



How common is hybridization in birds?

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Abstract

Hybridization—the interbreeding of different species—plays an integral role in the evolution of numerous bird species. However, it remains unclear how widespread this phenomenon is within and across different bird groups. Estimating the incidence of hybridization in different bird lineages can inform comparative analyses to uncover the evolutionary and ecological forces that promote or prevent the formation of hybrids. Estimates on a species level have varied from about 10% to almost 20% of hybridizing bird species. The variation among the latest estimates largely depends on the choice of global species checklists with differing decisions on the taxonomic status of certain (sub)species. However, the hybrid records in these estimates have generally been taken at face value. Detailed assessments of these records revealed that some cases are unreliable or incorrect. Removing of these faulty records and discovery of novel hybrids will result in a fluctuating percentage of hybridizing species that can best be captured in a living document (e.g., a regularly updated website or checklist). Estimating hybridization on an individual level is more challenging. A first attempt, using citizen science data from the eBird project, reported 0.064% hybrid individuals in the United States. This percentage is probably an underestimate due to underreporting of hybrids by birdwatchers and remains to be finetuned by considering other confounding factors, such as spatial and temporal variation in hybridization dynamics. Future efforts in estimating avian hybridization will need to rely on a combination of data sources and techniques, such as genetics, museum specimens, and citizen science.

Keywords Hybridization · Citizen science · Reproductive isolation · Speciation · Taxonomy

Zusammenfassung

Wie häufig ist Hybridisierung bei Vögeln?

Hybridisierung—die Kreuzung unterschiedlicher Arten—spielt eine wesentliche Rolle in der Evolution zahlreicher Vogelarten. Unklar ist jedoch, wie verbreitet dieses Phänomen innerhalb und zwischen verschiedenen Vogelgruppen ist. Eine Schätzung, wie ausgeprägt die Hybridisierung in verschiedenen Vogelstämmen ist, kann als Grundlage für vergleichende Analysen dienen, um die evolutionären und ökologischen Faktoren aufzuzeigen, die die Bildung von Hybriden fördern oder verhindern. Solche Schätzungen auf Art-Ebene schwanken zwischen etwa 10% und fast 20% der hybridisierenden Vogelarten. Die Unterschiede zwischen den jüngsten Schätzungen hängen weitgehend von der Zusammenstellung der globalen Arten-Checklisten ab, die auf unterschiedlichen Entscheidungen bezüglich des taxonomischen Status bestimmter (Unter-)Arten basieren. Aber die Hybriden-Datensätze in diesen Schätzungen wurden im Allgemeinen als Tatsache akzeptiert, wobei eine gründlichere Prüfung dieser Aufzeichnungen ergab, dass einige der Angaben unzuverlässig oder falsch sind. Das Weglassen solcher fehlerhaften Datensätze und die Entdeckung neuer Hybriden wird zu wechselnden Prozentsätzen an hybridisierenden Arten führen, die am besten in einem dynamischen Dokumentationssystem (z. B. einer regelmäßig aktualisierten Website

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oder Checkliste) erfasst werden können. Das Abschätzen der Hybridisierung auf individueller Ebene ist eine größere Herausforderung. Ein erster Versuch, bei dem von interessierten Laien (citizen science) beigetragene Daten aus dem eBird-Projekt verwendet wurden, ergab 0.064% hybride Individuen in den Vereinigten Staaten. Dieser Prozentsatz ist wahrscheinlich zu niedrig angesetzt, weil die Vogelbeobachter zu wenig Hybriden melden und muss durch die Berücksichtigung anderer Einflussfaktoren wie z. B. die räumlichen und zeitlichen Unterschiede in der Hybridisierungsdynamik noch verfeinert werden. Künftige Versuche, die Hybridisierung von Vögeln abzuschätzen, müssen sich auf eine Kombination von Informationsquellen und Techniken wie z. B. Genetik, Museumsexemplare und Bürgerforschung stützen.

Introduction

In his book *Animal Species and Evolution*, Ernst Mayr (1963) stated that ‘the available evidence contradicts the assumption that hybridization plays a major evolutionary role’. At the time of writing, this assertion was justified for animals (but not for plants, see for example Anderson and Stebbins 1954). Since the 1960s, however, the available evidence has been accumulating in favor of an important evolutionary role for animal hybridization (Abbott et al. 2013; Harrison and Larson 2016). Specifically, the development of genetic techniques for detecting hybridization revealed that it is a relatively common phenomenon across the Tree of Life (Mallet et al. 2016; Taylor and Larson 2019). Moreover, hybridization and consequent backcrossing of fertile hybrids can result in the exchange of genetic material between species (Ottenburghs et al. 2017). This interspecific gene flow—also known as introgression—has been extensively documented in hybrid zones (see Chapter 15 in Price 2008 for a comprehensive overview of avian examples) and might even lead to the transfer of adaptive traits across species boundaries (Hedrick 2013; Arnold and Kunte 2017). In addition to introgression, hybridization can contribute to the origin of new species through hybrid speciation (Schumer et al. 2014; Ottenburghs 2018). Although this mode of speciation is more common in plants, a handful of putative hybrid bird species have been reported, such as the Italian Sparrow (*Passer italiae*, Elgvin et al. 2017) and the Golden-crowned Manakin (*Lepidothrix vilasboasi*, Barrera-Guzmán et al. 2018). All in all, Mayr’s statement does not seem to apply to birds where the evolutionary role of hybridization—through introgression and hybrid speciation—is firmly established (Tobias et al. 2020).

The incidence of hybridization varies across the Tree of Life. For example, hybrids between European mammals have been recorded for at least 6% of the species (Gray 1972) and the incidence of hybridization in salamanders amounts to roughly 12% (Melander and Mueller 2020). For butterflies, the estimates of hybridization incidence range from 6 to 23%, depending on the family (Mallet 2005). In birds, estimates have varied from about 10% to almost 20% of species (for details, see section: Hybridization on the species level). On lower taxonomic levels, phylogenetic hotspots and coldspots for hybridization are also apparent (Ottenburghs et al. 2015), such as the striking contrast between

the bird orders Anseriformes (ca. 60% hybridizing species) and Caprimulgiformes (less than 5% of hybridizing species). Understanding the incidence of hybridization across the avian phylogeny can inform comparative analyses to uncover the evolutionary and ecological forces that promote or prevent the formation of hybrids (Randler 2006; Leighton et al. 2021). In some bird groups, hybridization might be limited by premating barriers, such as species-specific courtship behavior or the duration of pair bonds (Uy et al. 2018; Leighton et al. 2021). Specifically, song has been shown to be an effective premating barrier in passerines (e.g., leaf warblers, Wu et al. 2023; white-eyes, Cowles and Uy 2019). In other bird groups, postzygotic barriers might be more important, such as genetic incompatibilities that result in hybrid sterility or unviability (Pulido-Santacruz et al. 2018; Irwin 2020; Ottenburghs 2022). Moreover, hybridization dynamics might also be influenced by postmating prezygotic barriers, such as interspecific sperm competition and sperm–egg interactions, although this aspect has received less attention (Birkhead and Brillard 2007). Disentangling the relative importance of premating and postzygotic barriers—and their interactions (see Irwin 2020)—will require reliable estimates of the frequency of hybrids across different lineages (Westram et al. 2022).

Reliably quantifying the incidence of hybridization within larger taxonomic groups is a challenging exercise. Here, it is important to distinguish between hybridization on the species and on the individual level (Mallet 2005). The species level concerns the percentage of bird species that have hybridized with at least one other species. This estimate is relatively straightforward to calculate: a species has interbred with another species or it has not. One hybrid individual is thus sufficient to conclude that hybridization has occurred. However, identifying hybrids can be difficult for morphologically similar species (Randler 2004) as shown by the occasional misclassification of aberrant individuals as hybrids (e.g., Clark et al. 2017). Although these mistakes can be easily rectified with more detailed morphological and genetic analyses, the erroneous hybrid records might still be present in the scientific literature and run the risk of being included in larger analyses.

In comparison to the species level, quantifying the incidence of hybridization on the individual level is more difficult and time-consuming. To calculate the percentage of hybrid individuals within a geographic region, one needs to

confidently identify hybrids (already challenging for the species level estimates) as well as determine population sizes for the parental taxa. Moreover, the definition of a hybrid can influence the final estimate. Are only first-generation hybrids included, or are later-generation hybrids and backcrosses also taken into account? And are hybrids detected with phenotypic or genetic methods? These questions need to be addressed to place estimates of hybridization on the individual level into context. I will return to these issues later on (see section: Hybridization on an individual level).

Several scientists have tried to quantify the incidence of avian hybridization on the species level (Grant and Grant 1992; Aliabadian and Nijman 2007; Ottenburghs et al. 2015) and on the individual level (Justyn et al. 2020; Justen et al. 2020; Ottenburghs and Slager 2020; Hill and Justyn 2021; Minor et al. 2022). Reliable estimates on the species level can inform macroevolutionary analyses and provide insights into how the incidence of hybridization varies among bird orders and how it compares to other taxonomic groups. And individual level estimates of hybridization will help researchers to assess the importance of premating and postzygotic barriers across time and space. However, due to methodological differences and technical limitations, the resulting estimates vary among studies. In this paper, I will provide an overview of the latest estimates and identify possible sources of bias and uncertainty. This overview will lead to several avenues for future research to confidently quantify the incidence of hybridization in birds.

Hybridization in the species level

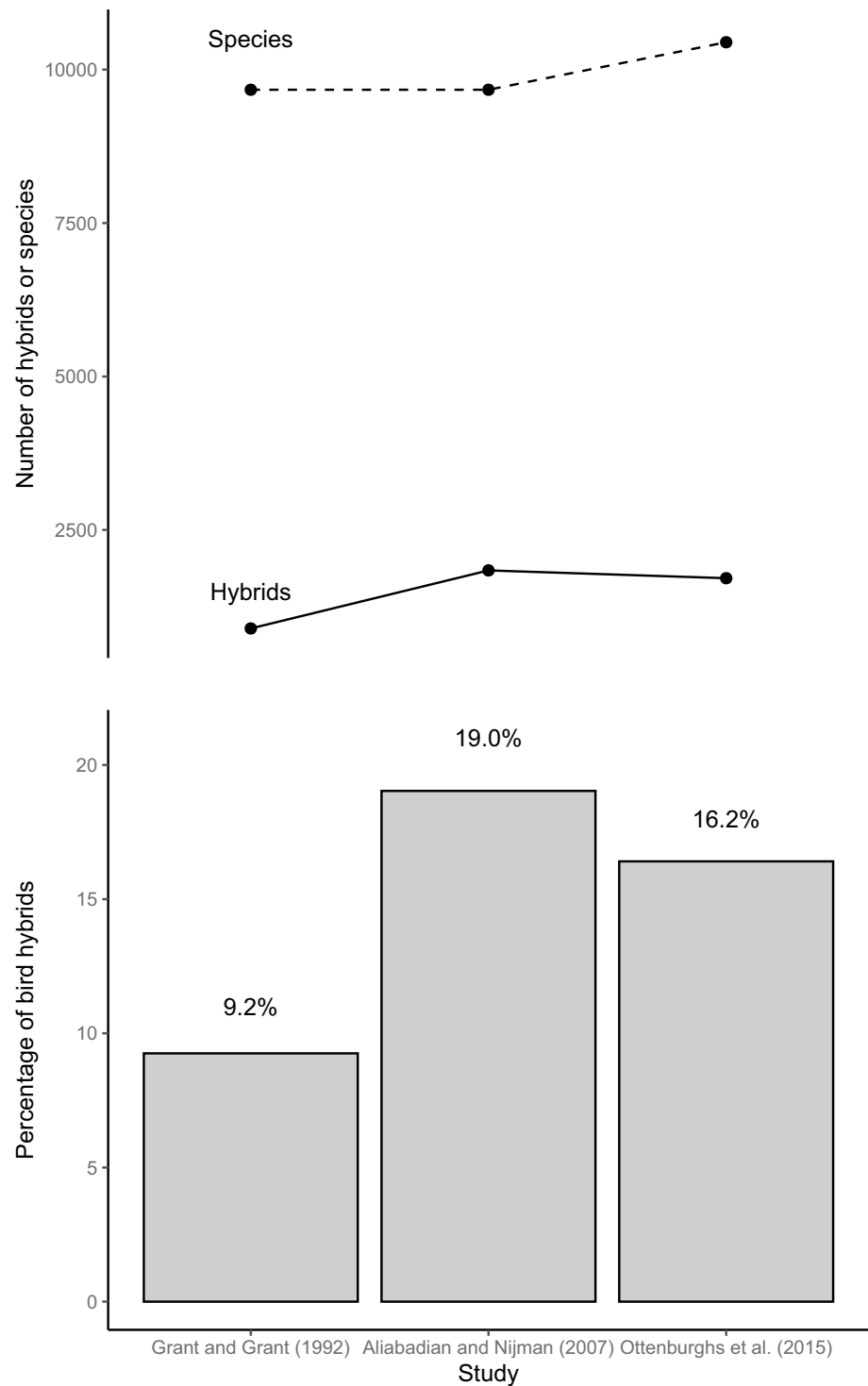
Scientists have been documenting bird hybrids for centuries. The French naturalist Georges-Louis Leclerc Comte de Buffon (1785), for example, described a cross between Canary (*Serinus canaria*) and Goldfinch (*Carduelis carduelis*)—along with several other animal hybrids—to support his incorrect hypothesis on embryonic development that the male determines the extremities of the body while the female accounts for the internal parts and the overall size and shape. In his book *The Variation of Animals and Plants under Domestication*, Charles Darwin (1868) documented several cases of avian hybridization, mostly involving crosses between wild birds and their domesticated counterparts, such as ducks and geese. However, these early reports were few and unsystematic. One of the first attempts to gather these scattered records was undertaken by André Suchetet (1896) who listed more than 200 bird hybrids.

Later checklists of bird hybrids focused on particular geographic regions (Cockrum 1952; Mayr and Short 1970). For example, Mayr and Short (1970) determined that 52 out of 516 non-marine species (10%) regularly hybridize in North America. A broader perspective was provided by Wilhelm

Meise (1975) who estimated that 2% of bird species regularly hybridize and another 3% occasionally hybridize. These numbers were updated by a more extensive analysis that used the most recent compilation of bird hybrids (Panov 1989) and the latest global catalogue of bird species (Sibley and Monroe 1990) available at the time to calculate that 895 out of 9672 species (9.2%) hybridized with at least one other species (Grant and Grant 1992). However, the list of bird hybrids by Panov (1989) was published in Russian, making it less accessible for the international scientific community. This hurdle was removed by Eugene McCarthy (2006) who produced an updated and extensively referenced overview in his *Handbook of Avian Hybrids of the World*. An analysis of the records in this book more than doubled the incidence of hybridization in birds from 9.2 to 19% (Aliabadian and Nijman 2007). This remarkable increase primarily reflects additional records of avian hybrids, although several taxonomic changes where subspecies were elevated to species rank also had an impact. A more recent analysis of McCarthy's book, supplemented with information from the Serge Dumont Bird Hybrids Database (www.bird-hybrids.com/), reported a slightly lower incidence of 16.2% hybridizing bird species (Ottenburghs et al. 2015). The discrepancy with the previous estimate (19%) can be explained by the use of different global checklists of bird species which disagree on the taxonomic rank of certain (sub)species: Aliabadian and Nijman (2007) relied on the survey of Sibley and Monroe (1990) with 9672 species whereas Ottenburghs et al. (2015) followed the IOC World Bird List (Gill et al. 2023) with 10,446 species. In summary, the estimates for the incidence of avian hybridization on the species level have increased from 9.2% (Grant and Grant 1992) to more than 15% (Aliabadian and Nijman 2007; Ottenburghs et al. 2015), although the exact number depends on the used global checklist of bird species (Fig. 1).

It is important to keep in mind that these percentages have a certain margin of error. The studies presented above have generally taken the reliability of the hybrid records at face value. However, detailed assessments of certain hybrids in the *Handbook of Avian Hybrids of the World* and the Serge Dumont Bird Hybrids Database revealed that some cases are questionable. For example, a putative hybrid between Chestnut-colored Woodpecker (*Celeus castaneus*) and Golden-olive Woodpecker (*Piculus rubiginosus*) can be traced back to an erroneous interpretation of a footnote in a checklist of Mexican birds (Miller et al. 1957). To capture the varying reliability of hybrid records, Ottenburghs (2021) introduced a scoring scheme that combines three criteria with different weights, namely (1) field observations or photographs (one point), (2) detailed morphological analyses (two points), and (3) genetic analyses (three points). The final tally of these three criteria (ranging from 0 to 6 points) indicates the level of confidence for a particular hybrid. To date, this

Fig. 1 Varying estimates of the incidence of avian hybridization on the species level. The resulting percentages are calculated by dividing the number of hybridizing species (solid line) by the number of bird species in global checklists (dashed line)



scoring scheme has only been applied to tinamous (order Tinamiformes) where it revealed one well-documented record (*Crypturellus boucardi* × *C. cinnamomeus*, based on a detailed description of museum specimens) and three doubtful cases that require further investigation (Ottenburghs 2021). Hence, only one out of four hybrid records in this bird group can be regarded as reliable. Clearly, a

thorough check of all hybrid records is needed to establish a more trustworthy estimate for the incidence of hybridization in birds. Moreover, when performing large-scale analyses of these hybrid records, such as macroevolutionary studies, it is advisable to discriminate between reliable and doubtful cases to avoid potential biases (see, for example, Leighton et al. 2021).

In addition to weeding out faulty records of avian hybrids, it is crucial to keep track of new cases. This can involve the discovery of previously undocumented hybrid individuals in the wild (Brennan et al. 2020; Cerqueira et al. 2020; Toews et al. 2018, 2020) or in captivity (Ottenburghs and Harteman 2021), but also taxonomic changes where currently interbreeding subspecies are elevated to species rank. It is thus likely that the percentage of avian hybrids at the species level will continue to fluctuate over time. A living document that keeps track of these changes and regularly updates this percentage with regard to the different bird checklists might be a viable solution, such as the Avian Hybrids Project (Ottenburghs et al. 2015) or the species accounts at the Birds of North America website (Justen et al. 2020). Such a living document would require strict criteria and expert guidance to include or exclude particular hybrid records.

Hybridization on the individual level

Another aspect of avian hybridization concerns the incidence on an individual level. Studies of avian hybrid zones have provided estimates for specific species pairs, but an overall estimate across multiple bird orders has rarely been attempted. Ernst Mayr (1963) used his experience with museum specimens to estimate the individual incidence of hybridization. He noted that about one in 60,000 specimens (0.00167%) was a hybrid individual. Recently, Justyn et al. (2020) tallied the number of hybrid individuals in the citizen science database eBird between 1 January 2001 and 31 December 2018. This analysis uncovered 212,875 hybrid records among 334,770,194 observations, amounting to an estimate of 0.064%. When they removed the ten most commonly reported hybrids, such as crosses involving the Mallard (*Anas platyrhynchos*), this number dropped to 0.009% (still slightly higher than Mayr's estimate). However, these percentages are most likely underestimates due to several biases, some of which are inherent to citizen science data. The study by Justyn et al. (2020) resulted in a back-and-forth discussion in the journal *Evolution* (Justen et al. 2020; Ottenburghs and Slager 2020; Hill and Justyn 2021; Minor et al. 2022). I will cover the main points from this debate in the following section.

First, not all hybrid individuals are readily recognized by birdwatchers. This failure to detect a hybrid can be due to the difficulty of identifying crosses between closely related species (Randler 2004), such as American Crow (*Corvus brachyrhynchos*) and Northwestern Crow (*C. caurinus*) that interbreed in western North America (Slager et al. 2020). In addition, birdwatchers might be reluctant to report hybrids because they are mainly focused on expanding their lists of observed species. This bias was nicely illustrated by Justen et al. (2020) who showed

that hybrids between Glossy Ibis (*Plegadis falcinellus*) and White-faced Ibis (*P. chihi*) were significantly underreported by local citizen scientists compared to experts extensively studying these birds. A more thorough analysis of hybrid sightings by citizen scientists remains to be conducted (e.g., using online surveys or interviews), but it seems likely that hybrids are being underreported by birdwatchers.

A second issue—largely unrelated to citizen science data—concerns the spatial and temporal variation in bird hybrids. Obviously, the percentage of hybrid individuals will be higher within or near a hybrid zone compared to an allopatric area. This spatial pattern raises the question whether it is meaningful to estimate the incidence of hybridization in areas where two species do not co-occur (Justen et al. 2020; Hill and Justyn 2021). The chosen approach will ultimately depend on the goal of the researchers and should be stated clearly in the study. In addition to spatial variation, hybridization dynamics are also expected to vary over time. This temporal effect was nicely captured in a survey of hybrid geese in the Netherlands. Citizen science data from a Dutch website (www.waarneming.nl) revealed that hybrids between migrating species were more commonly reported in winter whereas crosses between locally breeding species were observed year-round or peaked during the summer months (Ottenburghs 2017). Such spatial and temporal fluctuations are likely to be species-specific and will need to be taken into account when estimating the incidence of hybridization (for several approaches, see Minor et al. 2022).

As mentioned in the introduction, another source of potential bias relates to how a hybrid is defined in an estimate. In their survey of eBird data, Justyn et al. (2020) only considered phenotypic hybrids that showed intermediate features between the parental species. This approach misses cryptic hybrids (as explained above) and will probably not include later-generation hybrids or backcrosses. These different classes of hybrid individuals can be identified with genetic techniques. For example, a genomic survey of Mallards (*Anas platyrhynchos*) and American Black Ducks (*A. rubripes*) allowed researchers to confidently classify individuals for up to four generations of backcrossing using the software ADMIXTURE (Lavretsky et al. 2019). Another approach, based on remnants of recombination events, could even extend this classification beyond four generations, but these patterns became less reliable due to the genetic similarity between these duck species (Lavretsky et al. 2019). However, using a genetic strategy to estimate hybridization automatically changes the definition of a hybrid in the estimate (i.e., an individual with a portion of genetic variation from two parental species). Similar to the spatial and temporal patterns, it is thus important to clearly describe the aim of the study and

explicitly mention the definition of a hybrid (Justen et al. 2020; Hill and Justyn 2021).

The current estimate of 0.064% hybrid individuals among North American birds is thus probably an underestimate and remains to be refined with additional analyses and approaches. The effort of Justyn et al. (2020) and the subsequent discussion in the journal *Evolution* highlights the difficulty of estimating hybridization on an individual level. Different spatial, temporal and methodological factors need to be taken into account, which will require a combination of data sources and techniques, such as citizen science data, museum specimens and genetics (Minor et al. 2022). Moreover, hybridization dynamics are expected to be species-specific with differing importance of premating and postzygotic isolation mechanisms in particular species pairs (Pulido-Santacruz et al. 2018; Irwin 2020). The interplay of these reproductive isolation mechanisms will impact the number of hybrid individuals between the interbreeding species. This variation could be captured in an extensive meta-analysis of hybrid zone dynamics across the world that will provide insights into the incidence of hybridization across space and time.

Hybridization in the distant past

In addition to quantifying the contemporary incidence of hybridization, it is now also possible to infer patterns of hybridization in the distant past. Genomic analyses have revealed signatures of ancient hybridization events—ranging from thousands to millions of years ago—in several bird groups, such as *Passer* sparrows (Runemark et al. 2018), *Anser* geese (Ottenburghs et al. 2020) and *Aphelocoma* jays (Zarza et al. 2016). In some cases, these hybridization events even involved extinct species (e.g., Zhang et al. 2019), a phenomenon known as ghost introgression (Ottenburghs 2020). As more avian genomes are sequenced (Feng et al. 2020) and methods to detect (ancient) introgression events become more powerful (Hibbins and Hahn 2022), more hybridization events will undoubtedly be uncovered. At the moment, it is not feasible to confidently estimate the incidence of past hybridization in birds, but it is probably more common than previously thought. By studying the incidence of hybridization at different timescales, ornithologists will be able to pinpoint bird groups where hybridization is playing or has played a major evolutionary role.

Conclusion

This overview of historical and recent studies attempting to estimate the incidence of hybridization in birds revealed that it is a relatively common phenomenon on a species

level (between 15 and 20% of hybridizing bird species) while rare on an individual level (0.064% hybrid individuals in the United States). However, both estimates depend on methodological decisions, such as the choice of global bird checklists and the definition of a hybrid, and can be influenced by spatial and temporal variation. Hence, future research efforts will need to take into account these potential biases and combine several data sources to arrive at a reliable estimate of hybridization incidence in birds.

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Data availability There is no data associated with this paper. A data availability statement is not applicable.

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