COMMUNITY-SOURCED SIGHTINGS OF ATYPICAL BIRDS CAN BE USED TO UNDERSTAND THE EVOLUTION OF PLUMAGE COLOR AND PATTERN

Stepfanie M. Aguillon[1] and Allison J. Shultz[2]

[1] Department of Biology, Stanford University, 327 Campus Dr., Stanford, CA 94305

[2] Ornithology Department, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007

Corresponding authors: Stepfanie M. Aguillon (stepfanie.aguillon@gmail.com), Allison J. Shultz (ashultz@nhm.org)

ABSTRACT

Birds are known for their brilliant colors and extraordinary patterns. Sightings of individuals with atypical plumage often cause considerable excitement in the birding public, but receive little attention beyond reporting one-off sightings by the scientific community. In this perspective, we argue that sightings of individuals with atypical plumage submitted to community science platforms hold the potential to further our understanding of the evolution of plumage color and patterning in birds. As a demonstration, we outline two examples using sightings of leucistic individuals—those that lack melanin across the body or in certain feather patches. First, we discuss the potential for understanding carotenoid pigmentation with these sightings. Leucism influences melanins, but not carotenoids, and so the extent and distribution of carotenoids across the body are unmasked. In a leucistic individual, carotenoids may or may not be more extensive than what is typically visible and this could help to understand the energetic costs and constraints involved in obtaining, processing, and depositing carotenoids in different species. Second, we discuss how partial leucism could provide insights into plumage pattern evolution. We demonstrate that one can use the many observations present on community science platforms to identify repeated patterns in different partially leucistic individuals of the same species, and match these to patches present in related species. These patterns could be the result of shared

underlying genetic variation that controls plumage patterning in birds over long evolutionary timescales. With these examples we outline a few potential lines of inquiry possible with atypical sightings submitted to community science platforms and note that other plumage aberrations provide additional opportunities. We encourage researchers to take full advantage of these chance sightings when they occur and database managers to make it possible to more easily tag photos of individuals with atypical plumage or other traits.

LAY SUMMARY

- The fascination of the birding public with the brilliant colors and patterns of birds means sightings of individuals with atypical plumage receive extraordinary attention.
- We suggest these sightings should receive equal attention from the scientific community, as they could further our evolutionary understanding of bird color and patterning.
- As a demonstration, we outline two examples using sightings of leucistic individuals—those lacking melanin in some or all of their plumage.
- We encourage researchers to take full advantage of these rare sightings and managers of community science platforms to enable easier searches for atypical individuals.

The vibrant diversity of bird coloration and patterning made possible by just a handful of pigments and feather microstructures has fascinated ornithologists and birders alike for centuries (Hill and McGraw 2006, Mason and Bowie 2020, Terrill and Shultz 2022). Birds with “aberrant” or “atypical” plumage are thus easy to identify and, although rare, occur frequently enough in nature to become an attraction to be chased by the birding public (e.g., the sightings of “yellow cardinals” that occur every few years; Saha 2018). In the scientific literature, the focus has largely remained on reporting new, one-off sightings of individuals with atypical plumage, with the majority of these reports being published in smaller or regional journals (e.g., the 70 articles identified in Appendix

Table 1). It has remained difficult to move beyond individual sightings due to the limited ability to amass large sample sizes. However, some studies have compiled the published sightings from particular groups or from particular localities (e.g., Alaja and Mikkola 1997, Konter 2015, Bond and Diamond 2016, Mahabal et al. 2016, Lee and You 2016, Mikula et al. 2017, Abraham et al. 2020) or have performed intensive sampling to try to assess the frequency of atypical plumage in a species or clade (Jehl 1985, Møller et al. 2007, Martins-Silva et al. 2016). More rarely, studies will ask questions that move beyond sightings or frequencies of atypical individuals in the population (Hudon et al. 2017, Levinson et al. 2021, Besozzi et al. 2021, Hudon and Pyle 2022, Ocampo et al. 2022, Camacho et al. 2022). The rise in community-driven science presents an opportunity to study these sightings in large numbers in a way that was nearly impossible solely with museum holdings or an individual's own sightings (e.g., Leighton et al. 2016, Husby 2017, Izquierdo et al. 2018, Zbyryt et al. 2021). In this perspective, we argue that the large number of photographs now available on community science platforms (e.g., iNaturalist and eBird) make it possible to study atypically colored birds through an evolutionary lens for the first time.

There are a variety of potential plumage aberrations in birds, though terminology has varied greatly over time and across different interest groups (e.g., Davis 2007, Guay et al. 2012, Rodríguez-Ruíz et al. 2017, van Grouw 2021, Zbyryt et al. 2021; and see the variety of terms used in Appendix Table 1). In this perspective, we focus specifically on sightings of leucistic individuals to demonstrate the potential use of atypical sightings in an evolutionary framework. Leucism has previously been described as "amelanic" or incorrectly as "albino" or "partially albino" (Davis 2007, van Grouw 2021), and can be difficult to distinguish from "progressive graying," a condition that results in the loss of melanin in feathers over time due to aging (Izquierdo et al. 2018, van Grouw 2021). Here, we use "leucism" as a catch-all term for atypical plumage that is the result of the lack of melanin pigmentation in the feathers of certain body patches ("partial" leucism) or across the entire body ("full" leucism). This lack of melanin in the feathers reveals the patterns and colors that are present underneath, allowing us to see what is not normally visible in the plumage. We believe this “unmasking” of the plumage underlying melanins and novel plumage patterns present in partially leucistic individuals could provide important evolutionary insights into the evolution of color and pattern in birds. Below, we present two examples demonstrating the potential uses of sightings of leucistic individuals documented on community science platforms.

Example #1: leucism can unmask mechanisms involved in carotenoid pigmentation

Sightings of leucistic individuals are particularly useful for understanding the distribution and extent of carotenoid coloration (Figure 1). As carotenoid pigmentation is not influenced by the same biological processes that produce or deposit melanin pigmentation (Toews et al. 2017), a leucistic bird that possesses both melanin and carotenoid pigments in their feathers would have their carotenoid pigmented feathers on display. In some cases, the extent of carotenoid patches may differ in leucistic individuals from what is typically visible, as is the case in the Red-winged Blackbird (*Agelaius phoeniceus*; Figure 1A-B). In other cases they may be similar, as in the Yellow-rumped Warbler (*Setophaga coronata coronata*; Figure 1C-D). Both situations present an opportunity to understand the specificity of carotenoid pigment deposition across the body and the energetics costs to produce the carotenoid patch. If the carotenoid patch is more extensive in the leucistic individual (Figure 1A), then it may not be costly to produce the patch. As the energetic cost of carotenoid pigmentation has a long-history of study and debate (reviewed in Svensson and Wong 2011, Koch et al. 2018), assessing the extent of carotenoids in leucistic individuals could provide a clue to the ease of obtaining dietary carotenoids and the costliness of producing the patch. On the other hand, if the extent of the carotenoid patch is similar in the leucistic individual as in the typical plumage (Figure 1C), then this might suggest some kind of cost or constraint does exist. In both cases, the extent of hidden carotenoid patches may be constrained by evolutionary history, and so comparing leucistic individuals of closely related species could be particularly powerful.

As feather patches pigmented with carotenoids are often the subject of sexual selection (Hill and McGraw 2006), understanding the actual extent of the deposited carotenoids can influence our understanding of the evolution of these colors. For example, a common argument in birds is that females prefer males that are brighter in their carotenoid plumage as this represents an honest signal of the male's quality (Svensson and Wong 2011). This assumes some cost or constraint in obtaining or producing the bright coloration resulting in only the best quality males being able to produce the brightest colors. Assessing leucistic individuals in a particular species of interest can help determine if this kind of argument might apply. It might be possible to better pinpoint the stage in the carotenoid acquisition, processing, or deposition where constraints exist: it may be easy to obtain carotenoids in the diet (e.g., if carotenoids are more extensive in leucistic individuals than in the typical plumage), but there is a constraint in the carotenoid deposition (e.g., if there is variation in the extent of carotenoid plumage across leucistic individuals). Leucistic individuals might reveal that the constraint is more complicated than initially thought, or that the constraint does not exist at all. Importantly, sightings of leucistic individuals make this kind of assessment straightforward without the need to assess if carotenoids are present across the different patches of the body using more exhaustive and expensive methods.

Example #2: partial leucism can elucidate plumage pattern evolution

Partial leucism can be produced by different mechanisms, and can produce patterns ranging from a few aberrant feathers to entire body regions. When an individual has distinct leucistic plumage regions, they may be useful for understanding the evolution of typical plumage patterns across species. There have been great advances in the genetic and developmental mechanisms underlying plumage patterns in the genomic era, but many questions remain unanswered, particularly regarding the mechanisms underlying the spatial distribution of plumage colors on an individual (Price-Waldman and Stoddard 2021). Recent genomic studies of closely related species have identified regions of the genome associated with plumage patterns that contain sets of genes that demonstrate modular evolution and patch-specific control (e.g., genes that are shared across a radiation and seem to turn color in particular body patches on or off; Stryjewski and Sorenson 2017, Baiz et al. 2021, Estalles et al. 2022). However, we know very little about how plumage patterns might evolve or persist on longer evolutionary timescales. Studying partially leucistic individuals that demonstrate particular plumage patterns may be a way to bridge some of the gaps in our understanding. Many of the identified genomic differences occur in hypothesized gene regulatory regions (reviewed in Funk and Taylor 2019), so it is possible that partially leucistic individuals have mutations in regulatory regions of genes that exert control over particular patches of the body.

For some species, observations are made of many leucistic individuals that occur in different parts of their range, suggesting that they occur independently of each other. By quantifying where on the body leucistic patches occur, one could identify consistent patterns that occur across multiple individuals. These patterns may be indicative of genetic variation for color patterns that exist in the genome that are not usually expressed. For example, by using photographed observations of birds marked as “leucistic” on iNaturalist, we identified consistent patterns in the head of the Red-winged Blackbird (Figure 2A-C) and in the cheeks and crown of the House Finch (*Haemorhous mexicanus*) (Figure 2D-F). Photographs can be very useful for quantifying phenotypic trends, but cannot provide genotypes for the individuals in question. However, leucistic birds may persist in certain localities (e.g., the individual in Figure 2B is known as ‘baldy’ and has been observed on the same territory for several years) and a vigilant observer may be able to capture known individuals for DNA samples. Once consistent patterns have been identified within a species, identifying analogous patches from typical plumage of birds related to the species with leucistic patches may provide insight into genotype-phenotype relationships that are shared across long evolutionary timescales. In Figure 3, we provide four examples of leucistic patches that occur in typical individuals of species from the same family. With a large dataset, calculating evolutionary time between species could illuminate patterns of patch evolution across the bird phylogeny. Additionally, with larger sample sizes within or across species, it may eventually be possible to hypothesize when the genetic variation underlying observed plumage regions might have arisen, and for how long they might persist over evolutionary time.

The utility and opportunity of community science

Community science, also known as citizen science or participatory science, is an increasingly valuable tool in ecological and environmental science, particularly in applications of biodiversity (e.g., species distributions, abundances; Fraisl et al. 2022). However, community science can also offer opportunities for understanding the ecology and evolution of species traits (Drury et al. 2019, Laitly et al. 2021, Minor et al. 2022, Cosentino and Gibbs 2022), and, importantly, can enable novel opportunities for gathering observations of rare taxa, phenomena, or behaviors (e.g., Dylewski et al. 2017, Pesendorfer et al. 2018, Mesaglio et al. 2021). As discussed above, atypical plumage is an example of a biological phenomenon with enormous potential that may be increasingly realized with community science data (although collections biases need to be accounted for; Zbyryt et al. 2021, Fraisl et al. 2022), as has been demonstrated with distributional data (Johnston et al. 2020). To fully realize this potential, we recommend that the databases that collect these data improve metadata associated with observations. Different databases give users the ability to comment on or add metadata to their observations, but we recommend that databases give users the ability to flag observations of individuals with atypical phenotypes or behaviors. Even a simple checkbox for an atypical observation that either community scientists or identifiers could flag could save researchers from needing to manually score hundreds to thousands of observations to identify sightings of interest, and make sure that potentially important observations are not lost. Advancing research on these sightings will require accessible photos and documentation, and this will only become practical when it is easily possible to search and download sightings of atypical individuals.

In addition to being beneficial for scientific research, community science offers the opportunity for public engagement and informal science education. However, simply using data collected by community scientists is not sufficient for creating an opportunity for participants to learn and engage in the science enabled by their efforts (Phillips et al. 2019, Fraisl et al. 2022, Bruckermann et al. 2022). Researchers should fully engage with the individuals whose observations they use, at a minimum to notify them of the research their observation is contributing to, and potentially even in the study design or scientific writing process (Phillips et al. 2019, Bruckermann et al. 2022). Appropriate credit to community scientists should be included in publications that use their data, including authorship when appropriate (Ward-Fear et al. 2020a, b), as exemplified by Toews et al. (2018). There is enormous potential for public engagement in science with observations like those of animals with atypical coloration, and could lead to increased scientific literacy.

Concluding thoughts

In this perspective, we highlight how sightings of birds with atypical plumage documented with photographs on community science platforms (e.g., iNaturalist and eBird) provide a unique opportunity to understand coloration and patterning in birds, especially when viewed through an evolutionary lens. We used leucistic individuals as an example to outline just a small subset of the potential scientific applications for sightings of birds with atypical plumage, but note that similar lines of inquiry can be applied to individuals with different plumage aberrations. For instance, individuals with melanism could additionally provide insights into the evolution of color patterning (e.g., as in Figure 3) or individuals with aberrations that influence carotenoid pigment color (Gómez et al. 2013, Blondel and Kern 2022) could provide insights into the biochemical processing of carotenoids across birds. Plumage aberrations could serve as an important source of novel phenotypic variation for evolution to act upon (Hosner and Lebbin 2006, Ocampo et al. 2022), so it would be worthwhile to begin to view these sightings through an evolutionary lens.

We suggest researchers take full advantage of photographed sightings of atypical individuals of their particular species of interest when they occur and to mine community science databases for previous sightings. Particularly in species difficult to study, these fortuitous sightings could help complement or reinforce findings from current work or even provide useful starting hypotheses for future work.

ACKNOWLEDGMENTS

We thank the virtual Carotenoids in Ornithology reading group (organized by E. A. Webb) for their inspiration in writing this paper. Many thanks to the contributors to iNaturalist, Twitter, and various birding Facebook groups that post their photos of interesting, atypical bird sightings. Comments from two anonymous reviewers and an associate editor greatly improved this manuscript.

Funding statement: S.M.A. was supported by a Stanford Science Fellowship.

Ethics statement: The authors declare no conflicts of interest.

Author contributions: S.M.A. and A.J.S conceived the idea and wrote the paper.

Data availability: No new data were generated in this study. All photo credits are available in the figure captions.

LITERATURE CITED

Abraham, K. F., C. J. Risley, and D. V. C. Weseloh (2020). Aberrant colouration in some Ontario birds. Ontario Birds 38:36–48.

Alaja, P., and H. Mikkola (1997). Albinism in the Great Gray Owl (*Strix nebulosa*) and other owls. In Biology and Conservation of Owls of the Northern Hemisphere. pp. 33–37.

Baiz, M. D., A. W. Wood, A. Brelsford, I. J. Lovette, and D. P. L. Toews (2021). Pigmentation genes show evidence of repeated divergence and multiple bouts of introgression in *Setophaga* warblers. Current Biology 31:643-649.e3.

Besozzi, E., B. Chew, D. C. Allen, and A. Contina (2021). Stable isotope analysis of an aberrant

Painted Bunting (*Passerina ciris*) feather suggests post-molt movements. The Wilson Journal of Ornithology 133:151–158.

Blondel, N., and P. Kern (2022). Orange pigment variety in Black-bellied Crimson Finch *Neochmia phaeton phaeton* from West Kimberley, Australia. Australian Field Ornithology 39:171–173.

Bond, A. L., and A. W. Diamond (2016). Aberrant colouration in the Atlantic Puffin (*Fratercula arctica*), the Common Murre (*Uria aalge*), and the Thick-billed Murre (*U. lomvia*) from Atlantic Canada. The Canadian Field-Naturalist 130:140–145.

Bruckermann, T., H. Greving, M. Stillfried, A. Schumann, M. Brandt, and U. Harms (2022). I'm fine with collecting data: engagement profiles differ depending on scientific activities in an online community of a citizen science project. PLOS One 17:e0275785.

Camacho, C., P. Sáez-Gómez, P. Hidalgo-Rodríguez, J. Rabadán-González, C. Molina, and J. J. Negro (2022). Leucistic plumage as a result of progressive greying in a cryptic nocturnal bird. Scientific Reports 12:3411.

Cosentino, B. J., and J. P. Gibbs (2022). Parallel evolution of urban–rural clines in melanism in a widespread mammal. Scientific Reports 12:1752.

Davis, J. N. (2007). Color abnormalities in birds: a proposed nomenclature for birders. Birding 39:36–46.

Drury, J. P., M. Barnes, A. E. Finneran, M. Harris, and G. F. Grether (2019). Continent-scale phenotype mapping using citizen scientists' photographs. Ecography 42:1436–1445.

Dylewski, Ł., P. Mikula, P. Tryjanowski, F. Morelli, and R. Yosef (2017). Social media and scientific research are complementary—YouTube and shrikes as a case study. The Science of Nature 104:48.

Estalles, C., S. P. Turbek, M. José Rodríguez-Cajarville, L. F. Silveira, K. Wakamatsu, S. Ito, I. J. Lovette, P. L. Tubaro, D. A. Lijtmaer, and L. Campagna (2022). Concerted variation in melanogenesis genes underlies emergent patterning of plumage in capuchino seedeaters. Proceedings of the Royal Society B: Biological Sciences 289:20212277.

Fraisl, D., G. Hager, B. Bedessem, M. Gold, P.-Y. Hsing, F. Danielsen, C. B. Hitchcock, J. M. Hulbert, J. Piera, H. Spiers, M. Thiel, and M. Haklay (2022). Citizen science in environmental and ecological sciences. Nature Reviews Methods Primers 2:1–20.

Funk, E. R., and S. A. Taylor (2019). High-throughput sequencing is revealing genetic associations with avian plumage color. The Auk: Ornithological Advances 136:1–7.

Gómez, R. O., M. I. Stefanini, and G. F. Turazzini (2013). Carotenismo en un ejemplar de churrinche (*Pyrocephalus rubinus*). Nuestras Aves 58:46–48.

van Grouw, H. (2021). What's in a name? Nomenclature for colour aberrations in birds reviewed. Bulletin of the British Ornithologists' Club 141:276–299.

Guay, P.-J., D. Potvin, and R. Robinson (2012). Aberrations in plumage coloration in birds. Australian Field Ornithology 29:23–30.

Hill, G. E., and K. J. McGraw (2006). Bird Coloration: Function and Evolution. Harvard University Press, Cambridge, Massachusetts.

Hosner, P. A., and D. J. Lebbin (2006). Observations of plumage pigment aberrations of birds in Ecuador, including Ramphastidae. Boletín de la Sociedad Antioqueña de Ornitología 16:30–43.

Hudon, J., R. J. Driver, N. H. Rice, T. L. Lloyd-Evans, J. A. Craves, and D. P. Shustack (2017). Diet explains red flight feathers in yellow-shafted flickers in eastern North America. The Auk: Ornithological Advances 134:22–33.

Hudon, J., and P. Pyle (2022). Diet-Related plumage erythrism in the Western Tanager and other western North American birds. Western Birds 53:30–42.

Husby, M. (2017). Colour aberrations in Eurasian Magpies *Pica pica* in Europe. Ornithological Science 16:111–119.

Izquierdo, L., R. L. Thomson, J. I. Aguirre, A. Díez-Fernández, B. Faivre, J. Figuerola, and J. D. Ibáñez-Álamo (2018). Factors associated with leucism in the common blackbird *Turdus* *merula*. Journal of Avian Biology 49:e01778.

Jehl, J. R., Jr. (1985). Leucism in Eared Grebes in western North America. The Condor 87:439–441.

Johnston, A., W. M. Hochachka, M. E. Strimas-Mackey, V. R. Gutierrez, O. J. Robinson, E. T. Miller, T. Auer, S. T. Kelling, and D. Fink (2020). Analytical guidelines to increase the value of citizen science data: using eBird data to estimate species occurrence. [Online.] Available at https://www.biorxiv.org/content/10.1101/574392v3.

Koch, R. E., G. E. Hill, and B. Sandercock (2018). Do carotenoid-based ornaments entail resource trade-offs? An evaluation of theory and data. Functional Ecology 32:1908–1920.

Konter, A. (2015). Aberrant plumages in grebes Podicipedidae: an analysis of albinism, leucism, brown and other aberrations in all grebe species worldwide. Musée National d'histoire Naturelle Luxembourg, Luxembourg.

Laitly, A., C. T. Callaghan, K. Delhey, and W. K. Cornwell (2021). Is color data from citizen science photographs reliable for biodiversity research? Ecology and Evolution 11:4071–4083.

Lee, S.-Y., and Y.-H. You (2016). Plumage color aberrations of birds in Korea. The Korean Journal of Ornithology 23:1–11.

Leighton, G. R. M., P. S. Hugo, A. Roulin, and A. Amar (2016). Just Google it: assessing the use of Google Images to describe geographical variation in visible traits of organisms. Methods in Ecology and Evolution 7:1060–1070.

Levinson, P. M., A. E. Schmidt, V. Morandini, M. Elrod, D. Jongsomjit, and G. Ballard (2021). Breeding behaviour of colour-aberrant Adélie penguins (*Pygoscelis adeliae*) at Cape Crozier, Ross Island, Antarctica. Antarctic Science 33:335–343.

Mahabal, A., H. van Grouw, R. Sharma, and S. Thakur (2016). How common is albinism really? Colour aberrations in Indian birds reviewed. Dutch Birding 38:301–309.

Martins-Silva, J., M. B. Vecchi, and M. A. S. Alves (2016). First documented records of white plumage aberration in the White-necked Thrush (*Turdus albicollis*). The Wilson Journal of Ornithology 128:931–935.

Mason, N. A., and R. C. K. Bowie (2020). Plumage patterns: ecological functions, evolutionary origins, and advances in quantification. The Auk: Ornithological Advances 137:ukaa060.

Mesaglio, T., A. Soh, S. Kurniawidjaja, and C. Sexton (2021). 'First known photographs of living specimens': the power of iNaturalist for recording rare tropical butterflies. Journal of Insect Conservation 25:905–911.

Mikula, P., A. Čanády, and M. Hromada (2017). Aberrant plumage colouration in birds from the collection of the Sarisske Museum Bardejov, Slovakia. Zoology and Ecology 27:223–227.

Minor, N. R., P. J. Dougherty, S. A. Taylor, and M. D. Carling (2022). Estimating hybridization in the wild using citizen science data: a path forward. Evolution 76:362–372.

Møller, A. p, T. a Mousseau, F. de Lope, and N. Saino (2007). Elevated frequency of abnormalities in barn swallows from Chernobyl. Biology Letters 3:414–417.

Ocampo, D., A. Quesada, C. Oconitrillo, R. Lobo, and J. A. C. Uy (2022). Independent observations of phaeomelanic males of the Variable Seedeater (*Sporophila corvina*) with comments about its potential for evolutionary divergence. Ornitología Neotropical 33:79–83.

Pesendorfer, M. B., S. Dickerson, and J. W. Dragoo (2018). Observation of tool use in striped skunks: how community science and social media help document rare natural phenomena. Ecosphere 9:e02484.

Phillips, T. B., H. L. Ballard, B. V. Lewenstein, and R. Bonney (2019). Engagement in science through citizen science: moving beyond data collection. Science Education 103:665–690.

Price-Waldman, R., and M. C. Stoddard (2021). Avian coloration genetics: recent advances and emerging questions. Journal of Heredity 112:395–416.

Rodríguez-Ruíz, E. R., W. A. Poot-Poot, R. Ruíz-Salazar, and J. Treviño-Carreón (2017). Nuevos registros de aves con anormalidad pigmentaria en México y propuesta de clave dicotómica para la identificación de casos. Huitzil Revista Mexicana de Ornitología 18:57–70.

Saha, P. (2018). Why is this northern cardinal yellow? *Audubon*. [Online.] Available at https://www.audubon.org/news/why-northern-cardinal-yellow.

Stryjewski, K. F., and M. D. Sorenson (2017). Mosaic genome evolution in a recent and rapid avian radiation. Nature Ecology & Evolution 1:1912–1922.

Svensson and Wong (2011). Carotenoid-based signals in behavioural ecology: a review. Behaviour 148:131–189.

Terrill, R. S., and A. J. Shultz (2022). Feather function and the evolution of birds. Biological Reviews:brv.12918.

Toews, D. P. L., N. R. Hofmeister, and S. A. Taylor (2017). The evolution and genetics of carotenoid processing in animals. Trends in Genetics 33:171–182.

Toews, D. P. L., H. M. Streby, L. Burket, and S. A. Taylor (2018). A wood-warbler produced through both interspecific and intergeneric hybridization. Biology Letters 14:20180557.

Ward-Fear, G., G. B. Pauly, J. E. Vendetti, and R. Shine (2020a). Authorship: protocols should include citizen scientists. Nature 578:363–363.

Ward-Fear, G., G. B. Pauly, J. E. Vendetti, and R. Shine (2020b). Authorship protocols must change to credit citizen scientists. Trends in Ecology & Evolution 35:187–190.

Zbyryt, A., P. Mikula, M. Ciach, F. Morelli, and P. Tryjanowski (2021). A large-scale survey of bird plumage colour aberrations reveals a collection bias in internet-mined photographs. Ibis 163:566–578.

Figure 1

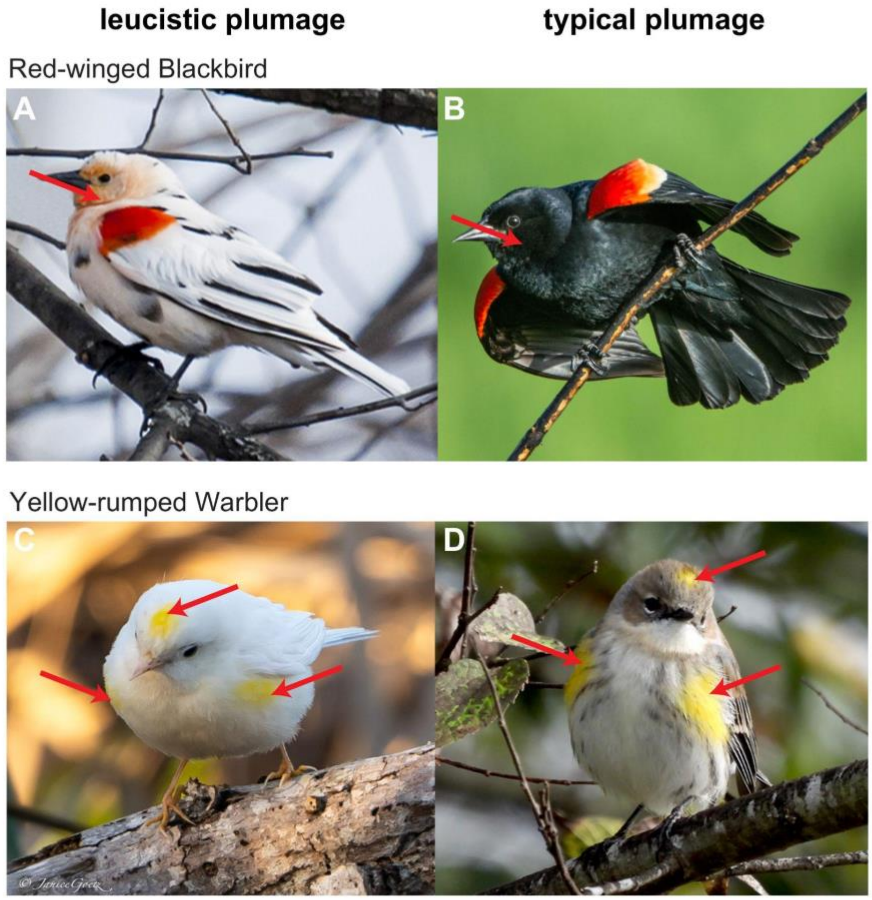

FIGURE 1. Red-winged Blackbirds (*Agelaius phoeniceus*) with (**A**) leucistic and (**B**) typical plumage demonstrating carotenoid coloration on the head, face, and throat that is hidden by melanin. Yellow-rumped Warblers (*Setophaga coronata coronata*) with (**C**) leucistic and (**D**) typical plumage demonstrating no hidden carotenoid coloration. Photo credits: (**A**) permission from Nancy Nabak; remaining photos obtained from iNaturalist and used under a CC-BY-NC license from (**B**) Jacob Collison, (**C**) Janice Goetz, and (**D**) Christa Denning.

Figure 2

FIGURE 2. Examples of similar patterns of partial leucism present in different (**A-C**) Red-winged Blackbirds and (**D-F**) House Finches (*Haemorhous mexicanus*). All photos obtained from iNaturalist. Photo credits: (**A**) CC-BY Jonathan Eisen, (**B**) CC-BY-NC-ND Randy Harwood, (**C**) CC-BY-NC Greg Lasley, (**D**) CC-BY Kalvin Chan, (**E**) CC-BY-NC Chris Bosacki, and (**F**) CC-BY-NC Reina Pearson.

Figure 3

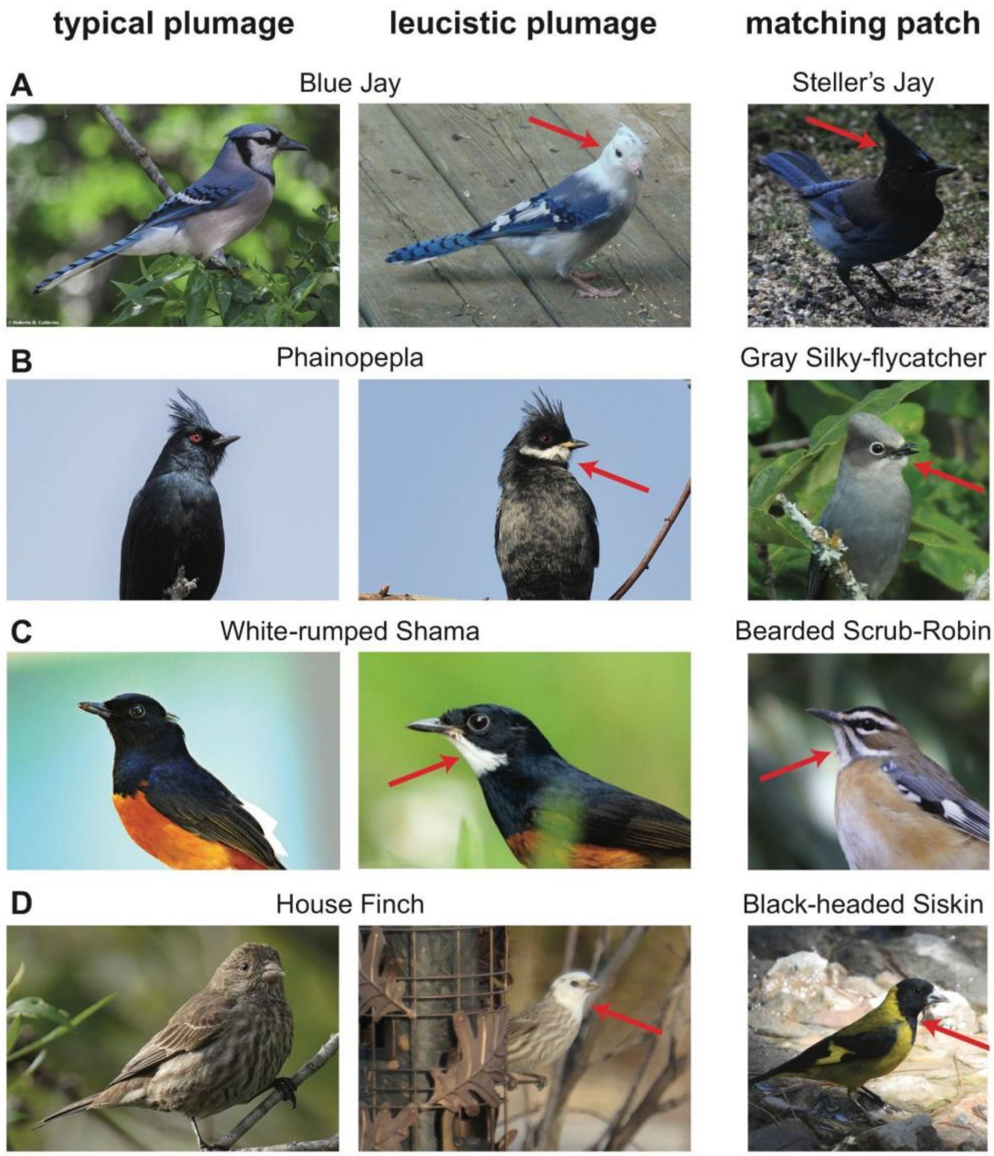

FIGURE 3. When specific regions of the plumage are leucistic, they may be similar to plumage patterns observed in other related species potentially due to mutations in gene regulatory regions that control patch-specific plumage coloration. These four examples each demonstrate a leucistic plumage patch that is matched by the plumage pattern of another species in the same family. (**A**) The leucistic head, upper back, and breast of the Blue Jay (*Cyanocitta cristata*) is similar to the black patch observed in the Steller's Jay (*Cyanositta stelleri*). (**B**) The leucistic chin of the Phainopepla (*Phainopepla nitens*) is similar to the light-colored chin of the Gray Silky-flycatcher

(*Ptiliogonys cinereus*). (**C**) The leucistic chin of the White-rumped Sharma (*Copsychus malabaricus*) is similar to the white chin of the Bearded Scrub-Robin (*Cercotrichas quadrivirgata*). (**D**) The leucistic head of the House Finch is similar to the black head of the Black-headed Siskin (*Spinus notata*). All photos obtained from iNaturalist. Photo credits (in order from left to right within panels): (**A**) CC-BY-NC Roberto R. Calderón, CC-BY-NC madworld1962, and CC-BY-NC macrhybopis. (**B**) CC-BY-NC Mark Otnes, CC-BY-NC brodiaea_max, and CC-BY Martín Márquez. (**C**) CC-BY-NC sunmr, CC-BY-NC Ben Tsai蔡維哲, and CC-BY-NC maritzasouthafrica. (**D**) CC-BY Daniel S. Katz, CC-BY-NC Susan Cahill, and CC-BY-NC Christopher Lindsey.

Appendix Table S1. Reports of one-off sightings of birds with atypical plumage (published 2000-present). The terminology used for the plumage aberrations are taken directly from the published articles. As many small or regional journals are not indexed in Google Scholar and many articles are likely not published in languages understood by the authors, this serves as a non-exhaustive list of reported sightings.