A black Page in the French partridge's history: the melanistic variety of Red-legged Partridge Alectoris rufa

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A black page in the French partridge's history: the melanistic variety of Red-legged Partridge *Alectoris rufa*

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Summary.—The melanistic variety of Red-legged Partridge *Alectoris rufa* was described from a small population in western France around the 1850s. In this region, the Red-legged Partridge population as a whole was hunted, but melanistic individuals were targeted for both private and museum bird collections, and by 1865 the variety was extinct in western France. An extensive search for extant specimens documented 13 melanistic birds in six museums, and their details are presented here. Remarkably, some of these specimens were collected in areas elsewhere in France or even in other countries. After 1915, the allele for melanism appears to have been lost within the Red-legged Partridge population as a whole, and we discuss possible reasons for this.

'…, nous sommes persuadé que cette perdrix qui tend à demeurer en Anjou [now Maine-et-Loire] se multipliera dans quelques années, au grand contentement des amateurs de la chasse et de l'ornithologie.' […, we are persuaded that this partridge which tends to remain in Anjou will multiply in a few years, to the great satisfaction of the amateurs of hunting and ornithology.] (de Soland 1861: 146).

Colour aberrations, especially melanistic varieties, have always confused ornithologists. In the past, when little was known concerning plumage pigmentation and mutations, aberrant-coloured birds were often viewed as new taxa, and were named scientifically. Perhaps the oldest and best-known example is the melanistic form of Grey Partridge *Perdix perdix*, which was named as a species, the Mountain Partridge *P. montana*, by Brisson (1760; Fig. 1).

Melanism is the only mutation in which there is no real loss of pigments or changes in the shape or size of the melanin granules (van Grouw 2017). Therefore the plumage of a melanistic bird often is not obviously aberrant, i.e. the plumage looks 'natural' but may be completely different to any known species. That melanistic birds were, especially in the past, mistaken for 'new species' is therefore understandable. Sometimes 'new species' were erected on the basis of a single specimen simply because it was differently coloured, like Sharpe's Rail (Hume & van Grouw 2014). Mostly, however, the confusion was based on melanistic forms that occurred, or still occur, quite commonly in the relevant species / populations. The fact that more individuals were found was, for many ornithologists, evidence that these aberrant birds were indeed species. An example is the melanistic form of Red-legged Partridge *Alectoris rufa*. This aberration was, for a period, quite common in a small area in western France, and it was consequently described as *Perdix Atro-rufa* (de Soland 1861; Fig. 2). The mutation also occurred sporadically elsewhere in Europe, as will be demonstrated later in this paper. A remarkable bird, occurring in small numbers, was inevitably the target of collectors, so specimens were deliberately obtained for museums and collectors of curiosities. Currently, the mutation is apparently not present in any extant Red-legged Partridge population, and just 13 melanistic specimens remain in museums.

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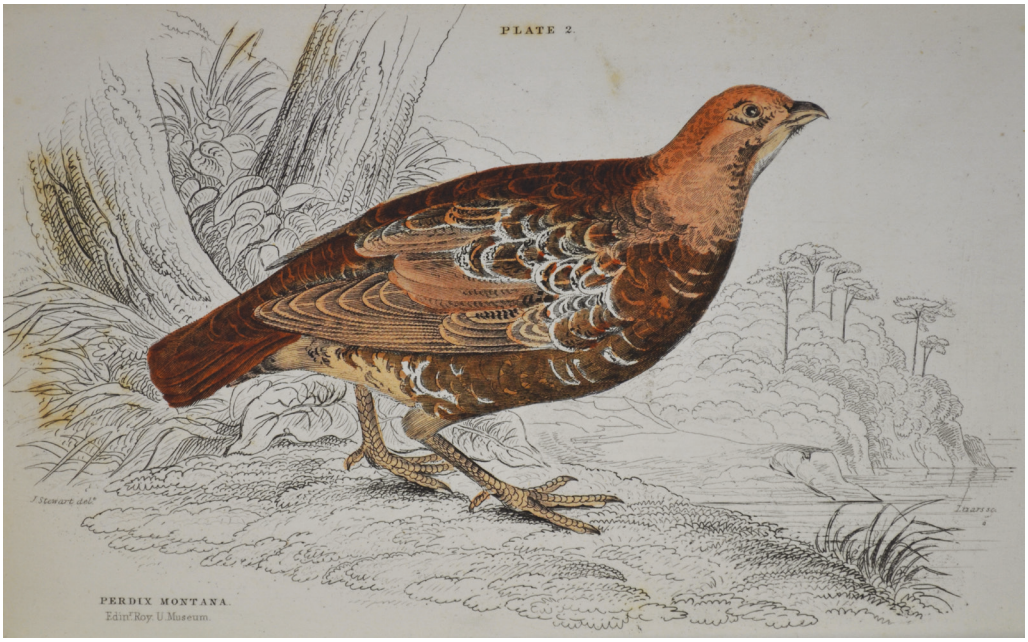

Figure 1. Mountain Partridge *Perdix montana.* Brisson knew this 'species' only from the mountains of Lotharingen, France, hence *montana*. However, subsequently '*montana*' was proven to occur all over Europe and to be a melanistic form of Grey Partridge *P. perdix*. From Sir William Jardine's *Naturalist's library,* 1834, *The natural history of game birds* (Hein van Grouw, © Natural History Museum, London)

Figure 2. *Perdix atro-rufa*, the melanistic variety of Red-legged Partridge, described taxonomically by de Soland (David Riou, © Musées d'Angers)

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Here, we discuss the nature of melanism in Red-legged Partridge and its history, and present information for all of the remaining specimens.

History of *Perdix atro-rufa* in France

The first records of melanistic Red-legged Partridges are from France in the mid-19th century. A small population was discovered south-west of Cholet, at the hamlet of Cou-Pinson, part of Saint-Aubin-des-Ormeaux, in the department of Vendée, Pays-de-la-Loire, western France. A specimen was sent to the Linnaean Society of Maine-et-Loire in May 1858 by Esprit Guillou (1798–1870), a naturalist from Cholet and member of the society. During the society's committee meeting on 18 May 1858, it was decided that the specimen represented a new 'race'. They named it *Perdix Atro-rufa* and a description with colour plate (Fig. 2) was published by de Soland (the society's president) in 1861. In the following years, various authors published information concerning the occurrence of *atro-rufa*, enabling us to compile a short history of the population.

The first melanistic bird was discovered by Guillou as early as 1846 (Millet de la Turtaudière 1868) in the area around Saint-Aubin-des-Ormeaux, Vendée department (de Soland 1861, Vincelot 1867). As this is only a few km from Cholet, Maine-et-Loire department, many authors considered the provenance of *atro-rufa* to be 'the vicinity of Cholet', but in fact the mutation was never observed in Maine-et-Loire (Millet de la Turtaudière 1865, 1868). After the first observation, at least 5–6 family groups including dark-coloured individuals were recorded in the area annually (de Soland 1861, Vincelot 1865), and the aberration would probably have become established in the population if it had not been targeted by collectors. Specimens were collected for private collections, as well as being sold as game at the markets in Cholet, or sent to Paris for research (Vincelot 1867).

De Soland (1861) already warned as to the negative effects of over-exploitation, and Millet de la Turtaudière (1865) reported that *atro-rufa* was killed by poachers and repeated that excessive hunting would threaten the population. By then, it was already too late as, according to Baugas (Lemetteil 1869), the last six individuals were killed in spring 1865. In less than 20 years after its discovery, the small population of melanistic Red-legged Partridges was wiped out. At that time, specimens were present in the private collections of Baugas (several), Guillou (four) and Lemetteil (one), and in the natural history museums of Angers (two), Saumur (at least one) and Paris (two) (de Soland 1861, Millet de la Turtaudière 1865, 1868, Vincelot 1865, Lemetteil 1869). Much of the above information was summarised by Mayaud (1947). He also mentioned specimens in different museums like Cholet and some English specimens. However, he did not mention the specimens held in Angers, Saumur and Paris. Remarkably, no-one appeared to be aware of a specimen collected in 1844 in the south of France, present in Marseille museum, which was depicted by Hachisuka (1928).

Perdix atro-rufa in England

In early 1900 the mutation appeared again, but this time in England, and three specimens are present in the Natural History Museum, Tring (NHMUK) collection (Fig. 8). Ogilvie-Grant (1912) mentioned and depicted (Fig. 3) the variety; 'The most extraordinary variety, however, that we have ever examined, is that shown in the second figure. It has the fore-part of the head, eyebrow-stripes, cheeks and throat black; the rest of the head, mantle, breast, and flanks dull vinous-red, with the exception of a few white feathers on the middle of the breast; and the abdomen, thighs, and under tail-coverts are dull greyish-brown, with the exception of a few buff feathers on the middle of the belly. The tail-feathers are dull greyish-

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Figure 3. Melanistic variety of Red-legged Partridge *Alectoris rufa* depicted in Ogilvie-Grant (1912), probably based on the specimen collected in Essex in October 1908, NHMUK 1908.10.22.1; see Figs. 8 and 10 (Hein van Grouw, © Natural History Museum, London)

brown, like the lower back, rump and wings.' He did not mention the earlier French history of this aberration, but he may have been unaware of it. Furthermore, he did not mention where the specimen came from, but it was in all likelihood that shot in Essex in 1908 (see Extant specimens). In March 1915, two *atro-rufa* specimens were present in what is now the NHMUK collection, and Ogilvie-Grant (1915) exhibited a series of aberrant partridges at the Zoological Society meeting. He noted: 'The remarkable variation which I now exhibit has the head, eyebrow-stripes, cheeks, and throat black, and the rest of the plumage dull vinaceous-red with a patch of white feathers in the middle of the belly, forming an irregular horse-shoe mark. … and it seems a remarkable coincidence that a second specimen of this quite unique variation of the red-leg should have been killed exactly six years after the first, and in nearly the same locality.' Coincidence or not, in September 1915, the museum received a third specimen taken near the same locality as the second bird the year before.

The English melanistic specimens were also described by Bateson & Bateson (1925) as the 'dull variety', which they named *Alectoris rufa rufa* Var. *obliterata*. Both Lowe (1945) and Ash (1966) mentioned the melanistic variety briefly without adding further details, although Ash also referred to the French population.

Red-legged Partridges in England originated from France, with the first introduction orchestrated by King Charles II in 1673 (Potts 2012). These birds came from Chambord, department Loir-et-Cher, in the Loire Valley, and were released in Windsor Great Park, on the Berkshire / Surrey border. This population apparently died out quickly. After several more attempts, the species eventually became well established on the Suffolk coast by *c*.1790. However, over the rest of England Red-legged Partridges remained uncommon until the late 1950s (Barbanera *et al*. 2015). It seems probable that the English melanistic birds derived directly from the French population. However, the French population described by de Soland came from Saint-Aubin-des-Ormeaux, Vendée department, which is *c*.250 km west of Chambord, Loir-et-Cher department, and it is unlikely that the rare allele for

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melanism was present in that population too. Furthermore, *contra* Potts (2012), molecular work demonstrates that English Red-legged Partridges are genetically closer to Italian and Corsican populations than to those of mainland France, with the three melanistic birds not diverging in this respect from other historical English specimens, and no relationship to birds from the Loire Valley is evident (Barbanera *et al*. 2015). Consequently, we consider the melanistic English birds as a fresh occurrence of the same mutation, rather than originating from the original French population.

Museum specimens of *Perdix atro-rufa*

Probably the oldest museum specimen, collected in 1844, is in Marseille but, apart from Hachisuka (1928), no other author seems to have been aware of it. Based on the pre-1870 literature (de Soland 1861, Millet de la Turtaudière 1865, 1868, Vincelot 1865, Lemetteil 1869) the following specimens were then known: four in Guillou's private collection, 'a few' in Baugas' collection, one in Lemetteil's collection, two in Angers, at least one in Saumur and two in Paris. Mayaud (1947) seemingly listed seven additional specimens; three in London (see above) and four in Cholet. The specimens in Cholet, however, are the same as the Guillou specimens mentioned by earlier authors. Following Guillou's death in 1870 his collection was donated to the Cholet museum (see Extant specimens).

The whereabouts of Baugas' collection are unknown and the specimens are considered lost. Edouard Leon Baugas (1824–1901) was also from Cholet and a friend of Guillou. The specimen from Lemetteil also appears to be lost. Eugène Lemetteil (1822–90), a keen amateur ornithologist from Bolbec, was particularly interested in the avifauna of the department of Seine-Maritime (formerly Seine Inférieure), in Normandy, northern France. The melanistic partridge was sent to him by Abbot Vincelot (Lemetteil 1869). Michel Honoré Vincelot (1815–77) was an abbot at Angers (Crépon 1877), an amateur ornithologist and a member of the Linnaean Society of Maine-et-Loire with a keen interest in the etymology of bird names. Probably initiated by Lemetteil's son-in-law Georges Pinchon, Lemetteil's collection, which comprised approximately 2,000 specimens, both birds and eggs, was sold 14 years after his death by the auctioneer Hommais in Bolbec, and bought by Lemaistre. Although it was Hommais' intention to sell the collection as a whole (letter PEN6 1904-018 in Rouen Museum archive), apparently Lemaistre purchased only part of it (P. Cantrel *in litt*. 2016). At the time, Edmond Lemaistre (1876–1953), a rich textile manufacturer and keen hunter, had just started to assemble a private collection of local birds. Lemaitre's collection as a whole is still at the Municipal Museum in Lillebonne, Seine-Maritime, having been bequeathed to the town in 1953. The melanistic partridge of Lemetteil, however, was never part of the bequest (P. Cantrel *in litt*. 2016), so Lemaistre may have parted with it earlier, as *atro-rufa* was not a local bird, or he never received it in the first place. If the specimen still exists, its whereabouts are unknown to us.

The Château-Musée de Saumur was founded in 1829 and based in the town hall until 1919; apparently an *atro-rufa* specimen was sent to this museum in the mid 1800s (Millet de la Turtaudière 1868). However, currently no melanistic specimen of Red-legged Partridge is present there (MB pers. obs.) and also we have not found any evidence that one was once in the collection (Courtiller 1868).

Extant specimens

Muséum d'Histoire naturelle de Marseille (MHNM), France

One mounted specimen, MHNM.0.394, originally labelled 'Basses Alpes, France 1844' (Fig. 4). No further details known. According to Hachisuka (1928) the specimen is a

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Figure 4. Mounted specimen (MHNM.0.394) at Muséum d'Histoire naturelle de Marseille, originally labelled 'Basses Alpes, France 1844'. A: figured in Hachisuka (1928) (Hein van Grouw). B: photographed in 2016 (Stéphane Jouve, ©Muséum de Marseille)

female, but no evidence of the bird's sex is recorded with the specimen. Until April 1970, 'Basses-Alpes' was the name of the Alpes-de-Haute-Provence, in southern France. If the date and locality are correct, then this specimen was collected before the population in Vendée was discovered, and is probably unrelated genetically.

Muséum national d'Histoire naturelle de Paris (MNHN), France

Two mounted specimens, Cat. Gén. 1858-1318 (other nos. 12436 and 562), originally labelled 'France. Collection du prince Charles Bonaparte, achetée par l'état en 1858', and Cat. Gén. 1859-610 (other nos. 12435 and 561), originally labelled 'femelle, Bretagne. Trouvé sur le marché de Paris en décembre 1859, venant de Bretagne, acquis à Mme Perrot le 15 décembre 1859' (Fig. 5). 12435 and 12436 are former registration numbers used in the 'Catalogue des Oiseaux n°4 placée dans la galerie du muséum d'histoire naturelle'. 561 and 562 refer to these specimens' entries in the 'Catalogue des Montages'. Bretagne (Brittany) traditionally included part of Pays-de-la-Loire, so this specimen probably emanates from the original population.

Muséum des sciences naturelles d'Angers (MHNAn), France

Two mounted specimens, both males, MHNAn.2003.522 and 2003.523 (Fig. 6). In the museum's register (2R24) both are mentioned under the same entry: 16 November 1863, two

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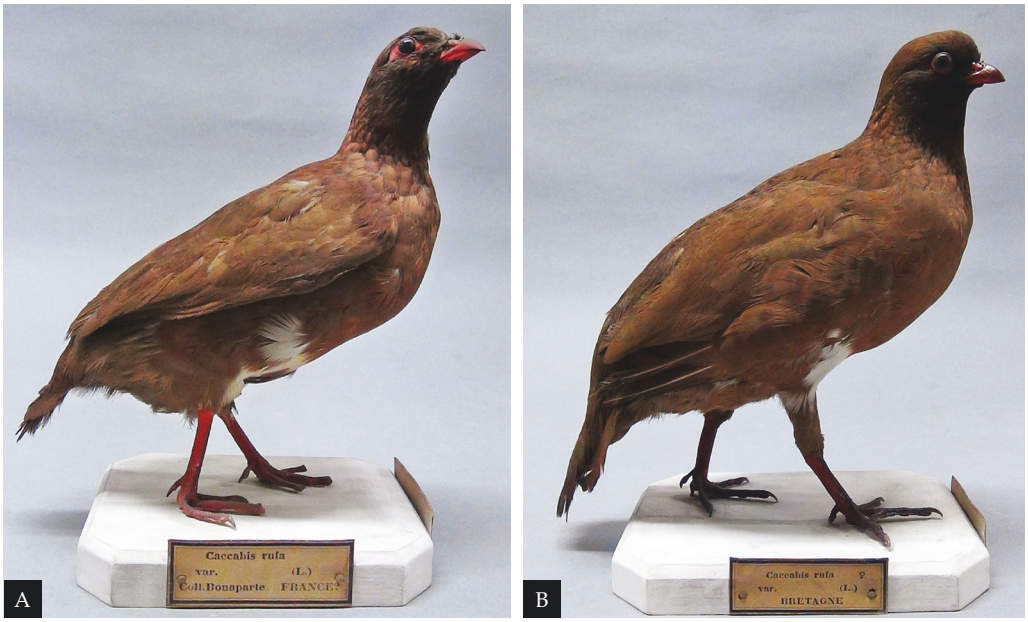

Figure 5. Mounted specimens at Muséum national d'Histoire naturelle, Paris: A: MNHN 1858-1318, originally labelled 'France. Collection du prince Charles Bonaparte, achetée par l'état en 1858'; B: MNHN 1859-610, originally labelled 'femelle, Bretagne. Trouvé sur le marché de Paris en décembre 1859, venant de Bretagne, acquis à Mme Perrot le 15 décembre 1859' (© Muséum national d'Histoire naturelle, Paris)

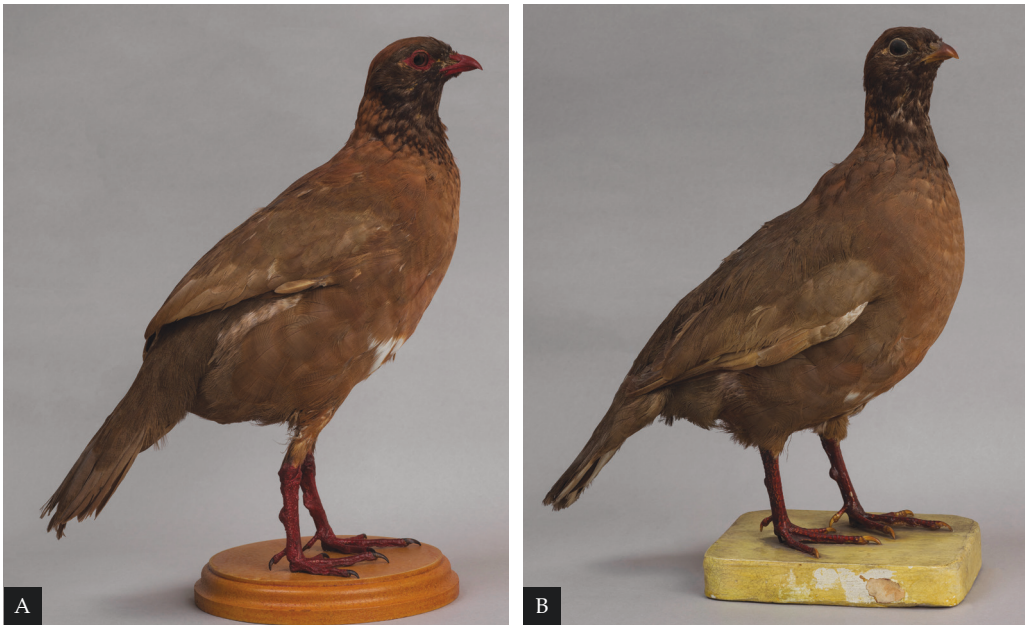

Figure 6. Mounted specimens at Muséum des sciences naturelles d'Angers, France. A: MHN.An.2003.522. B: MHN.An.2003.523 (David Riou, © Musées d'Angers)

'Perdrix lugubres, achetée 10 francs' It is unclear whether 1863 is the date of acquisition, collection or registration. 1863, however, appears to be incorrect for collection or acquisition as, based on de Soland (1861), these specimens must have been present in the museum

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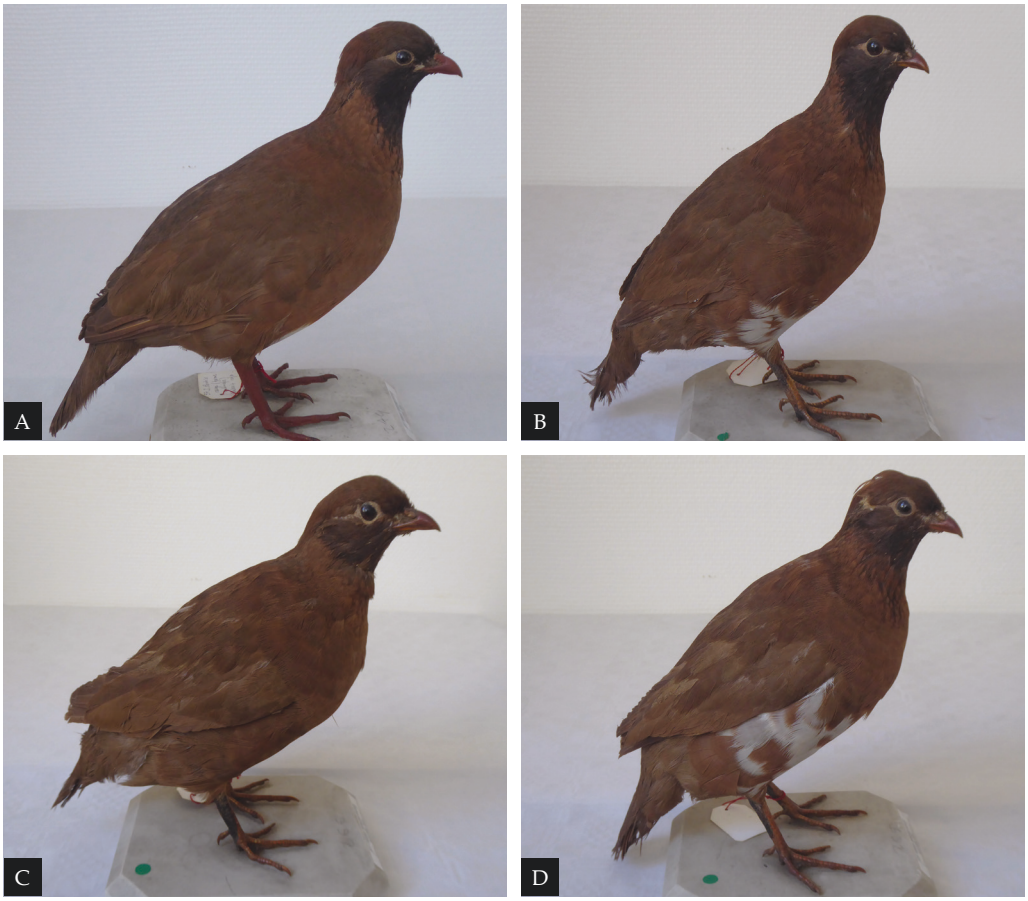

Figure 7. Mounted specimens at Museum de Société des Sciences Lettres et Arts de Cholet et sa région, France. A: SLA274-37.2. B: SLA288-37.6. C: SLA266-37.7. D: SLA265-37.8 (Fernand Lambert, © SLA, Cholet)

before 1861. According to Mayaud (1947) Deloche, the former taxidermist at Angers, obtained two specimens two years after Guillou presented one to the Linnaean Society of Maine-et-Loire in 1858, so these Angers specimens probably came to the museum in 1860, rather than 1863.

Museum de Société des Sciences Lettres et Arts de Cholet et sa région (SLA), France
Four mounted specimens, SLA 274-37.2, 288-37.6, 265-37.8 and 266-37.7 (Fig. 7). These were part of the private collection of Esprit Guillou (Mayaud 1947). His son, Arthur Guillou, donated the collection to the town of Cholet in 1905, when they were placed in the SLA (F. Lambert pers. comm.). E. Guillou was a keen naturalist, bird collector and member of the Linnaean Society of Maine-et-Loire. None of his specimens are accompanied by original data or labels, but we assume that all were collected at 'métairie du Cou-Pinson' of the village of Saint-Aubin-des-Ormeaux in Vendée between 1846 and 1861. One of these is probably that shown to the Linnaean Society and therefore the type of the name *atro-rufa*, although none agrees fully in shape and posture with the depiction in the type description (see Fig. 2).

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Figure 8. Specimens at the Natural History Museum, Tring. Ventral (A) and dorsal views (B), from left to right NHMUK 1915.1.15.1, 1915.10.5.1 and 1908.10.22.1 (Harry Taylor, © Natural History Museum, London)

Figure 9. Specimen (relaxed mount, MNCN-A4955) at Museo Nacional de Ciencias Naturales, Madrid, Spain, labelled 'Sur-oeste de Europa, probablemente España' (Josefina Barreiro, © Museo Nacional de Ciencias Naturales, Madrid)

Natural History Museum, Tring (NHMUK), UK

Three skin specimens, NHMUK 1908.10.22.1, male, Spaynes Hall, Braintree, Essex, shot 20 October 1908 and presented by A. W. Ruggles Brise; NHMUK 1915.1.15.1, male, Higham,

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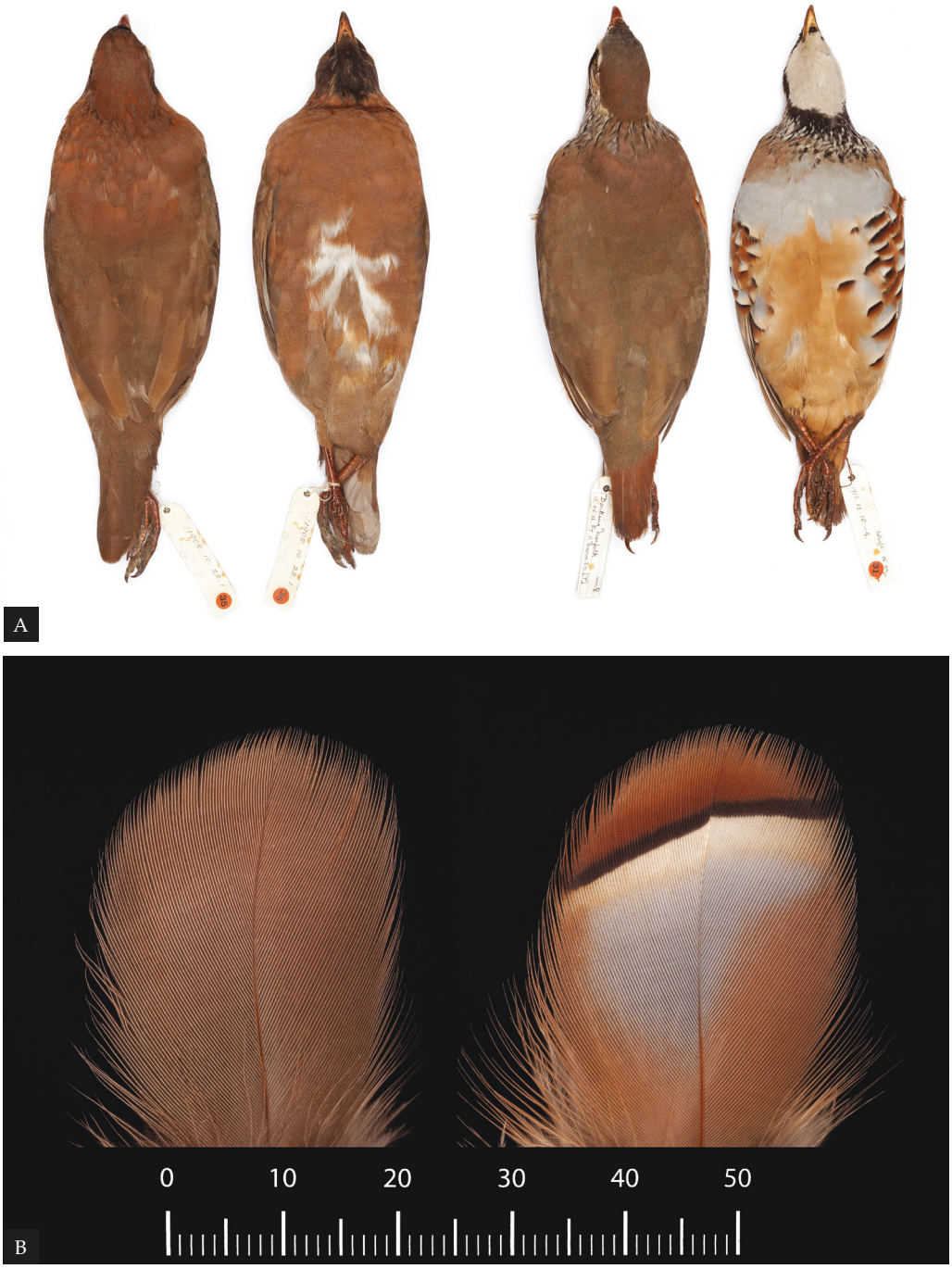

Figure 10. Melanistic form of Red-legged Partridge *Alectoris rufa* (left) compared with a normal-coloured specimen (NHMUK 1908.10.22.1 and 1912.12.18.4). A: the upperparts are hardly affected except the neck where phaeomelanin is increased, but the underparts are uniform reddish grey-brown due to an increase of both eumelanin and phaeomelanin, while the few white feathers are a form of leucism, which often occurs concurrently with certain forms of melanism; see Figs. 12 and 15. B: flank feathers of the same specimens (Harry Taylor, © Natural History Museum, London)

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near Gravesend, Kent, shot 20 October 1914 and presented by Dr Hammond Smith; NHMUK 1915.10.5.1, male, Mockbeggar, Rochester, Kent, shot 1 September 1915 and presented by Herbert Cobb (Fig. 8).

Museo Nacional de Ciencias Naturales (MNCN), Madrid, Spain
One skin specimen (relaxed mount), MNCN-A4955. Adult, originally labelled (in Spanish): 'South West Europe, probably Spain' (Fig. 9). The specimen was probably collected in Spain, but it is possible that it came from southern France, potentially from the same area (Alpes-de-Haute-Provence) as the Marseille specimen. The collection date is unknown, but it must be before 1912 when the museum's collection was inventoried (J. Barreiro pers. comm.)

Discussion

The pigments responsible for the Red-legged Partridge's plumage colour are melanins. Melanin comprises two forms: eumelanin and phaeomelanin. Depending on its concentration and distribution within the feather, eumelanin is responsible for black, grey and / or dark brown feathers, whereas phaeomelanin produces warm reddish-brown to pale buff feathers. Together, both melanins can produce a wide range of greyish-brown colours. Melanin is produced by cells called melanocytes, which are found mainly in the skin and the feather follicles (from which the feathers grow). Melanocytes within the feather follicles produce melanin, which is added to the feather cells as the feather grows. However, melanin distribution does not always occur at a constant rate. In most species, feathers have certain patterns and / or colour differences caused by the type, amount and distribution of melanin. During feather growth, sudden changes from the production of eumelanin to phaeomelanin may occur, giving rise to these different patterns (van Grouw 2017).

Many mutations in birds are known to cause plumage that is darker than normal (= melanism). Melanism, from the Greek *melanos* (= dark-coloured), is often defined as an increased amount of dark pigmentation (melanin). Aberrant dark plumage is, however, not necessarily the result of an increased amount of pigment. A change in the arrangement or distribution of pigment granules, rather than more granules being present, also causes darker plumage. Therefore a better definition of melanism is: 'a condition characterised by abnormal deposits of melanin in skin and feathers' (van Grouw 2017)

Although the melanistic form of Red-legged Partridge looks strikingly different from that with normal-coloured plumage, closer observation reveals that the original reddish grey-brown colour of the upperparts and wings in '*atro-rufa*' is hardly darker (Fig. 10A). Only on the neck is more phaeomelanin present, affording the plumage a more reddish appearance. Despite its name *atro-rufa* (Latin *ater* = black and *rufus* = red), the melanistic variety displays relatively little black in the plumage, perhaps even less than in normally coloured birds. The black head and throat markings typical of normal plumage are reflected in the solid black forehead and throat of the melanistic form, but the black stripes on the flanks have disappeared, instead the flanks and underparts are uniform reddish grey-brown (Fig. 10B). The normally reddish-brown tail feathers (produced by phaeomelanin alone) now contain both melanins, and are the same colour as the underparts.

In *atro-rufa* mainly phaeomelanin seems to be increased, although not to the same extreme as in *Perdix montana* (Fig. 11) and the phaeomelanistic variety of Northern Bobwhite *Colinus virginianus* known as 'Red Tennessee' (Fig. 12; Cole *et al*. 1949). Although in appearance these melanistic varieties are very similar to *atro-rufa*, large parts of their plumage contain only phaeomelanin, while in the melanistic Red-legged Partridge both pigments seem to be equally present in most feathers. In this respect, the mutation in Red-legged Partridge is highly comparable with 'recessive black' in Japanese Quail *Coturnix*

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Figure 11. Melanistic form of Grey Partridge *Perdix perdix*, originally named *P. montana*, a specimen in the Naturalis Biodiversity Centre, Leiden (Hein van Grouw)

Figure 12. Melanistic form of Northern Bobwhite *Colinus virginianus* known as 'Tennessee Red'; note the few white feathers (leucism) which often co-occur with certain forms of melanism; see Figs. 10 and 15 (© Joel Sartore)

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Figure 13. Melanistic form of Japanese Quail *Coturnix japonica* known as 'recessive black'. Both melanin pigments seem to be equally present in most feathers and the original patterns and markings are faint and therefore this mutation is very much comparable with the melanistic variety known as *atro-rufa* in Red-legged Partridge *Alectoris rufa* (© Nico van Wijk)

japonica, as in the latter, due to the mutation, each feather also contains both pigments and the original patterns and markings are faded (Fig. 13). In appearance, the varieties of both species do not look like each other at all, but in their normal colour the two are also totally different. In comparing mutations within different species, one must examine what happens to the pigmentation process, rather than just comparing the final result, as this can differ between species.

The inheritance of recessive black in Japanese Quail is, unsurprisingly, recessive, and the mutation is associated with the agouti gene (Hiragaki *et al*. 2008). Two important genes that regulate the production and deposition of the two types of melanin are agouti (A) and extension (E). The agouti gene regulates the distribution of eumelanin and phaeomelanin on each feather and over the surface of the body, while the extension gene is responsible for controlling the type of melanin being produced: eumelanin or phaeomelanin. Mutations of either of these genes can cause an abnormal deposition of melanins in the plumage (van Grouw 2017). Based on the similarity to recessive black in Japanese Quail, we assume the melanistic form of Red-legged Partridge was also recessive in inheritance.

Recessive black is also recorded in Common Quail *Coturnix coturnix* and this variety was described as a species, *Synoicus lodoisiae*, by Verreaux & des Murs (1862; Fig. 14). A similar mutation, which is rather common in northern Russia west of the Urals, chiefly in Perm and Olonetz Oblasts, also occurs in Hazel Grouse *Tetrastes bonasia*. Due to its frequency, Menzbier (1880) considered it a valid species and named it *T. gryseiventris* (Figs. 15–16).

The presumably recessive gene mutation responsible for the melanistic variety of Red-legged Partridge altered the deposition of both melanins in the feathers. In some species, like Northern Bobwhite, the melanistic variety (which mainly shows increased phaeomelanin) is weaker and less fertile than typical individuals (Cole *et al*. 1949). In Feral Pigeons *Columba livia* negative effects on fitness are also linked to strongly phaeomelanised plumage (van Grouw 2017). Furthermore, the reddish 'morph' of Grey Partridge, '*montana*', persistently

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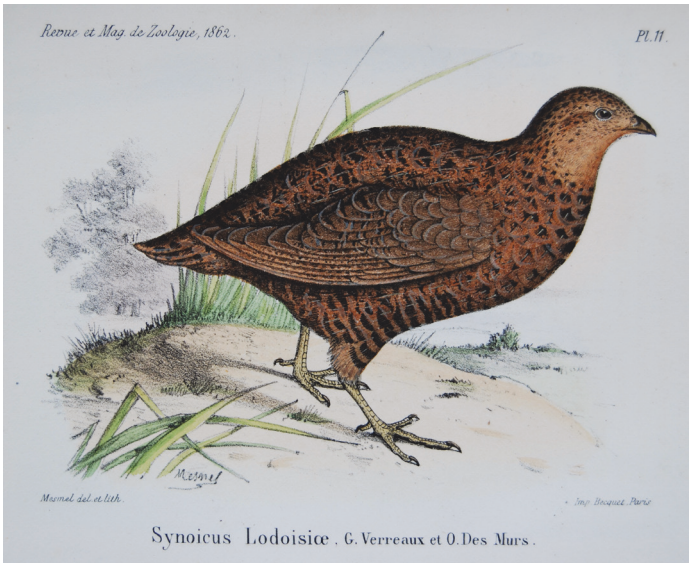

Figure 14. *Synoicus lodoisiae*, in Verreaux & des Murs (1862), which proved to be a melanistic variety of Common Quail *Coturnix coturnix* (Hein van Grouw, © Natural History Museum, Tring)

Figure 15. Menzbier's Hazel Grouse *Bonasa griseiventris* [*sic*], in Dresser (1896), proved to be a melanistic variety of Hazel Grouse *Tetrastes bonasia*; the specimen Dresser selected for the illustration had a small white bib and a few white feathers behind the eye, features which he assumed distinguished the 'species'. However, a few white feathers often co-occur with certain forms of melanism, but are certainly not usual (Hein van Grouw, © Natural History Museum, London)

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Figure 16. Melanistic specimen of Hazel Grouse *Tetrastes bonasia* formerly known as *T. gryseiventris*, in the Zoological Research Museum Alexander Koenig, Bonn (Hein van Grouw)

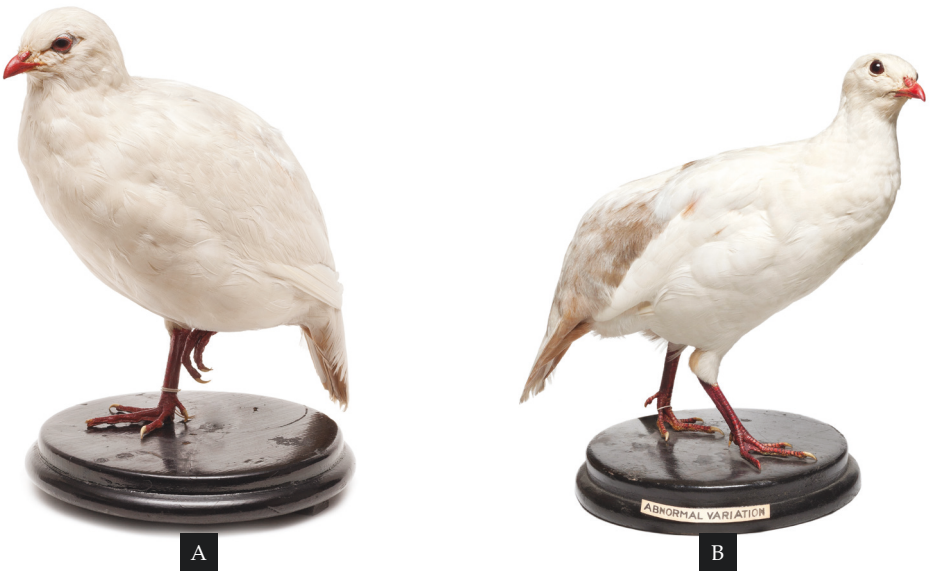

Figure 17. Leucistic Red-legged Partridges *Alectoris rufa*, collected *c*.1900 in England. A: NHMUK 1996.41.2098, B: NHMUK 1996.41.414 (Harry Taylor, © Natural History Museum, London)

re-appears due to the recessive nature of the mutation, but there is no evidence that this phaeomelanised variety increases numerically anywhere in the species' natural range. So mutations causing an increase of phaeomelanin apparently negatively affect fitness, whereas 'eumelanism' often has no effects or even contributes positively (van Grouw 2017)

The small population of melanistic Red-legged Partridges in the Pays-de-la-Loire region of north-west France became extinct less than 20 years after its discovery in 1846. In addition to being hunted for their meat, melanistic birds were consistently targeted by collectors,

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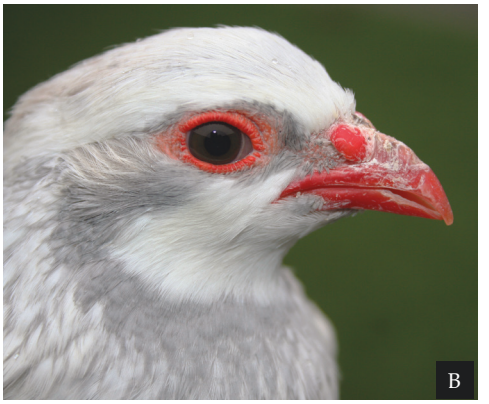

Figure 18. 'Diluted' Red-legged Partridge *Alectoris rufa*, bred and held in captivity (© Nico van Wijk)

Figure 19. 'Brown' Red-legged Partridge *Alectoris rufa*, bred and held in captivity (© Nico van Wijk)

which certainly contributed to their extirpation. Whether the mutation also had negative effects on fitness meaning that a thriving population would never have become established is unknown. Many mutations, however, like 'Leucism', 'Dilution' and 'Brown' (Figs. 17–19), in Red-legged Partridge are widespread in populations and appear repeatedly in the wild. In contrast, the melanistic variety is known only from three localities and for a period of *c*.70 years prior to 1915. A possible explanation for the loss of the melanistic variety is that the allele for this mutation has disappeared altogether from Red-legged Partridge populations due to hunting and an influx of genetically unrelated birds.

The estimated combined population of Red-legged and Grey Partridges in 1858 in France was *c*.20 million individuals. Subsequently, due to hunting and climatic changes, numbers of Red-legged Partridge declined dramatically and, in 1979, they were estimated at just 300,000–550,000 breeding pairs. Consequently, since the 1970s the species has been bred for hunting on a large scale in France (ONCFS 2018). In 1995, for example, no fewer than 2.5 million birds were released for sport hunting (Tupigny 1996). Due to the large influx of captive-bred birds into the wild, the genetic composition of the wild population has been

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diluted to the extent that the original population may become extinct sooner rather than later (ONCFS 2018).

In Britain the situation is little better. Although the species was by then well established in the wild in many parts of the UK, releasing captive-bred birds for sport commenced in 1963. For a time, the closely related Chukar *A. chukar* and Chukar × Red-legged Partridge hybrids were released too, but this practise was prohibited in 1992 to protect the genetic integrity of the wild population. Currently releases of captive-bred Red-legged Partridges are estimated at *c*.6 million birds p.a. in the UK (Game & Wildlife Conservation Trust 2018).

Whether it was unfitness, consistently being targeted by hunters, reduced genetic diversity, or a combination of these factors, the melanistic form has disappeared from Red-legged Partridge populations. All that remains are 13 museum specimens—the dark reminders of an even darker history.

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