

Hybridization patterns and the evolution of reproductive isolation in ducks

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Much of our knowledge of the evolution of reproductive isolation comes from studies of *Drosophila*. This body of work has revealed the following patterns: (1) reproductive isolation increases with phylogenetic distance between hybridizing species; (2) reproductive isolation is greater between sympatric than allopatric species with the same level of divergence; and (3) hybrid crosses conform to Haldane's rule. We tested for the existence of these patterns in ducks (subfamily Anatinae, *sensu* Livezey, 1997b) based on 1037 hybrids of known parentage. Our analyses of the number of interspecific crosses in relation to phylogenetic distance found a significant deviation between the observed and expected distribution of crosses controlling for the topology of the Anatinae phylogeny. In particular, we found both an excess of hybrid crosses among closely related species and a scarcity among distantly related species. The number of hybrid males also decreased with increasing phylogenetic distance between parental species, although the number of hybrid females remained low and constant. Sympatric species produced higher numbers of hybrid males than allopatric ones, despite no difference in phylogenetic distance among parental species in compared groups. The number of hybrid males exceeded the number of hybrid females, consistent with Haldane's rule. This was evident even though the analysis was restricted to a reduced set of phylogenetically independent crosses. However, the pattern was no longer significant after correction for the number of hybrid males by the male-biased sex ratio of adult ducks. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 77, 193–200.

ADDITIONAL KEYWORDS: ducks – Anatinae – hybrids – Haldane's rule – reproductive isolation.

INTRODUCTION

The hallmark of biological species is reproductive isolation and the study of evolution of isolating mechanisms has dominated much of the speciation literature for the last 50 years. Irrespective of its obvious importance to the study of sexually reproducing organisms including most vertebrates, much of our understanding derives from studies of invertebrates, notably *Drosophila* (see below). Among birds, waterfowl (family Anatidae) are exceptional in their propensity to hybridize under both natural and captive conditions (Gray, 1958; Johnsgard, 1960; Grant & Grant, 1992). It has been hypothesized that this is consequence of one or several of the following:

1. Extreme similarity of karyotypes among species reducing the probability of meiotic disjunctions (Shields, 1982).
2. Extensive sympatry increasing the potential for hybridization (Carboneras, 1992).
3. High opportunities for erroneous pairing because pairs are formed anew every year (Carboneras, 1992).
4. Strong selection pressure for early breeding especially in species at high latitudes (Rohwer & Anderson, 1988).
5. Behavioural similarity (Johnson *et al.*, 2000).
6. Male-biased sex ratios (Baldassarre & Bolen, 1994).

Waterfowl are one of the best-known groups of birds with respect to their phylogenetic relationships. These perspectives on evolutionary affinities within the Anatidae are based on analysis of morphological and behavioural characters (Livezey, 1986, 1991, 1995a,b,

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1996, 1997a,b), or molecular data (Johnson & Sorenson, 1999; McCracken *et al.*, 1999; Sorenson *et al.*, 1999). The high number of interspecific crosses together with the availability of phylogenetic information provide an excellent opportunity to study how reproductive isolation arose during evolutionary divergence in a group of higher vertebrates.

To date, the most comprehensive comparative analyses of prezygotic and postzygotic barriers in relation to phylogenetic distance involve the fruit fly genus *Drosophila* (Coyne & Orr, 1989a, 1997). These analyses showed that both prezygotic and postzygotic reproductive isolation increase with divergence time between taxa, that prezygotic isolation evolves faster than postzygotic isolation in sympatric species, and that hybrid sterility and inviability in *Drosophila* conform to Haldane's rule. The latter states that "... when in the F_1 offspring of two different animal races one sex is absent, rare or sterile, that sex is the heterozygous (heterogametic) sex" (Haldane, 1922).

In the present study, we describe patterns of hybridization in ducks based on different measures of phylogenetic divergence and sympatry/allopatry between parental species. In birds, females are the heterogametic sex (WZ). We thus predict that if ducks conform to Haldane's rule (Coyne & Orr, 1989b; Coyne, 1992), hybrid females should be rare compared to hybrid males.

METHODS

HYBRID DATABASE AND PHYLOGENY

The present analyses are based on 161 interspecific crosses totalling 1037 hybrids of known sex and parentage belonging to the subfamily Anatinae (*sensu* Livezey, 1997b), compiled in Gillham & Gillham (1996, 1998, 1999, 2000). Interspecific phylogenetic distances were estimated using the number of nodes connecting each species pair according to a cladistic phylogeny derived from Livezey (1997b). This measure underestimates the true interspecific distance because, at any point in the past, the reconstructed phylogeny generally has fewer lineages present (and never more) than the actual phylogeny (Nee *et al.*, 1995). To minimize such bias and to assess the robustness of the analysis, we also estimated interspecific distances by the number of apomorphic changes along the branches connecting all pairs of species (both including and excluding autapomorphies of the terminal taxa). These changes are described in Livezey (1986, 1991, 1995a,b, 1996, 1997a), and mapped on his cladograms.

Hybrid sex viability was estimated by comparing the number of males and females belonging to each interspecific cross. To avoid errors associated with sex

ratio estimation based on a reduced number of hybrids, some analyses were restricted to crosses in which five or more hybrids have been recorded. Since sex ratios of adult ducks are typically male-biased (Breitwisch, 1989; Baldassarre & Bolen, 1994; Promislow, Montgomerie & Martin, 1994; Johnsgard & Carbonell, 1996), we applied a 33% correction to the number of hybrid males produced. This correction assumes that most hybrids were sexed as adults and that typical adult sex ratios in ducks were about 1.5:1. Decisions regarding allopatric or sympatric designations of hybridizing species were based on distribution maps in Carboneras (1992). Only species with overlapping breeding ranges, irrespective of the area of overlap involved, were considered as sympatric.

It is important to note that although the hybrid duck dataset is probably the most complete for any group of higher vertebrates (Gillham & Gillham, 1996, 1998, 1999, 2000), it is far from ideal due to uncertainty concerning: (1) the original opportunities for hybridization between species; (2) the relative detectability of male vs. female hybrids under natural and captive conditions, and (3) the hybrid sex ratios at hatching. When appropriate, we make explicit assumptions regarding these three points and comment on the effect that possible data biases may have on the analyses and on the interpretation of the results.

STATISTICAL ANALYSES

Investigating the relationship between reproductive isolation and interspecific divergence requires that we do more than simply look at the number of hybrids present in all crosses, because hybrid crosses are not independent points of comparison. Many crosses shared one of the parental species, or were related through an internal branch of the phylogeny. To mitigate this problem, we also compared a subset of crosses involving species pairs that were phylogenetically linked through branches that never met with other species pairs. Mantel's test using Spearman rank correlations, and Kolmogorov-Smirnov tests were used to assess the relationship between hybridization and phylogenetic distances of the parental species. Statistical significance of Mantel's test was assessed using 9999 permutations of the distance matrix. Mann-Whitney non-parametric tests were employed to evaluate differences between sympatric and allopatric species crosses. Finally, hybrid sex ratio bias was evaluated using binomial tests. These analyses were performed using the R-Package 4.0 (Casgrain & Legendre, 2001) and Statistica 4.1 software.

RESULTS

FREQUENCY OF HYBRID CROSSES DEVIATES FROM NULL DISTRIBUTION

The results of our analyses were similar regardless of the measure of phylogenetic distance employed. We thus present only those based on the number of nodes.

Mantel's test revealed a negative relationship between the presence of hybrids and phylogenetic distance between parental species (Spearman $r = -0.145$, $P < 0.0001$). When considering closely related species, the number of interspecific crosses increased with phylogenetic distance and reached a maximum for species separated by between 6 and 12 nodes (Fig. 1). Beyond this range, increased phylogenetic separation between species was associated with a decrease in the number of crosses. In sum, most of the interspecific crosses were concentrated at intermediate phylogenetic distances. To further evaluate this pattern, we generated the expected distribution of interspecific crosses using the topology of the anatid phylogeny, assuming a uniform probability of hybridization. The expected distribution also showed a concentration of crosses at intermediate phylogenetic distances (by between 9 and 16 nodes; Fig. 1). This suggests that the shape of the observed distribution of interspecific crosses is driven by tree topology and is not directly related to reproductive isolation changes with phylogenetic distance. However, expected and observed distributions were significantly different (Kolmogorov–Smirnov test $D = 0.38$, $P < 0.01$). In particular, the

observed distribution showed more interspecific crosses between closely related and less crosses between distantly related species than predicted by the expected distribution.

HYBRID MALES DECREASE WITH PHYLOGENETIC DISTANCE BUT NOT WITH SYMPATRY

We found a decreasing trend in the number of hybrids with phylogenetic distance (Spearman $r = -0.25$, $t_{159} = -3.27$, $P < 0.001$). This trend is, however, a consequence of the reduction in the number of hybrid males ($r = -0.27$, $t_{159} = -3.47$, $P < 0.001$) rather than in the number of hybrid females ($r < -0.01$, $t_{159} = -0.05$, $P > 0.95$; see Fig. 2). Restricting the analysis to phylogenetically independent crosses with at least five hybrids of known sex, we obtained eight points of comparison. As all but one corresponded to sympatric species, we decided to present the analysis based on this reduced set of seven sympatric crosses. This analysis showed a non-significant decreasing trend in the number of hybrid males and females with phylogenetic distance ($r = -0.65$, $t_5 = -1.93$, $P > 0.10$; see Fig. 3).

Crosses between sympatric species produced a higher number of hybrid males than those involving allopatric ones (Table 1). This result cannot be attributed simply to differences in the degree of phylogenetic relatedness, because sympatric and allopatric species did not differ in their mean phylogenetic distance (Table 1).

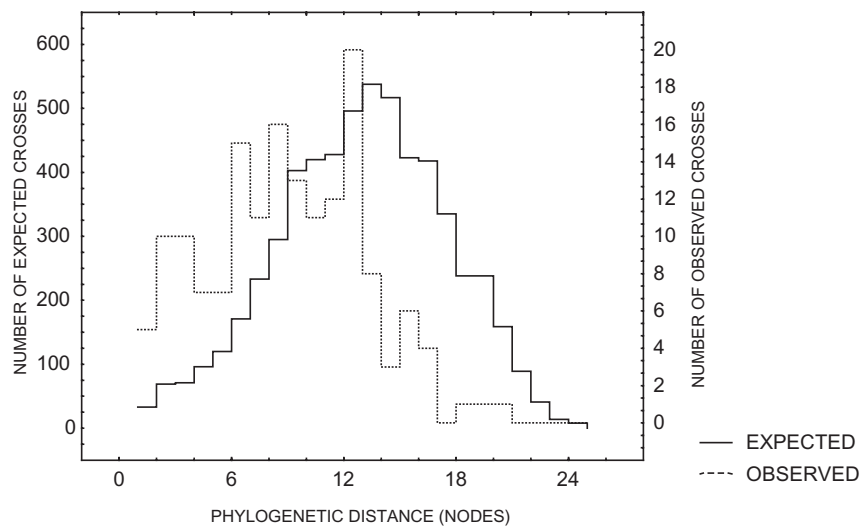


Figure 1. Expected and observed distribution of hybrid crosses in the subfamily Anatinae. The expected distribution was derived from the cladistic phylogeny of Livezey (1997b) assuming a uniform probability of hybridization. The observed distribution of hybrid crosses differed significantly from the expected distribution because of the excess of hybrids between closely related and the relative rarity of hybrids between distantly related species.

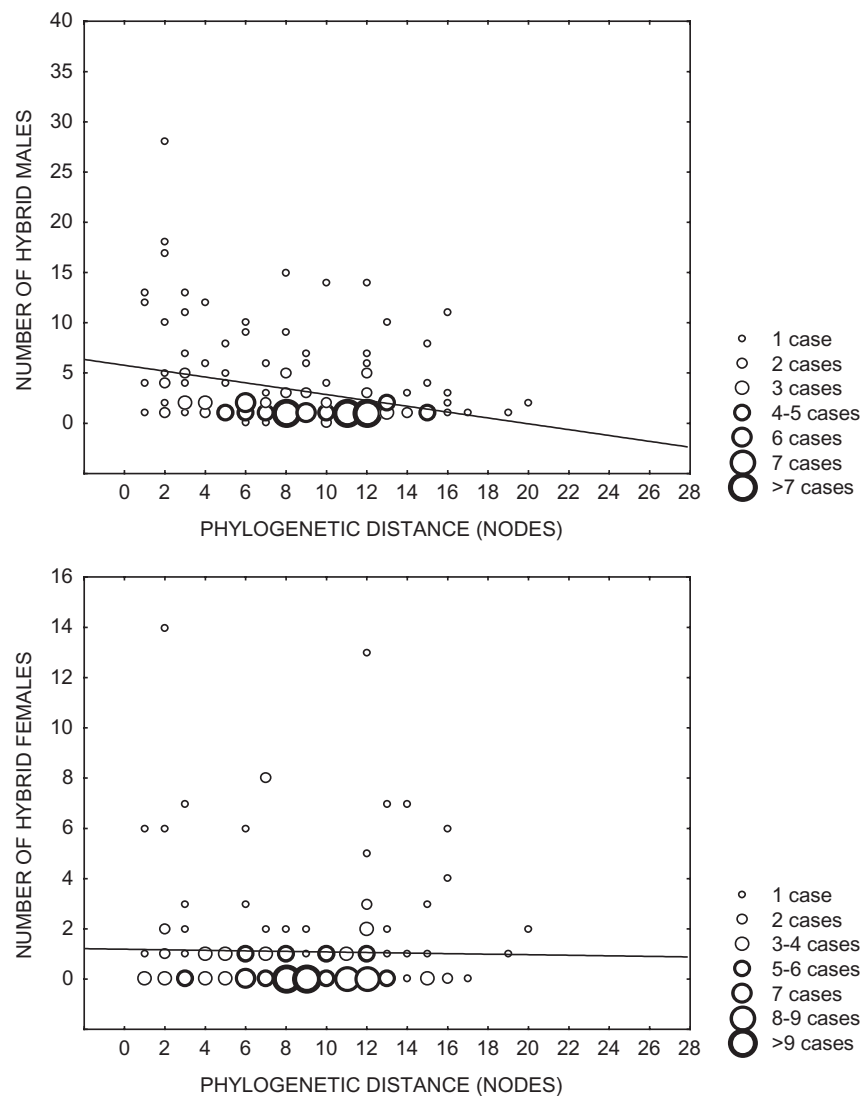


Figure 2. Scatterplots of the number of hybrids produced by different interspecific crosses. The number of hybrid males (upper diagram) significantly decreases with increasing phylogenetic distance between parental species. The number of hybrid females (lower diagram) remains approximately constant. For comparison, linear regression lines for the data are shown. Crosses *Anas penelope* × *Anas americana* (51 hybrid males, 1 node); *Anas platyrhynchos* × *Anas acuta* (73 hybrid males, 12 nodes); *Aythya ferina* × *Aythya nyroca* (46 hybrid males, 6 nodes); and *Aythya ferina* × *Aythya fuligula* (175 hybrid males, 7 nodes), were omitted for graphic simplicity.

NUMBER OF HYBRID MALES EXCEEDS THAT OF HYBRID FEMALES

Regardless of the phylogenetic distance of the interspecific crosses, the number of hybrid males significantly exceeded that of hybrid females. In 125 cases there were more hybrid males than females; in 23 cases sexes were equally represented. In only 13 cases were there more hybrid females than males (binomial test $P[z = -9.52] < 0.001$, two-tailed). The excess of males compared to females in the subset of phylogenetically independent crosses was still significant (binomial test $P[x = 0] = 0.032$, two-tailed, Fig. 3).

However, controlling for the effect of biased adult sex ratio of ducks (reducing the estimated number of hybrid males by 33%), the pattern was no longer significant (binomial test $P[x = 1] = 0.12$, two-tailed).

DISCUSSION

INTERSPECIFIC ISOLATION VARIES WITH EVOLUTIONARY DIVERGENCE

Our phylogenetic analyses of interspecific crosses in ducks revealed the following patterns: (1) a negative relationship between the number of interspecific

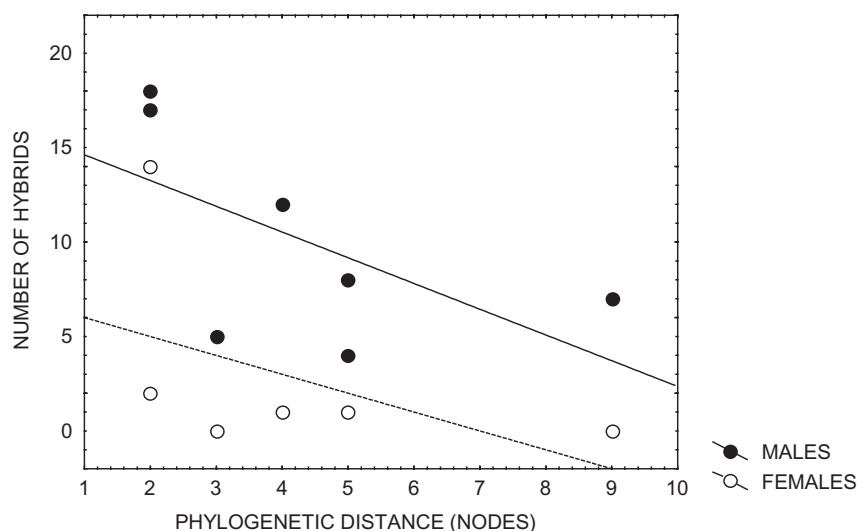


Figure 3. Scatterplots of the number of hybrids produced by a subset of phylogenetically independent crosses between sympatric parental species. The number of hybrid males (●) and females (○) tend to decrease with increasing phylogenetic distance between parental species. For comparison, linear regression lines for the data are shown. The number of hybrid males exceeds the number of hybrid females in all crosses, as predicted by Haldane's rule. See text for more details.

Table 1. Mean \pm standard deviation of the number of hybrids produced according to the distribution (sympatric or allopatric) of their parental species. In addition, the mean \pm standard deviation of the phylogenetic distances between parental species is given

Variable	Crosses between sympatric species ($N = 86$)	Crosses between allopatric species ($N = 75$)	Mann-Whitney adjusted z	P
Hybrid males	7.91 ± 20.77	2.40 ± 5.89	4.31	<0.0001
Hybrid females	1.50 ± 2.78	0.64 ± 1.02	1.30	0.194
Phylogenetic distance	8.52 ± 4.29	8.47 ± 4.00	0.02	0.982

crosses and the phylogenetic distance (2) a decreasing number of hybrid males, but not females, with increasing phylogenetic distance; and (3) an excess of hybrid males relative to hybrid females. These patterns were robust to different measures of phylogenetic distance and to treatments with and without phylogenetic correction. We interpret these results generally as evidence for the progressive appearance of reproductive barriers with increasing phylogenetic distance. It is important to note, however, that our analyses were based on data already available, which are far from ideal. In the following paragraphs we will discuss the potential biases affecting the data and the kind of experimental studies that would be needed for a better test of the questions addressed.

In contrast to experimental studies in *Drosophila* (Coyne & Orr, 1989a, 1997), we could neither discriminate between pre- and postzygotic barriers nor measure reproductive isolations directly, because our analysis was based on the number of produced hybrids

without reference to original opportunities for hybridization between species. In particular, although there are 5990 possible crosses among 110 species of typical Anatinae (reciprocal crosses are not considered as different), our study was based on only 161 crosses of known parentage. Even if some of the unreported crosses represent cases of complete prezygotic isolation and/or hybrid inviability, others (probably most) simply have not occurred because the species are not sympatric in nature or have not coexisted in captivity. Thus, our conclusion about the positive relationship between reproductive isolation and phylogenetic distance makes the important assumption that neither sympatry nor coexistence in captivity are associated with phylogenetic distinctiveness. The former assumption was confirmed because we detected no differences in the mean phylogenetic distances between sympatric and allopatric parental species (see Table 1). In contrast, nothing was known about the latter assumption because the source of data

did not discriminate between natural and captive hybrids. Moreover, any premating barriers that covary with phylogenetic distance have the potential to affect the results regarding the occurrence and number of hybrids, but not their sex ratios. Thus, in order to standardize opportunities for hybridization and overcome any premating barrier, captive crossings using the method of artificial insemination and artificial incubation of the eggs would be the ideal source of data for our study (Cheng, Burns & McKinney, 1983).

Only two previous studies have investigated the relationship between phylogenetic divergence and hybridization in ducks. Both of these (Johnsgard, 1960; Scherer & Hilsberg, 1982) concluded that most hybrids resulted from crosses between members of the same genus and tribe, the latter designations made using the classic taxonomic work of Delacour & Mayr (1945). Our finding that hybrids numbers decrease with phylogenetic distance agrees with their conclusions. However, our inclusion of cladistic perspectives (which include methods for correcting for lack of independence among interspecific crosses using the phylogenetic relationships of their parental species) gives us an important advantage over these previous studies. In addition, the use of a cladistic tree allowed us to build a null distribution of interspecific crosses for comparison with the real data, and to obtain more quantitative estimators of phylogenetic distances. Regarding this point, however, some caution is necessary because the number of nodes separating parental species could be an adequate measure of divergence if we assume no extinction and a punctuated mode of evolution in which all change occurs at the time of speciation. Therefore, we would prefer a measure of interspecific genetic distances, which is a direct measure of evolutionary change. Unfortunately, this information is still not available for all anatine species. Moreover, recent molecular studies (Johnson & Sorenson, 1999; McCracken *et al.*, 1999; Sorenson *et al.*, 1999) suggest that a revision of waterfowl phylogeny is needed. This would have consequences not only for the estimate of the null distribution of crosses but also for the phylogenetic distances employed in the analyses.

Strictly speaking, capacity to interspecifically hybridize is the symplesiomorphic retention of ancestral interfertility, while the raising of reproductive barriers is the apomorphic loss of the ability to interbreed (McKittrick & Zink, 1988). According to this, it would seem that there is no clear reason to expect that the number of hybrids should decrease with phylogenetic distance, a view apparently supported by the high number of intergeneric hybrids described in birds (Prager & Wilson, 1975; Grant & Grant, 1992). We think, however, that the existence of interespecific reproductive compatibility is increasingly unlikely as divergence augments because reproductive barriers

arise as a byproduct of genetic differences accumulated in diverging lineages, which interact negatively in the hybrids (Orr, 1993, 1995; Wu, Johnson & Palopoli, 1996; Orr, 1997). This agrees with the pattern we found in the subfamily Anatinae.

SYMPATRY, ALLOPATRY AND HYBRIDIZATION

A rather surprising result of our study was the finding that crosses involving sympatric species produced more hybrid males than those between allopatric species. This contrasts with the pattern exhibited by *Drosophila* where sympatric species showed greater degree of prezygotic isolation than allopatric species (Coyne & Orr, 1989a, 1997). However, we suspect that our result may derive from a bias in the data rather than a real phenomenon. This is because only sympatric species have the potential to hybridize in the wild while allopatric species pairs can hybridize either in captivity or because of accidental escapes from captivity. This would tend to inflate the number of sympatric compared to allopatric species hybrids.

This issue is not simply one of theoretical interest. Clarifying possible differences in the degree of isolation among sympatric and allopatric species of ducks may be important for their conservation because of the danger of extinction by hybridization and introgression when wild and introduced species of ducks come into contact (Rhymer & Simberloff, 1996). For example, the integrity of New Zealand and Australian populations of the Grey duck (*Anas s. superciliosa* and *A. s. rogersi*) is being compromised by interbreeding with the mallard (*Anas platyrhynchos*) (Dorst, 1972; Haddon, 1984; Lever, 1987). Hybridization with the mallard also has contributed to the decline of the endemic Hawaiian duck (*Anas wyvilliana*; Griffin, Shallenberger & Fefer, 1989) and the Florida mottled duck (*Anas f. fulvigula*; Mazourek & Gray, 1994). Regardless of the native sympatric or allopatric designations of these species, it is noteworthy that these examples involve closely related species, for which our analysis suggests that reproductive isolation is minimal.

DO DUCKS CONFORM TO HALDANE'S RULE?

One of the most interesting facets of the evolution of reproductive isolation relates to Haldane's rule. As females are the heterogametic sex in birds, our study suggests that the species included in the subfamily Anatidae conform to this rule because of the significant excess of hybrid males. However, we must be cautious due to the potential biases affecting the data, such as differences in relative detectability of the male and female hybrids. For example, if detectability is biased in favour of males (which is likely, particularly

under natural conditions), the pattern predicted by Haldane's rule would result. An additional problem relates to the estimation of hybrid sex ratio. Although data from several species show that the sex ratio during egg stage or at hatching is 1 : 1 (Bellrose *et al.*, 1961), adult sex ratios are usually male-biased in ducks. Fifty percent excess of adult males to females is not uncommon in wild duck populations (Bellrose *et al.*, 1961), and it can even be as high as 300% (McIlhenny, 1940). This means that if a fraction of hybrids reported in the literature are adults, or were sexed based on adult plumage, an excess of males cannot be unequivocally considered as a confirmation of Haldane's rule. Further, we note that if we reduce the estimated number of hybrid males by 33%, the excess of males produced by interspecific crosses is no longer significant. Alternatively, and in order to measure sex ratio bias related to hybrid inviability and to control for non-genetical (ecological) causes of bias such as differential predation (Promislow *et al.*, 1994), this variable should be evaluated at hatch.

Haldane's rule for inviability has been explained in terms of Dominance theory (Turelli & Orr, 1995; Presgraves & Orr, 1998). According to this theory, mutations in birds' Z chromosomes act as partial recessives in hybrids. These have deleterious effects when interacting with allospecific autosomes causing inviability in the heterogametic sex (Muller, 1942; Orr, 1993, 1997; Wu *et al.*, 1996). This theory also predicts an accelerating trend ('snowball effect') in the emergence of hybrid inviability with evolutionary divergence (Orr, 1995; Turelli & Orr, 1995). We observed a pattern not particularly consistent with the snowball effect; rather than finding a relatively equal number of male and female hybrids for close related crosses and then a steep decline in the number of female hybrids, we found greater differences in the number of hybrid males vs. females at the lowest levels of phylogenetic distinctiveness followed by a decline in the number of hybrid males (Figs 2,3). Here again, we should consider the effect of potential biases of the data. In particular, greater opportunities for hybridization among sympatric species and higher detectability of hybrid males (relative to hybrid females) in the wild would produce the patterns depicted in Figure 2 if a positive association between allopatric condition and phylogenetic distance exists. We think, however, that this is not the case because the mean phylogenetic distances separating sympatric and allopatric parental species in the global analysis were similar (Table 1). Besides, phylogenetically independent crosses involving only sympatric parental species always showed a male biased sex ratio, irrespective of their phylogenetic distance.

In sum, our study revealed that the interpretation of the hybridization patterns in ducks is complex due

to the confounding effect of phylogeny and the suspected bias of available data. In order to overcome these problems, further analyses should be based on hybrids obtained by artificial insemination and incubation, and sexed at hatching. This would control for differences in reproductive opportunities between sympatric and allopatric species, and for non-genetic causes of sex ratio bias.

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