, paler towards the midline, resembling the pattern of most *A. w. oweni*, less like the even tone below of *A. w. whitei*. The holotype and paratype are the central two specimens in Figs. 5–6.

Diagnosis.—The subspecies is small, wing and tail lengths being in the lower range and bill lengths below the range of those for *A. w. whitei*. Its measurements resemble those of *A. w. oweni* except that wing lengths are at the upper extreme. Tail/wing ratios for male and female of 1.38 and 1.44, respectively resemble mean figures for *A. w. whitei* (1.39 and 1.42) rather than *A. w. oweni* (1.51 for each sex). It differs from both subspecies in habitat, especially from that of *A. w. oweni*.

Etymology.—The epithet *parvus* is from *parvus* -a -um, the Latin adjective for small.

Taxonomic rank.—The subspecies appears to be a diminutive variant of the nominate subspecies, its tail and wing lengths slightly reduced, but a much smaller bill being diagnostic. Note that two other passerine species are represented on the North West Cape Peninsula by diminutive isolates, Grey Shrikethrush *Colluricincla harmonica kolichisi* Ford, 1987, and Western Bowerbird *Chlamydera guttata carteri* Mathews, 1920 (Schodde & Mason 1999, Johnstone *et al.* 2013).

Type locality, distribution and habitat.—Carter observed grasswrens only twice, and ‘at the same locality – viz., a rocky kopje’ (Carter 1903: 37) ‘on the tableland lying behind the ranges [inland from] the Yardie [Creek]’ (Carter 1902: 84), i.e. towards the southern extremity of the range. He described the Cape Range plateau as ‘broken table-land, mostly very rugged, with much spinifex, [where] in one place a few cabbage-tree palms occur, which is somewhat remarkable’ (Carter 1903: 31). Those relict palms *Livistona alfredii* occur at just one locality on the Cape Range (c.22°23’S, 113°54’E), 280 km or more from the nearest populations in the Pilbara (Humphreys *et al.* 1990), and rocky outcrops, perhaps Carter’s ‘kopjes’, are prominent nearby (SRM pers. obs.). We infer that grasswrens are restricted to the limestone plateau of Cape Range and perhaps only to its undissected southern portion. They are isolated from the nominate subspecies by 160 km of lowlands without suitable habitat (R. E. Johnstone pers. comm.). Carter (1903:37) described the type locality as having ‘low scrub and patches of spinifex round [sic] with bare patches and emergents, such as ‘a [native] fig tree’ (*Ficus* sp.). In contrast, G. Lodge (pers. comm. *per* R. E. Johnstone) observed a pair in spinifex on sand hills at the top of the range in the 1980s. The Cape Range is broadly



Figure 6. Bill profiles of the same specimens as in Fig. 5, from above in reverse order; *A. w. whitei* female AMNH 598127; *A. whitei* (Cape Range) female AMNH 598126; *A. whitei* (Cape Range) male AMNH 598125; *A. w. oweni* male AMNH 598115; note the small size and diminutive bills of the Cape Range specimens (B. Bird)

vegetated with *Acacia* and other shrubland with isolated eucalypts over hummocks of spinifex (*Triodia*) (Keighery & Gibson 1993). Sand hills are present on the southern plateau and extend onto adjacent dissected plateau (SRM pers. obs.). This evidence distinguishes its habitat on the limestone plateau from that of *A. w. whitei*, spinifex with or without shrubs on ironstone ranges, and of *A. w. oweni*, spinifex with or without low shrubs and eucalypts among desert dunes and interdunes (Higgins *et al.* 2001, Johnstone & Storr 2004, Johnstone *et al.* 2013).

Conservation.—Despite living at Point Cloates near the southern end of the Cape Range for 13 years, Carter (1903: 37) saw the new subspecies at just one locality and we can report just one further corroborated sighting among nine reports (Johnstone *et al.* 2013; R. E. Johnstone pers. comm., Atlas of Living Australia [<http://www.ala.org.au>], A. Silcocks [BirdLife Australia] pers. comm.). When details have been accessed, most sightings were not from the range itself and misidentification of Rufous Fieldwren *Calamanthus campestris* is likely. A recent unsuccessful transect by S. & N. McGregor on the southern plateau of the Cape Range covered over 20 km of *Triodia* hummock grasslands on both rocky substrate and red dunes. Some areas had been adversely affected by overgrazing, fires and invasion by exotic grasses, but the potential total area is vast, with limited access, and good patches of potential habitat remain on the Cape Range (SRM pers. obs.).

With few observations since Carter's, the subspecies' conservation status is Data Deficient, but it is implausible to assume that it is secure. Depending on whether its distribution includes all or only the southern portion of the Cape Range plateau, its extent of occurrence is between 160 km² and 1,600 km². We infer that it is probably Endangered (IUCN 2012).

Yellabinna Rufous Grasswren

Although North (1901–04: 251) described the distribution of the Black-cheeked [=Striated] Grasswren *Amytis striata* as extending 'from east to west right across the central portion of the Australian continent', he cited no specimen or observational record linking the Great Sandy Desert, Western Australia or central Australia with the Victorian Murray Mallee.

The presence of this grasswren complex on the Eyre Peninsula was first documented by Frank Parsons, who obtained a female (SAMA B23396) near 'Kelly', eight miles (c.13 km) south of Kimba on 29 April 1926. Sutton (1926) described its rufous plumage as much lighter than Murray Mallee birds, but Condon (1951: 53) 'was unable to separate [it] from a fairly large sample from the mallee areas of eastern SA and north-western Victoria'.

The Striated Grasswren (group) was first recorded from the southern Yellabinna, western Eyre Peninsula by a party that included ABB & LPP on 21 August 1983. A single specimen was obtained and is described here as the holotype of a new subspecies.

Amytornis whitei aenigma Black, subsp. nov.

Holotype.—Adult male, SAMA B37658, collected by L. P. Pedler in the southern Yellabinna, 50 km [travelled] north of Ceduna, Eyre Peninsula, South Australia (c.31°41'S, 133°44'E) on 21 August 1983. Wing (max. flattened chord) 63 mm, tail (central rectrix from emergence to tip) 92.7 mm, bill length (skull attachment to tip of maxilla) 12.2 mm, bill depth (at level of frontal feathering) 4.3 mm.

Paratype.—Adult male ANWC 52262, collected by L. P. Pedler in the southern Yellabinna, 96.6 km [travelled] north of Ceduna, Eyre Peninsula, South Australia (c.31°29'S, 133°58'E) on 12 August 2007. Wing 61 mm, tail 90.5 mm, bill length 13.1 mm, bill depth 4.3 mm.

Description of holotype.—Resembles specimens of *A. striatus*, from which it differs in the following plumage details: upperparts paler but brighter and more orange-rufous (cinnamon-rufous rather than russet) with less defined brownish (not black) edges to white streaking of dorsal feathers.

Description of paratype.—More closely resembles specimens of *A. striatus*, from which it differs in its upperparts being very subtly more orange-rufous rather than russet-toned.

Plumage variation.—The variation in depth of tone and strength of striation is shown in Figs. 2–3. The holotype and paratype are specimens four and three from the left, respectively.

Diagnosis.—Differs from *A. w. whitei* by its smaller bill and less evenly toned underparts, and in habitat. It is larger than *A. w. oweni* with longer wings but its bill is relatively slender. It is distinguished from *A. striatus* and *A. rowleyi* by mtDNA sequencing.

Etymology.—The epithet *aenigma* is a Latin feminine noun for puzzle or riddle.

Taxonomic rank.—The population lies disjunctly between those of the eastern Eyre Peninsula and the Great Victoria Desert but has been little studied, being represented by just a single specimen until recently. The resulting gap in knowledge has hindered resolution of the systematics of the Striated Grasswren complex, now recognised as comprising three species. Ford & Parker (1974) followed Condon (1951) by including Eyre Peninsula representatives within the south-eastern subspecies *A. s. striatus*, and not with all other western forms, which they recognised as *A. s. whitei*. Alternatively, Schodde (1982) and Schodde & Mason (1999) found Eyre Peninsula and Yellabinna populations transitional in a cline between south-eastern and inland desert forms, all included in *A. s. striatus*. Hence, after ‘Striated Grasswrens’ were detected in the Yellabinna, a component of the Great Victoria Desert, in 1983 they were assumed simply to be of the desert form, now *A. w. oweni* (Carpenter *et al.* 2003). Christidis *et al.* (2013) speculated that the Eyre Peninsula population might be a subspecies of *A. oweni*. The evidence indicates otherwise, yet even now the inclusion of eastern Eyre Peninsula representatives within this subspecies is provisional.

Distribution and habitat.—The subspecies, as described, is known only from the mallee-vegetated dune fields of the southern Yellabinna, western Eyre Peninsula, South Australia. Delimiting records are along a transect between *c.*31°05’S, 133°58’E and *c.*31°41’S, 133°44’E, and in five localities west of that to *c.*31°37’S, 133°13’E (LPP pers. obs., B. Backhouse pers. comm.). Grasswrens have been recorded only from this, the least arid (mean annual rainfall 250–300 mm) and most floristically diverse part of the 44,000 km² Yellabinna region (Copley & Kemper 1992). Its habitat of southern Yellabinna sandplain open scrub of mallee species, including *Eucalyptus yumbarrana* over mid and understorey shrubs and tussock grass *Triodia scariosa* (Copley & Kemper 1992; G. Carpenter and ABB pers. obs.) resembles that of other members of the species complex (Higgins *et al.* 2001). Other records of grasswrens, including specimens, which resemble and are predicted to be included in this subspecies are from the mallee of the eastern Eyre Peninsula, 250–350 km to the south-east, in a similar landform and rainfall regime.

Conservation.—Our present understanding is that this subspecies is restricted to two subpopulations *c.*250 km apart. The conservation status of each is examined separately.

The Yellabinna subpopulation is known from nine sites within less than 2,000 km². Its distribution is patchy and, while it is plausible that more populations will be found in the southern Yellabinna, we do not anticipate a tenfold increase. Recent loss of habitat, e.g. at the holotype locality, and failure to confirm its presence at known sites indicate decline and warrant a status of Near Threatened or Vulnerable under IUCN criteria.

Ford & Parker (1974) inferred from limited information that the eastern Eyre Peninsula subpopulation was ‘probably not uncommon’, but records are known from only eight

general localities within a broadly triangular region of *c.*100 km by 50 km. Clearance of the mallee for agriculture has eliminated much potential habitat and, since 1980, there have been reports from just ten sites at six general localities (K. Jones pers. comm.) within *c.*650 km² of its former distribution. One site no longer harbours grasswrens (LPP pers. obs.) following a fire that has eliminated all spinifex *Triodia*. Such a limited extent of occurrence, together with continuing losses warrants this subpopulation being categorised as Endangered (IUCN 2012).

We suggest that, if each subpopulation is of the same taxon, the subspecies is Vulnerable.

Conspectus of subspecies in *Amytornis whitei*

A. w. whitei Mathews, 1910.—The nominate subspecies of the Pilbara, Western Australia, is a large rufous form with an exceptionally large bill, but relatively short tail compared to other larger representatives of the Striated Grasswren complex (Black *et al.* in press). Its distribution across the ironstone Chichester, Hamersley, Ophthalmia and Parry Ranges is bisected by the Fortescue River, with an outlying population south of the Ashburton River in the Barlee Range. It is widely but patchily distributed and generally uncommon (Johnstone & Storr 2004, Johnstone *et al.* 2013).

A. w. oweni Mathews, 1911.—This small rufous form is sparsely distributed through the Tanami, Great Sandy, Little Sandy, Gibson and Great Victoria Deserts, and in sandy landforms among the Central Australian ranges, but extinct in parts of its eastern range beyond Uluru ('Ayers' Rock'). Outlying populations are present west of Wiluna, in the south-west around Queen Victoria Spring (Johnstone & Storr 2004) and in the south-eastern Great Victoria Desert (ABB pers. data). While this and the nominate subspecies are distinct in morphometrics and ecology, their potential zone of interaction has not been studied in detail (Schodde & Mason 1999; R. E. Johnstone pers. comm.).

A. w. parvus Black, 2020.—The Cape Range isolate, although among the earliest to be reported, is little known. Similar to the nominate subspecies but smaller, its tail and wing lengths slightly reduced and the tail/wing ratio similar, but with a much smaller bill. It occurs on a substrate of limestone rather than ironstone. Further investigation is required.

A. w. aenigma Black, 2020.—Eyre Peninsula representatives occur in two separate subpopulations and are larger birds that resemble *A. striatus*. In the west, they have been detected in only a limited part of the southern Yellabinna, *c.*400 km south-east of the closest record of *A. w. oweni* in the Great Victoria Desert. Eastern records are from mallee areas *c.*250–350 km further south-east. A survey of this subspecies is planned.

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First records of Piping Plover *Charadrius melodus* for Venezuela, with a revision of its non-breeding distribution

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SUMMARY.—The non-breeding distribution of Piping Plover *Charadrius melodus* outside the USA has only recently been elucidated, with new records in Central American and Caribbean countries during the last decade. A specimen from Ecuador was the only definite record in South America prior to 2018. We present two records of Piping Plover in Venezuela; the first at the Paraguaná Peninsula, Falcón state, on 25 February 2018, and the second in the northern part of Ciénaga de Los Olivitos Wildlife Refuge and Fishing Reserve, Zulia state, on 5 March 2020.

Piping Plover *Charadrius melodus* is a small shorebird of international conservation concern. Its population has declined significantly since the 1950s, but concerted conservation action slowed the trend and has led to overall increases since 1991 (BirdLife International 2020). Global numbers are now calculated at more than 5,700 breeding birds (Elliott-Smith *et al.* 2015). Nevertheless, *C. melodus* has been lost as a breeding bird in several US states (Elliott-Smith & Haig 2020) and is still one of the most threatened shorebirds in the USA and Canada, being federally listed in both countries (Elliott-Smith *et al.* 2015) and considered globally Near Threatened (BirdLife International 2020). Its non-breeding range outside the USA has only recently been elucidated, with new records from several countries.

The species breeds in North America and winters on the Atlantic coast of the south-eastern USA, the Gulf of Mexico coast south to the Yucatán Peninsula, in the Bahamas, Turks & Caicos, and Cuba (Wiersma *et al.* 2018, Elliott-Smith & Haig 2020). Although it overwinters in small numbers in Puerto Rico (Lewis *et al.* 2006), it is scarce on Hispaniola (Latta *et al.* 2006), and only a vagrant to Jamaica (Haynes-Sutton *et al.* 2009) and the Virgin Islands (seven records on St. Croix; Yntema *et al.* 2017; and at least three on Anegada; Raffaele 1989, McGowan *et al.* 2007, eBird 2018). There are no records from the Cayman Islands (Bradley & Rey-Millet 2013, Kirwan *et al.* 2019). In the Lesser Antilles, it is a vagrant on Anguilla (Holliday *et al.* 2015), St. Martin (eBird 2018), St. Kitts (Steadman *et al.* 1997), Antigua (Elliott-Smith *et al.* 2009), Guadeloupe (Levesque & Jaffard 2002, Levesque & Saint-Auret 2007), Martinique (Levesque *et al.* 2005) and Barbados (Buckley *et al.* 2009). Furthermore, there are two records from the Atlantic coast of Central America: a bird photographed in Honduras in October 2012 (Gallardo 2014), and a flock of six in Nicaragua in February 2000 (Martínez-Sánchez 2007). In the southern Caribbean there are at least two documented records on Bonaire, 96 km off the Venezuelan coast (Prins *et al.* 2009, eBird 2018). On the Pacific coast, it is rare and irregular in Mexico, from Sonora to Nayarit (Howell & Webb 1996), and there is one record from Costa Rica in November 2009 (Zook 2010). A specimen from south-west Ecuador, collected in October 1955 and now held at the Natural History Museum, Tring (NHMUK 1956.5.6), is the only confirmed record in mainland South America (Marchant 1956). Although there is a published record from far northern Brazil (Azevedo *et al.* 2003), this has not been repeated elsewhere (see Elliott-Smith & Haig 2020).

and the reported specimens are actually of Semipalmated Plovers *Charadrius semipalmatus* (Piacentini *et al.* 2015, Pacheco & Agne 2019).

We present two more records for South America, more than 50 years since the first record in Ecuador. On 25 February 2018, several of us were undertaking shorebird counts on the Paraguaná Peninsula, Falcón state, north-west Venezuela, as part of a Western Hemisphere Shorebird Reserve Network study. Field work commenced shortly after dawn at the sandy spit of Playa El Pico on the west side of the peninsula (11°51'20"N, 70°18'00"W; Fig. 1). A mixed flock of small shorebirds was foraging on the south side of the spit. It comprised 43 Sanderling *Calidris alba* and three Semipalmated Sandpipers *C. pusilla*. At 07.30 h, JM, who had moved further west along the spit to photograph the flock, flushed what he initially thought to be a Snowy Plover *Charadrius nivosus*, a low-density species on the Caribbean coast of Venezuela. The flock flew closer to the other observers while the bird in question landed amongst seaweed 1–2 m higher up the beach and began foraging c.30 m away. The behaviour did not match *C. nivosus* and, as its head shape, more vertical stance and short runs were more reminiscent of *C. melodus*, CJS suggested that the observers move closer to the bird to ascertain its identity. Almost immediately the bright orange legs were seen, eliminating *C. nivosus* and reinforcing identification as *C. melodus*. Over the next 30 minutes, the bird was observed from 10 m by four observers and photographs (Figs. 2–3) were obtained by JM & CJS. This individual was not ringed.

The bird was distinctly larger than the superficially similar *C. nivosus* (the only other pale ash-grey *Charadrius* in the region), with an erect rather than horizontal stance, assumed after short runs of just a few paces. The crown was rounded, rather than flattened as in *C. nivosus*, and the forehead steep. Legs were conspicuously bright orange, while the bill was black with a tiny orange base (only visible at close range and in photographs), characteristic of non-breeders. The forehead was white, the ear-coverts pale grey, separated from the

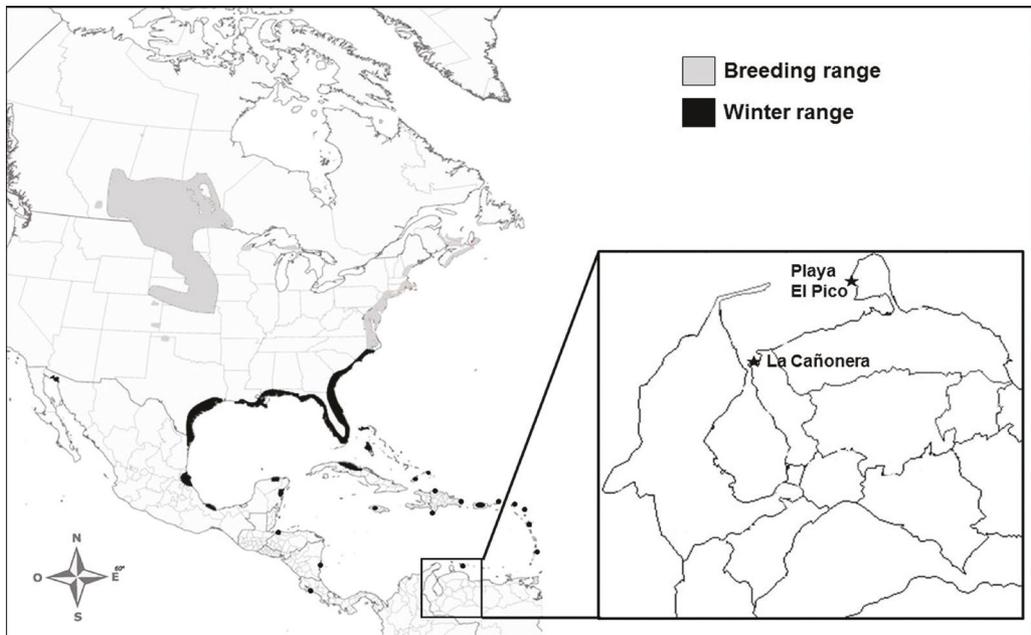


Figure 1. Distribution of Piping Plover *Charadrius melodus*: grey shading denotes breeding range, black areas indicate winter range and recent records (for sources, see bibliography), and stars indicate record localities for Venezuela described here.



Figures 2–3. Non-breeding Piping Plover *Charadrius melodus*, Playa El Pico, western Paraguaná Peninsula, Falcón, Venezuela, February 2018 (Jhonathan Miranda)

crown by a broad white supercilium, creating a plain face, within which the large black ‘button eye’ was prominent, producing an overall ‘innocent expression’. The sooty lateral breast-band was the darkest area of feathering, with no black in the rest of the plumage. This is the first record for Venezuela and the second for continental South America.

Two years later, on 5 March 2020, another single *C. melodus* was recorded in La Cañonera sector within the northern part of Ciénaga de Los Olivitos Wildlife Refuge and Fishing Reserve, Zulia state, also in north-west Venezuela (10°57'36"N, 71°22'41"W). In the area there were several plovers, including 19 Wilson's *Charadrius wilsonia*, 32 *C. semipalmatus* and two Grey *Pluvialis squatarola*. The Piping Plover was observed by LT at 10.30 h, together with a Wilson's Plover on a dry mudflat. When LT moved closer in order to observe the bird better, it moved away and closer to a Semipalmated Plover *C. semipalmatus*. In this case, the size, coloration and behaviour of the *C. melodus* were unmistakably different to the other plovers present in the area. LT also obtained photographs and observed that the plover was not ringed (Figs. 4–5).

North-west Venezuela, especially its coastal areas, is poorly studied from an ornithological perspective, nor is it a preferred destination for birders. The Paraguaná



Figures 4–5. Non-breeding Piping Plover *Charadrius melodus*, Ciénaga de los Olivitos Wildlife Refuge and Fishing Reserve, Zulia, Venezuela, March 2020 (Lermith Torres)

Peninsula, in particular, is an ideal ‘migrant trap’ due to its geographic location. A handful of visits has generated new bird records for Falcón state or Venezuela as a whole, both shorebirds (e.g. Buff-breasted Sandpiper *Calidris subruficollis*; Azpiroz & Rodríguez-Ferraro 2006) and landbirds (White-eyed Vireo *Vireo griseus*, Northern Parula *Setophaga americana* and Magnolia Warbler *S. magnolia*; Rodríguez *et al.* 2017). In terms of conservation, Playa El Pico, in particular, may be an important site for shorebird conservation as breeding Snowy Plover and American Oystercatcher *Haematopus palliatus* have been recorded there (Azpiroz & Rodríguez-Ferraro 2006). This beach, however, lacks legal protection and is frequently visited by fishermen and tourists, who drive vehicles along the sand disturbing breeding and resting birds. Feral dogs are also observed there, and may pose an additional threat to shorebirds. In the case of Ciénaga de los Olivitos Wildlife Refuge and Fishing Reserve and the nearby Salina Solar Los Olivitos, these areas are very important for shorebird conservation, not only because of the large concentration of wintering birds, but also because uncommon species in Venezuela have been recorded there in recent years. The first record of Red-necked Phalarope *Phalaropus lobatus* for the country was reported in February 2016, and in the same year the first record of Wilson’s Phalarope *P. tricolor* was reported in Zulia state (Torres *et al.* 2016), with large numbers of the latter recorded since, most recently a flock of 512 individuals in January 2020. Additionally, since 2008, there have been frequent records of Marbled Godwits *Limosa fedoa* (Giner *et al.* 2017) and Buff-breasted Sandpipers wintering there, as well as breeding records for Snowy Plover (L. Torres & F. Espinoza *in litt.* 2013). These two areas are protected and receive few visitors, thus potential threats to shorebirds are minimal there.

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Breeding biology and biometrics of Silver-beaked Tanager *Ramphocelus carbo connectens* in south-west Brazilian Amazonia

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SUMMARY.—We present new data on the breeding biology and biometrics of Silver-beaked Tanager *Ramphocelus carbo* in south-west Brazilian Amazonia. *R. carbo* is widely distributed in South America, but its reproductive ecology is little studied. We made observations on the species in a *terra firme* forest fragment in the capital city of the state of Acre, between 1999 and 2020. We monitored 12 nests between 2012 and 2020, built at a mean height of 1.3 m above ground. Clutch size was two eggs, incubated for 13 days. We monitored the development of 11 nestlings: minimum hatch weight was 1 g and young fledged with a mean mass of *c.*18.9 g. The constant growth rate (*K*) of nestlings was 0.48 with a growth asymptote of 22.1 g. Daily survival rate was 91% and 98% during the incubation and nestling periods, respectively. Mayfield success in the incubation and nestling periods was 28% and 74%, respectively. Apparent nesting success in the incubation and nestling periods was 62% and 82%, respectively. We recorded a minimum longevity of 11 years, six months and 28 days. The subspecies *R. c. connectens* breeds mainly in the rainy season (October–January) overlapping with the moult period.

Studies of the reproductive biology of birds reveal important data that can aid understanding of ecological relationships and contribute to conservation of species (Martin 2004). The start of a breeding season is influenced, for example, by the availability of food (Sick 1997). Reproduction in the appropriate period combined with choice of nest site and time invested in parental care are crucial for the survival of nestlings (Saether 1985, Mezquida & Marone 2001). Aspects such as incubation and nestling period are of practical and theoretical importance, but not all studies of avian breeding biology have given these issues the attention they deserve (Skutch 1945). Overall, very little is known concerning the reproduction of Neotropical birds (del Hoyo *et al.* 2020) and in Amazonia basic details on the breeding cycle of many species, even common birds such as Silver-beaked Tanager (Hilty 2020), are still unknown.

The genus *Ramphocelus* comprises ten species (del Hoyo *et al.* 2020), three of which occur in Brazil (Piacentini *et al.* 2015), two of them in Brazilian Amazonia (Sick 1997). Of these, the commonest and most widely distributed is Silver-beaked Tanager *R. carbo* (Hilty 2020). Eight subspecies of *R. carbo* are recognised (Hilty 2020) of which that in south-west Brazilian Amazonia (Acre state) is *R. c. connectens* (Pinto & Camargo 1954, Novaes 1957, Guilherme 2016). Despite its widespread distribution, including throughout Amazonia, knowledge of the reproduction of Silver-beaked Tanager is still limited (Carvalho 1957, Skutch 1968, Valente 2000, Greeney *et al.* 2018, Hilty 2020). Here we present new information on the breeding biology and biometrics of *R. c. connectens* from a lowland *terra firme* forest in south-west Brazilian Amazonia.

Methods

Study area.—We conducted this study at the Zoobotanical Park of the Federal University of Acre (UFAC), in Rio Branco, capital of the Brazilian state of Acre. The Zoobotanical Park (09°57'08.9"S, 67°52'22.5"W) is a forest fragment with an area of c.100 ha surrounded by an urban matrix. For detailed descriptions of its vegetation, climate and avifauna see Meneses-Filho *et al.* (1995), Duarte (2006) and Guilherme (2001), respectively.

Nest searches.—Nests were found during non-systematic observations made between 2012 and January 2020. We monitored all nests found, irrespective of stage, until they became inactive. We measured eggs and nestlings using a millimetre ruler and analogue (2012–14) or digital callipers accurate to 0.01 mm (2015–20). We weighed eggs and nestlings using a Pesola® scale with a capacity of 100 g and accurate to the nearest 1 g (2012–14) or a digital scale accurate to 0.05 g (2015–20). We collected nests after they became inactive and deposited them in the collection of the UFAC ornithology laboratory. Nests were described according to the standardised scheme proposed by Simon & Pacheco (2005).

Biometrics.—We trapped and ringed Silver-beaked Tanagers in the years 1999–2002 (1,624.8 net / hours), 2004–06 (1,367.3 net / hours) and 2009–19 (57,948.2 net / hours). We used 12.0 × 2.5 m mist-nets with 36-mm mesh and banded individuals with numbered metal rings supplied by CEMAVE (Centro Nacional de Pesquisa e Conservação de Aves Silvestres), under the scope of project 1099, coordinated by EG (senior bird bander, reg. no. 324654). Morphometric data (wing, tarsus, bill, head, tail, total length and cloacal temperature) were collected from 2002 following the protocol outlined by Proctor & Lynch (1993). We used a Pesola® scale with a capacity of 100 g (1 g precision) to weigh birds and nestlings prior to 2014, and a digital scale (0.05 g precision) during 2015–20. We used a millimetre ruler to measure wing, tail and total length, and analogue callipers (0.05 mm precision) until 2014 and digital callipers (0.01 mm precision) in 2015–20 to measure bill and tarsus. For each biometric, data were taken from each individual only the first time it was trapped, for males and females separately. During ringing, we distinguished adults and juveniles based on the presence of juvenile plumage (basic plumage from first and second juvenile cycles, see Sibley 2010, Johnson *et al.* 2011). We examined each trapped individual to determine moult in the remiges and rectrices (Sibley 2010) and presence or absence of a brood patch (Redfern 2010). We measured cloacal temperature with a digital thermometer (32.0–42.9°C, accurate to 0.1°C) and calculated minimum longevity from the first day an individual was banded to its final recapture (Scholer *et al.* 2018).

Incubation and nestling development.—The incubation period was calculated from the date the last egg was laid until the second chick hatched. Post-hatching, we measured the mass of nestlings every two days to minimise our impact on nests. We banded young with a numbered metal ring while still in the nest. We considered the nestling development period based on the hatching of the first nestling and the abandonment of the nest by the second chick. The day of hatching was treated as day 0 (Oniki & Willis 2001). For nests found with nestlings, we estimated age based on the mass of the nestlings, comparing them with data for young monitored from hatching. We applied the equation proposed by Ricklefs (1967) to determine the growth rate of the nestlings: $W(t) = A/(1+e^{-K(t-t_i)})$, where $W(t)$ is the mass of the nestling at age t , A is the asymptote of the growth curve, K is the constant growth rate and t_i is the inflection point of the growth curve. This equation was run in R software, version 3.5.1 (R Core Team 2018). We used the Mayfield (1961) method to calculate reproductive success rates, and determined apparent success as the ratio between the number of successful nests and the total number found (Jehle *et al.* 2004).

Results

Nest characteristics.—We found 12 Silver-beaked Tanager nests, of which 11 were active (Table 1). All nests were constructed in open areas or at the edge of forest on different substrates. Two nests were built in a stump of the palm *Attalea butyracea* (Fig. 1A–B), three in forks of *Theobroma grandiflorum* (Fig. 1D) and four nests in ornamental plants such as *Dracaena fragrans*, *D. terminalis* and *Polyscias guilfoylei* (Table 1). We did not identify the support plant at one nest. On average, nests were placed 1.30 m above ground (range 0.87–2.10 m). We found one nest under construction, six with eggs (three of which had been abandoned), four with nestlings in the first day of life, and one was empty. Most nests were built of dry leaves (Fig. 1D) lined internally with narrow, pliable blades of dry grass arranged concentrically (Fig. 1E). In one nest we found blue plastic threads in its inner lining. All nests conformed to the low cup / base, low cup / lateral or low cup / fork types (Figs. 1A, 1D, 2D). Mean measurements of nests ($n = 9$) were: height of the external wall = 68.66 mm (range 55.66–93.8 mm; SD = 13.7); wall thickness = 16.68 mm (12.12–22.25 mm; SD = 3.21), internal diameter of cup = 63.90 mm (52.93–77.85 mm; SD = 6.9), external diameter of cup = 97.26 mm (85.21–116.41 mm; SD = 10.42), depth of cup = 49.08 mm (40.05–60.35 mm; SD = 6.0) and mass = 12.38 g (8.30–17.37 g; SD = 3.77).

Eggs and incubation.—In six nests found with eggs, clutch size was two. Only nest 6 contained a single egg that had been abandoned (Table 1). Eggs were predominantly white with pale and dark brown blotches, generally concentrated at the larger end (Fig. 1C). Mean egg ($n = 13$) mass was 3 g (range 2.0–3.5 g) and size 21.23 × 16.00 mm (20–22 × 15–17 mm). Only females were seen incubating. Of all the nests monitored with eggs, only at nest 2 did one of the eggs fail to hatch (Table 1). Incubation period was 13 days (nest 5; Table 1).

TABLE 1

Characteristics of Silver-beaked Tanager *Ramphocelus carbo connectens* nests found between 2012 and 2020, in a *terra firme* forest fragment in Acre, Brazil, south-west Amazonia.

Nest	Date of discovery	Supporting plant	Height above ground (m)	Clutch or brood size	Type/insertion	Date of hatching	Date of fledging (n of nestlings)
1	27 Jan 2012	<i>Theobroma grandiflorum</i>	1.0	2 nestlings	Low cup/lateral		
2	14 Nov 2012	<i>Attalea butyracea</i>	2.1	2 eggs	Low cup/base	16 Nov 2012	1–26 Nov 2012
3	21 Nov 2012	<i>Dracaena fragrans</i>	1.75	2 eggs	Low cup/base	27/28 Nov 2012	2–12 Dec 2012
4	16 Jan 2013	<i>Attalea butyracea</i>	2.1	2 eggs	Low cup/base	24/25 Jan 2013	2–4 Feb 2013
5	21 Jan 2013	<i>Dracaena fragrans</i>	1.61	2 eggs	Low cup/base	5/6 Feb 2013	0
6	22 Feb 2013	<i>Coffea arabica</i>	1.2	1 egg/abandoned	Low cup/fork		
7	8 Oct 2013	<i>Polyscias guilfoylei</i>	1.0	2 eggs/abandoned	Low cup/lateral		
8	16 Jan 2014	Not identified	1.0	2 eggs/abandoned	Low cup/base		
9	7 Oct 2015	<i>Dracaena fragrans</i>	1.15	2 nestlings	Low cup/base		
10	26 Nov 2019	<i>Theobroma grandiflorum</i>	1.0	2 nestlings	Low cup/fork	Almost 22 Nov 2019	2–4 Dec 2019
11	6 Feb 2020	<i>Theobroma grandiflorum</i>	0.87	2 nestlings	Low cup/fork		
12	20 Feb 2020	<i>Dracaena terminalis</i>	1.3	Empty	Low cup/base		



Figure 1. Nests of Silver-beaked Tanager *Ramphocelus carbo connectens* found in a *terra firme* forest fragment in south-west Amazonia: (A) *Attalea butyracea* palm stump where nests 2 and 4 (Table 1) were sited (red circle); (B) detail of nest 2 with the female incubating (red arrow); (C) detail of the eggs; (D) lateral and (E) internal view of nest characteristics (A–C and E: Jônatas Lima; D: Edson Guilherme)

Nestlings.—We monitored the development of 11 nestlings in eight nests, three of which are depicted in Fig. 3. Nestlings hatch with dark pink skin, plumes on the back and head, and eyes closed (Fig. 2A–B). After five days, the eyes are slightly open, and the feathers of the remiges and rectrices start to develop (Fig. 2C). Nestlings in nests 2–4 were monitored from hatching (Table 1). Minimum hatch weight was 1 g (range 1.0–4.0 g; SD = 1.5; $n = 4$) and nestling mass reached a mean 20 g ($n = 3$) after 9–10 days, and 21.5 g ($n = 2$) on day 12 (Figs. 2D, 3; nest 10), the heaviest recorded of any nestling (Fig. 3; nest 10). Chicks at nests 2 and 4 fledged on days 10 and 11, respectively (Table 1, Fig. 3; nest 4) while those from nests 3 and 10 fledged on day 12 (Table 1, Fig. 3). Only the chicks at nest 3 were ringed in the nest (ring codes G105802 and G105801). Of the 11 nestlings monitored, the two at nest 5 were predated eight days after hatching (Table 1), when they weighed 12 and 15 g. The longest nestling period was 12 days (Fig. 3, nest 10; Table 1) and chicks fledged at a mean mass of 18.9 g (range 17.0–21.1 g; SD = 1.9; $n = 8$).



Figure 2. Development of Silver-beaked Tanager *Ramphocelus carbo connectens* nestlings in a terra firme forest fragment in south-west Amazonia: (A–B) recently hatched nestlings (nest 10; Table 1); (C) five-day-old nestlings (nest 3; Table 1); (D) 12-day-old nestlings (nest 10). (A, B and D: Edson Guilherme; C: Jônatas Lima)

The constant growth rate (K) of the nestlings was 0.48 (range 0.35–0.57; SE = 0.05) with a growth asymptote of 22.1 g (20.81–23.82 g; SE = 6.2; Fig. 4). Daily survival rate for nests during the incubation period was 91% and for nestlings 98%. Mayfield success during the incubation period was 28%, assuming a duration of 13 days, and 74% in the nestling period, assuming chicks remained in the nest for 12 days. Apparent success was 62% in the incubation period and 82% in the nestling period.

Breeding season.—We trapped and banded adults ($n = 246$) and young individuals ($n = 59$) in all months of the year. However, the vast majority of young were mist-netted between September and March ($n = 40$; Fig. 5). Active nests were found in January, February, October and November (Fig. 5), and we recorded individuals with a brood patch between October and March ($n = 12$; Fig. 5) while the majority of individuals in moult were mist-netted in January–May ($n = 78$; Fig. 5).

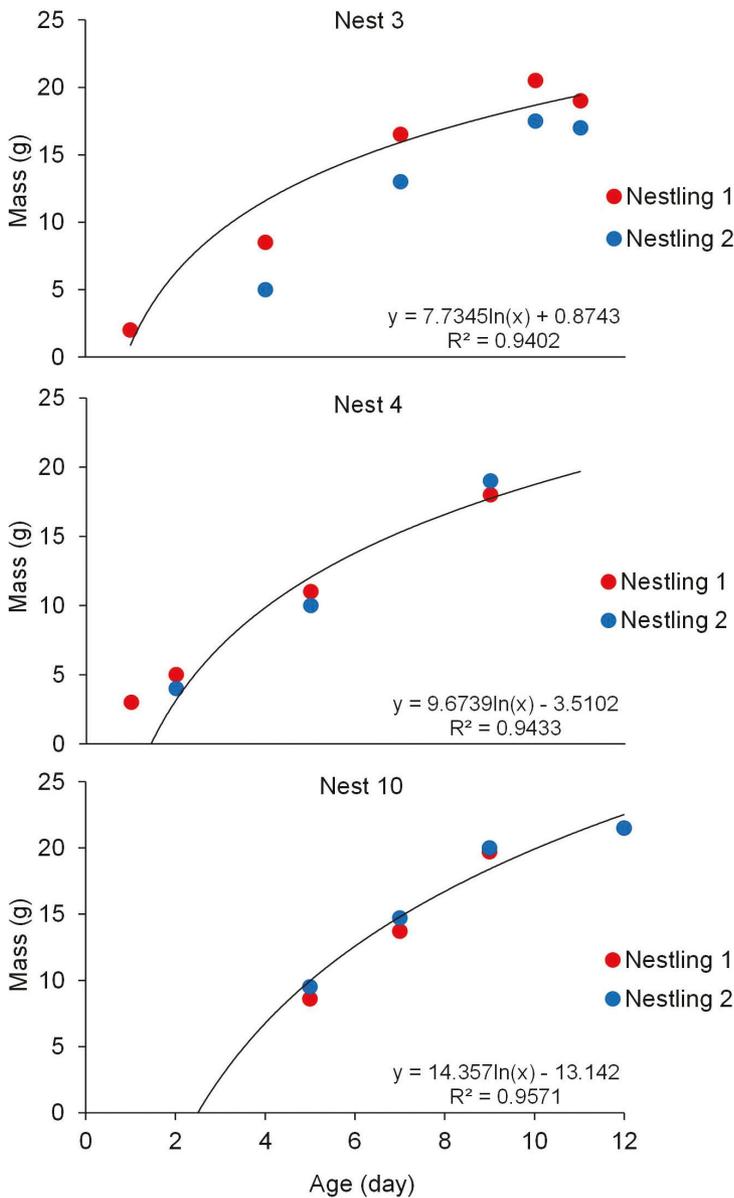


Figure 3. Development and body mass of six nestlings of Silver-beaked Tanager *Ramphocelus carbo connectens*, monitored in a terra firme forest fragment in south-west Amazonia between 2012 and 2019. The logarithmic equation is based on the most developed chick. Other nests found with nestlings (Table 1) are not shown here because they were predated or because we did not obtain continuous development data.

Morphometrics.—Between 2002 and 2019 we trapped and banded 99 females and 147 adult males. Morphometrics for females and males, respectively, were: mass 26.6 and 27.0 g (range 22–38 g, SD = 2.7, $n = 99$; 22–37 g, SD = 2.5, $n = 145$); wing 75.0 and 78.3 mm (65–85 mm, SD = 3.9, $n = 99$; 60–89 mm, SD = 3.8, $n = 146$); tarsus 20.2 and 21.5 mm (14–28 mm, SD = 2.5, $n = 97$; 17–28 mm, SD = 2.8, $n = 141$); bill 15.8 and 16.1 mm (12–20 mm, SD = 2.0, $n = 54$; 12–20 mm, SD = 1.7, $n = 76$); head 35.7 and 35.6 mm (34.9–36.7 mm, SD = 0.7, $n = 5$; 34.4–37.2 mm, SD = 0.8, $n = 14$); tail 75.5 and 77.0 mm (54–85 mm, SD = 5.2, $n = 98$; 58–89 mm, SD = 4.3, $n = 143$); total length 178.1 and 182.1 mm (164–189 mm, SD = 6.0, $n = 88$; 156–200 mm, SD = 7.3, $n = 132$) and cloacal temperature 41.9 and 42.4°C (41.3–42.5°C, SD = 0.6, $n = 3$; 41.7–42.9°C, SD = 0.5, $n = 4$).

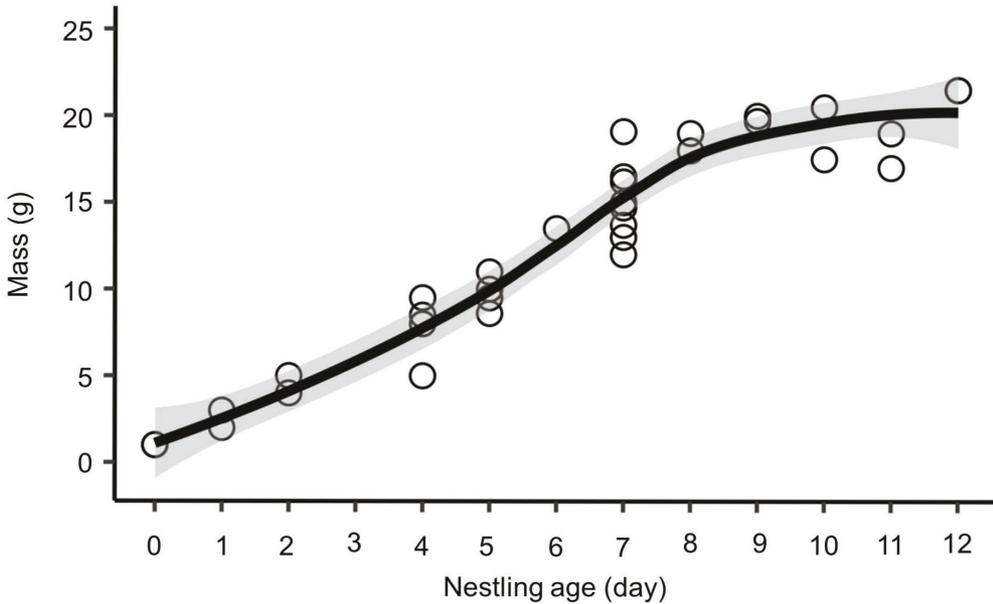


Figure 4. Logistic growth curve for 11 nestlings of Silver-beaked Tanager *Ramphocelus carbo connectens*, monitored in a *terra firme* forest fragment in south-west Amazonia between 2012 and 2020. Each circle represents a different nestling.

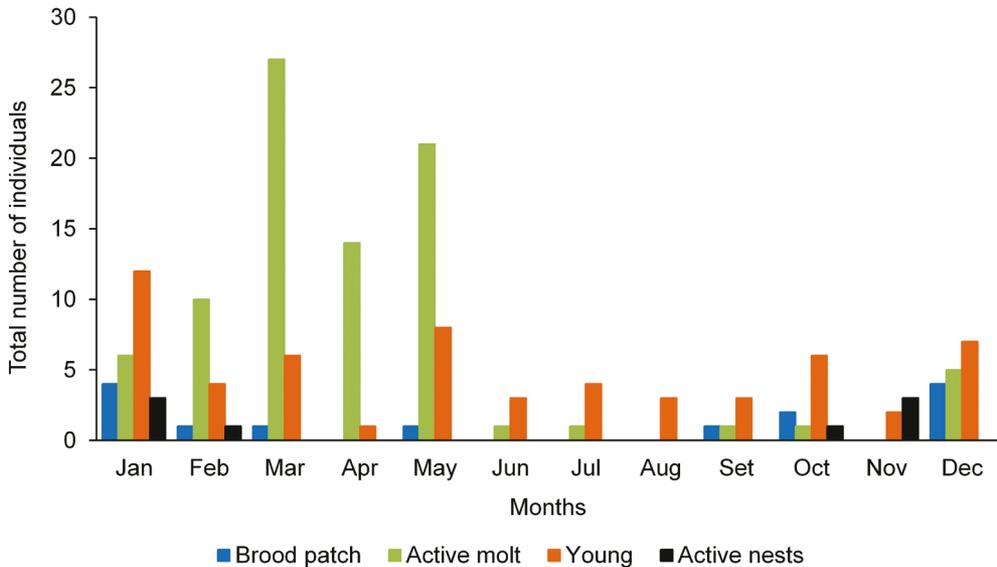


Figure 5. Silver-beaked Tanagers *Ramphocelus carbo connectens* trapped during the study period in a fragment of *terra firme* forest in south-west Amazonia in 1999–2002, 2004–06 and 2009–19, and active nests during 2012 to 2020. The bars show the numbers of ringed juveniles, moulting individuals, the presence of vascularised brood patches and active nests. Re-traps are not shown.

Minimum longevity.—Between 1999 and 2019 we made a total of 423 captures, 309 individuals which we banded and 114 of which involved re-traps. Of the ringed individuals, 53.5% were recaptured more than once ($n = 61$). Longest minimum longevity

was recorded for a male (G39942) banded as an adult by EG on 1 September 1999 and last re-trapped on 28 June 2011 (11 years, six months and 28 days, or 4,226 days after banding). The second longest-lived individual was a female (G91795), banded in 2011 and re-trapped in 2018 (seven years, two months and 25 days, or 2,642 days later). Males G39983 (2004–11) and G39984 (2004–10) had a minimum longevity of six years or 2,499 and 2,243 days, respectively. We re-trapped two females (G39954, G121045) and two males (G57713, G34989), all after four years (1,468–1,768 days); two females (G 39981, G34960) and one male (G91811) after three years (1,129–1,245 days); five males (G34958, G14447, G14452, G91725, G91854) and a female (G39979) after two years (766–1,091 days) and the other 44 individuals at intervals of <2 years (1–711 days).

Discussion

Silver-beaked Tanager is common in open areas of the campus and inside forest at the Zoobotanical Park (Guilherme 2001). It inhabits the edge of forest, near reservoirs and secondary vegetation undergoing regeneration. In Acre, it is very common in gardens and urban areas (Guilherme 2016). In the region, *R. carbo* occurs sympatrically with Masked Crimson Tanager *R. nigrogularis* (Guilherme 2016). The latter is less common and preferentially inhabits floodplain forest, avoiding upland forests and urban areas, thereby minimising competition with Silver-beaked Tanager.

The few data concerning reproduction by Silver-beaked Tanager pertain to subspecies that occur in central and northern Brazil (Carvalho 1957, Lopes *et al.* 2013) and in Venezuela, Suriname and Ecuador (Skutch 1968, Isler & Isler 1987, Greeney *et al.* 2018). The breeding information presented here is the first for *R. c. connectens* (south-east Peru, adjacent north-west Bolivia, and extreme south-west Brazil). In our study area, Silver-beaked Tanager appears to prefer to nest in largely open areas and uses exotic (cultivated) plants or palms in sites with much human activity. Nesting by this species in disturbed areas was also observed elsewhere in Amazonia (Carvalho 1957, Skutch 1968, Lopes *et al.* 2013, Lima *et al.* 2019). The species constructs its nest low above ground (<3 m) as reported in French Guiana (Ingels 1977), Suriname (Isler & Isler 1987), Ecuador (Greeney *et al.* 2018) and Brazil (Almeida *et al.* 2012).

Nest shape (low cup / base, lateral or fork types) was similar to those of *R. c. venezuelensis* and *R. c. carbo* described by Skutch (1968) and Ingels (1978) from Venezuela and French Guiana, respectively, and Collins & Araya (1998) for Trinidad, as ‘a compact open cup’, and those of *R. c. carbo* that Carvalho (1957) followed in Brazilian Amazonia. This nest type is typical of many Thraupidae, such as Brazilian Tanager *R. bresilius* (Castiglioni 1998). Use of man-made material to construct nests is not uncommon in *R. carbo*. In a *cerrado* in south-west Mato Grosso, Almeida *et al.* (2012) reported that several bird species used synthetic wool, fabric and plastic in their nests, including Silver-beaked Tanager. As it is a species highly adapted to anthropogenic environments, the availability of suitable plant material may sometimes be insufficient for nest construction, which leads to the birds using material discarded by humans (Borges & Marini 2010, Marini *et al.* 2012, Suárez-Rodríguez *et al.* 2017, Batisteli *et al.* 2020).

Clutch size and egg characters are similar to Skutch’s (1968) descriptions from Venezuela, Gibson (1987) based on captive birds, and those that Carvalho (1957) and Hellmayr (1910) described in Brazil. We recorded an incubation time equal to that reported by Skutch (1968) in Venezuela, by Isler & Isler (1987) in Suriname, and data for Brazilian Tanager in coastal *restinga* in south-east Brazil (Castiglioni & Gonzaga 1999). Nestling morphology and mass at hatching were similar to the data reported by Carvalho (1957), who found that two nestlings remained in the nest for 11 days. In the same study, he reported that one

of the chicks fledged with a mass of 19.6 g, similar to our findings. Regarding the growth rate of nestlings, ours are only the second calculations for Silver-beaked Tanager. Our rate (0.48) was very similar to that calculated by Oniki & Ricklefs (1981) for *R. carbo* in Manaus (0.50) and higher than those calculated for Multicoloured Tanager *Chlorochrysa nitidissima* in Colombia (Loaiza-Muñoz *et al.* 2017) and White-winged Shrike-Tanager *Lanio versicolor* in Peru (Céron-Cardona *et al.* 2018). Growth rate was similar but marginally higher than that calculated for Hauxwell's Thrush *Turdus hauxwelli* at the same study site (Guilherme & Lima 2019).

Predation of Silver-beaked Tanager nestlings has also been observed in other studies (Carvalho 1957, Pinho & Marini 2014). Pinho & Marini (2014) found that of 27 active nests of Silver-beaked Tanager in the Pantanal, 92.6% were predated, with a success rate of just 7.4%. In contrast, only one of the nests with chicks that we monitored failed as a result of such pressures, indicating that locally the species' nests do not appear to be heavily predated.

Although young birds were trapped year-round, in Acre Silver-beaked Tanager breeds largely during the rainy season, in October–April. This seasonal relationship was demonstrated by active nests and individuals trapped with a brood patch during this period, unlike in central Amazonia, where the percentage of individuals with an incubation patch was higher in the dry season than the wet (Stouffer *et al.* 2013). Other studies of the species' breeding cycle in Brazilian Amazonia corroborate the hypothesis that Silver-beaked Tanager starts nesting in the late dry season (September) or the early rainy season (October) (Carvalho 1957, Valente 2000, Lopes *et al.* 2013, Lima *et al.* 2019). In the Pantanal, nests were found mainly during the rainy season (Pinho & Marini 2014), and the same was true at a *cerrado* enclave near Santarém, in the Brazilian state of Pará (Sanaiotti & Cintra 2001). In contrast, Skutch (1968) monitored active nests of *R. carbo* in Venezuela during April–May, which are months of low rainfall, while Hellebrekers (1942) reported eggs in Suriname from every month except November, but mostly January to July. Oniki & Willis (1999) recorded brood patches also in the dry season in a Brazilian *cerrado*. Molt was similar to data collated by Valente (2000) from specimens collected across the Brazilian Amazon and deposited at the Goeldi museum (Belém). According to the latter study, the majority of moulting birds were collected during the wettest months, December–June, thus overlapping with breeding activity.

Mean body mass for the species is consistent with other studies (King & Laarhoven 2003, Silva *et al.* 1990, Guilherme *et al.* 2018), and variation in this character was similar to data for the species from the Brazilian Cerrado (Marini *et al.* 1997). Based on just one individual of the subspecies *R. c. centralis*, also from a Brazilian *cerrado*, Piratelli *et al.* (2001) presented bill and tarsus data similar to ours for both sexes, but wings and tail were longer. Wing, tail and bill lengths of both sexes measured by Pinto & Camargo (1954) in the environs of Rio Branco and Plácido de Castro, both in Acre, and Hellmayr (1910) in Rondônia, are similar to those observed by us. Males measured in Rondônia by Guilherme *et al.* (2018) had a mean total length less than that of males at our study site, but values in both studies are within the overall range for the species. Head length data had not previously been reported for Silver-beaked Tanager. The cloacal temperatures that we recorded were similar to those reported by Oniki & Willis (1999) for Silver-beaked Tanager in a Brazilian *cerrado*.

Few previous longevity data for wild Silver-beaked Tanagers were available, but individuals have lived as long as 17 years in captivity in Illinois, USA (Pingry 2000). Snow & Lill (1974) re-trapped two females with a minimum longevity of eight and 9.5 years on Trinidad. The variation in our minimum longevity records is consistent with the those available for other thraupids, e.g. Grey-headed Tanager *Eucometis penicillata* (eight years old) and Palm Tanager *Thraupis palmarum* (nine years old) in Venezuela (Lentino *et al.* 2003),

and Blue-capped Tanager *T. cyanocephala* (six years old) in south-east Peru (Scholer *et al.* 2018). With a diet of invertebrates and fruit (Wilman *et al.* 2014), Silver-beaked Tanager belongs to the same guild of bird species that is more long-lived in Madagascar rainforests (Woog *et al.* 2018). That Silver-beaked Tanager forages in monospecific flocks may explain its relative longevity, due to decreased mortality from predation, as observed by Julien & Clobert (2000) for other species of Neotropical birds.

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Species rank for *Rheinardia ocellata nigrescens* (Phasianidae)

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SUMMARY.—Crested Argus *Rheinardia ocellata* has two highly disjunct populations in Vietnam and Lao PDR (nominate *ocellata*) and Malaysia (subspecies *nigrescens*). When evidence from the small sample of museum specimens is supplemented by novel photographic and acoustic evidence, Malaysian *nigrescens* proves to be distinct on a suite of characters: yellower bill with blackish nares, buffier supercilium, throat and breast, different-coloured and -structured crest, different-patterned upperparts and tail, a purer, more fluent, longer, lower Short Call (used by advertising males), markedly divergent from the explosive, nasal, double-noted equivalent in nominate *ocellata*, and a higher number of loud notes in the Long Call including an unexplained bimodal vs. unimodal pattern (hence either average 8.6 or 14.5 vs. 7.1 loud notes per call). In combination these characters indicate a level of differentiation compatible with species rank for *nigrescens*, and this is strongly reflected in Tobias criteria scoring. The conservation of the two forms requires urgent reconsideration.

Crested Argus *Rheinardia ocellata* is a spectacular but reclusive species of pheasant with two subspecies in widely separated, highly restricted ranges in Vietnam and Lao PDR (nominate *ocellata*) and peninsular Malaysia (subspecies *nigrescens*), and largely owing to the trapping of birds in Vietnam, compounded by forest clearance, it is listed as Endangered on the IUCN Red List (BirdLife International 2020). Differences between the two taxa have never been considered particularly strong, but mentioned as a topic that needs examining (Liang *et al.* 2018), and the only close comparison between them was made at the time of the description of *nigrescens* nearly 120 years ago. However, as the conservation status of the species appears to be increasingly precarious (classified as Near Threatened in the years 2005–16), its taxonomic status has also become a matter worthy of further investigation.

The name *Argus ocellatus* was published by Elliot (1871) in reference to several very large pheasant feathers of unknown origin held in the Paris museum. These had been studied by Verreaux in the period 1835–59, who gave them the same name *Argus ocellatus* but only in manuscript (Delacour 1951). It was not until two skins were obtained during 1879–81, one from Commandant Rheinart and the other from the Governor General of Cochin China, that their origin was determined as present-day Vietnam and the genus name *Rheinardia* was published by Maingonnat (1882).

A similar taxon from the Malay Peninsula collected by Waterstradt (1902), although probably not quite on the mountain he assumed (Barlow 1969), was described by Rothschild (1902) as *Rheinardius ocellatus nigrescens*. All subsequent authorities (e.g. Peters 1934, Delacour 1951, McGowan 1994, Johnsgard 1999, Hennache & Ottaviani 2005) down to the four current world lists (del Hoyo & Collar 2014, Christidis *et al.* 2018, Clements *et al.* 2019, Gill *et al.* 2020) have followed Rothschild in treating *nigrescens* as a subspecies of *R. ocellata*. Nevertheless, the two taxa are disjunct by more than 1,000 km in a direct line (1,800 km by the shortest present-day land route), and they lie in two biogeographically

distinct provinces within the Oriental region, in mainland Indochina and on the Sunda Shelf (Whitmore 1984, Sterling & Hurley 2008, Corlett 2014).

In the original description of *nigrescens*, Rothschild (1902) distinguished nine characters in the male: (1) mantle and wings darker, brownish black, with chestnut-rufous mottling instead of dark brown; (2) spots of the upper surface mostly quite round and pure white, instead of more or less buff and irregular or elongated; (3) markings on the rump less numerous but larger and with more white; (4) white spots on the outer secondaries mostly quite round, instead of taking the form of irregular oblique lines; (5) upper crest feathers black, instead of dark brown, the white feathers of the crest apparently more numerous; (6) outer webs of the enormously elongated rectrices deeper in colour, more of a blackish brown, and at the same time more uniform; (7) broad superciliary stripe not greyish white, but strongly tinged rufous; (8) bill somewhat stouter; and (9) tail perhaps less elongated. The female is not appreciably different from her counterpart, but 'is somewhat brighter and more rufous, but this may be due to the freshness of the plumage'.

Nine points of distinction is a relatively large number for a taxon being described as a subspecies, and certainly suggests a level of divergence worthy of reassessment in the light of modern taxonomic trends. We do so here, based on re-examination of museum material, and on sound recordings as well as newly available information from observations on live individuals of both taxa.

Methods

Morphological study.—We inspected specimen material of both taxa at the American Museum of Natural History (AMNH), New York, USA, and the Natural History Museum (NHMUK), Tring, UK, made plumage comparisons between them and took biometrics. Material measured involved six full-tailed adult male *nigrescens* (three in AMNH, including the type, 544050; three in NHMUK) and nine full-tailed adult male *ocellata* (five in AMNH, four in NHMUK); registration numbers are given in Table 1. Mensural data were taken from males in millimetres using tape measures, long rulers and digital callipers accurate to two decimal places, for bill (skull to tip), crest (base to tip of longest straightened filoplume), tarsus (tarsometatarsus from back of 'ankle' to distal side of the joint-covering scute at the base of the longest toe), wing (curved) and tail (from point of insertion to tip, shafts as straight as possible). We also examined colour photographs of captive birds of both taxa on the internet and in our own and others' private collections, and, through the courtesy of J. Corder, World Pheasant Association, we examined footage of a series of videos he made of wild and captive male *nigrescens* several decades ago (no captive population of *nigrescens* currently exists).

Vocal study.—To evaluate possible vocal differences, we gathered as many sound-recordings as possible (Appendix). The established bird sound archives (Macaulay Library, Xeno-canto, AVoCet, BLNS) proved to have very few recordings, none of them involving *nigrescens*. However, between 2015 and 2019 we made our own digital recordings of more than 20 captive birds of nominate *ocellata* in Saigon Zoo, Ho Chi Minh City, Vietnam, predominantly in April–May and November, and of wild *nigrescens* at Gunung Rabong Forest Reserve, Kelantan, Malaysia, over the same period, using a Sony™ ICD-PX470 hand-held recorder without an external microphone. These recordings were saved as MP3 files and archived online in bird sound databases (see Appendix). Sonograms were derived from these recordings using CoolEdit Pro software and Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY, USA). Sound parameters were measured manually on these sonograms.

In addition, descriptions of calls of *nigrescens* are based on fieldwork at Gunung Rabong in 1976, 1977 and 2015–2019, and at an unnamed mountain just south of Gunung Rabong in 1984. Counts of the number of loud notes per Long Call and Sharp Call were made of more than ten captive males and seven females of *ocellata* while under direct visual observation in Saigon Zoo, and of possibly ten wild unsexed individuals of *nigrescens* not under visual observation in Malaysia. We considered a ‘note’ to be any continuous line on a sonogram prior to a pause. Within a note, ‘syllables’ are distinct parts of a note which typically are audible and on a sonogram usually can be seen as changes in the continuous line (e.g. from falling to rising, etc.). We defined separate calling bouts as vocalisations from a given individual separated by more than 60 seconds.

To gauge the degree of difference between taxa in plumage, dimensions and voice we made use of the system of scoring proposed by Tobias *et al.* (2010), in which an exceptional character (radically different coloration, pattern, size or sound) scores 4, a major character (pronounced difference in body part colour or pattern, measurement or sound) 3, medium character (clear difference, e.g. a distinct hue rather than different colour) 2, and minor character (weak difference, e.g. a change in shade) 1; a threshold of 7 is set to allow species status, species status cannot be triggered by minor characters alone, and only three plumage characters, two vocal characters, two biometric characters (assessed for effect size using Cohen’s *d* where 0.2–2 is minor, 2–5 medium, 5–10 major and >10 exceptional) and one behavioural or ecological character (allowed 1) may be counted. The notation ‘ns’ (‘no score’) with a value in square brackets is to indicate the degree of difference but, because of the restriction on the number of characters, the score is disallowed.

Results

Morphological evidence.—Our review of specimen material confirms the diagnosis of *nigrescens* by Rothschild (1902), with the exceptions that in his first character (darker wings and tail) we could not see ‘chestnut-rufous mottlings instead of dark brown’ and in his eighth (stouter bill) we could detect no obvious distinction (Table 1). Below we condense the differences into six plumage/bare-part characters, using ‘vs.’ to indicate comparison with nominate *ocellata*, and with Tobias criteria scores in brackets at the end of the description of each character (scores, as opposed to no scores [ns], allocated to the differences we judge most prominent):

1. supercilium buff vs. stony white, usually broader and stronger, and contrasting more strongly with the blacker crown and ‘face’ (area around eye and on ear-coverts) (Fig.1a,b; score at least 2);
2. nareal area blackish, adjacent area of bill (distal to nares) rosy (as noted in Ogilvie-Grant 1908), rest of bill yellowish horn with a paler tip and cutting edge vs. bill including all

TABLE 1

Means and ranges of five variables in fully adult male specimens of *Rheinardia* held in the American Museum of Natural History, New York (AMNH), and Natural History Museum, Tring (NHMUK). Sample sizes are nine for *ocellata* (eight for bill) and six for *nigrescens*.

Specimens contributing data are: (*ocellata*) AMNH 258935, 259081, 544045–047, NHMUK 1907.12.13.1, 1927.6.5.25, 1928.6.26.98 (bill unmeasurable), ‘H.1888’ (unregistered); (*nigrescens*) AMNH 544049–51, NHMUK 1903.5.1.1, 1906.7.23.384, ‘Mus. FMS’ (unregistered).

	bill	crest	tarsus	wing	tail
<i>ocellata</i>	41.1 (37.2–44.3)	79 (62–92)	88 (86–91)	339 (333–350)	1,369 (985–1,494)
<i>nigrescens</i>	41.7 (40.7–42.3)	100 (89–110)	96 (92–100)	366 (355–377)	1,278 (930–1,642)



Figure 1. Adult male (a) *nigrescens* and (b) *ocellata* to show supercilium and bill (N. J. Collar, © Natural History Museum, London)



Figure 2. Adult male (a) *nigrescens* and (b) *ocellata* to show chin and throat (N. J. Collar, © Natural History Museum, London)

but the base of the nareal area rosy pink, slightly paler at the tip, deeper pink above and behind the nostril, as noted by Delacour (1951) and apparent in many photographs of c.15 live individuals in Saigon Zoo (Figs.1a,b, 4a,b; score 3);

3. white of throat more contrasting, buffier (in an echo of the supercilium differences) and more extensive, vs. a less striking greyish white shading quickly into a dull rufous-brown lower neck (present in *nigrescens* as a very narrow zone where the white lower throat grades into the spotted body) (Fig.2a,b; ns[2]), in both taxa the throat feathers forming a little forward-projecting beard when the crest, head and neck feathers are all erected;
4. occipital crest pointing directly backwards rather than tending to spread laterally, in museum skins, with much longer and coarser filoplumes (lacking the fluffiness of the nominate), and consisting of two colours in different proportions, namely a relatively sparse number of elongate black feathers positioned above 5–10 times as many much longer white feathers, vs. soft, decurving sooty-brown feathers shading first to slightly rufous-tinged brown and then creamy white, producing an obviously different profile in display (discussed below; Figs. 3a,b, 4a,b; score 3);
5. white spots on the blacker body and wings much more distinct, being smaller and fewer (hence more widely spaced) and more linearly arranged compared to the dense buffy-white speckling of the nominate (Fig.5a,b; ns[2]);

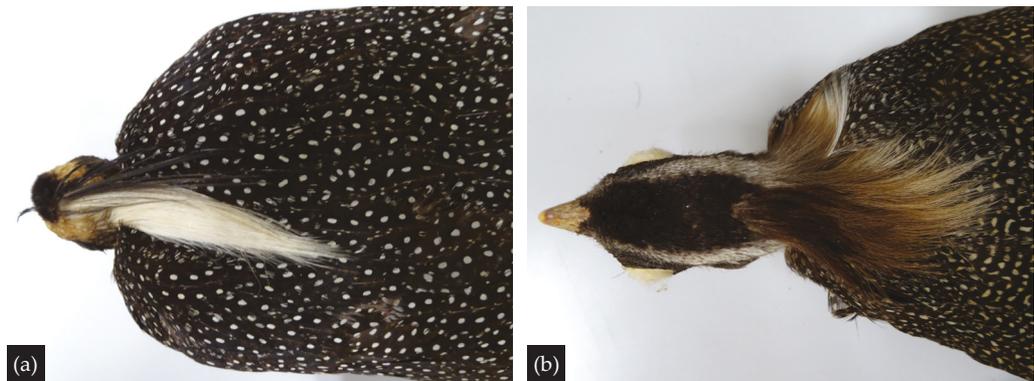


Figure 3. Adult male (a) *nigrescens* and (b) *ocellata* to show crest (N. J. Collar, © Natural History Museum, London)



Figure 4. Adult male (a) *nigrescens* and (b) *ocellata* to show different crest structure in display (also bill colour): (a) still from J. Corder video (made at Sungkai Wildlife Conservation Centre, Malaysia); (b) photograph by J. Bordonné, www.zoospassion.com (in Saigon Zoo, Vietnam)

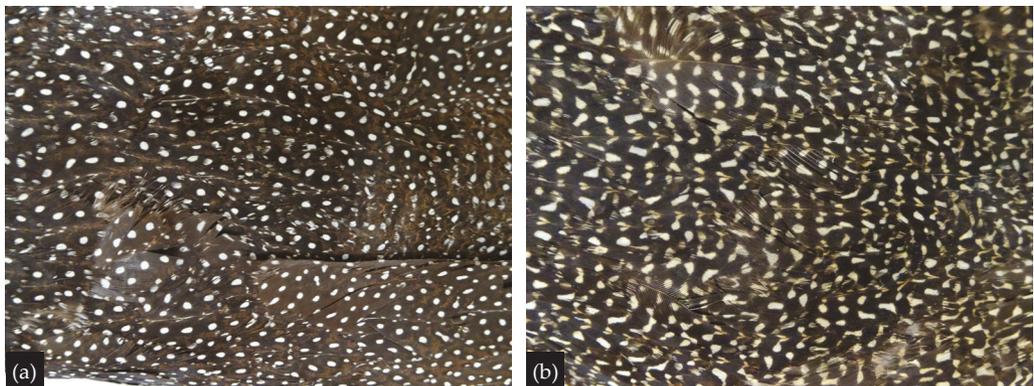


Figure 5. Adult male (a) *nigrescens* and (b) *ocellata* to show dorsal spotting (N. J. Collar, © Natural History Museum, London)

6. inner vanes of the largest rectrices with dull matt rufous-orange background on which white spots are inset in broad grey rings, vs. with grey background, the dull matt rufous-orange contracting to islands between the white spots (Fig.6a,b; ns[2]).

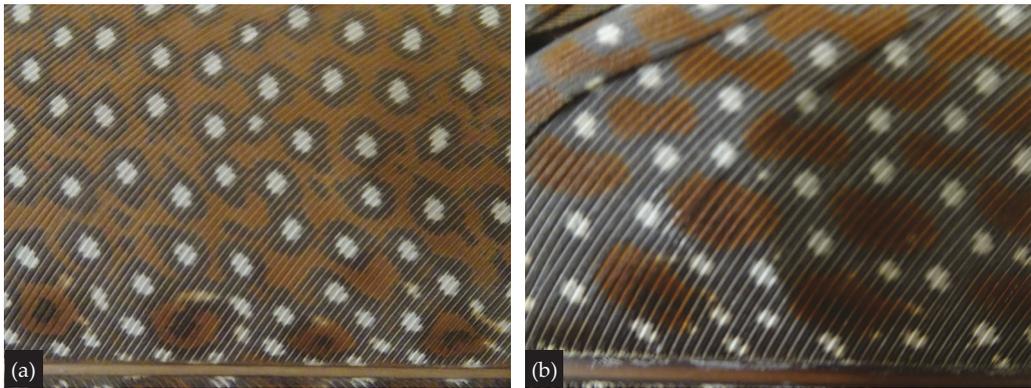


Figure 6. Adult male (a) *nigrescens* and (b) *ocellata* to show colour pattern on largest rectrices (N. J. Collar, © Natural History Museum, London)

In morphometrics *nigrescens* emerges slightly larger overall, with no overlap in tarsus or wing (Table 1). There is also very little overlap in length of crest, which shows much the greatest degree of difference between means (Table 1); we do not emphasise this as it is correlated with body size, but the crest is proportionately longer in *nigrescens* and the colour and shape differences are evident in display (next paragraph). The tail of *nigrescens* averages slightly shorter, but this is almost certainly an effect of sample size: tails in *Rheinardia* possibly increase in length with age (McGowan 1994), and in fact one *nigrescens* (NHMUK 1903.5.1.1) has a tail of 1,642 mm, far longer than the next longest, an *ocellata* (NHMUK 1928.6.26.98) at 1,494 mm. The sample sizes are too small to subject to statistical analysis, but the evidence suggests that the longer tarsus of *nigrescens* might involve a score of 2.

When erected, the crest of male *nigrescens* forms a very spiky pure white radiating mass of untidy feathers, while the long black feathers that lie over the white ones when at rest are projected far forward, overhanging the forehead and bill, apparently straightening under their own weight (Fig. 4a). Contrastingly, the crest of male *ocellata* forms a fluffy, bouffant powderpuff of golden-buff feathers, while the short brown feathers project above the forehead and in profile view form a short rounded curl (Fig. 4b; also Seth-Smith 1932, Huxley 1941). The difference in crest colour and length is striking when the crest is being raised, as their movement causes the long spiky feathers of *nigrescens* to scatter outwards (J. Corder, video).

Vocal evidence.—From the recorded and published material available to us we find both taxa possess three loud call types, which we term Short Call, Long Call and Sharp Call. In nominate *ocellata* all three calls have been sound-recorded; in *nigrescens* only the Short Call has been digitally recorded while the other two have written descriptions based on experience in the field. The Short Call is given by males at or near display sites, apparently in advertisement, and as far as is known it is not given by females. The Long Call and Sharp Call are given by both sexes.

Short Call.—In nominate *ocellata* (Fig.7a,b) this call is a loud, explosive, slightly nasal *woOh-WAWh* delivered as two clearly separated and equally accentuated notes (structurally similar to the homologous vocalisation of Great Argus *Argusianus argus*; as in that species the separation of the notes is not always as clearly defined on sonograms as appreciated by ear, owing to reflections and reverberation). The first note is slightly rising, the second overslurred and reaches a higher maximum pitch. It has been heard given once (rarely twice) per calling bout (by captive males) but few of these calls were heard during the observation periods, which were seasonally limited, and the regional literature indicates the

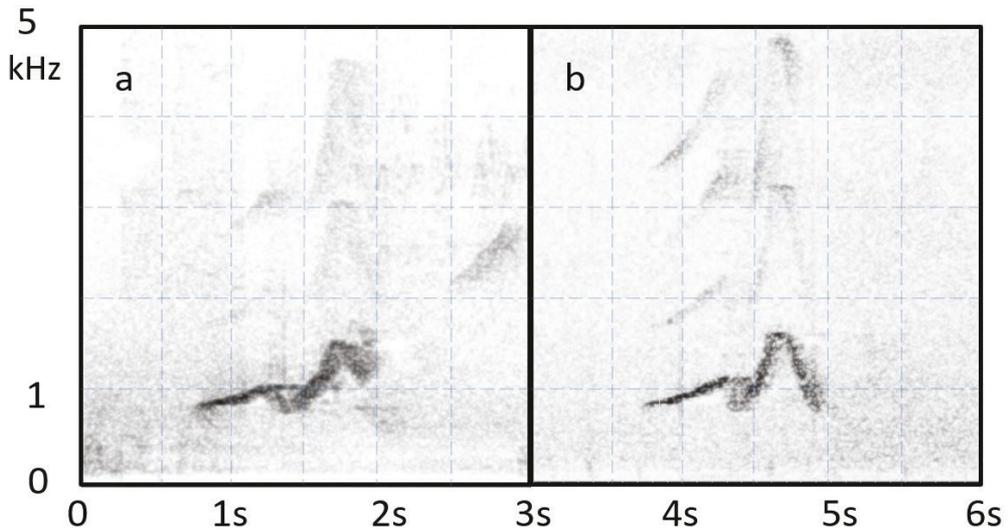


Figure 7. Short Call of *Rheinardia ocellata*: (a) in captivity (ML273908: male, Saigon Zoo, Ho Chi Minh City, Vietnam, 18 April 2019, GWHD); (b) in the wild (AV7666: Bach Ma National Park, Vietnam, 10 February 2003, P. Verbelen).

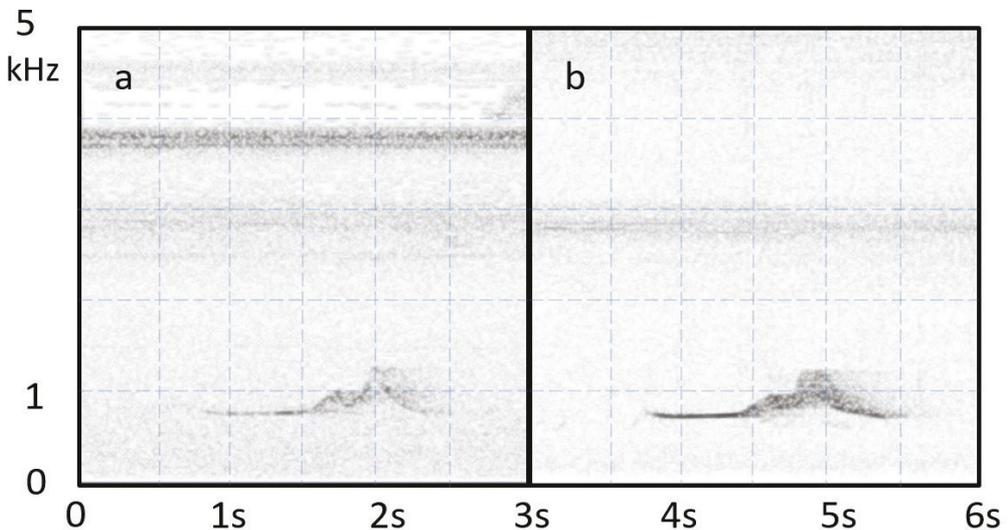


Figure 8. Short Call of *Rheinardia nigrescens* in the wild: (a) Gunung Rabong, Malaysia, 4 April 2018, GWHD (ML273906); (b) Gunung Rabong, Malaysia, 23 April 2019, GWHD (ML273907).

call can be repeated multiple times (see Discussion). In *nigrescens* (Fig.8a,b) the Short Call is a rather pure whistled *whuuhuhHUhuuu*, sounding less forceful and delivered fluently in one breath at fairly consistent amplitude, hence resembling a protracted single note with different internal emphases. The whistled note starts on a flat pitch, followed by a quavering middle part and ends again at about stable pitch. It is typically given once per calling bout, but has been heard repeated up to eight times in succession. When repeated, which is often when responding to extraneous sounds such as gibbons, hornbills, thunder or tree-falls, it can be with a distinct interval of a few seconds between calls, or as a rolling uninterrupted sequence.

TABLE 2
Measured sound parameters of the Short Call in males of the two taxa.

Recording no. (see Appendix)	<i>ocellata</i>		<i>nigrescens</i>	
	ML273908	AV7666	ML273907	ML273906
Total duration of call	1.34 s	1.19 s	1.64 s	1.60 s
Start frequency	780 Hz	800 Hz	780 Hz	760 Hz
Max. frequency	1,600 Hz	1,650 Hz	1,225 Hz	1,250 Hz
Number of notes	2	2	1	1
Number of oscillations	2	2	3–4	3–4
Max. time at stable frequency	<0.2 s	<0.2 s	0.64 s	0.75 s
Clear harmonics?	yes	yes	no	no

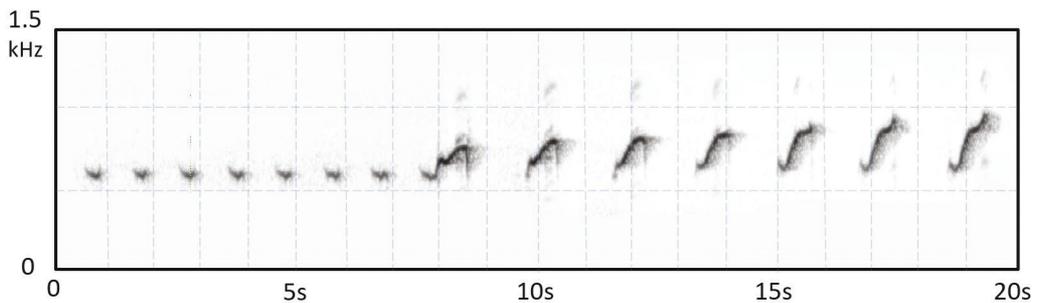


Figure 9. Section from Long Call of male *Rheinardia ocellata* in captivity (ML273918: Saigon Zoo, Ho Chi Minh City, Vietnam, 22 November 2019, GWHD) showing seven of the soft preliminary notes, and an eighth preliminary transitioning into all of the complete seven very loud rising disyllabic notes.

Sonograms were made of these calls and measurements of them reveal that male *nigrescens* has a longer (mean 1.62 vs. 1.27 seconds) but lower-pitched call (mean max. frequency 1,238 Hz vs. 1,625 Hz; Table 2) consisting of a diagnostic single continuous whistle on level pitch followed by quavering modulations, vs. two emphasised overslurred notes. The three recordings are too few to calculate effect sizes; for example, the methodology of Isler *et al.* (1998) requires calculation of percentiles in the *t*-distribution of measurements drawn from a sample of vocalisations. Donegan (2018) assessed strengths and weaknesses of the method. However, given this is a very stereotypic call (heard >100 times in various field situations but not recorded, and immediately recognisable), we can confidently estimate Tobias scores for the three differences to reach respectively 2 (for length), [ns]² (for pitch) and 4 (for 1 vs. 2 notes), resulting in a total score for this vocal character of 6. Isler *et al.* (1998) also used three differences between pairs of taxa, in their case for suboscine *Thamnophilidae*.

Long Call.—This call is given by both sexes of nominate *ocellata* (Fig. 9). It starts with a series, often prolonged over several minutes, of up to several hundred very soft notes that can be heard only from a few metres away and detected visually by slight throat movements, before suddenly transitioning into very loud disyllabic notes, usually *c.*5–9 in a series delivered with wide open bill and straining hyoids. This series of rising whistles, each of which lasts *c.*1 second, often gradually increases in pitch, every whistle reaching a slightly higher frequency than the previous one. The very soft preliminary notes are delivered at a rate of *c.*1 per second, and each lasts approximately 0.4 seconds. In *nigrescens* soft preliminary notes have not been heard, but if present they would not have been detected because of distance in the field. The known part of the call is a single introductory

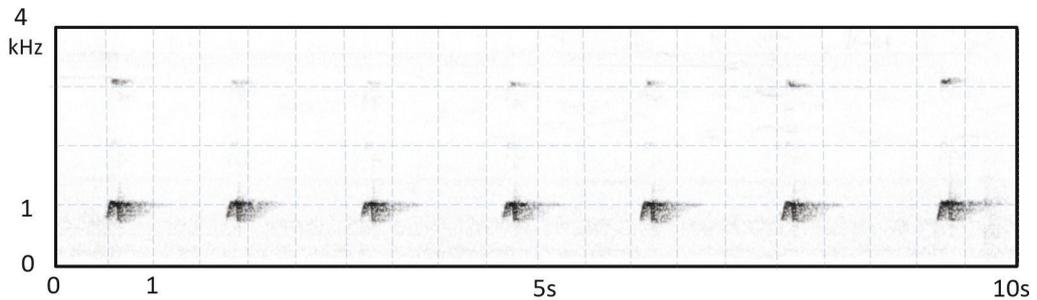


Figure 10. Seven notes from a prolonged Sharp Call of a male *R. ocellata* in captivity (ML273916: Saigon Zoo, Ho Chi Minh City, Vietnam, 22 November 2019, GWHD).

whistled note that morphs into a series of 8–17 very loud inflected disyllabic notes. It is uncertain whether both sexes of *nigrescens* give this call, as no direct observations have ever been made.

The Long Call of nominate *ocellata* could be transcribed as ...*u, u, u, uKIAU; KIAU; KIAU; ...* (here, the last four of the very soft preliminary notes followed by three very loud notes). The Long Call of *nigrescens* could be transcribed as *woooKI-IAU; KI-IAU; KI-IAU; ...* (here, the introductory whistle morphs into three of the subsequent very loud inflected notes). The introductory whistle is similar to that which introduces each Short Call in *nigrescens*. Once a Long Call was ended as well as begun by a whistled *wooo*.

Long Calls by captive male *ocellata* involved 4–11 loud notes per call (preliminary soft notes not counted) with a mean of 7.12 ($n = 109$ calls). They had a unimodal distribution, with 74% of calls containing 6–8 loud notes. Long Calls by captive female *ocellata* ranged from three to 12 loud notes per call with a mean of 6.74 ($n = 42$ calls). They almost had a unimodal distribution, with 81% of calls containing 5–9 loud notes (slightly fewer calls with six than with five or seven loud notes). Long Calls by unsexed wild *nigrescens* ranged from seven to 17 loud notes per call, with a mean of 11.6 ($n = 22$ calls), and were therefore longer on average than Long Calls of *ocellata*, with nine (41%) of the *nigrescens* calls containing more loud notes (13–17) than any *ocellata* Long Call (max. 12 loud notes, from a female). A Kruskal-Wallis test revealed that there was a highly significant difference between the three groups ($\chi^2 = 37.889$, $p < 0.001$), with number of notes from *nigrescens* significantly different from those of *ocellata* females (Dunn's pairwise test; Bonferroni corrected $p < 0.001$) and *ocellata* males ($p < 0.001$). However, the distribution of loud notes in *nigrescens* was arguably bimodal, with 11 calls containing 7–10 loud notes, and 11 containing 12–17 loud notes. These are based on field notes from a broad area of forest covering at least three separate mountain flanks, and therefore unlikely to reflect individual call differences between two birds. If these are treated as two non-overlapping classes (e.g., females vs. males, or perhaps non-court-holding vs. court-holding males), their means are (*nigrescens*-1) 8.6 ($n = 11$) vs. (*nigrescens*-2) 14.5 ($n = 11$) loud notes per call. A Kruskal-Wallis test revealed a highly significant difference between all four groups ($\chi^2 = 41.976$, $p < 0.001$), with the numbers of notes from *nigrescens*-1 and *nigrescens*-2 significantly different from those of *ocellata* females and *ocellata* males (Dunn's pairwise tests; Bonferroni corrected $p < 0.05$). A biological difference is evident between *ocellata* (difference between males and females of only 0.38 in mean number of notes per Long Call, and unimodal distribution of call notes within a large sample of males) vs. unsexed *nigrescens* (two non-overlapping categories of Long Call, and more notes on average in both these categories than in male and female *ocellata*). Accepting that further additions for vocal differences are ineligible under the Tobias criteria, if we assess the difference between these calls in terms of their constituent elements, we might

allow a score of 1 for the more inflected loud note in *nigrescens*, 1 for the introductory *wooo*, and 2 for the greater number and bimodal nature of the loud notes per call, yielding a score for this vocal character of [ns]4).

As a non-parametric test Kruskal-Wallis is not powerful, which is why we also applied Dunn's pairwise test and Bonferroni correction, considering these a reasonable option given the non-normal distribution and different sizes of samples. Larger sample sizes could provide a basis for improved statistical treatment.

Sharp Call.—A Sharp Call is given by both sexes of *ocellata* (Fig. 10). Based on the absence of fear behaviour among all birds before and during the call, it is not necessarily an alarm call. It is similar to the Long Call only in that it consists of a series of notes, but it is quieter and higher pitched, and consists of more notes (but a more variable number, from 12 up to 191 heard), and these are delivered at less regularly spaced intervals than notes in the Long Call. The notes are each much shorter than those of the Long Call, and appear on a sonogram as an inverted U shape. Each note lasts less than 0.5 seconds and is delivered at roughly 1.5–2.0 second-intervals, sometimes with pauses. Although the volume of the individual notes can increase over the series, there are no distinct soft preliminary notes, and no sudden transition to very loud notes. A seemingly identical Sharp Call has been heard only once in the wild from *nigrescens*, but at a distance and was not attributable to sex.

Discussion

Using the Tobias *et al.* (2010) criteria, museum skins alone provide a sufficiently high score (8) to indicate that *R. nigrescens* and *R. ocellata* merit species status. To that we are able to add the distinctive appearance and deportment of the crest, a significant display feature, and considerable differences in advertising calls (totalling 6).

The Short Call and Long Call of the Malaysian taxon were described by Wells (1975, 1999), Medway & Wells (1976), Davison (1978) and Jeyarajasingam & Pearson (1999), all based on fieldwork by D. R. Wells in 1972 and by Wells and GWHD in 1976. Three calls of nominate *ocellata* were described by Robson (2008), apparently corresponding to the Short Call and Long Call described above, as well as an alarm call. That alarm call may correspond to what we term the Sharp Call, although our observations of captive birds suggested it was not (or not necessarily) delivered in an alarm situation. Craik & Lê (2018) also described two loud calls, but possibly conflated descriptions of the two taxa, by incorporating details of Wells' (1999) account of the Short Call of extralimital *nigrescens* ('trisyllabic "WOO KIA'WAU" ... in series of up to 12', although correctly noting that it is usually uttered singly), followed by a correct description of the Long Call of *ocellata* ('6–8 far-carrying "oowaaa" calls'), the latter similar to the description by Robson (2008).

Our observations demonstrate that the Short Call, delivered by males at their display sites (Davison 1978), differs in structure between *R. nigrescens* and *R. ocellata*. As its function appears to be in mate attraction, any vocal differentiation in this call must be considered important. It is interesting to note that the Short Call of *ocellata* is very similar to allopatric *Argusianus argus*, while the Short Call in *nigrescens* (sympatric with *A. argus* but separated by elevation) is quite different, suggesting that the voice of *nigrescens* evolved to differentiate it from *A. argus*, while *ocellata* retained more ancestral features. Their respective Long Calls also differ in structure, in number of notes, and probably in the degree of difference between males and females.

The calls of *R. ocellata* analysed here were mainly from captive individuals, and those of *R. nigrescens* were made by wild birds. In general non-passerine vocalisations are not learnt. Forebrain areas that are similar in morphological appearance, location and connectivity to the song control areas of oscine passerines (songbirds), some parrots and hummingbirds are

lacking in various suboscine passerines, owls, doves, gulls and gallinaceous species (Gahr 2000) that do not learn vocalisations. These are reasons to suppose that the forms and types of calls of *R. ocellata* were not, or not greatly, affected by captive conditions; the validity of this assumption was further affirmed by comparing our recordings with the few available of *ocellata* in the wild (AV7666, XC69377, BLNS46837).

The total Tobias score for *R. nigrescens* reaches a relatively high 14 (double the threshold the criteria set for species rank), which ostensibly exaggerates its distinctiveness but underlines the value of assessing all aspects of phenotypic divergence. Outside the Galliformes an interesting parallel exists in the case of African Houbara *Chlamydotis undulata* and Asian Houbara *C. macqueenii*, two species that look extremely similar at rest but which differ significantly in feather deportment and pattern in display, including the crest, as well as in the number of call notes (Collar & Combreau 2017). Among Galliformes, several splits made employing the Tobias criteria have been validated by various parallel or follow-up studies and observations, e.g. Hainan Peacock-pheasant *Polyplectron katsumatae* (Davison *et al.* 2012), Elgon Francolin *Scleroptila elgonensis* (Hunter *et al.* 2019, Turner *et al.* 2020) and Taiwan Hill-partridge *Bambusicola sonorivox* (Hung *et al.* 2014), all involving considerably lower scores. We predict that if future molecular work becomes possible it will confirm species rank for *R. nigrescens* and *R. ocellata*. We prefer use of Tobias criteria rather than simple comparison with other pairwise cases in the family, but if the latter method is employed our findings indicate that phenotypic differences between *R. nigrescens* and *R. ocellata* outlined above are greater in number and larger in degree than those that separate, e.g., Rock Partridge *Alectoris graeca* from Chukar *A. chukar* and Gunnison Grouse *Centrocercus minimus* from Sage Grouse *C. urophasianus*.

Our recognition of what we propose to call Malaysian Crested Argus *R. nigrescens* as a species distinct from Vietnamese Crested Argus *R. ocellata* is likely to have several conservation implications. First, for planning purposes, the IUCN conservation status of the two resulting species-level taxa will require re-assessment, and is likely to result in heightened concern for both. Second, for the conservation of wild populations, awareness of species status might place them at heightened risk of poaching for trade. In Vietnam *R. ocellata* occurs in several protected and proposed protected areas such as Bach Ma National Park, Ngoc Linh Nature Reserve and Song Thanh Nature Reserve, all in Quang Nam province, and Khe Nuoc Trong Proposed Nature Reserve, Quang Binh province (Gray *et al.* 2014, Vū *et al.* 2017a,b, Vu & Tran 2020), but a sharp decline in advertisement calls in some former strongholds including both Laos (Brickle *et al.* 2008) and Vietnam (Gray *et al.* 2014) indicates the need for a new full assessment of its status and needs (Le Trong Trai pers. comm. 2019; BirdLife International 2020). Fortunately, in Malaysia the bulk of the *R. nigrescens* population lies within the boundaries of Taman Negara National Park (Mamat & Yasak 1998, Liang *et al.* 2018), but no uninhabited area with a long boundary that is difficult to patrol can be considered totally secure. However, there are in principle multiple levels of protection, with permits being required to enter forest (National Forestry Act, most recent major revision 2010), total protection of all species of plants and animals within Taman Negara, and total protection for the species anywhere, under the Protection of Wild Life Act (most recent major revision 2010). Third, improved knowledge of the calls of both species (including whether they are delivered by males or females) should improve the interpretation of survey and census results which, for these elusive birds, are largely based on sound records.

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Appendix: sources of calls used in the analyses in this paper

AV = AVoCet (Avian Vocalization Center)
 BLNS = British Library (Wildlife and Environmental Sounds)
 ML = Macaulay Library, Cornell Laboratory of Ornithology
 XC = Xeno-canto, Naturalis Biodiversity Center

Rheinardia ocellata nigrescens

Short Call: ML273906 and ML273907 (Gunong Rabong Forest Reserve, Kelantan, Malaysia, G. W. H. Davison)

Rheinardia o. ocellata

Short Call: ML273908 (Saigon Zoo, Ho Chi Minh City, Vietnam [in captivity], G. W. H. Davison), AV7666 (Bach Ma NP, Vietnam, P. Verbelen)

Long Call: ML273909–273915 and ML273918 (all Saigon Zoo, Ho Chi Minh City, Vietnam [in captivity], G. W. H. Davison), AV5578/XC69377 (Ho Ke Go, Vietnam, F. R. Lambert), BLNS46837 (Vu Quang Nature Reserve, Vietnam, J. C. Eames)

Sharp Call: ML273916–273918 (all Saigon Zoo, Ho Chi Minh City, Vietnam [in captivity], G. W. H. Davison), BLNS46837 (Vu Quang Nature Reserve, Vietnam, J. C. Eames).

Species limits and English names in the genus *Gygis* (Laridae)

by H. Douglas Pratt

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<http://zoobank.org/urn:lsid:zoobank.org:pub:89EF1BBB-D400-417C-832D-2C905D1E5B6C>

SUMMARY.—The alpha taxonomy of the genus *Gygis* is controversial, with limited molecular studies contradicting distributional and phenotypic evidence that two Pacific forms, larger *candida* and smaller *microrhyncha* are separate species. This paper reviews evidence from the subfossil record, morphology, distribution and hybridisation, and vocalisations to conclude that *Gygis* comprises three biological species, nominate *alba* in the Atlantic, and two Pacific species. It also reviews historical English vernacular names and proposes ‘fairytern’ as a group name for these members of the newly recognised subfamily Gyginae. This name maintains popular tradition but requires a minor exception to some current naming conventions. Proposed English names are Atlantic Fairytern, Common Fairytern, and Little Fairytern. The name White Tern should now apply only to the historical single species, and Fairy Tern remains for *Sternula nereis*.

The genus *Gygis* (Laridae) is distributed around the world in tropical and subtropical seas. It comprises three morphologically distinct populations: Atlantic *alba*; the Indo-Pacific *candida* group with several named subspecies; and *microrhyncha*, with a relictual distribution in the Marquesas Islands of the eastern tropical Pacific (Wingate & Watson 1974, del Hoyo & Collar 2014, Thibault & Cibois 2017). The genus is currently classified variously as comprising one (Yeung *et al.* 2009, Dickinson & Remsen 2013, Thibault & Cibois 2017, Scott 2018, Gill & Donsker 2019), two (Thomas *et al.* 2004, del Hoyo & Collar 2014) or three species (Olson 2005, Steadman 2006, Howell & Zufelt 2019). Yeung *et al.* (2009) studied two mitochondrial genes in search of differentiation among four Pacific *Gygis* taxa, three named subspecies of the *candida* group plus *microrhyncha*, and concluded that none of these populations was diagnosable even at the level of subspecies. They found significantly smaller size in *microrhyncha*, but classified all Pacific populations as a single monotypic species. Thibault & Cibois (2017) expanded the Yeung *et al.* (2009) dataset geographically but did not alter the conclusions. The eclectic study of Thomas *et al.* (2004), with a different molecular dataset, considered *microrhyncha* a species. Subsequently, Jackson *et al.* (2012) showed that molecular studies of Charadriiformes that depend entirely on mitochondrial DNA can be problematic and would profit from additional nuclear markers. No such study has yet been published. With no current consensus, and molecular studies at odds with other data, a thorough systematic review is timely. This analysis includes published subfossil evidence (Steadman 2006) along with new information from biogeography, evidence of ongoing hybridisation, and previously overlooked differences in vocalisations. It also reviews the history of English names in *Gygis*, and proposes new ones that reflect current understanding of the taxonomy and evolutionary position of the genus.

Archaeology

Steadman (2006) summarised the now quite extensive literature on subfossil remains from the Pacific and showed that *G. microrhyncha* and *G. candida* (by using the epithet *candida*,

he tacitly acknowledged nominate *alba* as a third species) were broadly sympatric across the tropical Pacific, from the Marianas (Tinian) in Micronesia to several sites in south-eastern Polynesia (two sites in Tonga, one in Samoa, Mangaia in the Cook Islands, and Tahuata in the Marquesas) in geologically recent times. Bones of both forms were found together at several sites, with no intermediates reported, which would not have been possible if, as Cibois & Thibault (2009) suggested, a continuum in size existed, with the smaller bones assigned to *microrhyncha*. Unfortunately, Steadman (2006) did not specify his criteria for identifying bones of the two Pacific *Gygis*, but the fact that he cited Pratt *et al.* (1987) suggests that he was aware of and took into account qualitative, as well as quantitative, differences. Thibault & Cibois (2017: 247) later criticised Steadman's (2006) work as based solely on 'geographical and morphological evidence', without mentioning that the geographical evidence involved a vast prehistoric zone of sympatry. Given that, *candida* and *microrhyncha* meet the gold standard of the biological species concept, i.e. sympatry without (apparent) interbreeding. Allopatric *alba* presumably forms a third species but must be evaluated using the character comparisons discussed below.

Morphology

Pacific members of *Gygis* exhibit two strikingly different bill shapes (Wingate & Watson 1974, Olson 2005; Fig. 1; note that legends may refer to online images in the Internet Bird Collection + Macaulay Library www.macaulaylibrary.org). Widespread *candida* exhibits a uniquely wedge-shaped or dagger-like bill quite unlike those of its congeners or, indeed, most other terns. The wedge-shaped look is enhanced because the insertion of the maxilla forms, in profile, a nearly straight line at an acute angle to the tomia, with the feather insertion of the mandible also appearing straight but at a less acute angle. The insertion thus inscribes a straight line bent slightly at the tomia (Fig. 1a). The culmen does not indent the forehead, so that, viewed from above or in front (Fig. 2a), the insertion line forms an inverted V or Greek lambda. The gonydeal angle is at the midpoint, and the bill is notably rich cobalt-blue over approximately the basal third (Figs. 1a, 3). Perhaps because of the thicker bill, this species has a subtly more rounded head profile, with a more bulbous forehead, than its congeners (pers. obs.; Figs. 1a, 3).

G. alba and *G. microrhyncha* have more conventional tern bill shapes with the culmen and gonyes roughly parallel, then tapering to a very sharp awl-like tip (sharper in *microrhyncha*; Figs. 1b, 3). The inconspicuous gonydeal angle is set further back on the mandible. The insertion line of the maxilla is deeply bowed downward rather than straight. In *microrhyncha*, the feathers may extend into the nasal groove, often to an acute point, but in *alba* the forward protrusion is rounded (Fig. 3). From above or from in front, these insertion lines inscribe a rounded, shallow letter W, with the midpoint indenting the forehead (Fig. 2b; see video ML 201638871 for *alba*). Similarly, the base of the mandible is indented by a forward protrusion of feathers rather than squared off. This bill shape is conspicuously different, even at a distance, from the dagger-like bill of *candida* (Pratt *et al.* 1987, Morris & Beaman 2017; Figs. 1, 5). In *alba* and *microrhyncha*, the bill is entirely black, sometimes with a 'trace of blue at base' (Pratt *et al.* 1987: 187) in *microrhyncha* (often difficult to discern in photographs because of problematic light conditions). Note, however, that blue bill colour in *microrhyncha* could result from hybridisation with *candida* as discussed below. Although the bills of *alba* and *microrhyncha* are similar in general shape (*alba* somewhat thicker at the base) they differ strikingly in size, with *alba* the largest and *microrhyncha* the smallest in the genus (Fig. 3). Both have concave forehead profiles.

The bill bases of downy *Gygis* chicks resemble each other more than their respective adults but are by no means identical (Figs. 3, 6h; for image of same age *microrhyncha*, see



Figure 1. The two Pacific forms of *Gygis*: (a) *candida* and (b) *microrhyncha* perched showing characteristic bill shape and dark primary shafts; (c) *candida* and (d) *microrhyncha* in flight, with the latter appearing a more compact, goggle-eyed bird with shorter, more rounded wings and less deeply forked tail; Marquesas Islands, French Polynesia (© Pete Morris) For comparable images of Atlantic *alba*, see ML 144554051 (for a and b) and ML 205939691 (for c and d).

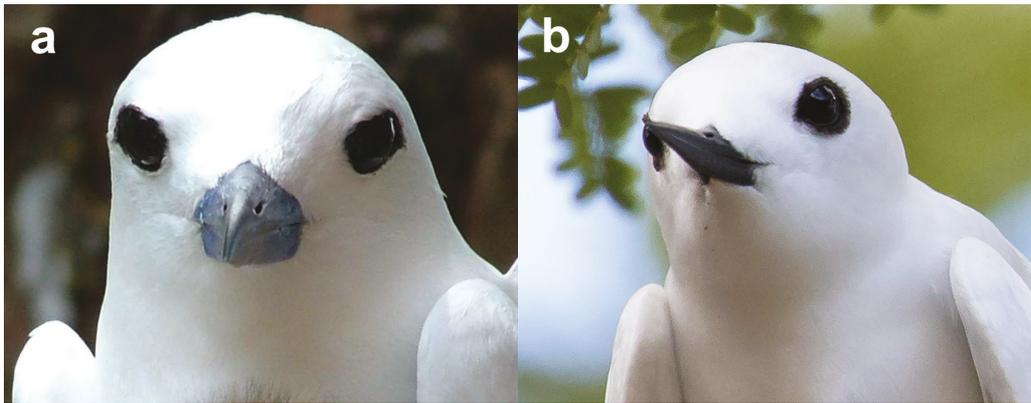


Figure 2. Head-on views of Pacific *Gygis* showing different bill insertion contours: (a) *candida* with inverted V or lambda-shaped basal contour, Honolulu, Hawaiian Islands (© Darcy Fiero); (b) *microrhyncha* with rounded or W-shaped contour, Nuku Hiva, Marquesas Islands (© Pete Morris). For comparable image of Atlantic *G. alba*, see ML 201638871.

ML 198094251; and for *alba* see video ML 201638871). By the time contour feathers start to emerge, the characteristic adult configuration of each species begins to take form, and adult base contour is achieved by the time juvenile plumage is complete (Fig. 4).

Certain plumage differences accompany the three *Gygis* bill morphotypes. In *alba* and *candida*, the shafts of the outer 3–4 primaries and the rectrices are darkly pigmented, sometimes on both surfaces. In *microrhyncha*, these feathers are immaculate or only the outermost primary has a dark shaft, and usually on the upper surface alone. All have black around the eye, thicker in front and behind it, the rest covering only about half of the feathered eye-ring, but the eye-ring of *microrhyncha* is broader, enhancing the endearing large-eyed appearance for which the genus is well known. The most noticeable morphological difference in flight is the shape of the tail. In *candida* and *alba*, the tail is deeply forked, usually

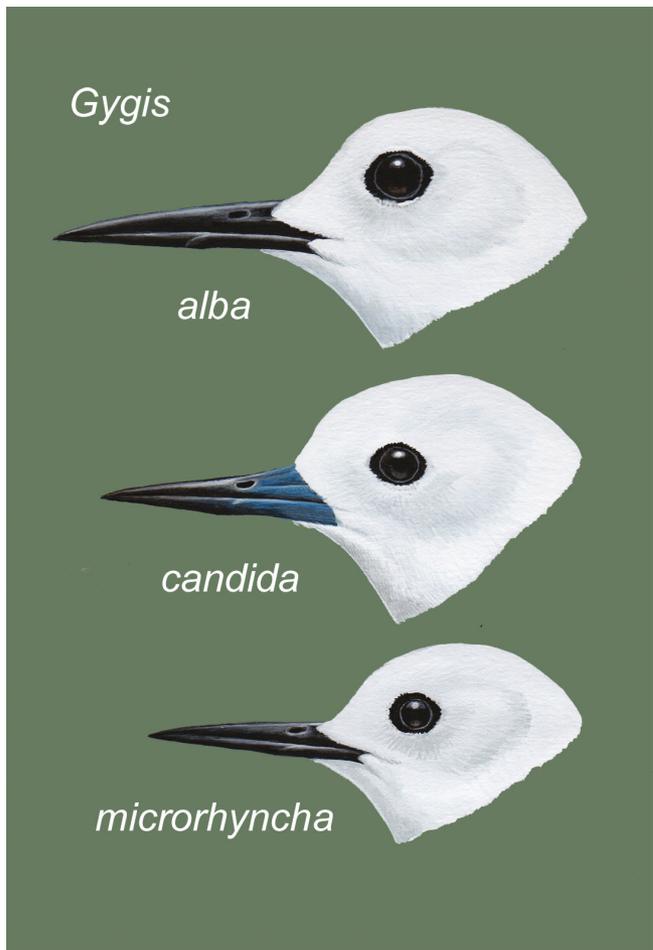


Figure 3. The three morphotypes of genus *Gygis* (H. Douglas Pratt, based on museum specimens and images of live birds)



Figure 4. Developmental stages of young *Gygis candida*, Kiritimati, Kiribati: above, young chick just beginning to grow contour feathers; below, full juvenile plumage with bill not fully grown, but showing adult insertion contour (© E. A. VanderWerf)

with the outermost rectrix longest (Fig. 5a). The tail fork is much shallower in *microrhyncha* with the outer two rectrices often shorter than the third, so that the fork disappears entirely when the tail is spread and it becomes almost spoon-shaped (Fig. 5b). In flight (Figs. 1c–d, 5) the wings of *candida* also look slightly longer and narrower than those of *microrhyncha*.



Figure 5. *Gygis* in overhead flight, showing differences in wing and tail shape, Marquesas Islands, French Polynesia: (a) *candida* with long narrow wings, deeply forked tail; (b) *microrhyncha* with shorter, slightly more rounded wings, rounded tail showing no fork in this configuration (© Pete Morris)

Yeung *et al.* (2009), Cibois & Thibault (2009), and Thibault & Cibois (2017) overlook, or dismiss as trivial, these qualitative differences among *Gygis* (Wingate & Watson 1974, Olson 2005) perhaps because bill shape in particular is not easily revealed by use of conventional bill measurements (Baldwin *et al.* 1931), nor did they consider the possibility that bill shape and colour can be important potential isolating mechanisms (Pratt *et al.* 1987: 185–186, Pratt 2010). Some of these phenotypic differences were the basis for splitting *G. microrhyncha*, but enigmatically not *G. candida*, from *G. alba* by del Hoyo & Collar (2014) employing the Tobias *et al.* (2010) scoring system. However, this taxonomy is untenable if Olson (2005) is correct that *G. alba* and *G. microrhyncha* are sister taxa, as morphology suggests.

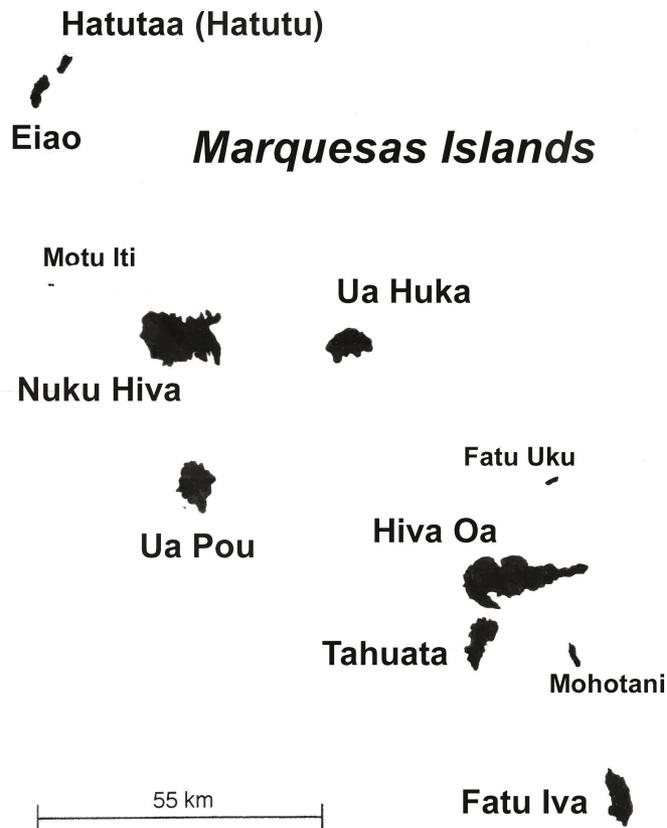


Figure 6. Map of the Marquesas Islands showing the localities mentioned in the text.

Hybridisation and genetic swamping

Olson (2005) suggested that *microrhyncha* fell victim to a rapidly expanding *candida* that replaced it over vast areas by genetic swamping. S. L. Olson (unpubl. data; pers. comm.) examined a series of specimens in the US National Museum (USNM; Smithsonian Institution, Washington DC) of both Pacific taxa, including some with intermediate characters that may be hybrids, collected in the 1920s and 1930s from the Line and Phoenix Islands, where only *candida* apparently occurs today. I also examined these specimens but made no detailed notes. I have found evidence that genetic swamping is ongoing in the remaining relictual range of *microrhyncha*. Traditionally, *G. candida* and *G. microrhyncha* have been said to be parapatric within the Marquesas Islands (Fig. 6), with *candida* on the northernmost large island, Hatutaa (in most older literature referred to as Hatutu), and the relictual population of *microrhyncha* in the rest of the archipelago (Pratt *et al.* 1987). But the situation is more complex and dynamic than that. In 1983, I examined specimens at the American Museum of Natural History (AMNH; New York) collected in the Marquesas by the Whitney South Seas Expedition in 1921–22. I categorised each specimen as *candida* or *microrhyncha* based on the qualitative bill differences described above. Among seven specimens taken on Hatutaa, five were typical of *candida*, but two



Figure 7. A series of photographs of *Gygis* spp. taken on Hatutaa (Hatutu), Marquesas Islands, September 2013: (a) an individual very close to *G. candida*, but with a slightly thinner bill, reduced blue at the base, and shallow tail-fork; (b) another bird, also superficially like pure *candida*, but with no blue at the base of the bill; (c) a bird with a much thinner bill than typical *candida* but with a blue basal third and irregular margin to the maxilla, with white feathers intruding into the nasal groove as in *microrhyncha*; (d) a mated pair with dagger-shaped bills, both of which show evidence of mixed ancestry, with the left-hand bird showing some blue at the bill base but an irregular margin, and that on the right an all-black bill with margin that bows outward and only the outermost primary has a dark shaft; (e) a bird approaching the morphology of *G. microrhyncha*, but with a somewhat thicker blue bill base; (f) a bird that appears to be pure *microrhyncha*; (g) a bird in juvenile plumage (compare with Fig. 4) that appears to be *G. microrhyncha*; and (h) a juvenile bird just starting to lose its natal down, with a bill base typical of *microrhyncha* but with more blue tinge than usual for that species. Images (g) and (h) suggest that *G. microrhyncha* may still breed on Hatutaa, which island was long thought to harbour only *G. candida* (© David Sargeant)

(AMNH 194874 and 194888) were intermediate. Likewise, two (AMNH 220772 and 194881) of three specimens from neighbouring Eiao could not be identified by bill type. All other specimens from the Marquesas were typical *microrhyncha* ($n = 39$) except one specimen of *candida* (AMNH 194905) from Mohotani. Holyoak & Thibault (1984) reported that among 17 specimens (apparently including the seven I examined at AMNH) from Hatutaa, 13 were intermediate, three looked like *candida*, and one like *microrhyncha*. From nearby Eiao, the same authors found two intermediates and three typical *microrhyncha*. Ten specimens from Mohotani, much further south in the archipelago (Fig. 6), included three each resembling *candida* and *microrhyncha* and four intermediates. If their specimens included any collected after the early 1920s, those later specimens might provide evidence of progressive changes during the 20th century (or Holyoak & Thibault may simply have used different methods to categorise specimens).

In September–October 2013 a group of prominent birders visited both Hatutaa and Ua Huka (Sargeant 2013). Among their images from Hatutaa are several birds with intermediate bill structure, thicker than in typical *microrhyncha* but not as heavy as in *candida*, with a proximal border not as straight, and no blue at the base. These probably represent hybrids or intergrades. Sargeant himself obtained a heretofore unpublished series of images from Hatutaa that reveal a highly variable *Gygis* population on the island (Fig. 7). He photographed several birds that resemble typical *candida* but have all-black bills whose rear margins are not quite straight; one adult that approaches typical *microrhyncha*; and another adult, a juvenile, and a much younger chick that appear to be intermediate between the parental morphotypes. These images are the first photographic evidence of possible hybridisation and intergradation between *candida* and *microrhyncha* in the Marquesas. They reveal that a few *G. microrhyncha* may persist in nearly pure form on Hatutaa, and that many of the birds most observers would identify as *G. candida* there differ noticeably from typical members of that species.

G. candida appears to be slowly invading the Marquesas from north to south and displacing *microrhyncha* by hybridisation and genetic swamping (Todesco *et al.* 2016) as Olson (2005) suggested had occurred in the Line Islands. Thus, across the Pacific, the *microrhyncha* phenotype may have disappeared completely from previously inhabited islands, but left a trail of *microrhyncha* genes, a possibility not considered by molecular systematists. Importantly, such hybridisation does not necessarily imply that the two taxa are conspecific (e.g. Fowler *et al.* 2009, Lavretsky *et al.* 2015) but it may lead to the extinction of the species being genetically swamped (Todesco *et al.* 2016), which suggests that *G. microrhyncha* should probably be considered an endangered species. No one has suggested any obvious reason for the displacement of the formerly sympatric *G. microrhyncha* by *G. candida*, but it was broadly coincidental with human colonisation of the Pacific (Steadman 2006). The genetic interactions of *G. candida* and *G. microrhyncha* in the Marquesas are fertile ground for further research. The variations in Fig. 7 suggest that for most hybrids, traits are inherited in a blending, rather than mosaic, pattern. The fact that both parental types appear to persist in the zone of intergradation also suggests a non-random pattern of hybridisation. But these observations are mere speculation until further genetic and field studies can be undertaken.

Vocalisations

Although Yeung *et al.* (2009) did not study *microrhyncha* in the field, they claim that it and *candida* have ‘no subspecific distinctions in behavior or vocalizations’. That statement overlooks Holyoak & Thibault’s (1984) report that *microrhyncha* sounds different to the

human ear, and that chicks in the Marquesas, presumably *microrhyncha*, utter a begging call not heard in other populations (which requires further investigation; apparently no recordings exist). I searched recordings of all forms of *Gygis* in the two major online archives: Macaulay Library (ML; www.macaulaylibrary.org; now incorporating the former Internet Bird Collection); and Xeno-canto (XC; www.xeno-canto.org). Both permit one to listen to a recording and simultaneously view its sonogram. Sound-recordings of *candida* are plentiful, but those of *alba* and *microrhyncha* are relatively few in these collections, and many more samples are required before firm conclusions can be drawn.

Vocalisations of *G. candida* are remarkably uniform throughout the Indo-Pacific (pers. obs.). Most frequently heard is a series of identical short raspy notes, *yik-yik-yik...etc.*, c.5 per second, spanning 2 KHz to 10 KHz (e.g. ML 32673). These are contact notes that may be given by perched birds or groups flying over a colony. Sometimes these notes take on a more structured pattern that rises to a crescendo, then falls symmetrically (e.g. ML 32586 2:21–2:29). Another vocalisation, possibly used for chick defence because it is often uttered when humans approach, is a series of low-pitched twangy notes, consisting of a short sharp whistle followed very quickly by a more structured lower-pitched note or two such notes given in harmony (e.g. ML 5410, ML 96891). It recalls the sound of a stretched rubber band plucked near the ear. These notes may be interspersed with loud raspy upslurred notes, longer in duration than those of birds flying over (e.g. ML 94998 0:21–0:32), which indicate heightened alarm.

Only two recordings were available that I could confidently identify as pure *G. microrhyncha*, but they yielded some surprises. One (ML 203895301) of several birds includes a series of short, sharp rasps similar to flight calls of *G. candida*, plus a series of five two-syllable raspy notes, *shi-dick, shi-dick,...* quite unlike anything I have heard or found in archives for *G. candida* elsewhere in the Pacific. So distinctive are these calls that I question whether they were uttered by *G. microrhyncha*, but no other species is identified on the recording, and in the sonogram these calls appear to be continuous sounds from the same bird or birds giving more typical vocalisations. A recording from Hatutaa (ML 203895611) identified as *G. microrhyncha* sounds very much like typical *G. candida* and, as discussed above, could represent an intergrade. T. Mark recorded *G. microrhyncha* calls on Ua Huka (XC 75212) that are probably homologous to the 'rubber band' calls of *G. candida*. They have a similar twangy quality, but sound higher pitched, cover a narrower sound spectrum (2.5–10.0 KHz), and possess a simpler structure with an initial loud note followed by a faint but identical 'echo' that equates to the 'rubber band' effect.

The voice of Atlantic *G. alba* is even more distinctive. All of its vocalisations are strikingly lower pitched than those of either Pacific species, making homologies less obvious. The rapidly repeated notes (XC 431353) are much heavier sounding because they are sustained longer and are pitched at only 2–3 KHz. A structured rising and falling version (XC 14680) reaches no higher than 7 KHz. The 'rubber band' call is similarly low-pitched (1–8 KHz) and the individual notes possess a unique structure with only one 'echo' note that in a sonogram appears like a hook dangling from the initial note. Another low-pitched vocalisation (XC 431354) has long-sustained notes with a far more complex structure than anything uttered, as far as is known, by either Pacific species.

In summary, although homologies can be discerned, each species of *Gygis* appears to have a unique vocal repertoire easily distinguishable from the other two. Further recordings of *G. alba* and especially *G. microrhyncha* are a critical research requirement. The most obvious gap in sound collections are the reportedly distinctive begging calls of *microrhyncha* chicks (Holyoak & Thibault 1984).

Conclusions

Yeung *et al.* (2009) and Thibault & Cibois (2017) present a view, based on studies of two mitochondrial genes, that the genus *Gygis* has no genetic structure across the vast tropical Pacific Ocean. This paper summarises a large body of phenotypic and biogeographic evidence that suggests otherwise. The subfossil record demonstrates broad sympatry, the ultimate test of the biological species concept, of two Pacific species in pre-human times. Qualitative shape differences among the three species have been overlooked because standard measurements are not adequate to detect such differences. New and historical evidence of hybridisation, as *G. candida* continues its hypothesised range expansion and genetic swamping of *G. microrhyncha*, suggests a possible source of genetic bias. Striking vocal differences, described here for the first time, also suggest that *Gygis* comprises three species. Nevertheless, molecular systematists (Thibault & Cibois 2017) and list-makers (Gill & Donsker 2019) have seized upon the Yeung *et al.* (2009) study to make generalisations that dismiss other lines of evidence. However, the findings of Jackson *et al.* (2012) suggest that fresh research, including both nuclear and mitochondrial genes, is sorely needed in this complex before genetic data can be seriously weighed against seemingly overwhelming non-molecular evidence. For now, the only meaningful taxonomy is to regard *G. alba*, *G. candida* and *G. microrhyncha* as biological species.

English names redux

Readers have undoubtedly noticed that, until now, I have avoided using English names. Vernacular names in this genus have a long, highly controversial, and still unresolved history, in which I have been involved for several decades as a member and advisor to committees that led up to what was the International Ornithological Congress' committee on English names (Gill & Donsker 2019). Now, the split into three species and recent genetic studies of higher categories within the Laridae (see below) have fundamentally altered the discussion and require that we reconsider English names in this genus.

As an iconic single species, *G. alba* has long been popularly known as the fairy tern, a name that has served it well and is a difficult one to abandon, given the birds' popularity in areas where it is conspicuous to large human populations (Morgan 2007). Unfortunately, when *Sternula* (formerly *Sterna*) *neréis*, a little-known small tern restricted to temperate waters of Australia and New Zealand, was discovered in the 19th century, it was also called 'fairy tern'. Nevertheless, in much of the rest of the world, 'fairy tern' continued to be used for *G. alba*. Ornithologists began employing the rather insipid 'White Tern' for *G. alba*, which gained fairly wide acceptance, particularly among list compilers, but the general public was less easily persuaded (although see Scott 2018). To this day, ordinary folk and popular publications around the world know and love the 'Fairy Tern', and not in reference to *S. neréis* (e.g. Floyd 2019 and comments). Even when White Tern is used, it is usually followed by 'also known as Fairy Tern' or similar, or given as alternatives (White / Fairy Tern). In Honolulu, Hawaii, where the bird is a city icon (Morgan 2007, Scott 2018), the hybrid name 'White Fairy Tern' has taken hold (Yuen 2012, Allen 2019, Vollbrecht 2019). Pratt *et al.* (1987) offered a compromise that involved hyphenating 'fairy-tern' in the case of *Gygis*, while keeping 'Fairy Tern' for the austral bird, but current trends on the use of hyphens in bird names (Gill *et al.* 2009) make this problematic. However, the guidelines of the American Ornithological Society's checklist committee (Chesser *et al.* 2019) would still consider hyphenated fairy-tern viable.

Meanwhile, molecular systematists have been studying evolutionary relationships within the family Laridae, i.e. terns, gulls, jaegers and skuas, and skimmers. One important finding is that noddies (*Anous*, probably including *Procelsterna*; Cibois *et al.* 2016), traditionally thought to be terns, are a basal offshoot and sister to the rest of the Laridae, forming their own subfamily Anoinae (Bridge *et al.* 2005, Pons *et al.* 2005, Baker *et al.* 2007). Because a few narrower studies (Ödeen *et al.* 2010, Cibois *et al.* 2016) considered *Gygis* a sister group to noddies, Gill & Donsker (2019) prematurely proposed such names as 'White Noddy' or 'Fairy Noddy' for the then-single species. A consensus topology (Thibault & Cibois 2017: 246) now positions *Gygis* as an independent basal offshoot of Laridae forming its own subfamily Gyginae (grouping it with the noddies would render the Anoinae paraphyletic). However, the precise position of *Gygis* at the base of the larid tree remains unsettled (Jackson *et al.* 2012). Unfortunately, Howell & Zufelt (2019), whose book is likely to be very influential among birders, unwisely call the members of *Gygis* 'white noddies', a name that now appears to be misleading or wrong (Thibault & Cibois 2017).

Because these birds are neither noddies nor typical terns, the three species in the Gyginae need a name that will distinguish them as a group, which the unhyphenated 'white tern' fails to do. I propose the unhyphenated compound name 'fairytern' as a group name for *Gygis* (leaving Fairy Tern for *Sternula nereis*). That way, the Gyginae would be indexed under F, but *S. nereis* under T with other Sterninae. I understand that this name violates, slightly, one rule proposed by Gill & Donsker (2019) but I believe 'fairytern' should be granted an exception comparable to those made for such traditional names as 'goldfinch' and 'skylark'.

Use of 'fairytern' would allow non-professionals to maintain a beloved and widely used name without being scolded by pedants. Note that 'fairytern' has a subtly different pronunciation from 'fairy tern'. For the three species, Howell & Zufelt (2019) use the epithets Atlantic, Indo-Pacific, and Little. I suggest 'Common' in place of 'Indo-Pacific', which, although appropriate, is an unfamiliar construct among the general public. Common Fairytern is appropriate, despite 'Common' as a modifier of bird names being often denigrated (*pers. obs.*), because the bird is indeed common most places where it occurs, it is the species most people will see, and the epithet has been used by birders in the Pacific at least since publication of the Pratt *et al.* (1987) field guide, until recently the only such reference for the region. 'White Tern' should now be reserved for the monotypic species before it was split, as required by American Ornithological Society rules (Chesser *et al.* 2019). As for *Sternula nereis*, if an additional modifier is deemed necessary, 'Austral Fairy Tern' would suffice, but I do not advocate such a change.

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New documented records of Ring-billed Gull *Larus delawarensis* and Roseate Tern *Sterna dougallii* for Colombia

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The most recent updates to the avifauna of continental and insular Colombia listed 1,909 species (Avendaño *et al.* 2017) and 1,941 species (Donegan *et al.* 2018), respectively. Of these, Avendaño *et al.* (2017) included 57 and 63 hypothetical and vagrant species, respectively. The former involve birds whose presence in the country is based solely on published sight records without supporting materials (i.e., museum specimens, published photographs, videos or audio recordings). These authors called upon the ornithological community 'to publish their data and to improve the evidence supporting future new records for the country'. Documentation and formal publication is necessary to consolidate knowledge of Colombian avifaunal diversity and distribution patterns (Arbeláez-Cortés 2013, Avendaño *et al.* 2017). Here we report new documented records of two seabirds that are currently classified as 'hypothetical', 'unconfirmed' or 'vagrant' in the Colombian bird lists (Avendaño *et al.* 2017, Donegan *et al.* 2018).

On 22 November 2017 several seabirds were observed and photographed by one of us (ABA) a few km north-east (10°27'02"N, 75°31'06"W) of Cartagena de Indias, dpto. Bolívar, on the Caribbean coast of Colombia. The birds were feeding on fish scraps discarded by fishermen, and subsequently many of them gathered in a flock nearby on the beach. The group was dominated by Sandwich Terns *Thalasseus sandvicensis* and Laughing Gulls *Leucophaeus atricilla* but also included several Royal Terns *Thalasseus maximus*, two Common Terns *Sterna hirundo*, a Roseate Tern *S. dougallii* and a Ring-billed Gull *Larus delawarensis*. The latter two represent noteworthy records for Colombia.

RING-BILLED GULL *Larus delawarensis*

Breeds in Canada and the northern USA, and winters mainly throughout the USA, West Indies and Mexico south to the Pacific coast of Costa Rica; it is casual in central Panama and exceptional in Colombia, Ecuador and Amazonian Brazil (Howell & Dunn 2007). The bird at Cartagena de Indias was apparently a first-winter based on the dark scales on the breast and belly, pink bill with a black tip and retained juvenile wing-coverts (Sibley 2000, Howell & Dunn 2007; Fig. 1). Its overall appearance and size made the bird easily separable from the nearby Laughing Gulls.

The species' first record in Colombia was a specimen collected on 8 December 1964 (Instituto de Ciencias Naturales, Bogotá; ICN 14953) at Lago de Tota, dpto. Boyacá, recently reported by Donegan *et al.* (2010). Subsequently, this gull has been observed occasionally on both coasts of Colombia. On the Pacific coast, it was first recorded at Buenaventura, on 19 January 1978, 9 February 1984 and 28 September 1990 (Hilty & Brown 1986, Naranjo & Franke 1995); and inland at Laguna de Sonso in the Andes of dpto. Valle del Cauca on 10 March 2001 (Downing 2005). There are at least seven additional sight records between early November and late March on the Pacific coast in recent decades (eBird); however, the only documented records (i.e. supported by photographs) are from Tumaco, where it appears to be a rare but annual visitor (V. E. Góngora Fuenmayor unpubl., eBird). These records



Figure 1. First-winter Ring-billed Gull *Larus delawarensis*, just north-east of Cartagena de Indias, dpto. Bolívar, Colombia, 22 November 2017 (A. B. Azpiroz)

are in line with the presence of vagrants on the northern Pacific coast of Ecuador (Nilsson *et al.* 2014). On the Caribbean coast, it was first recorded at Camarones, near Riohacha on 7 January 1998, then at Santa Marta on 9 January 2007 (Mazar Barnett *et al.* 1996, Donegan *et al.* 2010). Seven additional sight records are available in the last decade from between Sincelejo and Riohacha, all during late August to mid March (eBird), with one photographed at Camarones on 12 March 2015 (L. E. Ureña unpubl., eBird). Our documented record at Cartagena adds to the increasing evidence from both coasts of Colombia that suggest that this gull is probably a rare but regular winter visitor. However, additional field work is necessary to understand the precise status and distribution of this and other 'rare' gulls, especially on the Pacific coast (Ellery & Salgado 2018) and along the coast from the Gulf of Urabá to Barranquilla, a well-known knowledge gap for seabirds in Colombia (Estela *et al.* 2010).

ROSEATE TERN *Sterna dougallii*

New World populations of the species breed from Nova Scotia to New York and Florida, south through the Gulf of Honduras and West Indies to islands off northern Venezuela. They winter primarily on northern and eastern coasts of South America, with records in Brazil south to 21°04'S (Gochfeld *et al.* 2020). The US Fish & Wildlife Service lists the north-eastern population as 'Endangered' and the Caribbean population as 'Threatened'. Hays *et al.* (1997) reported recoveries of Roseate Terns in South America, noting the predominance of records ($n = 146$) between 10°N and the equator (along the north coast of South America), with most in November–December, suggesting that they moved elsewhere in December. More than half of these recoveries were of first-year birds. In another paper, Hays *et al.* (1999) described a major non-breeding area for the species on the east coast of Brazil. Current work in Brazil by P. Lima (pers. comm.) has confirmed that these remain important areas for non-breeding Roseate Terns in December–March.



Figure 2. First-year Roseate Tern *Sterna dougallii*, just north-east of Cartagena de Indias, dpto. Bolívar, Colombia, 22 November 2017 (A. B. Azpiroz).

The bird seen at Cartagena de Indias was in non-breeding plumage (Fig. 2). Overall appearance in flight was reminiscent of a *Sternula* tern. At rest, the most obvious characteristic was its size: the bird appeared significantly smaller than the nearby Common Terns. Based on the bird's blue plastic field-readable band (CS2) and a partial reading of the USGS Bird Banding Lab band number (1402-18260), it was identified later (J. Spendelow *in litt.* 2017) as a first-year Roseate Tern. The bird was banded as a chick by GC under H. Hays' permit, on Great Gull Island, New York, USA, on 22 June 2017, making it five months old when photographed in Colombia.

Roseate Tern can be difficult to distinguish from Common Tern in non-breeding plumage: adults are similar in size and both have a dark bill and legs, and a white forehead. Roseate Tern has pale upperparts and a white underwing, which separate it from Common Tern (Harrison 1983), but these differences are subtle. At this season, all Roseate Terns lack the long tail-streamers typical of breeding plumage. A dark carpal bar, as seen on CS2, is characteristic of a first-year. The Colombian individual probably appeared smaller than the nearby Common Terns, not only because Roseate Tern is slimmer than Common, but also because this young bird's tail feathers may not have been fully grown.

The bird reported here is the second verified record for Colombia to be published. The first was a bird that was also banded as a chick at Great Gull Island, New York, on 8 August 1969, and was recovered on Gorgona Island, off the Pacific coast, on 27 October 1969 (Hays 1971). In an analysis of Roseate Tern recoveries in the Western Hemisphere, Nisbet (1984) reported seven additional records from Colombia (six from the Caribbean and one from the Pacific coast during the period 1927–79). When not individually verified, however, banding data may include errors in reporting or processing that can result in significant uncertainties regarding actual geographic locations (Nisbet 1984). For example, at least one of Nisbet's Colombian records referred to a bird on a ship at an unspecified distance off the coast, while some other observations might have been of birds found dead or dying

onshore (Nisbet 1984: 11). Other occasional sight records of Roseate Terns have been made along the Caribbean and Pacific coasts of Colombia; records are from Isla Salamanca on 14 January 1975, Cartagena harbour on 21 January 1978 (Gochfeld *et al.* 1980), Punta de la Cruz, Casablanca and Buritaca on the Guajira Peninsula in February 1979 (Naranjo 1979). Recently, Arzuza *et al.* (2008) reported the species at Ciénaga Grande de Santa Marta, Isla Salamanca, and Gorgona Island, but without dates or documentation.

Earlier references to ringed birds (Hays 1971, Nisbet 1984) were apparently overlooked by Donegan *et al.* (2010) and Avendaño *et al.* (2017), who considered the species hypothetical or unconfirmed in Colombia, which may reflect differences of interpretation regarding supporting materials, with photographs and specimens being perceived as better verified than banding or radio-tracking data (Donegan *et al.* 2018). It is noteworthy that, to date, the only two Colombian records verified by colour-banding are those reported by Hays (1971) and the individual described here.

Although Gochfeld *et al.* (2020) speculated that the few Roseate Tern sightings in Caribbean Colombia might involve birds from the Venezuelan colonies, both verified records have involved birds from the Great Gull Island (USA) colony. That described here may have been blown off course by either of the two major hurricanes (José and María) in the Caribbean during September 2017. Satellite-tracking data from four Common Terns reveal that two flew through the hurricane, to the coast of Venezuela; one was only c.100 km from the Colombian border (P. Loring pers. comm.). Perhaps Roseate Tern CS2 encountered one of these hurricanes and was blown towards Colombia. Like the other birds in the flock at Cartagena, it was presumably attracted by the fish scraps. H. Hays (pers. comm.) and GC have observed Roseate and Common Terns in Brazil feeding on bycatch and fish scraps thrown overboard.

In sum, the records summarised here suggest that this tern is a vagrant to Colombia. However, given the identification challenges involved with mid-sized terns (especially non-adults), it is possible that the species has been overlooked. That Roseate Terns seem to feed some distance offshore and visit land primarily at night (Nisbet 1984, Hays *et al.* 1999) may also explain the scarcity of records. Additional observations of banded birds might enable a better understanding of the occurrence of Roseate Tern in Colombian waters.

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The New Guinea bird names Macgregor's Bowerbird and Macgregor's Honeyeater

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Macgregor's Bowerbird *Amblyornis macgregoriae* of the uplands of New Guinea was named by Charles W. De Vis and was 'Dedicated to Lady Macgregor', wife of Sir William McGregor (*sic*) who was Administrator of British New Guinea during 1888–98 (knighted in 1889) by the specific name *macgregoriae* (De Vis 1890). Sir William's surname was originally, and thus formally, McGregor but he adopted the spelling MacGregor while in New Guinea as his personal preference.

Similarly, what was long called Macgregor's Bird of Paradise of the highlands of New Guinea was originally named *Macgregoria pulchra* by De Vis (1897) 'after Lady Macgregor' and was known thereafter as Macgregor's, or by some MacGregor's, Bird of Paradise. Having long been thought to be a bird of paradise, it is now established that *Macgregoria pulchra* is in fact a large honeyeater with extensive facial wattling, and was therefore re-named Macgregor's Honeyeater (Cracraft & Feinstein 2000).

In their Introduction del Hoyo *et al.* (2009: 46–47) discussed the issue of the English name spelling for the bowerbird and honeyeater, and their confusion as to the correct usage. They undertook 'an extensive search', which 'did not prove totally conclusive'. Because these authors found that Lady Mary McGregor signed her letters 'MacGregor' they considered it proof of what the McGregors 'used themselves'. Del Hoyo *et al.* (2009) apparently did not, however, appreciate that their formal name was McGregor and that Lady Mary's signature merely reflected her husband's idiosyncratic personal preference. Jobling (1991: 136) used the correct spelling Lady Mary McGregor but subsequently (Jobling 2010: 234) employed MacGregor, perhaps influenced by del Hoyo *et al.* (2009).

Contrary to the widespread use of the vernacular name Macgregor's for the bowerbird and what is now the honeyeater for some 120 years in major publications dealing specifically with the bowerbirds and birds of paradise (e.g. Gilliard 1969, Cooper & Forshaw 1977, Everett 1978, Peckover 1997, Frith & Beehler 1998, Lenz 1999, Frith & Frith 2004, 2008, 2010) some authors (e.g. Iredale 1950, Gregory 2019) use MacGregor's in one or both cases. It is difficult to see any point or benefit in changing Macgregor's to MacGregor's for the name for the bowerbird and honeyeater, as the former was consistently used in the majority of the relevant ornithological literature. The argument that MacGregor's should be used because McGregor personally preferred it is fundamentally weak. A far stronger argument is that the names should be changed to McGregor's Bowerbird and McGregor's Honeyeater because that was the man's official name (but see below).

The rules for zoological nomenclature do not apply to vernacular names. Pertinent points that should be considered, however, are:

(1) That the International Ornithological Committee (IOC; Gill & Wright 2006) listed ten rules or principles that should be considered in applying common names. The first was that 'Existing usage would be the predominant guideline'. The spelling Macgregor's for the two bird species involved here could not be more long established—that spelling having been used by most authoritative authors since both birds were named. Thus to apply the first rule correctly the name should be Macgregor's.

(2) Had De Vis applied a common name to *Amblyornis macgregoriae* and *Macgregoria pulchra* in describing them he would doubtless have used Macgregor's Bowerbird and Macgregor's Bird of Paradise respectively, as is consistent with his dedications.

(3) Gregory (2019: 320) stated 'the long-standing usage' of Macgregor's is wrong and that MacGregor's is correct because that is how 'Sir William signed his name' but this is erroneously selective history because Sir William's original surname was McGregor.

(4) Changes such as this lead to confusion and inconsistent misuse in the literature: such as in del Hoyo & Collar (2016) in which both MacGregor's Bowerbird and Macgregor's Honeyeater are conflictingly applied!

(5) In Rand & Gilliard (1967) MacGregor's Bowerbird and Macgregor's Bird of Paradise are used, whereas in Gilliard (1969) Macgregor's is used, suggesting Gilliard, specialist in these two bird groups (or his colleagues, as his monograph was published posthumously), came to consider the latter the correct usage.

(6) Similarly Sibley & Monroe (1990) used MacGregor's for both birds but Monroe and Sibley (1993) use Macgregor's, possibly having realised the error of their former spelling.

(7) Contrary to the last, and emphasising my point, Pratt & Beehler (2015) use Macgregor's Bowerbird, while Beehler & Pratt (2016) use MacGregor's Bowerbird.

(8) Rule 8 of the IOC, in applying vernacular names to birds, noted that 'brevity and simplicity are virtues'. Surely having an (unnecessary and erroneous) upper case letter in the middle of a common name makes for complexity and confusion rather than simplicity.

I am not arguing for a change of names to McGregor's (Sir William's correct name) Bowerbird and McGregor's Honeyeater. This would be change for the sake of change, and no more helpful than the change to MacGregor's from the original and long and widely used Macgregor's—an unnecessary and erroneous change for no good, logical or justifiable reason.

Future confusion and contradictory usage, as is clearly demonstrated above as occurring in recent literature, is best avoided by using the long-standing vernacular name Macgregor's for the bowerbird and honeyeater.

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