

Birds rarely hybridize: A citizen science approach to estimating rates of hybridization in the wild*

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The rate of hybridization among taxa is a central consideration in any discussion of speciation, but rates of hybridization are difficult to estimate in most wild populations of animals. We used a successful citizen science dataset, eBird, to estimate the rates of hybridization for wild birds in the United States. We calculated the frequency at which hybrid individuals belonging to different species, families, and orders of birds were observed. Between 1 January 2010 and 31 December 2018, a total of 334,770,194 species records were reported to eBird within the United States. Of this total, 212,875 or 0.064% were reported as hybrids. This estimate is higher than the rate of hybridization (0.00167%) reported by Mayr based on impressions from a career studying museum specimens. However, if the 10 most influential hybrid species are removed from the eBird dataset, the rate of hybridization decreases substantially to about 0.009%. We conclude that the rate of hybridization for individuals in most bird species is extremely low, even though the potential for birds to produce fertile offspring through hybrid crosses is high. These findings indicate that there is strong prezygotic selection working in most avian species.

KEY WORDS: Aves, citizen science, hybridization, eBird, prezygotic selection, speciation.

The process of speciation is a central topic in evolutionary biology. Species boundaries occur where the gene flow between populations is disrupted (Coyne and Orr 2004; Petit and Excoffier 2009). The amount of gene flow that is permitted before populations are no longer recognized as species is the foundation of species concepts (De Queiroz 2007). It follows, then, that knowledge of rates of hybridization between taxa is fundamental to any discussion of speciation (Mallet 2005; Abbott et al. 2013). However, rates of hybridization are difficult to estimate in most wild populations of animals (Randi 2008).

From the standpoint of biogeography and population structure, birds are undoubtedly the best characterized of all animal taxa (Mayr 1963; Hill 2017). Birds are largely diurnal, conspicuous, and their primary signaling modalities—coloration and

song—are easily perceptible to human observers. Thus, birds have long been a central focus in discussions of the process of speciation and the evolutionary forces that structure populations (Mayr 1963; Cracraft 1983). Even for birds, however, the literature does not sufficiently distinguish between the widespread ability of different species to mate and produce offspring (Grant and Grant 1992), and the rate at which individual species actually engage in hybrid pairings in nature. Statements such as “Hybridisation is commonly recorded in birds” (Aliabadian et al. 2007), “Hybridization is common in birds” (Miller et al. 2014), and “In birds it [hybridization] is widespread” (Grant and Grant 1992) are frequently encountered in the literature. These statements are sometimes associated with observations of birds producing F1 hybrids in captivity (Mallet 2005) or crosses between different subspecies (Amadon and Short 2006), which can confuse discussions about the rates of hybridization between species of wild birds.

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Mallet (2005) drew the critical distinction between rates of hybridization calculated on a per-individual basis versus rates calculated on a per-species basis. Many of the claims of high rates of hybridization in birds are based on per species calculations, and Mallet (2005) argued that “we would not be able to distinguish species if hybridization were common [on a per individual basis].” However, with strong postzygotic selection against hybrids, there could be both high rates of hybridization and maintenance of species boundaries (Hill 2017, 2019). Therefore, estimating the proportion of hybrid individuals in populations of birds provides critical data for assessing the role of pre- versus postzygotic processes in structuring populations. To date, the only effort to quantify the per individual rates of hybridization across multiple orders of wild birds was made by Mayr (1963). As a summation of years working in museum collections, Mayr (1963, p. 114) estimated that he observed approximately one hybrid individual for every 60,000 (0.00167%) bird study skins that he examined. This rate of per individual hybridization was an after-the-fact gross estimate and was not based on actual tallies of specimens. Nevertheless, Mayr’s one-in-sixty-thousand estimate remains the only published estimate of the per-individual rate of hybridization by wild birds.

Until recently, there was no way to replicate the work of Mayr—short of spending another lifetime examining museum specimens. However, with the onset of “big citizen science data,” the number of biodiversity records has increased vastly (Bonney et al. 2009; Dickinson et al. 2010; La Sorte et al. 2018). Citizen science data are revolutionizing ecological and conservation research (Jordan et al. 2015; Chandler et al. 2017; Soroye et al. 2018), contributing to ecological and biological studies including global climate change, phenology, landscape ecology, and macroecology (Dickinson et al. 2012). One of the most successful citizen science projects to date is eBird, initiated in 2002 by the Cornell Lab of Ornithology (Sullivan et al. 2014). eBird is a massive global citizen science project that has generated over 600 million global observations as of early 2019, including observations of hybrid individuals. As far as we are aware, however, citizen science datasets such as eBird have not yet been used to assess rates of hybridization. In this paper, we rely on over 300 million eBird citizen science records in the United States to provide a novel estimate of hybridization events in different species, families, orders, and class Aves as a whole.

Materials and Methods

eBIRD: DETAILS OF BIRD OBSERVATIONS

We investigated the eBird basic dataset to summarize the number of hybrid and nonhybrid birds reported. eBird is a semistructured project, enlisting volunteer birdwatchers to submit bird sightings in “checklist” format, including the time, date, location, and a

list of all birds seen and/or heard (see Sullivan et al. 2014; Wood et al. 2011; Kelling et al. 2019 for details). Birdwatchers can submit lists from any date and time, allowing for back-filling the dataset. We used data collected between January 1, 2010 and December 31, 2018 (version ebd_relDec-2018), the period for which the data are the richest in eBird at the time of our analysis because most of the data in the dataset has been submitted contemporaneously with bird observations. Although birdwatchers can submit “historical lists,” we decided to exclude lists that were added too far in the past because, in adding historical records, birdwatchers are more likely to favor “odd” records, such as hybrids, compared with the comprehensive records made in real time. Although eBird is a global project, we restricted our analysis to the United States because eBird was initiated in the United States and the data are accordingly most numerous and complete for this area. An extensive network of regional volunteers (Gilfedder et al. 2019) use their local expertise to filter eBird submissions, reviewing observations based on unexpected species or abundances of species that are not aligned with a priori expectations based on spatiotemporal coordinates.

Importantly, hybrids are a special case when reported to eBird, and are often heavily reviewed by field experts before being accepted—often being discussed on forums and listservs at length. Even hybridization involving Mallards (*Anas platyrhynchos*), which are among the most common hybrids, are sometimes flagged as “rare” on eBird, causing them to warrant review. This review generally involves detailed field notes and preferably photographs, before the record is accepted into the eBird dataset by a regional reviewer. Generally, it is common practice to further limit the number of eBird checklists included in analyses based on effort (e.g., time spent or distance traveled) associated with individual checklists (e.g., Johnston et al. 2019). In our analysis, we included all eBird checklists from the dates and geographic areas stated above that had been released after field expert review. We think that hybrid records would have a high probability of occurring on checklists that would otherwise be excluded from analyses, and we wanted to ensure we included as many hybrid records as possible and associated non-hybrid records were treated the same for comparable estimates.

OVERALL HYBRIDIZATION IN BIRDS

We defined the overall rate of hybridization in birds as the number of hybrid observations divided by the total number of individual bird observations in the eBird dataset. In other words, following the approach of Mayr (1963), we used observer records to classify each bird in the database as “hybrid” or “not hybrid” and estimated the proportion of free-flying birds that were classified by observers as a hybrid. Observations categorized as a “spuh” (genus or identification at a broad level) or “slash” (a difficult to distinguish species pair) were omitted from the

Table 1. A summary of the 10 most frequently reported hybrids in the United States (see Table S1 for the complete list of hybrids).

Common name	Scientific name	No. of observations
Western × Glaucous-winged Gull	<i>Larus occidentalis</i> × <i>L. glaucescens</i>	80,391
Mallard × American Black Duck	<i>Anas platyrhynchos</i> × <i>A. rubripes</i>	32,386
Mallard × Mottled Duck	<i>Anas platyrhynchos</i> × <i>A. fulvigula</i>	21,714
Tufted × Black-crested Titmouse	<i>Baeolophus bicolor</i> × <i>B. atricristatus</i>	19,582
Herring × Glaucous-winged Gull	<i>Larus argentatus</i> × <i>L. glaucescens</i>	9150
Mallard × Mexican Duck	<i>Anas platyrhynchos</i> × <i>A. diazi</i>	6223
Mallard × Hawaiian Duck	<i>Anas platyrhynchos</i> × <i>A. wyvilliana</i>	5381
Eurasian × American Wigeon	<i>Mareca penelope</i> × <i>M. americana</i>	2899
Domestic goose sp. × Canada Goose	<i>Anser sp. (Domestic type)</i> × <i>Branta canadensis</i>	2483
Carolina × Black-capped Chickadee	<i>Poecile carolinensis</i> × <i>P. atricapillus</i>	2386

calculations because no specific bird species is reported under such categories. For more details on eBird treatment of categories, see <https://ebird.org/science/the-ebird-taxonomy>. Additionally, because many vagrant and escapees are present in the eBird dataset, we only first omitted any known vagrants and/or escapees using *a priori* knowledge from the possible records included, and when we were uncertain, we included the species that were submitted >100 times to the eBird dataset during our specified timeframe; thus, the species included are likely to be free-flying birds throughout at least a portion of the United States. Because of the potential for birders to preferentially chase rare or unique sightings such as hybrids, and because observations of a single bird can often be reported multiple times by birders frequenting the same location, we estimated three different overall rates of hybridization in birds. We calculated the overall hybridization: (1) by using all records in eBird, as described above; (2) by subsetting hybrid birds that were submitted from unique coordinates and collapsing such instances into only one hybrid record (i.e., reducing spatial autocorrelation) and dividing by all records in eBird; and (3) by subsetting hybrid birds to unique coordinates and dividing by all records subsetted to unique coordinates. For these latter analyses, we filtered records by their “LOCALITY_ID” in the eBird dataset (i.e., the unique latitude and longitude coordinates that an observation corresponds with).

SPECIFIC HYBRIDIZATION RATES

We investigated the order- and family-specific rates of hybridization for each of the 25 orders and 95 families in the United States that met our aforementioned criteria. We used the Clements checklist (version 2018; <http://www.birds.cornell.edu/clementschecklist/>) to assign each species its corresponding order and family. For each order and family, we calculated an order- and family-specific rate of hybridization defined as the number of hybrid observations in that order or family divided by the total number of observations in that order or family.

We recorded a complete list of all hybrid observations in our dataset (see Table S1). For each species of interest, species specific hybridization rates can be determined by splitting the species pair and then searching the eBird dataset for each specific species. Some hybrids submitted do not necessarily have two corresponding parents that can be assigned to a species (e.g., a species can hybridize with an unknown Anseriformes species). Subspecies should not be included in these calculations. We simply defined the species-specific hybridization rate as the total number of observations for that species divided by the number of times that species was involved in a hybridization event. As a worked example, we compared estimated species hybridization rates to the number of hybrid individuals and parent species reported on Vertnet (<http://vertnet.org/>) for Lazuli (*Passerina amoena*) and Indigo Buntings (*Passerina cyanea*).

Results

OVERALL HYBRIDIZATION IN BIRDS

Between January 1, 2010 and December 31, 2018, 334,770,194 species records were reported to eBird and of this total 212,875 or 0.064% were identified by the observer as a hybrid. In total, 242 species were implicated in hybrid events, forming 214 unique hybrid pairs, with 59 putative hybrid events involving mating between individuals from different genera. In total, 242 of the 1146 (21.117%) species in the eBird dataset for the United States were implicated in a hybridization event. Of the 214 hybrid pairs reported, 33 of the 214 (15.421%) were implicated as the parent of a hybrid offspring only a single time.

Filtering eBird records by location to reduce the risk of multiple records of the same hybrid resulted in a drastic reduction in the number of observations remaining for analysis. When we recalculated the number of hybrids by their unique coordinates, we found that the number of hybrids decreased from 212,875 to just 35,729, highlighting that hybrids are often reported from the same unique locations. When using this new number of hybrids

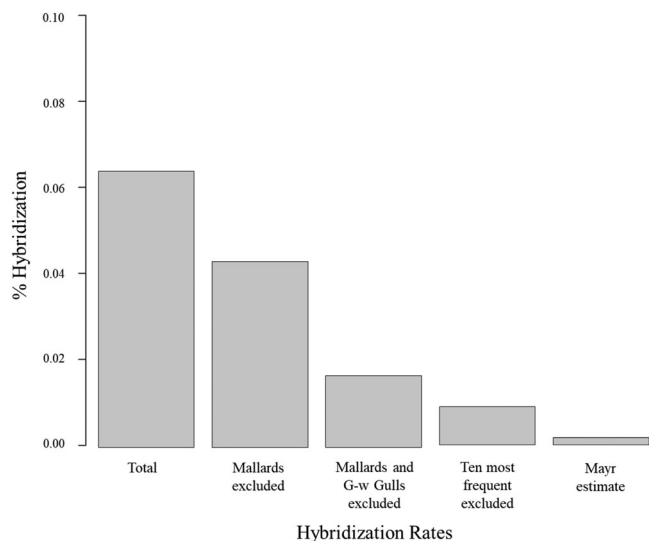


Figure 1. A comparison of hybridization rates between (1) the entire eBird dataset (0.064%), (2) the eBird dataset excluding Mallards (0.043%), (3) the eBird dataset excluding Mallards and Glaucous-winged Gulls (0.016%), (4) the eBird dataset excluding the 10 most common hybrids (0.009%), and (5) the estimated hybridization rate of Aves given by Ernst Mayr (0.00167%).

to calculate the total rate of hybridization, we obtain a hybridization rate of 0.011%. However, if the total number of observations is also filtered by unique coordinates, it decreases from 334,770,194 observations to 46,812,869. This new calculation provides an estimated overall rate of hybridization of 0.076%.

Among the 212,875 hybrid observations submitted to the eBird dataset, the top 10 most common putative parental crosses—which involved only 16 of the 1,146 species in the dataset—made up 182,595 or 85.776% of all hybrids reported (see Table 1). Recalculating the hybridization rates after removing these 10 most commonly reported hybridizing species from the analyses provides a hybridization rate of about 0.009%. Thus, inclusion of a few putative species in calculations of rates of hybridization can skew perceptions for the significance of hybridization across Aves as a whole (Fig. 1).

SPECIFIC HYBRIDIZATION RATES

The number of hybrids varied greatly among the different orders. Of the 25 orders of birds in the United States, 16 had species involved in a hybridization event. Orders Cathartiformes, Ciconiiformes, Coraciiformes, Cuculiformes, Gaviiformes, Phaethonitiformes, Phoenicopteriformes, Pterocliiformes, and Trogoniformes were not reported in a hybridization event (Fig. 2A and Table S2 for a summary of order hybridization rates). The order with the highest rate of hybridization was Charadriiformes contributing 93,384 of the 212,875 hybrid observations (43.868%). Charadriiformes had an overall

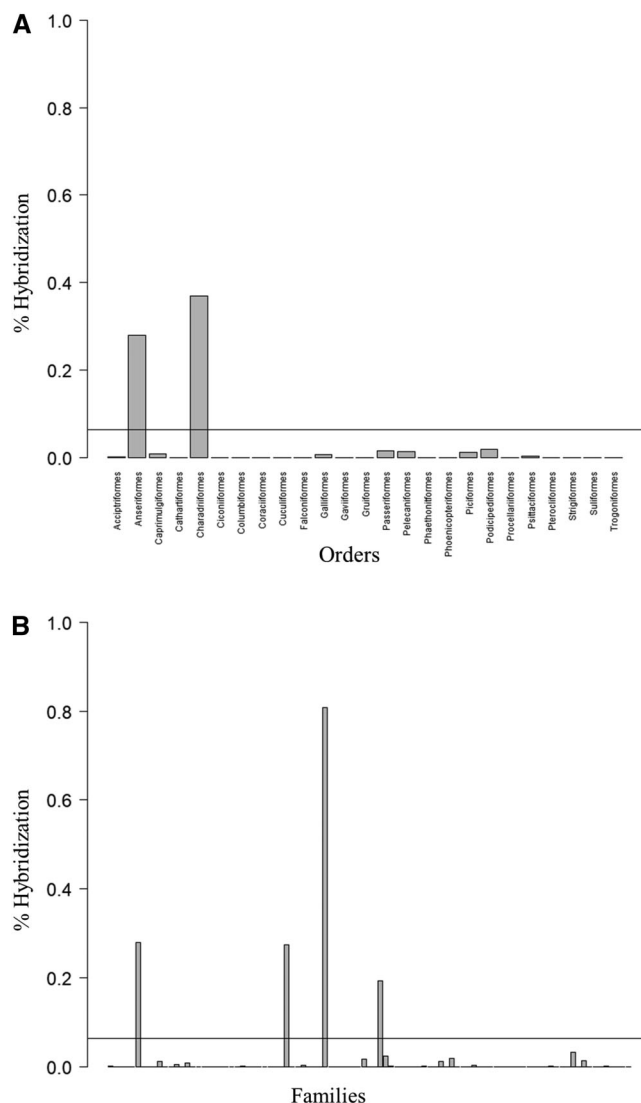


Figure 2. A comparison of hybridization rates between each of the (A) 25 orders and (B) 95 families. Orders are listed in alphabetical order and families are shown in alphabetical order (see Tables S2 and S3 for the complete lists). Line at 0.064% represents the calculated average rate of hybridization from all of the observations in the eBird dataset.

hybridization rate of 0.369%. Order Anseriformes had a hybridization rate of 0.279% and this order contributed 83,636 (39.289%) of all hybrid records.

There were large differences between the rates of hybridization among families. Of the 95 families with species present in the United States, only 35 had species that were implicated in hybridization. Thus, 60 of the 95 families of birds did not have a single hybrid record. Just two families of birds, ducks (Anatidae) and gulls (Laridae), contributed 82.770% of all hybrids in the United States dataset. Laridae was the family with the highest number of hybrid observations (92,561), which was largely a consequence of rampant hybridization between the

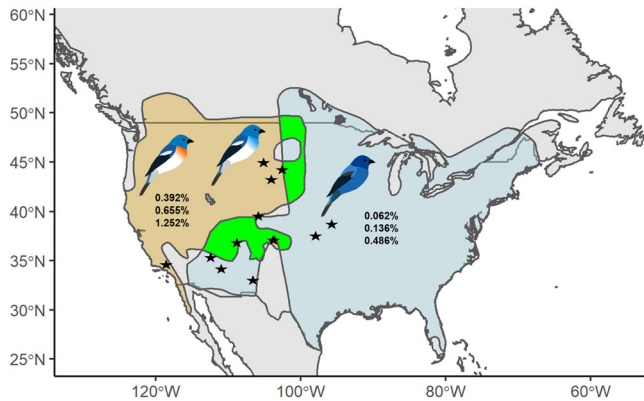


Figure 3. A summary of the estimated rates of hybridization for Lazuli (*Passerina amoena*) and Indigo Buntings (*Passerina cyanea*), calculated using the total number of eBird observations available, unique observations filtered by locality ID, and specimen numbers on Vertnet. The light blue region represents the range for the Indigo Bunting, and the light orange region represents the range for the Lazuli Bunting. The shaded green patches indicate where the two ranges overlap. The black stars on the map represent locations where museums report collecting hybrids to Vertnet.

Western Gull (*Larus occidentalis*) and Glaucous-winged Gull (*Larus glaucescens*) reported in the eBird dataset. Among families of birds in which hybrids were reported, there was also a wide range of variation in rates of hybridization, although most rates were low when compared to Anatidae and Laridae (Fig. 2B and Table S3 for a summary of family hybridization rates).

In contrast to these families and orders of birds that include taxa that hybridize relatively frequently, Passeriformes contributed 189,108,693 (56.581%) of all birds observed, yet only 29,902 (14.047%) of hybrid observations involved passerines. Order Passeriformes had an overall hybridization rate of 0.016%. Among families in Passeriformes, Paridae had by far the highest rate of hybridization. When Paridae is removed from the calculations, the rate of hybridization for Passeriformes drops to just 0.004%.

When examining the species-specific hybridization rates of Lazuli and Indigo Buntings, we calculated the estimated rates of hybridization using the total number of eBird observations, unique eBird observations filtered by locality ID, and Vertnet specimen numbers. Our estimated species-specific hybridization rate ranged from 0.392 to 1.252% for Lazuli Buntings and 0.062 to 0.486% for Indigo Buntings (Fig. 3).

Discussion

For more than 50 years, Mayr's (1963) back-of-the-envelope estimation of approximately one hybrid individual for every 60,000

study skins examined (0.00167%) was the only rate available for hybridization among wild birds. Here, for the first time, we use empirical data to estimate hybridization rates in Aves. We calculated the individual hybridization rate to be about 38 hybrid individuals for every 60,000 birds observed (0.064%) in the United States. Our estimate is substantially higher than the rate of 1 in 60,000 originally reported by Mayr (1963), but our estimate of the rate of hybridization among all birds was inflated by the large number of hybrid observations produced by just a few species. For example, Mallards, which make up nearly 1.5% of all eBird observations, have a hybridization rate over 20 times higher than the calculated average hybridization rate for all birds. Simply removing Mallard hybrids from our calculations drops the overall rate of hybridization among birds by almost one-third, to about 26 in 60,000 (0.043%). The Glaucous-winged Gull was another highly influential species. More than one-third of all individuals with Glaucous-winged Gull parentage were reported as hybrids. Removing Glaucous-winged Gulls, in addition to Mallards, reduced the overall hybridization rates in birds to about 10 in 60,000 (0.016%). Removing the 10 most influential hybrid species from our estimate produces a rate of 5 in 60,000 (0.009%), which is of the same magnitude as the estimate by Mayr (1963). It seems possible that when stating his estimate of hybridization rates, Mayr also took into account and devalued influential species, which he likely did not view as distinct species given his well-documented view on species boundaries. Whether we take the uncorrected 0.064% or some lower rate procured by excluding certain taxa, our calculations from the eBird dataset confirm Mayr's conclusion from 50 years ago—hybridization among individual birds in nature is a rare event.

The data produced through the eBird citizen science effort is not without errors and biases that undoubtedly affected our hybridization estimates. Some hybrids will not be recognized, and some observers—especially non-experts—may be reluctant to report unusual birds. On the other hand, a hybrid with visibly distinct plumage will be easier to recognize, and a recognizable hybrid at a location frequented by birders might be counted multiple times, creating pseudo-replication of records. The extent to which hybrids may or may not be under- or overreported is difficult to address using the current eBird dataset. Yet, we did find that our range of hybridization estimates—accounting for some effects of pseudo-replication—were all relatively comparable: 0.011–0.076%. We also compared hybridization estimates at an individual species level to see how they compared to estimates of hybridization from published museum specimens. The Lazuli and Indigo Bunting have a well-studied zone of hybridization and the resulting hybrids are easily visually distinguished (Carling and Brumfield 2008; Carling et al. 2010). The rates of hybridization for these buntings that we calculated from eBird data are comparable to rates that we calculated from museum specimens,

but there appears to be an overestimation of species-specific hybridization from museum specimens compared with eBird. Many of the largest series of specimens for Lazuli and Indigo Bunting were made during studies of gene flow between these taxa, and these series are likely biased toward hybrid individuals. From all of these considerations, we conclude that no database that can be used to estimate hybridization is without bias and error, but despite sampling problems they all provide approximately the same conclusions—hybridization is rare among wild birds.

Seasonality will also play a large role in birdwatching activity, as well as the detectability of hybrids. In the period following breeding (typically autumn months), numbers of hybrids will be at a maximum before mortality arising from hybrid dysfunction begins to cull the hybrid population. At this time of maximum hybrid numbers, however, many birds wear drab plumage and do not sing, making hybrids harder to detect. In spring, with birds in nuptial plumage and full song, hybrids should be most easily detected, but some hybrids will have been lost to mortality in the winter and migration. Given all of these considerations, we elected to include data from all seasons of observations in generating our estimates. Because our goal was a gross determination of whether hybridization among wild birds was frequent or infrequent, we propose that the eBird tallies provided a meaningful assessment.

Ottenburghs et al. (2015) reported that in the wild 16.4% of bird species had at least one record of hybridization and that in captivity 21.1% of bird species were reported to have been involved in at least one hybridization event that resulted in F1 hybrids. From the eBird database, we calculated that 242 of 1146 (21.12%) species were involved in hybridization at least once. Thus, our species-level rate of hybridization based on eBird observations was higher than had previously been reported for wild birds. A rise in the number of species involved in at least one hybridization event is almost certainly a consequence of the orders-of-magnitude increase in sampling effort offered by eBird. Nevertheless, the total number of species reported to be involved in hybridization is remarkably similar to what has previously been published (Ottenburghs et al. 2015). For the first time, we were also able to calculate the rates of hybridization for higher level taxa: we observed that 16 of 25 orders and 35 of 95 families were involved in at least one hybridization event. One conclusion from these observations is that hybridization is such a rare event in Aves that it has never been recorded in the wild for numerous families and even orders. Price and Bouvier (2002) provided compelling data that, in captivity, most congeneric and even most confamilial species can produce F1 offspring from hybrid pairings. Thus, we do not attribute the paucity of hybrid observations to developmental failure when individuals pair with heterospecifics.

The very low rates of mating outside of species boundaries in wild birds has important implications for speciation theory, indicating that gene flow among populations of birds is impeded by prezygotic sorting. Birds are very good at species recognition, which results in mating with conspecifics and avoidance of heterospecifics (Gill 1998; Hill 2015). The observation that most wild birds avoid hybridization helps to reconcile two fundamental observations: (1) nearly all species of birds have a unique mitochondrial DNA (mtDNA) sequence and (2) crosses between most species of birds within a genus produce offspring. More than 95% of birds show a mitochondrial DNA barcode gap between species (Kerr et al. 2007, Tavares and Baker 2008). This barcode gap indicates that there is limited gene flow between species (Hill 2016). Despite this strong evidence that there is limited gene flow across species boundaries, captive breeding programs have shown that most birds can mate with and produce offspring with other birds in their genus (Price and Bouvier 2002). The evidence for strong prezygotic sorting among bird species, which we document in our analysis, presents a solution to how birds maintain sharp genetic boundaries even with the potential for producing offspring. Premating isolation best explains the sharp boundaries in plumage pattern, song, and mtDNA genotype between most bird species (Hill 2018), but for some species, strong postzygotic selection must be invoked. For instance, Carolina Chickadees (*Poecile carolinensis*) and Black-capped Chickadees (*Poecile atricapillus*) have a very narrow zone of overlap that occupies less than 1% of the total range of each species. Nevertheless, there were as many as 2386 observations of hybrid chickadees in the eBird dataset. This high rate of hybridization within the narrow zone of contact should rapidly lead to a broadening zone of contact and a blending of genotypes (Irwin et al. 2009), neither of which is observed. In the case of these chickadees, postzygotic selection against hybrids likely maintains the tight suture zone between the species.

Our calculations are the first attempt to empirically estimate the rate at which individual animals in the wild mate with heterospecifics and produce hybrid offspring. Our analysis was made possible by eBird, a broad-scale empirical citizen science dataset. We acknowledge a number of biases, in multiple facets, that could potentially influence our results, but clearly, eBird citizen science data provide a useful dataset to investigate novel analyses of hybridization patterns in birds. Our analysis highlights a number of important research avenues that can investigate hybridization rates in birds using these citizen science data (e.g., spatiotemporal patterns in hybridization and further comparisons with multiple data sources of “known” hybridization rates). Regardless of our methodological approach (e.g., removing pseudo-replicates or not), hybridization appears to be extremely rare for individuals across families and orders of birds in the United States.

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AUTHOR CONTRIBUTIONS

All authors helped to conceive the study, N. M. J. and C. T. C. performed data analyses, N. M. J. took the lead in writing the manuscript, and all authors contributed to writing and revising the manuscript.

DATA ARCHIVING

eBird data are freely available to researchers and practitioners at the following link (<https://ebird.org/data/download>). The list of hybrid species and corresponding orders and families analyzed are presented in the Supporting Information.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supporting Information Table 1. List of all 214 hybrid pairs reported, the number of each reported, and their corresponding family.

Supporting Information Table 2. List summarizing (1) the total number of hybrids, (2) total number of observations, (3) calculated hybridization percentage, and (4) the number of unique hybrid species for each of the 25 orders

Supporting Information Table 3. List summarizing (1) the total number of hybrids, (2) total number of observations, (3) calculated hybridization percentage, and (4) the number of unique hybrid species for each of the 95 families.