

Colour aberrations in extinct and endangered birds

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SUMMARY.—Several groups of birds have suffered high extinction rates, especially rails, pigeons, parrots and passerines. Some island species that disappeared in the early 19th century, e.g. Lord Howe Gallinule *Porphyrio albus*, Rodrigues Parakeet *Psittacula exsul* and Mascarene Parrot *Mascarinus mascarinus*, are known from only a few skins and illustrations, whereas the Huia *Heteralocha acutirostris* of New Zealand is known from hundreds of specimens. Furthermore, two North American species—Passenger Pigeon *Ectopistes migratorius* and Carolina Parakeet *Conuropsis carolinensis*—which became extinct in the early 20th century, are also represented by hundreds of specimens. Other supposedly extinct bird species are enigmatic. Confusion exists concerning the unique specimens of Sharpe's Rail *Gallirallus sharpei* and Townsend's Bunting *Spiza townsendi*, paintings of a parrot from the West Indies and an aberrant white Huia, as well as aberrant specimens of the Critically Endangered Kakapo *Strigops habroptilus*. Much has been written concerning these birds and why they became extinct, or have become extremely rare, but few data are available concerning colour aberrations in certain specimens; the literature is also riddled with incorrect terminology. This paper addresses this shortfall and describes the various colour aberrations in these extinct and endangered birds and why they have occurred.

The Rallidae (rails and coots), Columbidae (pigeons and doves), Psittacidae (parrots and macaws) and Passeriformes (passerines) are all widely distributed, occurring on every continent except Antarctica. All have suffered extremely high extinction rates (Hume & Walters 2012), especially those genera endemic to oceanic islands. This is primarily due to severe anthropogenic factors, especially over-hunting, deforestation and introduction of exotic species. Many of these extinct taxa are known from very few specimens, particularly those that disappeared in the 19th century. These include Lord Howe Gallinule *Porphyrio albus* (ex. c.1844), Rodrigues Parakeet *Psittacula exsul* (ex. c.1875) and Mascarene Parrot *Mascarinus mascarinus* (ex. c.1800) (Hume 2007, Hume & Walters 2012), all of which are represented by just two known skins. In contrast, Huia *Heteralocha acutirostris* (ex. 1907) of New Zealand is known from hundreds of specimens (Fuller 2000) and the Critically Endangered Kakapo *Strigops habroptilus* by >1,000; both were particularly sought after during the 19th century (Butler 1989, Hume & Walters 2012). Carolina Parakeet *Conuropsis carolinensis* (ex. 1918) and Passenger Pigeon *Ectopistes migratorius* (ex. 1914), of the continental USA, are known from at least 720 skins (Luther 1996) and 1,532 skins (Hahn 1963), respectively. Much has been written about these birds and why they became extinct (Rothschild 1907, Greenway 1958, 1967, Fuller 1987, 2000, Butcher 1992, Hume 2007, Hume & Walters 2012), but little documentation exists for specimens exhibiting unusual colour aberrations. The unique specimens of Sharpe's Rail *Gallirallus sharpei*, obtained in 1865 and of unknown provenance but considered an extinct species (Olson 1986), and Townsend's Bunting *Spiza townsendi*, collected once in 1834 and also considered extinct (Paynter 1970), are discussed. Some aberrant-coloured skins of Kakapo, illustrations of an enigmatic *Amazona* parrot from the West Indies, and a white Huia are also described.

This paper addresses the probable reasons why these colour aberrations occurred, and elucidates some of the erroneous misconceptions associated with these birds. In particular, the much-used term ‘partial albinism’ is an incorrect terminology that cannot be used to describe any avian taxon exhibiting partial white feathering (van Grouw 2006, 2012, 2013).

Rallidae

LORD HOWE GALLINULE (SWAMPHEN) *Porphyrio albus* (White, 1790)

Endemic to Lord Howe, a small, remote island between Australia and New Zealand in the Tasman Sea, c.600 km east of Australia, *P. albus* was considered common when discovered in 1788 (Hutton 1991), but soon fell victim to over-hunting and introduced mammalian predators, becoming extinct between 1832 and 1844 (Hindwood 1940). The population was derived from Purple Gallinule *P. porphyrio*, but differed in its white plumage and bill, wing and leg proportions (Forbes 1901, Ripley 1977); thus Lord Howe Gallinule is given specific status. Two specimens, as well as several contemporary illustrations and subfossil remains, are available (Forbes 1901, Iredale 1910, Fuller 2000, Holdaway & Anderson 2001). Neither skin has accurate provenance data.

The first illustration was probably by Arthur Bowes Smyth, surgeon on one of the First Fleet vessels, the *Lady Penrhyn*, which arrived at Lord Howe on 16 May 1788 (Hutton 1991). The drawing depicts one white and two pied gallinules, and Smyth described the birds as ‘some white, some blue and white, others all blue’. Other contemporary images demonstrate that the species was variably coloured, with some completely white, others white with blue speckling, some entirely blue. Phillip (1789) described the adult female



Figure 1. Watercolour of live Lord Howe Gallinules *Porphyrio albus* showing the various stages of progressive greying discussed in the text. Fig. 1a (left) shows a pair exhibiting the same colour aberrations as the extant specimens; illustration by George Raper c.1790 (from Hindwood 1940). Fig. 1b (above) shows the three colour stages described by White (1790); illustration by Thomas Watling c.1792 (from Fuller 2000).



Figure 2. Comparison of the two extant specimens of Lord Howe Gallinules *Porphyrio albus*, both of which exhibit progressive greying, with a normal-coloured Purple Gallinule *P. porphyria*: Fig. 2a (top) holotype NMW 50761; Fig. 2b (above left) WML D3213; Fig. 2c (above right) artist's impression of the Liverpool specimen (Julian P. Hume); Fig. 2d (left) Eastern Purple Gallinule *P. p. melanotus* BMNH 1887.5.2.66 dorsal and ventral views (Hein van Grouw). Note that the holotype is completely white.

as all white, but was informed that the male had some blue on the wings. White (1790), followed by Latham (1824) and Gray (1862), stated that young were all black, turning bluish grey, then pure white with maturity (Fig. 1b). White's (1790) statement that juveniles were normal-coloured before developing white feathers (= feathers without melanin) at maturity, strongly suggests that the species exhibited the aberration progressive greying, which can be defined as 'the progressive loss of pigment cells with age' (van Grouw 2013). From the onset of this condition, the bird gains an increasing number of white feathers with every moult. In the early stages, they are usually spread randomly over the bird, but eventually the entire plumage is white. Progressive greying may or may not be inheritable; some forms are related to age, while in others the progressive loss of pigment cells is due to inheritable disorders such as vitiligo (van Grouw 2013). Progressive greying is common in birds, especially in the Corvidae, Passeridae and Turdidae (van Grouw 2012). The aberration affects only the melanin, not the carotenoid pigments (reds and yellows), therefore Lord Howe Gallinule's bill and legs retained normal coloration.

The widespread Australasian subspecies of Purple Gallinule, *P. p. melanotus* (Fig. 2d), still occurs on Lord Howe and some exhibit blue and white feathering (Mayr 1941, Ripley 1977), but it appears that these birds had disappeared entirely by 1977. Mayr (1941) considered the survival of blue individuals was due to them being less conspicuous, after the original population of white birds had disappeared; however, Hindwood (1965) thought that blue birds occasionally arrived from Australia and interbred with the resident white population. Unsurprisingly, the differences in coloration resulted in a wealth of confusing taxonomic literature (Rowley 1875, Forbes 1901, Rothschild 1907, Mathews 1928), exacerbated by confusion over provenance (Hume & Walters 2012). This has led to doubts concerning the specific status of the Lord Howe birds. Regardless of this, what is certain is that a population of probably flightless, white or partially white gallinules was formerly resident on Lord Howe.

NMW (Naturhistorisches Museum Wien) 50.761, type (Fig. 2a). This specimen was obtained from the sale of the Leverian collection in 1806, and labelled '*Fulica albus*, Norfolk Island' (Pelzeln 1873) in error. It is considered the type, as White (1790) mentioned that the bird on which his drawing was based was deposited in the Leverian collection (Pelzeln 1873). The skin, which was originally mounted, is in good condition, and the natural red coloration of the bill and shield is visible. Although faded, the legs are pale orange-brown, and thus were probably reddish in life. The specimen is all white, with no trace of yellowish sheen or any purple feathering (*contra* Rothschild 1907: 144). The remiges and rectrices are soft, and the remiges almost completely covered by the uppertail-coverts. Wing length is shorter than in the Liverpool specimen (Greenway 1967).

WML (Liverpool World Museum) D3213 (Fig. 2b–c). A mount, this specimen was originally obtained by Sir Joseph Banks, but the collection date is unknown. It must have been collected post-1778, when the island was first discovered (Hutton 1991). The skin went to the Bullock collection, was purchased at auction by Lord Stanley in 1819, then bequeathed to Liverpool by the 13th Lord Derby and finally donated to the museum c.1850 (Forbes 1901). It is generally in good condition, considering its age, but with extensive feather loss on the head and neck. General coloration is white with yellowish reflections on the neck and breast. Purplish-blue speckling occurs on the top of the head, cheeks and neck, and is more concentrated on the head, especially near the dorsal surface of the shield. There are several purplish-blue feathers on the back, scapulars and lesser coverts, and some of the lateral rectrices are purplish brown. The remiges and rectrices are soft, and the primaries shorter than in *P. porphyrio* (Forbes 1901, Greenway 1967). The bill, shield, iris, legs and

feet were bright red or yellow in life (Philip 1789, White 1790), but the bill and feet in the Liverpool skin have been painted red.

Rothschild (1907) correctly suggested that *P. albus* was not albinistic, but that the population was in the evolutionary process of becoming pure white. Our analysis of museum skins confirms that albinism was not present in the population (*contra* Taylor & van Perlo 1998, Fuller 1987, 2000, Hume & Walters 2012), and that white coloration in the two extant specimens is caused by a presumably inheritable form of progressive greying. The Liverpool bird had not yet reached the final stage of this condition, hence the retained normal-coloured feathers, whereas the Vienna specimen was in the final stage and therefore all white. The individuals that occurred on Lord Howe until 1977 exhibiting white and blue coloration were probably a local population of *P. p. melanotus*, which also carried the gene for progressive greying. They too are now extinct.

SHARPE'S RAIL *Gallirallus sharpei* (Büttikofer, 1893)

Several rails are known from unique skins or illustrations, and the enigmatic Sharpe's Rail *Gallirallus sharpei*, first described in 1893 (Büttikofer 1893), is one such. It is considered to be closely related to Buff-banded Rail *Gallirallus philippensis* (Olson 1986), an extremely widespread species found on many islands and archipelagos in the South Pacific, New Guinea, New Caledonia and New Zealand, as well as Australia and Indonesia (Ripley 1977, Taylor & van Perlo 1998). Buff-banded Rail has been treated as at least 21 subspecies, most of which are not threatened, but Macquarie Island Rail *G. p. macquariensis* became extinct c.1870 due to the introduction of feral cats and Wekas *G. australis* (Hume & Walters 2012). The type of *G. sharpei* was received at the Rijksmuseum van Natuurlijke Historie, Leiden (now Naturalis), in 1865 from the Amsterdam natural history dealer, G. A. Frank (Büttikofer 1893, Olson 1986). The original range is unknown, but H. Schlegel thought that the bird was a juvenile of the South American Spotted Rail *Pardirallus maculatus* (Büttikofer 1893), an error that initiated great confusion over its true provenance (R. B. Sharpe *in* Büttikofer 1893). In 1893, J. Büttikofer, Schlegel's successor and probably biased by the latter's provenance allocation (Olson 1986), described it as a distinct species from South America in honour of Sharpe, who had brought it to his attention (Büttikofer 1893). O. Bangs (*in* Peters 1934) placed the rail in *Hypotaenidia* and, as it was never recorded again, this prompted Peters to suggest that it might be an extinct species. *Hypotaenidia* has been applied to bar-winged or buff-banded rails of the genus *Gallirallus* (Olson 1986), and Olson concluded that Sharpe's Rail, which was similar in many aspects of size and morphology to volant *G. philippensis*, should be placed there too.

On many occasions, unique bird skins have been ignored by modern ornithologists, especially those collected on islands during the 18th and 19th centuries, which has commonly resulted in their relegation to dubious status. Based on the available evidence, Olson (1986) thought that, as the bird differed significantly in plumage pattern and coloration, it probably represented an extinct species, and speculated that the skin was procured from Java, Sumatra or Borneo. Unusually among island rails, which are often characterised by flightlessness (Olson 1973, Livezey 2003), Sharpe's Rail exhibited no reduction in wing length (Olson 1986).

RMNH (Rijksmuseum van Natuurlijke Historie, Leiden) 87485 (Fig. 3). Sharpe's Rail is a mid-sized, dark-coloured bird, upperparts brownish black, paler and more brownish on upperwing; white-spotted mantle, scapulars, upperwing-coverts, undertail-coverts and tail; remiges dull brown, strongly barred white; sides of head, chin, throat and neck grey; rest of underparts brownish black; flanks irregularly marked with small white spots; bill, legs and



Figure 3. Sharpe's Rail *Gallirallus sharpei* RMNH 87485 (left) exhibiting category 3 melanism compared with a normal-coloured Buff-banded Rail *G. philippensis* RMNH 185133 (right) (© Steven van der Mije / Naturalis)

feet reddish. Sharpe's Rail lacks the chestnut-coloured nape and ocular stripe, ochraceous pectoral band and pale superciliary of Buff-banded Rail (Fig. 3).

The dark and spotted appearance of Sharpe's Rail vaguely resembles that of Spotted and Buff-banded Rails, therefore it is not obviously an aberrant specimen. The plumage appears 'natural', and thereby convinced previous authors that it differed from any known species. But the 'natural look' is an important distinguishing feature of melanism, as this aberration does not cause a qualitative and / or quantitative loss of pigment.

In general the appearance of a melanistic bird is dark, predominantly blackish, but this is not always the case. There are at least three ways in which melanism can affect plumage (van Grouw 2013): (1) normally dark markings become bolder and noticeably 'overrun' their usual boundaries (the rest of the plumage is often somewhat darker too); (2) all plumage becomes darker, appearing dark brown or black; and (3) normal pattern and / or pigment distribution is changed, but plumage is not necessarily darker.

Melanism can therefore be defined as 'an abnormal deposit of melanin in skin and / or feathers', which means that melanism is not necessarily an increase of pigment, but may be the result of a changed distribution or 'abnormal deposit' of the same amount of melanin (van Grouw 2013).

The possibility that *G. sharpei* represents a colour aberration was not considered until mtDNA revealed that the specimen can be referred to *G. philippensis* (Naturalis unpubl. data). Therefore the unique specimen of Sharpe's Rail is not an extinct species (van Grouw 2010), but is in fact an outstanding example of category 3 melanism of Buff-banded Rail.

Columbidae

PASSENGER PIGEON *Ectopistes migratorius* (Linnaeus, 1766)

Probably once the most abundant bird species on Earth, its extinction is one of the most damning acts of human greed and thoughtlessness: it defies belief that a species so abundant could be exterminated so quickly. Its range was inextricably linked to the eastern deciduous forests of North America and Canada, from the Great Plains east to the Atlantic, north to southernmost Canada, and south to Virginia and northern Mississippi. In winter they migrated to the south-eastern USA, the Caribbean slope of central Mexico, and even Cuba (Schorger 1955, Gibbs *et al.* 2001). Early accounts describe the immense numbers of individuals that congregated during the nesting season and especially on migration, although such concentrations were irregular (Hume & Walters 2012). The decline began in the early 1800s, and coincided with an increase in deforestation and commercial exploitation, particularly following the development of new railroads and telegraph systems after the American Civil War. Wherever the pigeon concentrated in numbers, it was subject to wanton slaughter; they were in huge demand for meat and the feather trade (Butcher 1992). By the end of the century the species was almost extinct. The last recorded wild specimen was shot on 24 March 1900 (Fuller 2000). A few were kept in private aviaries, but they proved poor breeders; the last, a captive female called Martha, outlived the rest by four years. She died on 1 September 1914 in Cincinnati Zoo (Shufeldt 1915).



Figure 4. Passenger Pigeon *Ectopistes migratorius* BMNH 1939.12.9.4071 exhibiting the brown aberration (left) lateral view; (second from right) dorsal view; compared with normal-coloured bird BMNH 1918.12.3.3 (Hein van Grouw / © Natural History Museum, Tring).

Passenger Pigeon is known from at least 1,532 skins and 16 skeletons (Hahn 1963). It was a large dove with long wings and a long graduated tail, and adults were sexually dichromatic. Males had the head bluish grey; display area at back of neck iridescent bronze, green or purple depending on the light; back tinged slate-grey with olive-brown; lower back and rump greyish blue and greyish brown on uppertail-coverts; two central rectrices brownish grey, rest white; wing-coverts brownish grey with irregular subterminal spots; primaries and secondaries darker greyish brown; secondaries edged white; throat and breast rich pinkish rufous, becoming paler on lower breast to white on undertail-coverts; bill black, iris carmine-red, bare orbital ring purplish red, legs and feet red. Female similar but overall duller, greyish-brown head, neck and back; reduced iridescent markings; underparts buff-brown, less rufous and tail shorter; legs and feet paler red, iris orange-red, and orbital ring greyish blue.

BMNH (Natural History Museum, Tring) 1939.12.9.4071 (Fig. 4). This aberrant specimen, an adult female, has no provenance other than it formed part of the Rothschild collection at Tring. Rothschild had a great interest in colour aberrations and this specimen is probably the only aberrant-coloured Passenger Pigeon in existence. It differs from normal-coloured birds in being washed brown on the upperparts, wing-coverts, secondaries and tail where grey normally occurs; the primaries, lower breast and belly are white; the black subterminal spots brown; the top of head, lower back and uppertail-coverts pale grey, but the neck iridescence is unaffected. The aberration is caused by the mutation brown, 'an inheritable qualitative reduction of eumelanin due to incomplete synthesis (oxidation) of eumelanin' (van Grouw 2013). This mutation is the most common in wild birds, and the probable reason is that the gene for brown is sex-linked. In birds, males have two Z-chromosomes, whereas females have a Z and W (Bellott & Page 2009), thus in sex-linked mutations the gene is located on the Z-chromosome alone. This explains why only brown females occur in the wild, as females need only one gene to express the recessive brown mutation. In contrast, to produce a brown male, a heterozygous father and brown mother are essential; the likelihood of this occurring under natural conditions is extremely remote. The bill and feet are usually slightly paler in brown (not discernible in this specimen), but eye colour remains the same (van Grouw 2012). The result of this aberration is that the black eumelanin pigment becomes brown, but the reddish or yellowish-brown phaeomelanin is unaffected. The white coloration is due to further bleaching by exposure to natural light, whereby old feathers can be much paler than fresh ones (van Grouw 2012, 2013). The original un-faded brown coloration is clearly visible in this individual on the inner webs of the flight feathers, which have not been exposed to light.

Psittacidae

RODRIGUES PARAKEET *Psittacula exsul* (Newton, 1872)

Known from two specimens, the last collected in 1875 (Newton & Newton 1876). Their coloration appears to differ from normal-coloured wild birds, which has resulted in much confusion. Rodrigues Parakeet was first mentioned by the Huguenot, François Leguat, in 1692–93 (Leguat 1708), and then by the Réunionnais mariner, Julien Tafforet (1725–26), who also observed other parrots (our translation from the original manuscript):

'The Parrots are of three kinds and in quantity. The largest [*Necropsittacus rodericanus*] are larger than a pigeon and have a very long tail, the head big as well as the beak; most are from the southern islets to the south of island where they eat a small black seed that produces a small shrub whose leaves have the scent of lemon, and come to the mainland to drink water; others remain on the mainland, where they find these

small shrubs. The second species [σ^7 *Psittacula exsul*] is slightly smaller, and much more beautiful, because it has its plumage green like the previous, a little blue, and a little red above the wings as well as their beaks, the third species [♀ *P. exsul*] is small, all green and the beak black.'

The parrots were extremely abundant, but Tafforet noted that they generally occurred on offshore islets (probably due to the presence of rats on Rodrigues itself: Hume 2007), only visiting the main island for water. The astronomer Pingré, who was on Rodrigues to observe the transit of Venus in 1761 (Alby & Serviabile 1993), noted that both parrots had become rare, *Necropsittacus* especially; this was the last time the latter species was mentioned. Over the next century, slash-and-burn agriculture and free-roaming livestock turned the island into a wasteland (Cheke & Hume 2008). Remarkably, the parakeet survived; it was not until 1871 that the first specimen, an adult female, was collected and the species formally described (Newton 1872). A second transit expedition to the island took place in 1874, which included several naturalists, and the first natural history survey was undertaken (North-Coombes 1971). The Revd. H. H. Slater wrote a manuscript describing the surviving birds on Rodrigues, but only small extracts were published (Günther & Newton 1879, Slater 1879, Hume *et al.* 2014). The parakeet was by now extremely rare, and Slater remarked on the single specimen he saw during his three-month stay at the Plaine Corail, south-west Rodrigues. The following is taken verbatim from his field notes (Slater 1874):

Palaeornis exsul. I saw one specimen of this bird as I was going from my camp to a distant cavern: unfortunately I had not my gun with me or I could easily have shot it as



Figure 5. The two extant specimens of Rodrigues Parakeet *Psittacula exsul* exhibiting the parblue aberration. Male UMZC18/Psi/67/h/I (right) lateral and dorsal views; holotype female UMZC18/Psi/67/h/I (left) lateral and dorsal views (Julian P. Hume).

it came within thirty feet of me: I believed it to be a male at the time, and it is probably the one procured since by Mr Caldwell; I never had time to hunt for it subsequently. I was informed by a native (Quibus minime credendum pot [who cannot be trusted]) that he had seen two specimens at the N. end of the Island, but I had never time to visit that region.

Assistant Colonial Secretary, William James Caldwell (1875), who arrived on Rodrigues 12 May 1875, saw several parakeets during his stay, but was unable to obtain a specimen himself. However, he did receive a male from a local resident and ship's pilot, William Vandorous, who had killed and sexed the bird on 14 August 1875 (Newton & Newton 1876); it was probably that seen by Slater. This was the last time the parakeet was recorded.

CUMZ (University Museum of Zoology, Cambridge) 18/Psi/67/h/I ♀ holotype (Fig. 5). Newton (1872) and Newton & Newton (1876) described the female in fresh plumage as overall dull greyish glaucous, darker above, with a blue or green sheen depending on the light; primaries deep greenish blue, secondaries slightly darker; rump and belly verditer-blue, becoming greener on vent; black collar from nostrils to sides of head; bill black, iris black with yellow ring, legs and feet greyish black. Originally preserved in alcohol, the specimen was removed from solution when it was described (Newton 1872).

CUMZ (University Museum of Zoology, Cambridge) 18/Psi/67/h/I ♂ (Fig. 5). Differs in being larger and in having the top of head clearer glaucous, less grey; black stripe more distinct, extending upwards from nostrils to nape of neck and almost meeting there; primaries with dull black patch on inner web near tip; central secondaries dusky black; maxilla deep crimson, becoming horn at tip, mandible dark reddish brown (Newton & Newton 1876). The feathers exhibit more wear than the female, and thus are less well preserved.

The unusual coloration of *P. exsul* has caused much debate, so it is important to establish a general overview of parrot coloration. The predominant greens of most parrots are not true colours as they are not formed by green pigments; instead, the green is produced by two different pigments (eumelanin and psittacin) in combination with feather structure. As in all birds, melanin, or more precisely, eumelanin, is one of the pigments that determines colours in parrots. Eumelanin is normally black or dark brown, but depending on the way the microscopic pigment granules are arranged (i.e. their density) in the feather cells, it appears black (dark brown) or as different shades of grey. The eumelanin granules in the deeper cells of the feather barbs, together with their special structure, distort the light as it passes through, making the feathers appear blue. Thus, blue is a structural colour and not a pigment. The second pigment, psittacin, is unique to parrots. Yellow is the commonest colour of psittacin, but the related colours red, orange and pink can also be produced by it. Psittacin, when present, is distributed in the cortex, the outermost layer of a feather barb, and combined with the structural blue coloration, creates the bright shades of green characteristic of most parrot species (Martin 2002).

The inheritable absence of psittacin, which causes blue feathers instead of green, is probably the commonest mutation in parrots and is, for obvious reasons, called blue. In all parrot species inheritance is recessive and not sex-linked (Martin 2002). For a recessive mutation to appear, a bird must inherit a gene for the mutation, in this case blue, from both parents. The coloration caused by blue mutations varies in shade, depending on the normal colours (wild type) in the relevant species. For example, in *Psittacula* the blue coloration will be evenly distributed and intense, as is the original green of these species. In contrast, an uneven distribution and intensity of green can result in an uneven distribution of blue (see Kakapo).

The allele responsible for the total absence of psittacin in parrots is often referred to as true blue, but several other alleles produce reduced quantities of psittacin (Martin 2002). Due to the 'diluted' psittacin exhibited by such mutations, overall colour will lie somewhere between green and blue, an aberration known as parblue. Newton & Newton (1876) described *P. exsul* as being greyish glaucous, with green or blue reflections depending on the angle of light. This suggests that the cause of the colour aberration was due to a parblue mutation rather than true blue.

MASCARENE PARROT *Mascarinus mascarinus* (Linnaeus, 1771)

Endemic to Réunion, the youngest of the Mascarene Islands (Cheke & Hume 2008), this species disappeared before anything was recorded of its ecology. A few captive birds arrived in Paris during the late 18th century, by which time it was probably already extinct in the wild. The last individual, a specimen in King Maximilian of Bavaria's menagerie, reportedly died in 1834 (Hahn 1834, Milne-Edwards & Oustalet 1893, Hachisuka 1953, Greenway 1958, 1967, Fuller 1987, 2000, Forshaw 1989); however, this is extremely unlikely and the species was almost certainly extinct by c.1800 (Hume 2007). The specimen described by Hahn was not preserved, but two exist, the holotype in Paris (MNHN 211; Fig. 6a,c) and another in Vienna (NMW 50.688) (Fig. 6b–c). The latter has frequently been described as 'partially albinistic' (Pelzeln 1873, Fuller 2000, Hume & Walters 2012) or as a 'variety' of Mascarene Parrot (Latham 1781), as the skin has some white feathering (Fig. 6c). Latham (1781: 265) gave the first detailed description of the specimen:

'In the Leverian Museum is one of these [*Mascarinus*], with the mask in front. The ground colour of the plumage the same as in the above [as Brisson (1760), see below], but irregularly sprinkled with white feathers throughout; the tail, part white, part brown, but not regular; some of the quills and tail feathers being wholly white, while the opposites, which should have answered them, were white and brown: it is a particular and beautiful *lusus naturae*.'

Both skins are now faded, and in the 1790s, the wings and tail of the Paris specimen were severely damaged due to sulphuric acid fumigation in an attempt to eliminate pests (Milne-Edwards & Oustalet 1893). Most depictions of Mascarene Parrot are biased by the faded coloration of the specimens and early descriptions and illustrations, which depict the bird with a purplish head, black mask, pale brown body with darker wings and tail, and white bases to the lateral rectrices (see Hume 2007). However, birds described in life differed significantly, with Dubois (1674: 172) in 1671–72 providing the best description: 'Parrots a little bigger than pigeons, with plumage the colour of squirrel fur [blackish brown: see Mourer-Chauviré *et al.* 1999], a black hood on the head, the beak very large and the colour of fire.'

Brisson (1760: 315) gave the following description of a fresh skin: 'head and neck ash-grey; back, wings, rump and underparts very dark ash-grey; tail dark ash-grey, with lateral feathers white at base; bare skin around eye region, bill, bare skin around upper bill and iris bright red; legs and feet pale flesh; claws grey-brown' (translation from Hume 2007). Little of the original coloration is discernible in the two extant skins (Fig. 6); only the black mask and red bill are clearly visible.

MNHN (Muséum National d'Histoire Naturelle, Paris) 211 (Fig. 6a). No details exist as to this specimen's provenance, but probably it was one of the live individuals that resided in Paris in the late 1700s (Hume 2007). Overall coloration uniform pale brown, with slightly darker primaries and secondaries; first two primaries with white bases; underparts



Figure 6. The two extant specimens of Mascarene Parrot *Mascarinus mascarinus*: Fig. 6a (top left) holotype MNHN 211 (Julian P. Hume); Fig. 6b (top right) NMW 50.688, dorsal and lateral views (Julian P. Hume); Fig. 6c (below) illustration of both specimens, drawn to scale (Julian P. Hume). The greyish-blue head of the Paris holotype (centre left and centre) is not discernible in the Vienna specimen, and the tail has been reconstructed. The irregular white feathering in the Vienna skin is due to poor diet in captivity.

paler; head brown with black mask; tail dark brown with white bases to lateral feathers; bill bright red; legs greyish brown.

NMW (Naturhistorisches Museum Wien) 50.688 (Fig. 6b). The Vienna specimen was purchased from the sale of the Leverian collection in 1806 (Pelzeln 1873, Schifter 1994). Nothing else is known about it. Overall uniform brown, greyer on the head and neck, with individual white feathers on mantle, back, rump and underparts; primaries pure white (one side has been clipped), secondaries white with dark brown tips; head brown with black mask; tail has white and dark brown feathers; legs and feet reddish brown.

The pale brown coloration is clearly an artefact of fading due to light exposure, from grey to brown (Hume 2007, van Grouw 2013), which has occurred in other ancient skins that were predominantly grey or black in life, but are now brown, e.g. a Captain James Cook specimen of Hawaii 'O'o *Moho nobilis*, and Townsend's Bunting *Spiza townsendi* (pers. obs., this paper). The red bill and black mask are unaffected. The Vienna skin exhibits random white feathering on the body, with white primaries and asymmetrical white tail feathers, which is almost certainly a result of food deficiency. It is more than likely that the bird was a long-term captive (H. Schifter pers. comm.), perhaps being another of those birds alive in Paris during the 1770s (Hume 2007). The clipped primaries further suggest that it was caged. The dietary requirements of parrots were doubtless poorly known in the 18th century, and almost certainly inadequate for maintaining a healthy bird. This specimen of *Mascarinus* was probably therefore unable to extract sufficient quantities of the amino acid tyrosine from its food, which is necessary for normal melanin synthesis. In consequence, white feathers appeared in the plumage. In nearly all other parrots, the affected feathers would be yellow (or orange / red) instead of white because psittacin would still have been present. However, vasa parrots *Coracopsis* sp. and Mascarene Parrot are the only species that naturally lack psittacin in their plumage (HvG unpubl.).

The affinities of *Mascarinus* are obscure and not satisfactorily resolved. Based on coloration and skeletal morphology, it has been considered related to south-east Asian Psittaculini (Hume 2007), whereas molecular evidence places it with Lesser Vasa Parrot *Coracopsis nigra* (Kundu *et al.* 2012); however, the latter result has been questioned (Joseph *et al.* 2012, Safford & Hawkins 2013). Whether the lack of psittacin in both genera represents convergent evolution or supports a close relationship remain unclear.

CAROLINA PARAKEET *Conuropsis carolinensis* (Linnaeus, 1758)

Formerly present over much of the eastern USA, from Florida and southern Virginia west to eastern Texas, Oklahoma, Kansas and Nebraska. It has been divided into two subspecies, Eastern Carolina Parakeet *C. c. carolinensis* and Western Carolina Parakeet *C. c. ludovicianus*, separated by the Appalachians (Snyder & Russell 2002). Considered common when described in the late 1700s, but as early as 1831 the species was rapidly declining as a result of persecution due to its habit of damaging fruiting crops. The birds disappeared in advance of European settlement of the west and, as the species became rarer, there was an increase in collecting for aviculture. By the end of the 19th century, Carolina Parakeet was almost extinct, and the last confirmed report from the wild was in Florida on 18 April 1904 (McKinley 1985). Several parakeets were kept in captivity, but breeding success was low and mortality high. The last bird died in Cincinnati Zoo on 21 February 1918 (Hume & Walters 2012), apparently in the same enclosure in which the last Passenger Pigeon had expired just four years earlier.

Carolina Parakeet is known from at least 720 skins and 16 skeletons (Hahn 1963, Luther 1996) and c.50 eggs, but not all of the latter are considered authentic (McKinley 1977). The nominate subspecies was generally green with a bluish tint, paler on the underparts;



Figure 7a (left). Carolina Parakeet *Conuropsis carolinensis* NMW 50.795 showing the red suffusion aberration; Fig. 7b (right) normal-coloured bird BMNH 1896.12.1.57, dorsal, ventral and lateral views (Julian P. Hume / © Natural History Museum, Tring). This condition is due to long-term confinement and poor diet

forehead, lores, bare skin around eye and upper cheeks orange; rest of head and upper part of neck, bend of wing, carpal edge and thighs yellow; outer webs of primaries yellow at base; tail green; bill yellowish horn; iris pale brown, legs and feet pinkish-brown. The western race differed in being greener, with less bluish tint, having less yellow on wings and being generally paler. As far as we are aware, there has not previously been any description of colour aberrations in the species.

NMW (Naturhistorisches Museum Wien) 50.795 (Fig. 7a). Purchased from the Leverian sale in 1806, it appears that it may have been a captive individual (data from label). It differs dramatically from normal-coloured specimens (Fig. 7b), the green of the mantle and back being replaced by brownish orange and the underparts with yellow, with more orange in the central breast. The wing-coverts are green, richly suffused orange, whereas the primaries and tail are unaffected, being the usual green. The yellow of the head is also replaced by orange, but the bill, legs and feet are normal. A second captive specimen (NHMW 50.682) exhibits similar coloration and was also purchased from the Leverian sale.

The aberrant coloration exhibited by these birds is caused by an increase and abnormal distribution of red / orange psittacin, a condition known in parrots as red suffusion (Martin 2002). In very rare cases, the increase of red pigment is due to inheritable factors (mutations), but usually it is ill health and / or food deficiency that are the cause (A. K. Jones pers. comm.). Protein deficiency and liver diseases are widely recognised as causing persistent reddish feathering, and lack of direct sunlight, presumably resulting in a lack of vitamin D, may also be a contributory factor. Given that the Vienna specimen was in captivity prior to 1806, when little was known about natural diet, the red suffusion was probably the result of poor physical condition and / or food deficiency.

GEORGE EDWARDS' PARROT *Amazona* sp. (Fig. 8a)

In 1764, George Edwards, the celebrated 18th-century naturalist, painter and author, produced a watercolour of an unknown parrot (see Fuller 2000: 209; Fig. 8a). The painting



bears the inscription: 'A very uncommon parrot from Jamaica. Drawn from Nature the size of life by G. Edwards, July 1764.' On the back in Edwards' own hand is a more detailed description, repeated here verbatim:

'The insides of the wings and under Side of the tail is of a Durlis [meaning unknown] yellow, the colours of the upper sides casting faintly through them. This bird was lent to me by Dr. Alexander Russel and is preserved in his collection. It was shot in Jamaica and brought Dried to England. The people on Jamaica did not remember Ever to have Seen one of this species of Parrots before.

Geo. Edwards, July, 1764.

Some of the fethers have their tipps red and Others have them yellow. The fethers on the under sides, Back and rump have yellow with fine transverse lines of red.'



Figure 8a (top). Watercolour dated July 1764 by George Edwards of an *Amazona* parrot, probably *A. collaria*, exhibiting the opaline aberration; the skin was taken on Jamaica and brought to England, but its whereabouts are unknown (© Errol Fuller). Fig. 8b (below). The two extant Jamaican *Amazona* parrots, Yellow-billed Amazon *A. collaria* BMNH 1891.4.1.32, far left dorsal, and second from right ventral views; Black-billed Amazon *A. agilis* BMNH 1845.4.29.3, second from left dorsal, and second from right ventral views, alongside a Cuban Amazon *A. leucocephala* BMNH1890.6.1.158, third from left dorsal, and far right ventral views (Hein van Grouw / © Natural History Museum, Tring).

TABLE 1

Measurements of Jamaican *Amazona* parrots compared with Edwards' Parrot painting. All specimens held at Natural History Museum, Tring. TL = Total length; WL = Wing length; HL = Head length (head and bill); BD = Bill depth. {n = number of specimens}; (M = mean); Range = smallest to largest; [SD = Standard deviation]. Edwards' Parrot falls within low range of *A. agilis* in all measurements except head length and bill depth, which are too large compared with other measurements, suggesting that the painting was not accurately drawn to scale.

Species	TL {n} (M) Range [SD]	WL {n} (M) Range [SD]	HL {n} (M) Range [SD]	BD {n} (M) Range [SD]
<i>Amazona collaria</i>	{8} (256.2) 225–280 [20.48]	{8} (178.7) 175–190 [5.82]	{8} (58.5) 53–70 [6.04]	{8}(27.1) 26.0–28.0 [0.99]
<i>Amazona agilis</i>	{6} (238.3) 225–245 [8.16]	{6}(166.0) 155–175 [7.79]	{6}(56.6) 55–60 [2.58]	{6} (24.0) 23.0–25.0 [0.89]
Edwards' Parrot	{1} (243)	{1}(165.0)	{1}(62.0)	{1} (25.0)

Because of the uniqueness of this specimen and the fact that it is associated with one of the West Indian Islands, where so many parrot species have become extinct (Rothschild 1907, Greenway 1967, Fuller 1987, 2000, Hume & Walters 2012, Wiley & Kirwan 2013), George Edwards' parrot has been discussed as a possibly extinct species (Shuker 1999, Fuller 2000). It bears a strong resemblance to an *Amazona* parrot, a widespread genus in Middle and South America as well as the West Indies (Forshaw 1989, Juniper & Parr 1998). Furthermore, two extant *Amazona* are native to Jamaica, Yellow-billed Amazon *A. collaria*, with a mean 25.62 cm in total length ($n = 8$), and Black-billed Amazon *A. agilis*, mean 23.83 cm ($n = 6$) (Table 1). The supposed life-size rendition of Edwards' Parrot measures c.24.3 cm long (from top of head to tail tip), is intermediate between *A. agilis* and *A. collaria*, and fractionally larger than *A. agilis*. However, wing length is shorter, while combined head and bill length is much larger than either species; bill depth is intermediate between the two. This suggests that Edwards' 'life-size' rendition is not accurate, and that any measurements from the illustration must be viewed with great caution.

Yellow-billed Amazon (Fig. 8b) is predominantly apple-green, with blue on the head merging into green, throat and lower cheeks pinkish, greater wing-coverts, alula and outer webs of flight feathers blue, uppertail green with yellow tips and red basally. Black-billed Amazon (Fig. 8b) is mainly green, with red primary-coverts, blue primaries, darker blue secondaries, and green uppertail with outer tail feathers red at base of inner webs. Edwards' depiction has predominantly red coloration, but more importantly it shows the blue in the primaries as being unaffected. Edwards' Parrot may have exhibited an inheritable form of red suffusion, but more probably the colour was caused by a mutation known as opaline (see Kakapo). This gene markedly reduces the distribution of melanin, especially in the body plumage, and increases the spread of psittacin; this pigment is strongly emphasised in species with red, orange or pink psittacin (Martin 2002). Normally, Yellow-billed Amazon has reddish-pink psittacin in its plumage, therefore we suggest that Edwards' Parrot was not an extinct species, but an opaline aberration of Yellow-billed Amazon, with increased deposits of psittacin. It is less likely to be an aberrant Black-billed Amazon due to the lack of red psittacin in the normal plumage coloration (wild type) and the black bill (Fig. 8b). Although not from Jamaica, if there is any doubt concerning the collection locality, Cuban Amazon *A. leucocephala* (Fig. 8b) might also be considered as another strong candidate for Edwards's Parrot. This species has even more reddish-pink psittacin in its plumage than *A. collaria*.

Strigopidae

KAKAPO *Strigops habroptilus* Gray, 1845

Formerly occurred on North Island, South Island and Stewart Island, and prior to human occupation of the islands had one of the widest distributions of any New Zealand bird (Gibbs 2007). It is the only known flightless parrot, which made it extremely vulnerable to human disturbance. Kakapo began to decline following Polynesian settlement and this accelerated with the arrival of European settlers. The introduction of mammalian predators, especially rats, mustelids, domestic cats and dogs (Sutherland 2002), rapidly eliminated it from most areas, and the demand for museum skins in the late 19th century, when thousands were collected (Butler 1989), reduced the species to a few remote localities. The last report on North Island was in 1927, three males were recorded on South Island in 1987, but have not been recorded since, and the last record on Stewart Island was in 1997, when a female was transferred to predator-free Codfish Island (Powlesland *et al.* 2006). Due to intense conservation management, around 126 individuals survive on four offshore islets (BirdLife International 2013), but the future of the Kakapo is far from secure.

A nocturnal, cryptic species, its plumage provides perfect camouflage in its natural habitat of mossy, damp forest. The upperparts are olive-yellow and moss-green barred or mottled black or dark brownish grey; underparts pale greenish yellow streaked brown, forehead yellowish brown; and face, neck, belly and undertail-coverts more yellowish, streaked pale green and finely mottled brownish grey. Nevertheless, there is much individual variation. The bill is pearly grey with an ivory tip, iris dark brown, and legs and feet greyish-brown. However, at least two wild-caught yellow specimens of Kakapo exist.

CMNZ (Canterbury Museum, New Zealand) Av2059 (Fig. 9a). This specimen was captured by the Bradshaw brothers in 1898 near Cromarty, Fiordland, which is in Kisbee Bay in Preservation Inlet (Galbreath 1989). Walter Buller, the New Zealand ornithologist and dealer, kept it alive on a diet of potatoes before it became part of his collection (Butler 1989). It was also illustrated in an originally unpublished painting entitled 'Two Kakapos' by J. G. Keulemans (Fig. 9c; Galbreath 1989). Buller (1905) recorded that the entire plumage was vivid canary yellow, fading to pale yellow on the cheeks and throat; the bill was white and the legs and feet flesh-coloured. It is very clear from Buller's account that he considered it to be one of his most precious specimens.

The yellow coloration is almost certainly due to the mutation *ino*, which can be described as 'a strong qualitative reduction of melanin' (van Grouw 2013). Among parrot breeders, this mutation is known as *lutino*, because of the predominant yellow colour. In *ino* mutations, melanin synthesis scarcely occurs, which results in the yellow psittacin becoming clearly visible. Because *ino* is a recessive and sex-linked mutation (van Grouw 2013), a wild-caught *ino* Kakapo is likely to be female (see Passenger Pigeon).

AM (Auckland War Memorial Museum) LB8526 (Fig. 9b). A second aberrant specimen, a relaxed mount, was collected by G. Mueller, a surveyor and engineer, in Jackson Bay, South Westland, prior to 1888 (Buller 1888: 178). Although superficially similar to the *ino* Kakapo described above (Fig. 9a), it differs in having natural green tips to the feathering (unaffected melanin deposits) in parts of its plumage, especially on the head, mantle and wings. This aberration vaguely resembles certain forms of recessive leucism in parrots (Martin 2002), but the overall appearance strongly suggests opaline (see Edwards' Parrot), a condition that alters pigment distribution. In this specimen, the presence of unaffected melanin only in the feather tips (especially on head and mantle), the absence of melanin (barring) in the tail and outer webs of the flight feathers, and because the melanin in the inner webs is unaffected, further supports an opaline aberration. Because this mutation is



Figure 9. Three colour aberrations exhibited by Kakapo *Strigops habroptilus*: Fig. 9a (top left). Ino aberration CMNZ Av2059, dorsal, lateral and ventral views (© Paul Scofield / Canterbury Museum, New Zealand); Fig. 9b (top right) opaline aberration AM LB8526, dorsal, lateral and ventral views (© Jason Frogatt / Auckland War Memorial Museum); Fig. 9c (centre left) originally unpublished painting of CMNZ Av2059 by John Gerrard Keulemans entitled 'Two Kakapos' (from Galbreath 1989); Fig. 9d (centre right) parblue aberration BMNH 1853.6.9.1 type of *S. greyi*, dorsal, lateral and ventral views (© Natural History Museum, Tring); Fig. 9e (bottom left) mounted bird in the collection of Errol Fuller (Julian P. Hume); Fig. 9f (bottom right) normal-coloured Kakapo BMNH 1927.12.18.1 (Hein van Grouw / © Natural History Museum, Tring) .

proven to be recessive and sex-linked in all parrots (Martin 2002), and if our opaline determination is correct, the AM specimen is probably female.

BMNH (Natural History Museum, Tring) 1853.6.9.1 (Fig. 9d). The reduction of melanin resulting in yellow is not the only colour aberration exhibited in Kakapo,

as similar reduction of psittacin produces individuals with predominantly blue plumage. One notable specimen (BMNH 1853.6.9.1) is the holotype of *S. greyii* (Fig. 9d), which has an intense blue hue to the upperparts and some on the underparts, and was originally considered to be a different species (Gray 1862). A second specimen, owned by E. Fuller, is extensively marked with turquoise-blue (Fig. 9e). In BMNH 1853.6.9.1, the tail and flight feathers are particularly worn, which strongly suggests that it was kept in captivity. In both specimens, the upperparts exhibit the more extensive and stronger blue hue. Although the BMNH specimen was seemingly a captive, the absence of psittacin is almost certainly not due to confinement. Reduction in intensity of yellow psittacin due to poor physical health (mostly liver diseases) or a chronically deficient diet is extremely rare in parrots (A. K. Jones *in litt.* 2013), so it is more likely that the Tring specimen was caught because it was an unusual coloration and subsequently kept in captivity. We believe, therefore, that both of the above-mentioned specimens exhibited the parblue aberration (see Rodrigues Parakeet).

Because this mutation can be extremely variable depending on the wild type, the phenotype can exhibit blue coloration that is unevenly distributed. In the case of a parblue Kakapo, the olive and moss-green upperparts in a normal-coloured bird (Fig. 9f) are more likely to exhibit stronger blue than the more yellowish-green underparts.

Callaeidae

HUIA *Heteralocha acutirostris* (Gould, 1837)

The largest member of the New Zealand endemic family, the Callaeidae (wattlebirds), and confined to North Island, Huia exhibited extreme sexual dimorphism in the bill, the male's being relatively short and slightly decurved, and the female's much longer and heavily curved. The sexes evolved different foraging techniques; males used their strong, short bill for chiseling at hard substrates such as decaying wood to extract insect larvae, whereas females used their long, thin bill for probing crevices (Buller 1873). The fossil record reveals that it was originally widespread on North Island (Worthy & Holdaway 2002), but by the time Europeans arrived the species was largely restricted to the south of the island. Huia declined rapidly as human settlement proceeded (Buller 1905) and widespread destruction of undisturbed, old-growth forest appears to have been a major factor in its demise (Morris & Smith 1995). As it became rarer, large numbers were taken for the feather trade and museums; by the late 19th century, Huia was effectively extinct (Hume & Walters 2012). A few were recorded between 1890 and 1907, with the last confirmed sighting on 28 December 1907 (Myers 1923) despite claims that it survived until at least the 1960s.

Huia is known from hundreds of skins (Fuller 2000); a unique egg and subfossil remains are at the Museum of New Zealand, Wellington. General coloration was black with green gloss; terminal tail band white; facial wattles orange; bill ivory; iris brown, legs and feet black. The sexes were similar; the juvenile duller, with a brownish wash. A specimen illustrated by Keulemans *c.*1900, London, for Buller (1905) entitled 'Three Huia', but never published, depicts a pure white individual (Keulemans & Coldewey 1982) (Fig. 10). Buller was told that the specimen was for sale, but when he inquired about it, the owner had already sold the bird (Buller 1905); its whereabouts are now unknown.

Although the painting by Keulemans was probably made from a mounted specimen and therefore the dark eye is not reliable; it is unlikely that the individual exhibited true albinism. Albinism, from the Latin *Albus* (= white), is defined as a 'total lack of melanins in feathers, eyes and skin' (van Grouw 2013). The complete lack of melanin is due to the hereditary absence of the enzyme tyrosinase in the pigment cells, as this enzyme is necessary for initiating melanin synthesis; melanin cannot be created without it (Fox &



Figure 10. Unpublished illustration by John Gerard Keulemans of a female ino Huia *Heteralocha acutirostris* (far right) (© Te Papa 1993-0029-6). We have been unable to locate this specimen.

Vevers 1960). In almost all cases, this results in a completely colourless bird, whereas the red or pinkish hue present in the eyes and skin is caused by blood being visible through the colourless tissue. Albinos rarely occur in the wild, although the mutation is not uncommon in birds. Their scarcity is due to the absence of melanin in the eye, which makes them extremely light-sensitive and susceptible to damage from sunlight, and they also have a poor depth of vision. Therefore, it is not primarily the white plumage that makes albinos vulnerable in the wild, but their poor eyesight; most succumb to starvation and predation soon after fledging (van Grouw 2013).

The bird illustrated by Keulemans (Fig. 10) appears to be adult, which almost certainly eliminates albinism as a cause. It is more likely that progressive greying, leucism or ino was involved. In progressive greying, the bird would have moulted several times before becoming entirely white, but an aberrant pied Huia would surely have been a target for collectors; it is unlikely that such a bird went unnoticed, especially as it survived to adulthood. Leucism, which is a congenital and heritable absence of pigment cells from all of the skin areas where they would normally provide the growing feather with pigment, is very rare in wild birds (van Grouw 2012, 2013), and thus probably can be ruled out. As ino is not uncommon in wild birds, and individuals can be all white, it is the most likely explanation for the aberration. The fresh plumage of an ino may show some very pale coloration, but it is the strong bleaching effect of natural light that rapidly turns the bird almost pure white. Furthermore, although the eyes of an ino are also reddish due to the reduction of melanin, they do not suffer the poor eyesight of an albino. As ino birds survive comparatively well in the wild and the mutation is not uncommon, we believe that Keulemans illustrated a Huia exhibiting this condition.

Although we cannot be absolutely certain about the colour aberration of this Huia without a specimen, the fact that the illustrated bird is a female strongly supports the recessive and sex-linked mutation characteristic of an ino (van Grouw 2012, 2103).

Cardinalidae

TOWNSEND'S BUNTING *Spiza townsendi* (Audubon, 1834)

The unique type (Fig. 11a) was collected by J. K. Townsend on 11 May 1833, at New Garden, Chester County, Pennsylvania, and described the following year (Audubon 1834). There has been much debate as to its status, it being variously considered an extinct species (e.g. Paynter 1970, AOU 1983), a colour variant of Dickcissel *S. americana* (Parkes 1985) or a hybrid female *S. americana* × male Blue Grosbeak *Passerina caerulea* (E. Coues in Sharpe 1888). The type (USNM 10282) is in poor condition, with the original coloration now barely discernible; the specimen has foxed, producing an overall wash of pale brownish beige (Fig. 11b).

Audubon (1834; Fig. 11c) described the fresh plumage as having the upperparts, head, neck, sides and upper breast slate-blue; back and upperwings tinged yellowish brown, streaked black on interscapular area; eyestripe, chin, throat, central line on underparts and edge of wing white; black-spotted line from lower corner of mandible down side of throat, connecting with crescent of streaks on upper edge of slate-blue breast. Adult male Dickcissel (Fig. 11d) has olive-grey crown and cheeks, brown mantle streaked black on back, wings darker, rusty patch on shoulder, and superciliary stripe and underparts yellow, becoming buff on belly, with a black throat patch. Variable dark streaking occurs on the flanks and sometimes the belly. Females (Fig. 11d) have a brown crown and cheeks, with black-streaked flanks. Juvenile males (Fig. 11d) are browner, and the throat patch is black-speckled. Juvenile females are duller and browner, and have black or brown speckling on upper breast.

Parkes (1985) suggested that Townsend's Bunting was a female colour variant of Dickcissel that lacked normal carotenoid pigments, resulting in the complete absence of yellow. Holt (2002–03) questioned this conclusion, as Townsend explicitly stated that the specimen was male, but considered that it was an aberrant first-year male Dickcissel. Our comparison of adult males, females and juvenile Dickcissels with the unique skin and original illustration of Townsend's Bunting (Audubon 1834) suggests that the situation is far more complex. For example, the lack of yellow due to diet or a single genetic change would result in the bird lacking all yellow pigments, leaving the melanins unaffected (Martin 2002).

If Townsend's Bunting was a female Dickcissel as suggested by Parkes (1985), the diagnostic brown crown and cheeks should still be present. Townsend stated that it was a male, so it should have exhibited the black throat patch, unless juvenile. Finally, Holt's (2002–03) suggestion that the specimen was a juvenile male is supported by the lack of a full black throat patch, but juvenile males are brown above, not grey. In the Townsend's Bunting specimen, there is black speckling (eumelanin) concentrated on the sides of the upper breast, no dark streaking on the flanks, and the upperparts are grey. This coloration and pattern is not found in any plumage of Dickcissel.

At this stage, we cannot determine if the specimen of Townsend's Bunting is the result of hybridisation, a colour aberration, or caused by some other genetic change. That it might be an extinct species is highly unlikely, but it cannot be ruled out. No molecular work has been undertaken on the skin, but mtDNA analysis may be the only way to resolve this conundrum.



Figure 11. Townsend's Bunting *Spiza townsendi*: Fig. 11a (top) holotype, USNM 10282, male (Julian P. Hume); Fig. 11b (above left) illustration showing the specimen today (above), and how it would have looked when described by Audubon in 1834 (below) (Julian P. Hume); Fig. 11c (above right) from Audubon (1834); Fig. 11d (left) Dickcissel *S. americana*, from left to right in lateral view, adult male BMNH 1899.2.1.4108, juvenile male BMNH 1885.13.14.147, and adult female BMNH 1899.2.1.4126 (Hein van Grouw / © Natural History Museum, Tring). The cause of this probable colour aberration is unclear.

Discussion

Colour aberrations are not uncommon in birds (van Grouw 2006, 2013), so it is unsurprising that they occur in extinct and threatened species. However, few of these extinct bird colour aberrations had been analysed, despite the specimens themselves being apparently well known. The factors involved in producing unusual coloration can be complex, and it appears that in some species discussed here, illness and poor diet in captivity resulted in aberrant plumage. There may also be a bias in collecting from wild populations, e.g. the parblue aberration of *Psittacula exsul*, white *Porphyrio albus* or parblue and yellow specimens of *Strigops habroptilus*, as it is more likely that an unusual-coloured example was collected rather than normal-coloured birds. However, despite >1,500 skins of Passenger Pigeon, >700 skins of Carolina Parakeet, and hundreds of Huias having been collected, we have only located single colour aberrations of Passenger Pigeon and Huia, and two Carolina Parakeets, none previously described in the literature. During the 19th century, the demand for unusual colour varieties of birds was extremely high and examples

TABLE 2

Causes and effects of colour aberrations of extinct and endangered birds discussed in the text. *Conditions caused by physical factors and not by true genetic aberrations.

Colour aberration	Cause	Effect	Species exhibiting mutation
Progressive Greying	Partial or total lack of melanins in feathers due to progressive loss of pigment cells in some or all of the skin areas with age.	All-white plumage or all-white feathers mixed with normal-coloured feathers. Bill and feet can be normal-coloured or pink. Always normal-coloured eyes.	Lord Howe Gallinule <i>Porphyrio albus</i>
Melanism	Abnormal deposit of melanin in skin and / or feathers.	Normal pattern and / or pigment distribution is changed, but plumage is not necessarily darker.	Sharpe's Rail <i>Gallirallus sharpei</i>
Brown	Qualitative reduction of eumelanin due to incomplete synthesis (oxidation) of eumelanin.	Black becomes brown.	Passenger Pigeon <i>Ectopistes migratorius</i>
Red Suffusion*	Poor physical condition in captivity.	Reddish-orange psittacin randomly spread through the plumage.	Carolina Parakeet <i>Conuropsis carolinensis</i>
Pigment loss*	Due to food deficiency, lacks sufficient quantities of tyrosine in diet, resulting in disturbed melanin synthesis.	Random white feathering intermixed with normal-colours; bill and feet normal-coloured.	Mascarene Parrot <i>Mascarinus mascarinus</i>
Opaline ⁽¹⁾	Reduced melanin distribution, especially in the body plumage, and an enhanced spread of psittacin, notably red psittacin.	A predominant reddish coloration with minimal dark (melanin) plumage markings.	Edwards' Parrot <i>Amazona cf. collaria</i>
Opaline ⁽²⁾	Reduced melanin distribution, especially in the body plumage.	Predominant yellow coloration with minimal dark (melanin) plumage markings.	Kakapo <i>Strigops habroptilus</i>
Ino ⁽¹⁾	Strong qualitative reduction of melanin.	Yellow psittacin (lutino) clearly visible	Kakapo <i>Strigops habroptilus</i>
Parblue ⁽¹⁾	Quantitative reduction of psittacin.	Coloration between green and blue.	Kakapo <i>Strigops habroptilus</i>
Parblue ⁽²⁾	As above.	Coloration between green and blue.	Rodrigues Parakeet <i>Psittacula exsul</i>
Ino ⁽²⁾	As above	Pale, cream-coloured feathering that is rapidly bleached to white by exposure to light. Paler bare parts, reddish eyes.	Huia <i>Heteralocha acutirostris</i>
Undetermined	Lack of lipochrome pigments? Hybridisation?	Loss of yellow pigmentation	Townsend's Bunting <i>Spiza townsendi</i>

of extinct or endangered species were particularly sought after; a yellow Kakapo owned by Buller was considered to be one of his most prized possessions.

In ornithology in general, colour aberrations are poorly understood, which has been further exacerbated by incorrect terminology (van Grouw 2006, 2012, 2013). For example, almost all birds that exhibit any white feathering are termed 'partially albinistic', and this is often applied to extinct birds too, e.g. the Vienna Mascarene Parrot. The inherent condition of true albinism cannot, by definition, be partial. Either true albinism is present, whereby the individual lacks the enzyme tyrosinase, or white feathering can be explained by other factors, e.g. leucism, ino, progressive greying and poor diet (van Grouw 2006, 2012, 2013). Studies of extant birds that exhibit unusual coloration can assist understanding of why similar aberrations occurred in extinct species, and can sometimes provide new information about the bird's ecology or a specimen's history. In these cases in particular, it is important to understand the processes involved and to use correct terminology (Table 2). The aim of this study is to highlight extinct or endangered bird species that exhibit colour aberrations and we would welcome hearing from curators with additional specimens of interest. It is probable that many more examples exist than those discussed here.

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