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Hybridization between sister taxa versus non-sister taxa: a case study in birds

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Capsule Sister taxa hybridize more frequently than non-sister taxa.

Aims To test whether the frequency of hybridization is higher in avian sister species than in non-sister species, based on molecular phylogenetic relationships and reports of hybridizing bird species globally.

Methods A literature based survey of hybridizing bird species was conducted on genera that: (1) have a completely known phylogenetic molecular tree for at least 90% of the total number of species, (2) have at least four species, (3) have an incidence of hybridization more than 25% recorded from the wild, and (4) have at least two pairs of hybridizing species. The frequency of hybridization for avian sister species was compared to that of non-sister species.

Results Twenty-nine genera were identified that met our four selection criteria. In 25 genera, sister species hybridized more than non-sister species (mean frequencies of 0.52 ± 0.35 versus 0.16 ± 0.13).

Conclusion The frequency of hybridization within sister species was found to be higher than within non-sister species.

Hybridization could play an important role in speciation, and hence provide new material for evolution (Newton 2003, Price 2008). Hybrids are formed when different species or subspecies interbreed, resulting in the combination of genetic material from previously isolated gene pools (Schwenk *et al.* 2008, Arnold 1992). Hybrid speciation was once thought to be rare in animals, but over the past decade, improved molecular analysis techniques and increased research attention have allowed scientists to uncover many examples of natural hybridization (Brelsford 2011). Hybridization is relatively common in birds: for example, there is a widely quoted figure of approximately 1 in 10 of the world's species of birds having hybridized in nature and having produced hybrid offspring (Grant & Grant 1992). Aliabadian and Nijman (2007) calculated a higher incidence of hybridization, increasing the estimate from 9.8% (Grant & Grant 1992) to 19% based on McCarthy (2006). This increase, to some extent, is inflated by the inclusion of some subspecies of Grant & Grant (1992) listed by McCarthy (2006) as good species. Different factors might enhance hybridization and these factors, in turn, might differ among families and orders. It has already been noted that close genetic relationships are a key factor facilitating hybridization (Randler 2006). Many evolutionary biologists take for granted that sister taxa hybridize more than non-sister taxa because of their similar morphology between members of sister taxa (Randler 2002, 2004, 2006) and where this is involved with speciation assume that hybridization most likely occur between the sister taxa (Grant & Grant 1997, sister taxa are those presented as most-closely related in a phylogeny). However, to the best of our knowledge, this hypothesis has not yet been tested.

Although there are some examples of hybrids between species of different genera, e.g. *Aix* with *Anas*, *Aythya*, *Bucephala* and *Lophodytes* (McCarthy 2006), it seems likely that hybridization occurs most frequently between species within the same genus. Many such

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examples can be extracted from literature concerning plants, insects, fish, birds and primates. Nevertheless, even inside the same genus, there can be large differences in the molecular divergences between species that hybridize. For example, hybrids occur within the closely related diver genus *Gavia* (Roselaar *et al.* 2006) and also within the distantly related *Heliconius* butterfly species (Dasmahapatra *et al.* 2007).

Systematic data on the incidence of hybridization in birds has been available since 1958, when Gray listed all known hybridizing bird species. McCarthy (2006) updated Gray's survey and provided an exhaustive compilation of all cases of avian hybridization under both wild and captive conditions. However, the hypothesis of 'hybridization in avian sister species occurs more than in non-sister species' still remains untested. This study examines the evidence for the hypothesis based on available molecular phylogenetic studies and known hybridizing bird species of the world as included in McCarthy's (2006) compendium.

METHODS

Based on the *Handbook of Avian Hybrids of the World* (McCarthy 2006), a complete checklist of the birds of the world (Dickinson 2003), and available molecular phylogenetic papers (in English, published prior to January 2012), a survey of the hybridizing species of avian genera was conducted regarding the following criteria: (a) have a completely known phylogenetic molecular tree for at least 90% of the total number of species within the genus, (b) have at least four species, (c) have an incidence of hybridization more than 25% recorded from the wild, and (d) have at least two pairs of hybridizing species. These thresholds were applied in order to have undisputed relations of species within each genus (which species are sisters and which are not; threshold a), informative genera in statistical terms (thresholds b, c and d) and hybridization only in natural conditions because many hybridizations reported in captive have never been seen in nature. The taxonomy and nomenclature of taxa of Dickinson (2003) was followed. McCarthy (2006) used a slightly different taxonomy resulting in exclusion of some of the species listed in McCarthy from our analysis. Genera with only one hybridizing species pair were ignored because in these cases the probability of hybridization is only present for sister or non-sister species and leads to biased results.

The distribution maps of each species in a pair were compared to identify which species pairs are in contact in their distribution range. To do so, the distribution maps of the *Handbook of the Birds of the World* (Del Hoyo et al. 1992–2011) and GIS maps of Birdlife data set (http://www.birdlife.org/) were used, as well as more detailed extended maps of handbooks for some bird orders (e.g. Hollom *et al.* 1988, Ferguson-Lees & Christie 2001, Shirihai *et al.* 2001, Madge & McGowan 2002). The frequency of hybridization for each genus was calculated for sister and non-sister species separately (Table 1). For this, within a genus, the total number of hybridizing sister pairs or non-sister pairs were divided by the total number of sister or non-sister species pairs which are in contact (extracted from Appendix). The incidence of hybridization for each genus was calculated as the total number of species involved in hybridization divided by total number of species. Then, a Wilcoxon signed-ranks test was conducted to test for a difference in hybridization frequency between the two groups. Contingency tables (2×2) and the Fisher's Exact Probability Test were also used to test the hypothesis (Appendix).

RESULTS

According to our literature reviews, 15 passerine and 14 non-passerine genera were found that comply with the applied thresholds in this study. They are: *Buteo*, *Larus*, *Sylvia*, *Turdus*, *Anas*, *Picoides*, *Pteroglossus*, *Hippolais*, *Aquila*, *Acrocephalus*, *Celeus*, *Malurus*, *Parula*, *Basileuterus*, *Dendroica*, *Grus*, *Oporornis*, *Icterus*, *Euplectes*, *Saxicola*, *Geothlypis*, *Progne*, *Spizella*, *Alectoris*, *Lophura*, *Gallus*, *Lampornis*, *Callipepla* and *Coeligena*. They are placed in 19 families, of which Parulidae is the most diverse family with five genera (Table 1). Fig. 1 shows that the mean of frequency of hybridization is higher within sister species than non-sister species in the studied genera and a Wilcoxon signed-ranks test revealed that the difference was significant ($z = -3.80$, $P < 0.01$, sister species mean: 0.52 ± 0.35 sd, se = 0.07, non-sister species mean: 0.16 ± 0.13 sd, se = 0.05). The proportion of sister taxa that hybridize compared with the hybridizing non-sister taxa is greater in all genera except in the genera *Grus*, *Geothlypis*, *Spizella* and *Alectoris* in which there are no hybridizing sister species. Distribution maps of sister species pairs within genera *Grus* and *Alectoris* do not overlap, but there is overlap in distribution within genera *Geothlypis* and *Spizella*.

Taking into account the four thresholds for inclusion of the studied genera, the mean incidence of hybridization of the species is high (55.8%). The

Table 1. Incidence and frequency of hybridization in sister and non-sister hybridizing species pairs within 29 genera of birds with overlapping ranges.

Genus	Family	No. species (Dickinson)	No. species involved in hybridization	Frequency of hybridization for sister species	Frequency of hybridization for non-sister species	Incidence of hybridization	References used to access the phylogenetic trees
Buteo	Acciptridae	26	7	0.67	0.07	0.27	Riesing *et al.* 2003
Larus	Laridae	43	25	0.66	0.22	0.58	Pons *et al.* 2005
Sylvia	Sylvidae	18	7	0.16	0.05	0.39	Bohning-Gaese *et al.* 2003
Turdus	Turdidae	65	18	0.30	0.06	0.28	Voelker *et al.* 2007
Anas	Anatidae	41	32	0.80	0.34	0.78	Johnson & Sorenson 1999
Hippolais	Sylvidae	8	6	0.67	0.12	0.75	Helbig & Seibold 1999
Aquila	Acciptridae	10	5	0.33	0.11	0.50	Lerner & Mindell 2005
Picoides	Picidae	12	7	0.50	0.15	0.58	Weibel & Moore 2002
Pteroglossus	Ramphastidae	12	9	0.33	0.17	0.75	Eberhard & Bermingham 2005
Acrocephalus	Sylvidae	31	8	0.20	0.07	0.26	Fregin *et al.* 2009
Celeus	Picidae	11	6	1	0.07	0.55	Benz & Robbins 2011
Malurus	Maluridae	13	7	0.25	0.04	0.54	Driskell *et al.* 2011
Parula	Parulidae	4	3	1	0.33	0.75	Lovette *et al.* 2010
Basileuterus	Parulidae	22	9	0.60	0.02	0.41	Lovette *et al.* 2010
Dendroica	Parulidae	29	17	0.50	0.05	0.59	Lovette *et al.* 2010
Grus	Gruidae	10	7	0.00	0.50	0.70	Fain *et al.* 2007
Oporornis	Parulidae	4	4	1	0.20	1	Lovette *et al.* 2010
Icterus	Icteridae	26	9	1	0.02	0.34	Jacobsen *et al.* 2010
Euplectes	Ploceidae	17	5	0.25	0.00	0.29	Prager *et al.* 2008
Saxicola	Muscicapidae	10	5	0.25	0.09	0.50	Illera *et al.* 2008
Geothlypis	Parulidae	9	3	0.00	0.12	0.33	Lovette *et al.* 2010
Progne	Hirundinidae	9	5	0.5	0.13	0.55	Sheldon *et al.* 2005
Spizella	Emberizidae	7	4	0.00	0.17	0.57	Canales-del-Castillo *et al.* 2010
Alectoris	Phasianidae	7	5	0.00	0.42	0.71	Randi, 1996
Lophura	Phasianidae	11	6	0.66	0.18	0.54	Randi *et al.* 2001
Gallus	Phasianidae	4	3	1	0.25	0.75	Eo *et al.* 2008
Lampornis	Trochilidae	7	4	0.50	0.28	0.57	García-Moreno *et al.* 2006
Callipepla	Odontophoridae	4	3	1	0.43	0.75	Eo *et al.* 2008
Coeligena	Trochilidae	10	6	1	0.11	0.60	Parra *et al.* 2009

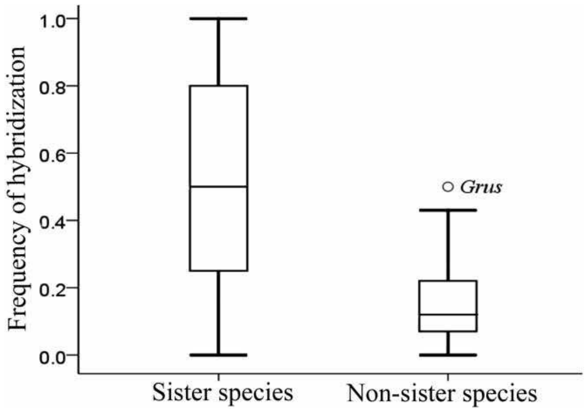

Figure 1. Boxplot of the rate of hybridization in sister and non-sister species pairs in birds with overlapping ranges.

highest incidence of hybridization was recorded for the genus *Oporornis*. The number of species in this genus is small (4 species), but all species are known to hybridize. The genus *Anas* also shows one of the highest incidence of hybridization (0.78) with a large number of species showing hybridization (32 out of 41 species).

Although overall frequency and probability of hybridization was significantly higher within sister species than in non-sister species where there is an overlap in their distribution ranges (Fig. 1), there were only eight individual genera (*Larus*, *Turdus*, *Celeus*, *Dendroica*, *Buteo*, *Icterus*, *Anas* and *Basileuterus*) where this reached statistical significance using Fisher's Exact Probability tests (Appendix).

DISCUSSION

Although many evolutionary biologists take it for granted that sister taxa hybridize more than non-sister taxa, hitherto this hypothesis had not been explicitly tested. Our data show that, for species with geographically overlapping distribution ranges, the frequency of hybridization within sister species is significantly higher than non-sister species within the same genus. The higher frequency of hybridization within sister species does not necessary means that the actual number of hybrids within sister species in nature is higher than in non-sister species because fewer sister species pairs were in contact than non-sister species pairs. In this study these numbers differed remarkably; 185 non-sister species were in contact and hybridized in contrast to 42 sister species.

Different approaches have tried to identify factors facilitating natural hybridization in birds, but it is not yet clear why hybridization is more common in some taxa and absent or rare in others (Randler 2004). Several factors such as environmental and behavioural factors are known as the main causes for hybridization in birds (Randler 2006, McCarthy 2006). It is argued that closely related species separated by small genetic distances can increase the propensity for hybridization, but this is not necessarily an indicator of hybridization. For example, Blue-winged Warbler (*Vermivora pinus*) and Golden-winged Warbler (*V. chrysoptera*), two sister species which regularly hybridize, are separated by a Nei's genetic distance of 0.001–0.012, while non-hybridizing species Yellow-rumped Warbler (*Dendroica coronata*) and Prairie warbler (*D. discolor*) have, when in contact, a genetic distance of zero (Hepp *et al.* 1988).

The spatial distribution of species is an important factor that determines opportunities for hybridization. Some species are entirely sympatric and exhibit a certain level of hybridization while maintaining their integrity (Mallet 1995, Coyne & Orr 2004). Other species are partially allopatric, and hybridize in the overlapping distribution areas forming hybrid zones which are maintained more or less stably. Hybridization can be promoted when two species enter in secondary contact, especially if those species are relatively young and reproductive isolation is still not complete (Machado-Schiaffino *et al.* 2010). In this study, distribution for some genera (*Alectoris* and *Grus*) overlap only with non-sister taxa so hybridization cannot occur in sister taxa although they may have a potential for hybridization. Sister species with a parapatric distribution (species with contiguous or narrow overlap zones) may not have developed perfect species recognition mechanisms. Therefore, rarity at the boundary of the range of a species plus similarity in appearance and mating signals between sister species might encourage mixed pairing and hybridization. Rapid radiation and recent speciation in a genus, and convergent adaptation to similar habitats, also may enhance hybridization between related taxa. In some cases, hybridization may be a function of divergence across a sharp ecological gradient while in primary contact, a model supported, for example, by various studies in the northern Rocky Mountains of North America (Irwin 2012). Moreover, there is abundant evidence that many bird species, oscine passerines especially, are reproductively isolated at the premating stage, a pattern that suggests a substantial and rapid radiation that is recent in geological time.

For some genera, all hybrids recorded by McCarthy (2006) indeed occur between subspecies, according to Dickinson's taxonomy, and for some genera the number of hybridizing bird pairs decreases from 5 to 1 when Dickinson's taxonomy is followed. Therefore, the frequency of hybridization for sister and non-sister species is different depending on which taxonomy is followed. Dickinson's taxonomy was followed in this study because it is most consistent with the biological species concept. Some species listed by McCarthy (2006) are controversial and some authors prefer to lump them.

Although frequency of hybridization was found to be higher within sister species than non-sister species in contact, the reasons that only eight genera in Fisher's Exact Probability test have significant *P* values are likely to be (1) the low number of species in some genera and (2) spatial distribution does not allow contact between sister taxa in some genera. The results of this study may therefore be biased because of some of the thresholds applied and the low number of species for many genera (for example, *Callipepla*, *Oporornis* and *Parula* had non-significant *P* values in Fisher's Exact Probability tests whereas genera with a large number of species had significant *P* values, e.g. *Larus*, *Turdus*, *Anas*). Access to more complete phylogenetic trees of the genera with a large number of species would probably increase these significances.

The question addressed in the study could be applied in a similar way for other groups of animals in order to test the sister taxa propensity for hybridization. In summary, on the basis of data culled from McCarthy's (2006) compendium of hybrid birds coupled with known phylogenetic molecular trees, we conclude that sister species do indeed hybridize more frequently than non-sister species, thus providing support for a long-assumed but previously untested assumption.

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REFERENCES

Aliabadian, M. & Nijman, V. 2007. Avian hybrids: incidence and geographic distribution of hybridisation in birds. *Contrib. Zool.* **76:** 59–61.

Arnold, M.L. 1992. Natural hybridization as an evolutionary process. *Ann. Rev. Ecol. Syst.* **23:** 237–261.

Benz, B.W. & Robbins, M.B. 2011. Molecular phylogenetics, vocalizations, and species limits in *Celeus* woodpeckers (Aves: Picidae). *Mol. Phylogenet. Evol.* **61:** 29–44.

Böhning-Gaese, K., Schuda, M.D. & Helbig, A.J. 2003. Weak phylogenetic effects on ecological niches of *Sylvia* warblers. *J. Evol. Biol.* **16:** 956–965.

Brelsford, A. 2011. Hybrid speciation in birds: allopatry more important than ecology? *Mol. Ecol.* **20:** 3705–3707.

Canales-Del-Castillo, R., Klicka, J., Favela, S. & González-Rojas, J.I. 2010. Molecular phylogenetic analysis of an endangered Mexican sparrow: *Spizella wortheni*. *Mol. Phylogenet. Evol.* **57:** 1319–1322.

Coyne, J.A. & Orr, H.A. 2004. *Speciation*. Sinauer Associates, Sunderland, MA.

Dasmahapatra, K.K., Silva-Vásquez, A., Chung, J.W. & Mallet, J. 2007. Genetic analysis of a wild-caught hybrid between non-sister *Heliconius* butterfly species. *Biol. Lett.* **3:** 660–663.

Del Hoyo, J., Elliot, A., Sartagal, J. & Christie, D.A. 1992–2011. *Handbook of the Birds of the World*: (Vols. 1–16). Lynx Edicions, Barcelona.

Dickinson, C.E. (ed.). 2003. *The Howard and Moore Complete Checklist of the Birds of the World*. Christopher Helm, London.

Driskell, A.C., Norman, J.A., Pruett-Jones, S., Mangall, E., Sonsthagen, S. & Christidis, L. 2011. A multigene phylogeny examining evolutionary and ecological relationships in the Australo-papuan wrens of the subfamily Malurinae (Aves). *Mol. Phylogenet. Evol.* **60:** 480–485.

Eberhard, J.R. & Bermingham, E. 2005. Phylogeny and comparative biogeography of *Pionopsitta* parrots and *Pteroglossus* toucans. *Mol. Phylogenet. Evol.* **36:** 288–304.

Eo, S.H., Bininda-Emonds, O.R.P. & Carroll, J.P. 2009. A phylogenetic supertree of the fowls (Galloanserae, Aves). *Zool. Scr.* **38:** 465–481.

Fain, M.G., Krajewski, C. & Houde, P. 2007. Phylogeny of 'core Gruiformes' (Aves: Grues) and resolution of the Limpkin–Sungrebe problem. *Mol. Phylogenet. Evol.* **43:** 515–529.

Ferguson-Lees, J. & Christie, D.A. 2001. *Raptors of the World.* (Helm Identification Guides.) Christopher Helm, London.

Fregin, S., Haase, M., Olsson, U. & Alström, P. 2009. Multi-locus phylogeny of the family Acrocephalidae (Aves: Passeriformes) – the traditional taxonomy overthrown. *Mol. Phylogenet. Evol.* **52:** 866–878.

García-Moreno, J., Cortés, N., García-Deras, G.M. & Hernández-Baños, B.E. 2006. Local origin and diversification among *Lampornis* hummingbirds: a Mesoamerican taxon. *Mol. Phylogenet. Evol.* **38:** 488–498.

Grant, P.R. & Grant, R.B. 1992. Hybridization of bird species. *Science* **256:** 193–197.

Grant, P.R & Grant, B.R. 1997. Genetics and the origin of bird species. *Proc. Natl Acad. Sci. USA* **94:** 7768–7775.

Gray, A.P. 1958. *Bird Hybrids.*: Commonwealth Agricultural Bureaux. Farnham Royal, Bucks, UK.

Helbig, A. & Seibold, I. 1999. Molecular phylogeny of Palearctic–African *Acrocephalus* and *Hippolais*Warblers (Aves: Sylviidae). *Mol. Phylogenet. Evol.* **11:** 246–260.

Hepp, G.R., Novak, J.M., Scrirbner, K.T. & Stangel, P.W. 1988. Genetic distance and hybridization of Black Ducks and Mallards: a morph of a different color? *Auk* **105:** 804–807.

Hollom, P.A.D., Porter, R.F., Christiensen, S. & Willis, I. 1988. *Birds of the Middle East and North Africa*. T. & A.D. Poyser, Calton UK.

Illera, J.C., Richardson, D.S. & Emerson, B.C. 2008. Phylogenetic relationships, biogeography and speciation in the avian genus Saxicola. *Mol. Phylogenet. Evol.* **48:** 1145–1154.

Irwin, D.E. 2012. Local adaptation along smooth ecological gradients causes phylogeographic breaks and phenotypic clustering. *Am. Nat.* **180:** 35–49.

Jacobsen, F., Friedman, N.R. & Omland, K.E. 2010. Congruence between nuclear and mitochondrial DNA: combination of multiple nuclear introns resolves a well-supported phylogeny of New World orioles (*Icterus*). *Mol. Phylogenet. Evol.* **56:** 419–427.

Johnson, K.P. & Sorenson, M.D. 1999. Phylogeny and biogeography of Dabbling Ducks (Genus: *Anas*): a comparison of molecular and morphological evidence. *Auk* **116:** 792–805.

Lerner, H.R.L. & Mindell, D.P. 2005. Phylogeny of eagles, Old World vultures, and other Accipitridae based on nuclear and mitochondrial DNA. *Mol. Phylogenet. Evol.* **37:** 327–346.

Lovette, I.J., Pérez-Emán, J.L., Sullivan, J.P., Banks, R.C., Fiorentino, I., Córdoba-Córdoba, S., Echeverry-Galvis, M., Barker, F.K., Burns, K.J., Klicka, J., Lanyon, S.M. & Berminghamg, E. 2010. A comprehensive multilocus phylogeny for the wood-warblers and a revised classification of the Parulidae (Aves). *Mol. Phylogenet. Evol.* **57:** 753–770.

Machado-Schiaffino, G., Juanes, F. & Garcia-Vazquez, E. 2010. Introgressive hybridization in North American hakes after secondary contact. *Mol. Phylogenet. Evol.* **55:** 552–558.

Madge, S. & McGowan, P. 2002. *Pheasants, Partridges & Grouses.* (Helm Identification Guides.). Christopher Helm, London.

Mallet, J. 1995. A species definition for the modern synthesis. *Trends Ecol. Evol.* **10:** 294–299.

McCarthy, E.M. 2006. *Handbook of Avian Hybrids of the World*. Oxford University Press, New York.

Newton, I. 2003. *The Speciation and Biogeography of Birds*. Academic Press, London.

Parra, J.L., Remsen, J.V., Jr., Alvarez-Rebolledo, M. & McGuire, J. A. 2009. Molecular phylogenetics of the hummingbird genus *Coeligena*. *Mol. Phylogenet. Evol.* **53:** 425–434.

Pons, J.M., Hassanin, A. & Crochet, P.A. 2005. Phylogenetic relationships within the Laridae (Charadriiformes: Aves) inferred from mitochondrial markers. *Mol. Phylogenet. Evol.* **37:** 689–699.

Prager, M., Johansson, E.I.A. & Andersson, S. 2008. A molecular phylogeny of the African widowbirds and bishops, *Euplectes* spp. (Aves: Passeridae: Ploceinae). *Mol. Phylogenet. Evol.* **46:** 290–302.

Price, T. 2008. *Speciation in Birds*. Roberts and Company, Greenwood Village, CO.

Randi, E. 1996. A mitochondrial cytochrome *b* phylogeny of the *Alectoris* partridges. *Mol. Phylogenet. Evol.* **6:** 214–227.

Randi, E., Lucchini, V., Hennache, A., Kimball, R.T., Braun, E.L. & Ligon, J.D. 2001. Evolution of the mitochondrial DNA control region and cytochrome *b* genes and the inference of phylogenetic relationships in the avian genus *Lophura* (Galliformes). *Mol. Phylogenet. Evol.* **19:** 187–201.

Randler, C. 2002. Avian hybridization, mixed pairing and female choice. *Anim. Behav.* **63:** 103–119.

Randler, C. 2004. Frequency of bird hybrids: does detectability make all the difference? *J. Ornith.* **145:** 123–128.

Randler, C. 2006. Behavioural and ecological correlates of natural hybridization in birds. *Ibis* **148:** 459–467.

Riesing, M.J., Kruckenhauser, L., Gamauf, A. & Haring, E. 2003. Molecular phylogeny of the genus *Buteo* (Aves: Accipitridae) based on mitochondrial marker sequences. *Mol. Phylogenet. Evol.* **27:** 328–342.

Roselaar, C.S., Prins, T.G., Aliabadian, M. & Nijman, V. 2006. Hybrids in divers (Gaviiformes). *J. Ornith.* **147:** 24–30.

Schwenk, K., Brede, N. & Streit, B. 2008. Introduction, extent, processes and evolutionary impact of interspecific hybridization in animals. *Phil. Trans. R. Soc. B* **363:** 2805–2811.

Sheldon, F.H., Whittingham, L.A., Moyle, R.G., Slikas, B. & Winkler, D.W. 2005. Phylogeny of swallows (Aves: Hirundinidae) estimated from nuclear and mitochondrial DNA sequences. *Mol. Phylogenet. Evol.* **35:** 254–270.

Shirihai, H., Gargallo, G. & Helbig, A. 2001. *Sylvia Warblers.* (Helm Identification Guides.). Christopher Helm, London.

Voelker, G., Rohwer, S., Bowie, R.C.K. & Outlaw, D.C. 2007. Molecular systematics of a speciose, cosmopolitan songbird genus: defining the limits of, and relationships among, the *Turdus* thrushes. *Mol. Phylogenet. Evol.* **42:** 422–434.

Weibel, A.C. & Moore, W.S. 2002. A test of a mitochondrial gene-based phylogeny of woodpeckers (Genus *Picoides*) using an independent nuclear gene, b-fibrinogen intron 7. *Mol. Phylogenet. Evol.* **22:** 247–257.

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Appendix. Contingency table for sister and non-sister hybridizing species pairs of birds.

Genus		No. hybridizing pairs	No. non-hybridizing pairs but in contact	*P* value
Acrocephalus	Sister taxa	1	4	0.33
	Non sister taxa	7	91	
Celeus	Sister taxa	2	0	0.01
	Non sister taxa	2	25	
Anas	Sister taxa	4	1	0.05
	Non sister taxa	55	105	
Malurus	Sister taxa	1	3	0.26
	Non sister taxa	1	24	
Parula	Sister taxa	1	0	1
	Non sister taxa	1	2	
Turdus	Sister taxa	3	7	0.03
	Non sister taxa	12	185	
Pteroglosus	Sister taxa	1	2	0.50
	Non sister taxa	5	22	
Picoides	Sister taxa	1	1	0.32
	Non sister taxa	5	27	
Basileuterus	Sister taxa	3	2	< 0.001
	Non sister taxa	2	102	
Dendroica	Sister taxa	4	4	< 0.001
	Non sister taxa	13	216	
Grus	Sister taxa	0	0	1
	Non sister taxa	6	6	
Oporornis	Sister taxa	1	0	0.33
	Non sister taxa	1	4	
Buteo	Sister taxa	2	1	0.02
	Non sister taxa	6	76	
Larus	Sister taxa	4	2	0.03
	Non sister taxa	29	105	
Hippolais	Sister taxa	2	1	0.10
	Non sister taxa	2	14	
Aquila	Sister taxa	1	2	0.35
	Non sister taxa	3	24	
Sylvia	Sister taxa	1	5	0.28
	Non sister taxa	4	86	
Icterus	Sister taxa	1	0	0.02
	Non sister taxa	3	152	
Euplectes	Sister taxa	1	4	0.08
	Non sister taxa	1	115	
Saxicola	Sister taxa	1	3	0.40
	Non sister taxa	2	20	
Geothlypis	Sister taxa	0	1	1
	Non sister taxa	2	15	
Progne	Sister taxa	1	1	0.33
	Non sister taxa	2	13	
Spizella	Sister taxa	0	1	1
	Non sister taxa	4	19	
Alectoris	Sister taxa	0	0	1
	Non sister taxa	5	7	
Lophura	Sister taxa	2	1	0.14
	Non sister taxa	3	14	
Gallus	Sister taxa	1	0	0.40
	Non sister taxa	1	3	
Lampornis	Sister taxa	1	1	1
	Non sister taxa	2	5	
Callipepla	Sister taxa	1	0	1
	Non sister taxa	3	4	
Coeligena	Sister taxa	1	0	0.14
	Non sister taxa	3	25	