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REVIEW

Chromatic disorders in bats: a review of pigmentation anomalies and the misuse of terms to describe them

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ABSTRACT

1. Chromatic disorders in bats are being reported worldwide at an increasing rate. However, there is widespread misunderstanding and misuse of the associated terminology and concepts in the scientific literature. We conducted an extensive assessment and standardisation of published and unpublished cases of chromatic disorders in bats worldwide.
2. Chromatic disorders have been recorded in at least 609 bats belonging to 115 species and 10 families (after correction of misused terms, 152 cases of albinism, 11 of leucism, 269 of piebaldism, 20 of hypomelanism, three of partial melanism and 94 of melanism; a further 60 records remain unclassified).
3. Of the 354 records in which a location was given, 297 bats were found in closed roost sites, mainly caves, buildings, and mines and galleries, while just three were found roosting externally. This difference could be attributed to the greater monitoring effort employed in underground areas than in forests, and to the greater detectability of bats dwelling in caves and buildings than forest-dwelling species.
4. Although reports of chromatic disorders in bats are reasonably well spread around the globe, there are large areas from which no disorders have ever been reported: the Central Amazon, almost all of Africa, northern Europe, and almost all of Asia and Oceania. This is likely to be attributable to either the disregard for information on chromatic disorders (e.g. Central Amazon) or to the low abundance of occurring species (e.g. northern Europe).
5. In all, 40% of the records of leucism and piebaldism were misclassified as 'partial albinism'; leucism was also often used to designate pied aberrations.
6. We propose a standardised classification to distinguish between albinism, leucism, piebaldism, hypomelanism, melanism and partial melanism. Due to frequent confusion, we encourage scientists to follow this classification and we highlight the need to employ comprehensive terminology when describing chromatic disorders in scientific publications.

INTRODUCTION

The broad variety of forms and colours found in mammals generally results from the presence of certain pigments, mostly melanin, in their integuments. Different combinations and intensities lead to a range of hues, which might persist during evolution (Pawelek & Körner 1982). Unravelling the biological functions behind organisms'

pigmentations has captivated scientists for centuries, and although the loss of pigments has evolved in a range of animals (mostly living in caves), the genetic processes responsible for these variations remain unknown in most mammals. Understanding the potential evolutionary costs and/or benefits arising from chromatic disorders is essential for explaining adaptations to the changing landscape (Bilandžija et al. 2013).

The progressive increase in bat research has engendered more publications and reports on bat ecology, natural history and conservation, thereby expanding knowledge of both rare and common species. As a result, interest in chromatic disorders in bats has grown worldwide and the number of reported cases has increased (Uieda 2000, Zalapa et al. 2016).

Chromatic disorders are pigmentation anomalies that cause abnormal colouration of the skin and derivatives (Rook et al. 1998). They have been reported in many mammals and are caused by either a deficiency in or an excess of melanin (Hofreiter & Schöneberg 2010, Abreu et al. 2013). Nevertheless, general confusion still exists as to the correct terminology for describing these disorders, especially for those related to hypopigmentation, which are most easily detected (Zalapa et al. 2016). The classification of hypopigmentary disorders into 'complete albinism' or 'partial albinism' has proved to be inaccurate and obsolete, and what was once termed 'partial albinism' is now better classified as either 'leucism' or 'piebaldism' (van Grouw 2006, 2013, Summers 2009, Abreu et al. 2013). The confusion still present in the literature seems to be associated with the incorrect use of the terms 'partial albinism', 'leucism' and 'piebaldism' (e.g. Geiger & Pacheco 2006, Boada & Tirira 2010, García-Morales et al. 2010, Olarte-González et al. 2014).

Albinism is an inherited, hypopigmentary disorder characterised by a complete lack of melanin. It is caused by an absence of the enzyme tyrosinase that causes individuals to have pale skin, white fur or feathers, and red eyes (van Grouw 2006, 2013, Hofreiter & Schöneberg 2010). Tyrosinase is an essential component of the chemical process that produces melanin pigments in vertebrates. The reddish colouration of the eyes is due to the fact that the blood capillaries at the back of the eye are visible. Albinism is controlled via inheritance by an autosomal recessive gene in all animal species (van Grouw 2006). Leucism is defined as the total lack of pigmentation in the whole body. This occurs despite normal production of the enzyme tyrosinase and melanin; however, no melanin deposition occurs in the skin cells, hair follicles or feathers due to an inherited defect in the pigment transfer process. Leucism can be caused by one of several different mutations and gives rise to seemingly similar phenotypes. Thus, leucistic animals are white or whitish all over but have normally coloured eyes (van Grouw 2006, 2013, Abreu et al. 2013).

A further type of hypopigmentation is what is commonly known as piebaldism, in which the absence of pigment is localised and is due to an absence of melanocytes in the affected skin and hair follicles or feathers, as a result of genetic mutations. This aberration is similar to leucism but differs in that the melanocyte development is only locally disrupted. Piebald animals have a variable patchy distribution of white spots on the body but have normally coloured eyes (Davis 2007, Abreu et al. 2013). The term piebaldism is considered inappropriate by Zalapa et al. (2016) as these mutations can occur in several genes, as opposed to only in the piebald gene (Lamoreux et al. 2010). Nevertheless, we decided to keep the term piebaldism to classify this phenotype, as it is not inherently incorrect and we could not find any other non-confusing and specific term to describe it. There are also non-hereditary (external environmental) forms provoked by factors other than piebaldism, such as malnutrition, disease, parasites and ageing (Červený 1980, Heise 1990, Bartel et al. 1999, Lanza 2012). In these cases, the colouration can be restored if the external factors are negated. Another type of hypopigmentation is hypomelanism, an inherited disorder resulting in beige, golden, yellowish or reddish individuals with insufficiently pigmented skin (Červený 1980, Zamolo et al. 2013). Melanism, unlike albinism, is an inherited hyperpigmentary disorder characterised by the abnormal deposition of melanin in the skin and/or hair follicles or feathers, which gives rise to exaggerated black or brown pigmentation. Partial melanism can occur, although it is not caused by a mutation but by disease, malnutrition or lack of exposure to the sun (van Grouw 2006, 2013, Davis 2007, Hofreiter & Schöneberg 2010).

Although they are supposedly rare, cases of chromatic disorders in bats have been reported globally (e.g. Buchanan 1985, Uieda 2000, López-Wilchis & León 2012, López-Baucells et al. 2013, Treitler et al. 2013). In bats, chromatic disorders can affect both fur and skin, including patagium, ears and muzzle, and their effect on bat survival and fitness has long been debated. Some authors (Marín-Vásquez et al. 2010) believe that hypopigmentation is detrimental for survival and leads to overexposure, higher predation risk and intra-specific conflicts, others believe that it has no impact, since bats generally select dark roosts and are active at night when their colour has no effect either on predation or on social behaviour (Buys et al. 2002). Moreover, aberrant individuals naturally roosting in sheltered places (i.e. caves, mines and buildings) may even have greater survival rates, whereas aberrant individuals in species that roost in the open (e.g. on leaves) could be more vulnerable to predation. Uieda's (2000) review reported cases of albinism in bats, listing 38 species and 64 individuals with this anomaly; 38 of 39 albino bats for which the roost site was known were found in sheltered roosts.

Some species that are naturally whitish or have white patches (e.g. *Diclidurus* spp. and *Ectophylla alba*) adopt camouflage strategies to confound visually oriented predators (they resemble paper-wasp nests or construct roosts from the leaves of *Heliconia* plants, respectively; Timm & Mortimer 1976, Ceballos & Medellín 1988).

The specific objectives of this literature review are to: (1) present an updated review of chromatic disorders in bats and use it to define a standardised terminology to describe them; (2) report hitherto unpublished cases of such anomalies only made public via the Internet, with commentaries on the trend in publication rates; (3) analyse how chromatic disorders are distributed in different families and countries; and (4) report roosting and other types of behaviour in aberrant bats.

METHODS

Data search and exclusions

This review was compiled by considering both published and unpublished records of chromatic disorders in bats (i.e. albinism, leucism, piebaldism, hypomelanism, partial melanism and melanism). All records we found were reclassified using the classifications given by van Grouw (2006, 2013) and Abreu et al. (2013) to exclude all improper and obsolete terms. Other previously described colour mutations exist in bats; however, we decided to focus our review on the principal anomalies, which are the most commonly observed aberrations in field studies and museum collections.

An extensive review of records published in peer-reviewed journals was conducted by checking scientific web-portals and data bases. In our search for scientific papers, we mainly used the Thomson Reuters (Web of Science) and Scopus data bases, Google Scholar and Google Books, using key words in different combinations and languages such as: 'albinism', 'bats', 'chiroptera', 'leucism', 'piebaldism', 'pied', 'melanism', 'chromatic disorders', 'pigmentation anomalies', 'colour aberrations', 'hypopigmentation' and 'hyperpigmentation'. For every record found, the following information was recorded: species, sex, age, locality, type of record (capture, photo, sighting), year of record, type of chromatic disorder and position on the body, location (if applicable), roosting strategy (Anonymous 2015), and type of colony (mixed or non-mixed, if applicable). When a scientific paper was located, we used the references and citation records therein to access other relevant information sources. Unpublished records were acquired from websites, Citizen Science platforms, bat recovery centres, social networks and personal communications (i.e. Google, Google Images, Facebook, Twitter, Flickr, YouTube and iNaturalist); from these unpublished records the same information as described for published records was derived. When the information was insufficient to classify a case of anomalous pigmentation, the record was classified as 'undetermined'.

In order to investigate the correlation between the publication rate of reports of chromatic disorders and overall publication rate globally of bat research, the number of papers per year on bats since 1950 was obtained from the Web of Science by searching for all publications with the terms 'Chiroptera', 'bats' or 'bat' in their titles. All data were normalised, and temporal linear regression trends were compared for the period 1950–2015. All the analyses were carried out using the R software v. 3.2.4 (R Foundation for Statistical Computing).

Geographical information and mapping

In order to analyse the data geographically, we excluded incomplete records and citations with no geographical information. Whenever possible, geographical coordinates were obtained and included in the data base; if these data were not available they were inferred from the publication or received via personal communication. If there was no information available regarding the location in a country, a central point within that country was taken for relatively small countries. Data were plotted and georeferenced onto world maps using QGIS v. 2.12.2 (Open Source Geospatial Foundation, Lyon).

In order to assess how records were distributed globally, a kernel density function (non-parametric method) was used. This method was developed as a general density estimation tool and is used to infer data about populations from finite data by predicting densities without considering previously known underlying distributions. This technique was directly applied in QGIS using the plugin 'Heatmap'. All maps and analyses were carried out with QGIS v. 2.12.2 (Open Source Geospatial Foundation, Lyon) using the base layer obtained from Bjorn Sandvik (thematicmapping.org), with an original shape derived by Schuyler Erle from public domain sources.

RESULTS

Chromatic disorders in bats

From a total of 224 reports and 15 personal communications (of which 15% were previously unpublished records), referring to 609 individual bats, we gathered 269 individual records of piebaldism, 152 of albinism, 94 of melanism, 20 of hypomelanism, 11 of leucism and three of partial melanism; in 60 bats the chromatic disorder was 'undetermined' (see Appendix S1). This classification is based on the corrected concepts of chromatic disorders. The records

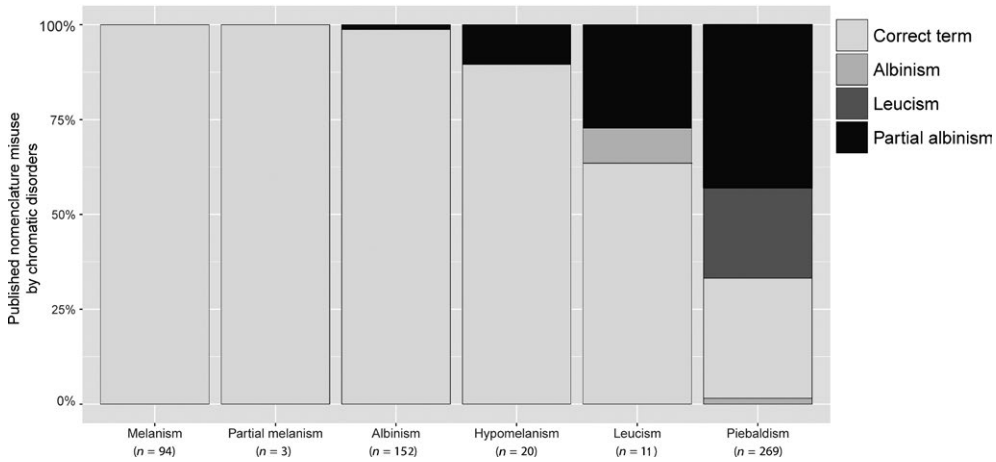

Fig. 1. Percentages of correct/incorrect usage of the different typologies of chromatic disorders. Sample sizes are numbers of bats (609 in total; in 60 bats, the chromatic disorder was not determined).

date from 1877 to the most up-to-date publications, and include reports by a total of 369 different authors.

Misuse of terms to describe chromatic disorders in bats

Before our corrections, 204 (34%) bats were incorrectly classified (Fig. 1); 136 bats were originally mistakenly classified as partial albinos (22% of the total; 40% of the cases described as leucistic or piebald); these disorders were reclassified as albinism (2 records), leucism (3), piebaldism (110) or hypomelanism (2); 19 records could not be properly determined. On the other hand, 62 bats were originally misclassified as having leucism (10% of the total; 23% of the cases described as piebaldism) and were reclassified as piebaldism (61 cases; one case could not be properly determined). Similarly, six records were misclassified as albinism (0.9% of total) and were reclassified as leucism (1) or piebaldism (5; Fig. 1). The misused terms we found in the literature included 'albino spots', 'white-cuffed bats' and 'bats with white patches'. Misidentifications were from countries throughout the world: there were 25 misclassifications from Asia (56% of all reports for Asia), 90 for Europe (31%), 36 from North America (29%), two from Oceania (25%) and 58 from South America (54%).

Taxonomical and geographical distribution of chromatic disorders in bats

The 609 individual bats that had documented chromatic disorders belonged to 115 species and 10 families (Fig. 2, Appendix S1). Globally, similar percentages of males and

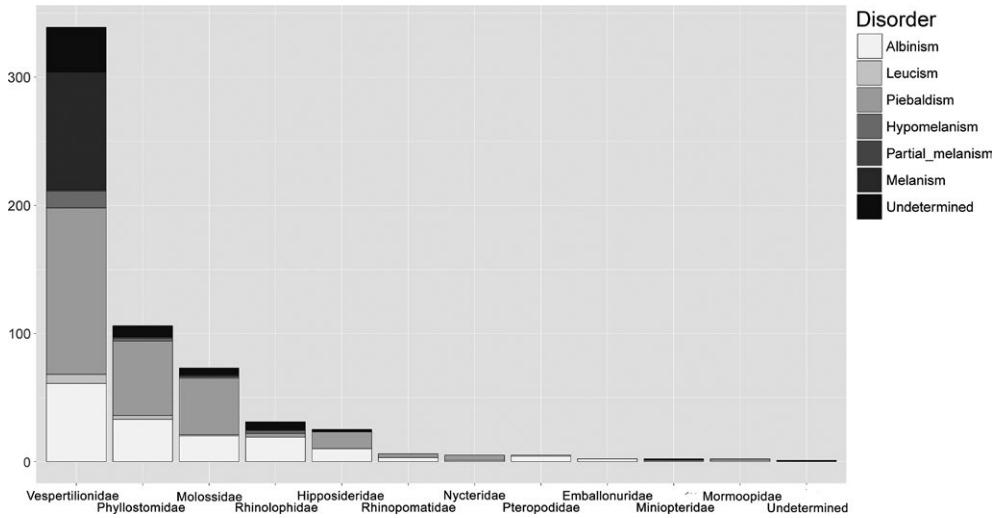

Fig. 2. Records of chromatic disorders for each family of bats.

females were recorded as having chromatic disorders (54% males and 46% females, respectively; sex was noted in 334 individuals); this proportion was maintained within each type of anomaly (albinism: 45% vs. 55%, $n = 82$; piebaldism: 56% vs. 44%, $n = 201$). The most represented families were the Vespertilionidae (53%) and Phyllostomidae (19%), followed by Molossidae (12%) and Rhinolophidae (5%). The USA was the country with the most records (70 records, 12%), followed by Germany and Slovakia (43 records each, 7%). In general, Europe and North and South America had the highest number of records, followed by Asia and Africa; Oceania was the continent with the fewest records (Figs 3 and 4). Important gaps in the available information were detected in northern North America, the Amazon in South America, almost all of Africa, northern Europe, and almost all of Asia and Australia (Figs 3 and 4). These distributions correspond chiefly to reports of albinism and piebaldism; the less abundant anomalies were only ever reported from central and southern Europe, eastern USA and Canada, and western South America. For the regions that lack useful data on chromatic disorders, data were either ignored during sampling (e.g. in the Central Amazon) or occurrences were low due to lower abundance and diversity of bat species (e.g. in northern Europe). Comparison of the global bat research publication rate with the publication rate of reports of chromatic disorders in bats showed that both rates display a positive trend and are increasing with time, the former at a slightly greater speed (b = 0.0152 and 0.0095, respectively, calculated with normalised [0–1 range] annual data; Fig. 5).

Roosting strategies and reported behaviour in aberrant bats

Of the 609 reports, only 354 contained detailed information about the location; in these cases, only 54 individuals (15%) were captured on flyways. Most individuals were found while roosting in closed roosts, mainly in caves (125 individuals, 35%), buildings (including houses, castles, churches, temples, stables and bunkers; 78 individuals, 22%), and mines, tunnels and galleries (72 individuals, 21%). 12 individuals (3%) were found in bat or bird boxes, two individuals (0.6%) in hollow trees and eight (2%) in other locations (e.g. water butt, dam). Only three individuals (0.8%) were found roosting externally: an albino *Artibeus jamaicensis*, an albino *Rhinophylla pumilio* and an aberrant *Artibeus phaeotis* sighted roosting on a tree (Fig. 6, Appendix S1). However, according to the information on roosting strategies provided by the International Union for Conservation of Nature, 48% of the individuals recorded as having anomalies belong to cave-dwelling species, 27% to species with variable and flexible roosting strategies, 14% to forest-dwelling species, 10% to species dwelling in buildings, and only 1.2% to species roosting under leaves. On occasions, aberrant individuals were reported for several consecutive years in the same colony or roost, and successful reproduction by aberrant females (that were either pregnant, lactating or post-lactating) has been reported.

DISCUSSION

Standardising terms to describe chromatic disorders in bats

We aimed to gather information on chromatic disorders in bats and to clarify and standardise the terminology used to describe such cases. The fact that 40% of cases of leucism and piebaldism were incorrectly classified as 'partial albinism' is evidence of the misuse of the term 'albinism' to describe these pigmentation disorders. By definition, the concept of partial albinism is a contradiction in terms - it is like 'partial pregnancy' (Buckley 1982). Albinism is a hereditary genetic anomaly that leads to a complete absence of melanin in the skin, hair follicles and eyes due to the lack of the enzyme tyrosinase in the melanocytes. It is not even possible to have only partially pigmented areas of the body. Despite being one of the most commonly mentioned anomalies, albinism is not the commonest of pigmentation disorders in nature.

Although many authors have now stopped using the improper term 'partial albinism', confusion still exists between the terms 'leucism' and 'piebaldism'. Piebaldism is underused, while leucism is often employed to designate both leucistic and piebald-type aberrations. In fact, of all the cases of leucism included in this review, 85% were misclassified and actually correspond to piebaldism. These results highlight the need to establish a comprehensive standardised terminology for describing pigmentation disorders in bats.

Despite the lack of data, scientists are increasingly beginning to discuss pigmentation disorders (Zalapa et al. 2016). In recent years, the number of publications on bat ecology and conservation has grown considerably, a fact that, combined with better access to data, has helped improve understanding of chromatic disorders in Chiroptera and their impact on natural populations. However, many cases are still misidentified in the literature due to poor quality pictures or difficulty when examining individuals in the field (e.g. during winter counts of bats in inaccessible colonies).

Much still needs to be investigated regarding the causes, symptoms and correct naming of these disorders. We therefore encourage scientists and bat experts to share their knowledge and data, and to report cases of these aberrations whenever they are encountered. More exhaustive classifications have been proposed for birds (e.g. Buckley

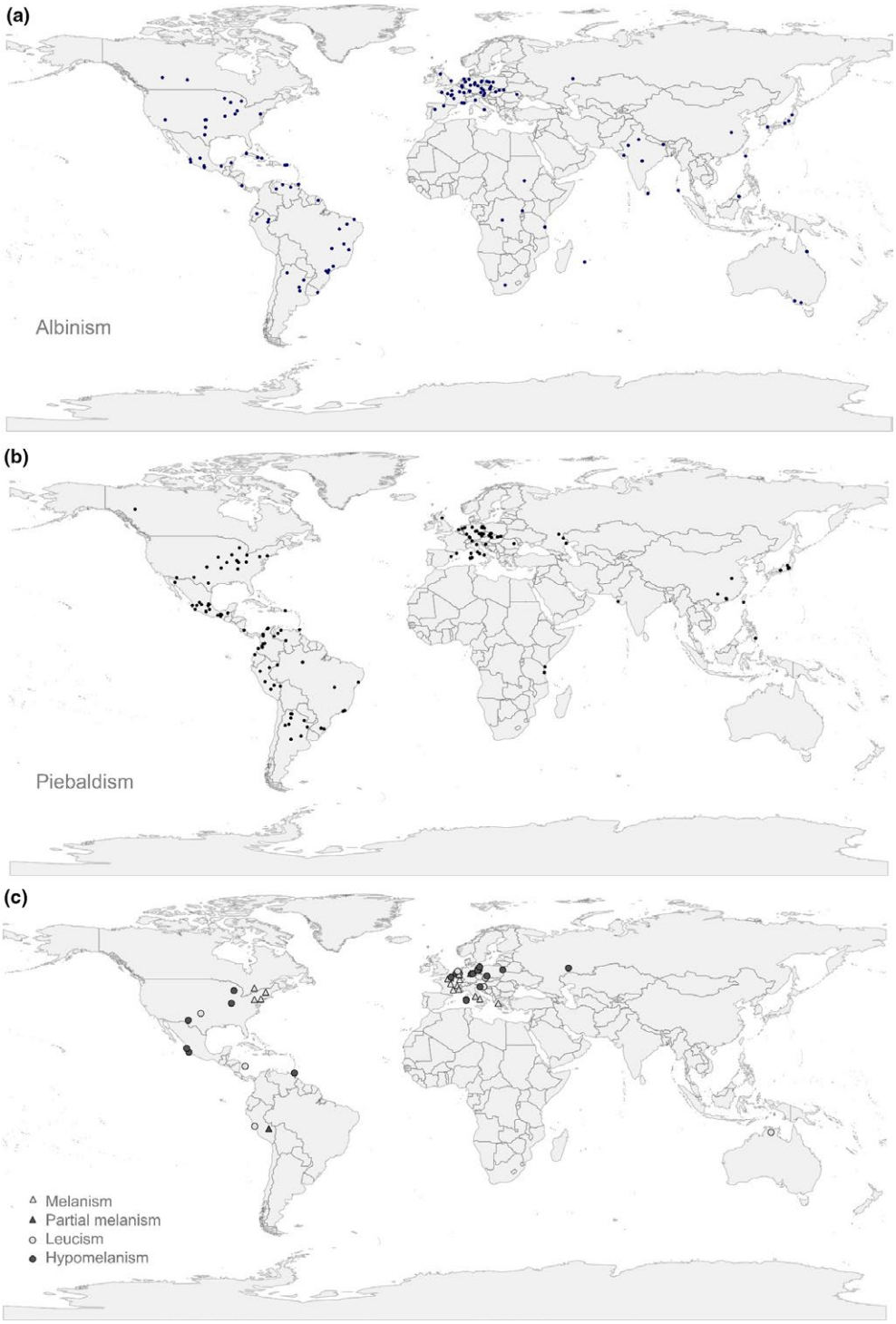

Fig. 3. Global distribution of chromatic disorders in bats. Each report is represented by a black dot: (a) albinism, (b) piebaldism and (c) other aberrations. [Colour figure can be viewed at wileyonlinelibrary.com]

1982, van Grouw 2006, 2013, Davis 2007), which are among the best-studied of all vertebrate groups. Recently, Zalapa et al. (2016) proposed an updated classification for bats based on that proposed by Lamoreux et al. (2010), which includes the following aberrations: 'white patches', 'albinism', 'pale' and 'no agouti'. Nevertheless, we believe that our study and the simple classifications we propose, illustrated with clear examples (Table 1), are useful tools

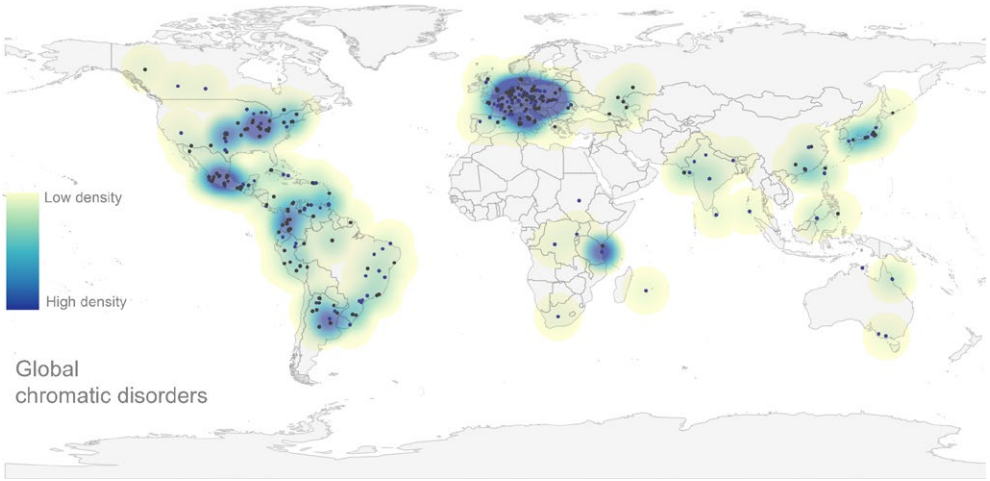

Fig. 4. Global distribution of chromatic disorders in bats. The density of anomalies is represented using kernel density maps generated using the whole data set. [Colour figure can be viewed at wileyonlinelibrary.com]

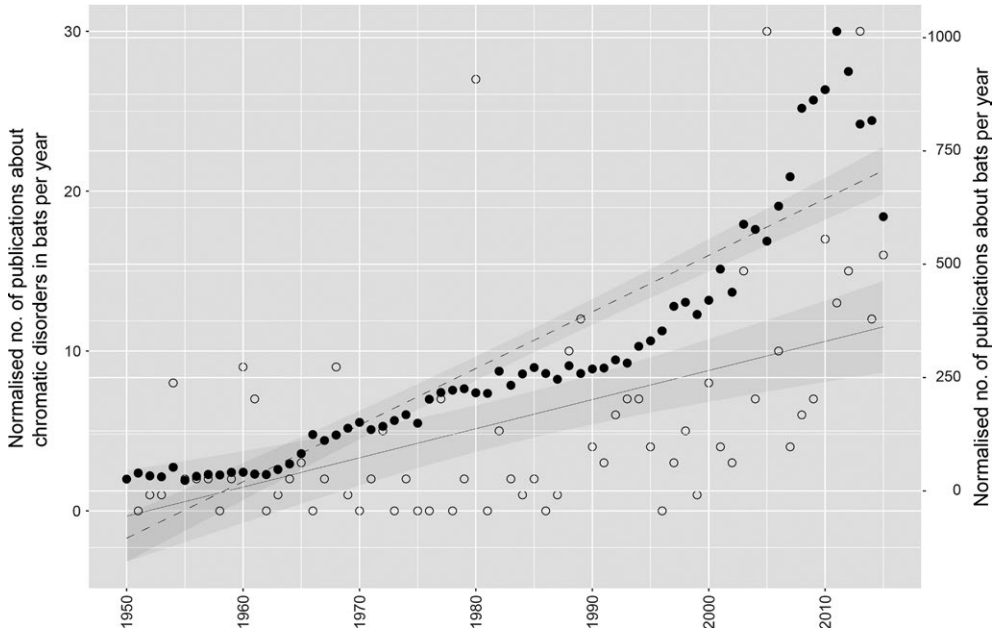

Fig. 5. Comparison of global publication trends in bat studies (open circles, solid line) and the publication rate on chromatic disorders in bats (filled circles, dashed line) from 1950 onwards.

for resolving classification discrepancies and clarifying any major doubts. Although many questions still need to be answered, our study highlights the potential of this field of research and paves the way for new findings.

Taxonomical and geographical distribution of chromatic disorders in bats

Since Uieda (2000) published the first review of albinism in bats, almost no extensive research has been conducted on the subject. Here we increase the number of reports of true albino bats from 64 (Uieda 2000) to 152, and include 457 cases of other chromatic disorders. Piebaldism and albinism are much more commonly described in the literature than other anomalies, but this may simply reflect the fact that they are much easier to detect in the wild; melanism might be the most difficult anomaly to detect, although we found 94 records in our bibliographic search.

Our classification is constrained by methodological limitations; in the absence of first-hand analysis, it was not

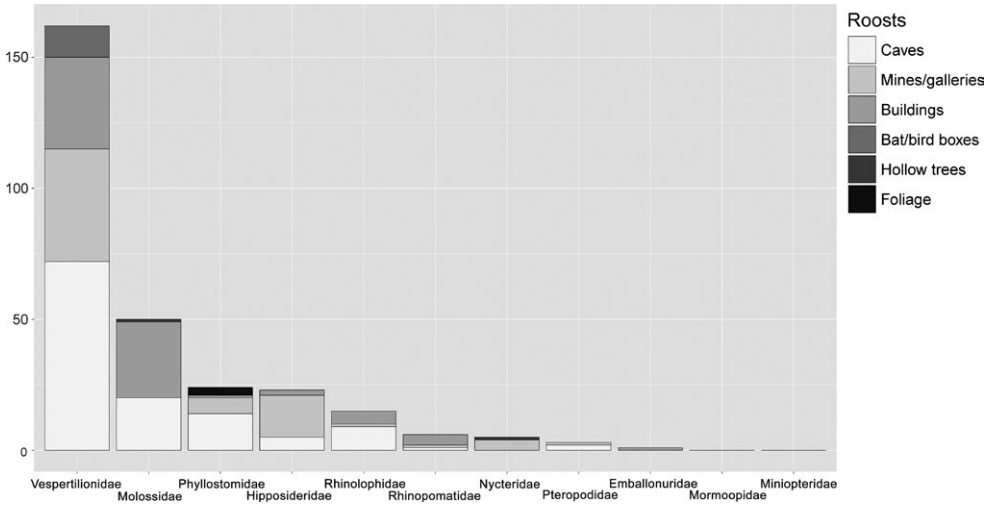

Fig. 6. Of the 609 bats with chromatic disorders, 300 were described as being found in specified roosts. The most common roost types in which they were found are shown per family.

always possible to determine the nature of a disorder from just pictures or written descriptions. Moreover, some reports are not entirely reliable, as identifying colour aberrations in the field is complex, and relevant limiting factors are usually not given. For instance, cases classified as albinism in bats in wintering caves, when it was not possible to check the eye colour (and thus confirm these as albinism and not leucism) are quite common in the literature. Furthermore, the phenotypic effects that we group together under the single term 'hypomelanism' could be due to certain gene mutations (and combinations thereof) that either affect melanin biosynthesis or pigment granule density and distribution in melanocytes (Barsh 2001, Hoekstra 2006). This subject has not yet been properly studied and may therefore complicate and mislead the interpretation of detected anomalies.

Nearly 85% of all records of chromatic disorders were from species belonging to the families Vespertilionidae, Phyllostomidae and Molossidae. These families are among the most numerous and diverse of all bat families and include many common and widely distributed species found in anthropic environments that are, as a result of this, very well studied. For instance, the three commonest species in the USA (the country that has the greatest number of records of chromatic disorders) are *Eptesicus fuscus*, *Myotis lucifugus* (Vespertilionidae) and *Tadarida brasiliensis* (Molossidae). No research has ever been conducted on whether some species are more prone to developing chromatic disorders than others. Our results show that the reports of chromatic abnormalities are highly biased towards the most-studied species from the best-studied areas. Glass (1954) reported that 49 of 79 *Myotis sodalis* captured in a cave in Oklahoma (USA) had the so-called 'chin-whiskers' trait in which the underside of the chin and throat is white; Herreid and Davis (1960) counted 149 *Tadarida brasiliensis* with white fur patches in four different caves in Texas (USA), while Geiger and Pacheco (2006) reported that 21% of the observed *Nyctinomops laticaudatus* in a building in Rio Grande do Sul (Brazil) had white fur patches. These data could be explained by the fact that colonial species such as these may be susceptible to inbreeding since they are usually highly faithful to their roost sites (Laikre et al. 1996, Sánchez-Hernández et al. 2012).

The areas with the lowest number of reports of chromatic disorders in bats are the least-prospected areas of the globe such as West Africa and Central and Northern Asia. This suggests that chromatic disorders may in fact be evenly spread on a geographical scale, and may be more likely to be detected in the most studied regions. We encourage bat workers and scientists in the least-studied regions to publish reports of chromatic disorders to complement the currently available data.

Reported behaviour and roosting strategies for aberrant bats

According to the data gathered on locations, the detectability of aberrant bats seems to be higher in closed roosts such as caves, mines and buildings than in open roosts. This is in agreement with the findings of Uieda (2000), who proposed that such roosting sites could offer albino bats protection from solar radiation and predators, thereby enhancing their survival possibilities. However, according to the information on roosting strategies gathered for the whole data set, only 10% of the individuals were species that normally roost in buildings. The higher number of

Table 1. Suggested classification for bat chromatic disorders.

Disorder	Causes	Phenotypic effects	Other designations	Normal colouration	Aberrant colouration
Albinism	Hereditary (genetic): total lack of melanin in skin, hair follicles and eyes due to the absence of the enzyme tyrosinase in the melanocytes.	All-white hairs, pale skin and red eyes.	Total or pure albinism, complete albinism, perfect albinism, total amelanism.		
Leucism	Hereditary (genetic): total lack of melanin in skin and hair follicles due to the failure of melanocytes to migrate to the skin and hair follicles.	All-white or whitish hairs, pale skin, eyes always normally coloured.			
Piebaldism	Hereditary (genetic): total lack of melanin in part of the skin and/or hair follicles due to the absence of melanocytes in the affected part.	All-white fur/skin patches, eyes always normally coloured.			
Hypomelanism	Hereditary (genetic): mutations affecting melanin biosynthesis, pigment granule trafficking or membrane sorting.	Beige, golden, yellowish or reddish fur and skin, eyes always normally coloured.	Erythrism, flavism, rufism, silvering, tawny.		
Melanism	Hereditary (genetic): abnormal deposit of melanin in the skin and/or hair follicles. Non-hereditary (environmental): malnutrition, disease, lack of exposure to sun.	Increase in black or brown pigmentation on the whole body (melanism) or just on a part (partial melanism).	Nigrism.		

Photographs: albinism (Nigel Milbourne), leucism (René Janssen and Carles Flaquer) piebaldism (Adrià López-Baucells), hypomelanism (Aja Zamolo) and melanism (René Janssen).

aberrant bats found in buildings (22% of individual records) could be explained by the fact that both underground and urban roosts have been widely monitored and repeatedly inspected worldwide, and probably harbour more of the best-known bat species. Thanks to the contribution of speleologists, geologists and other visitors to caves, cave-dwelling bats are generally well studied (Kunz 1982). In contrast, due to the difficulty of capturing them and the small size of their colonies, forest-dwelling species are poorly known (Vonhof & Barclay 1996, Lacki et al. 2007). Species detectability depends greatly on the roosting strategy and, unlike caves and buildings, where an albino specimen is easily detectable within a colony, hollow trees and crevices are difficult to monitor and aberrant bat abundances could be greatly underestimated.

Many authors describe how chromatic disorders – especially albinism – are known to have a negative effect on fitness in vertebrates (Caro 2005, Krecsák 2008). Studies conducted, for example, on reptiles (Krecsák 2008), birds (Lee & Grant 1986, Møller & Mousseau 2001) and mammals (Laikre et al. 1996, Caro 2005) reveal how hypopigmentation can lead to poor vision, greater predation risk, lower mating success and lower survival rates. Nevertheless, to date there is no proof that chromatic disorders are detrimental to bats. Bats use echolocation for foraging and orientation, usually prefer dark roost sites and are mostly active at night; pigmentation may therefore have no effect either on predation or social behaviour. Indeed, there are several reports of bats affected by hypopigmentation surviving for many years: Brack and Johnson (1990) observed

the same albino *Myotis sodalis* in a cave in Indiana (USA) in 1985, 1987 and 1989, Bartonička and Buřič (2007) observed the same albino *Rhinolophus hipposideros* every year from 2000 to 2007 in a cave in Jeseník (Czech Republic), while Sánchez-Hernández et al. (2010) recaptured several times the same two albino *Desmodus rotundus* in 2008–2009 in a tunnel in Guerrero (Mexico). Uieda (2001) kept an albino female *Desmodus rotundus* in captivity for two years in Brazil before it died from a bacterial infection. Furthermore, many authors describe pregnant or lactating aberrant bats. Brigham and James (1993) captured a pregnant albino *Myotis lucifugus* in Saskatchewan (Canada) and Sánchez-Hernández et al. (2010) captured a lactating albino *Desmodus rotundus* in Guerrero (Mexico). A pregnant leucistic *Nyctalus noctula* was captured in a building in Zagreb (Croatia), while a pregnant hypomelanistic *Artibeus jamaicensis* was captured in Colima (Mexico; Dulić & Mikuska 1968, Sánchez-Hernández et al. 2010). Similarly, Talerico et al. (2008) caught a pregnant piebald *Myotis lucifugus* in a building in Yukon (Canada), García-Morales et al. (2012) caught a pregnant piebald *Sturnira ludovici* in Hidalgo (Mexico), López-Wilchis and León (2012) captured a lactating piebald *Artibeus lituratus* in a cave in Oaxaca (Mexico), and Rocha et al. (2013) captured a pregnant piebald *Carollia perspicillata* in a cave in Sergipe (Brazil).

CONCLUSIONS

Although chromatic aberrations in bats seem to be a worldwide phenomenon, there is a huge bias towards the best-studied regions (North America and Europe – Africa and Australia have the fewest reports) and also towards the most abundant and best-sampled bat families and species. In the years since Uieda's (2000) first review of albinism in bats, and despite several attempts to generate ecological hypotheses, no clear or solid facts regarding how these anomalies might affect bat survival rates have ever been established. Even so, we did detect a high proportion of misused terminology in descriptions of chromatic disorders in the scientific literature and so here we have highlighted the need to standardise the nomenclature used as a means of reporting these findings. We therefore propose a classification (Table 1) based mainly on van Grouw (2006, 2013) and Abreu et al. (2013), which will act as a useful tool for resolving discrepancies and for clarifying any major doubts in the future. We encourage scientists from less well-studied regions to publish their findings in order to complement available data on the subject.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Summary of records of chromatic disorders in bats.