

Biased introgression of mitochondrial and nuclear genes: a comparison of diploid and haplodiploid systems

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Abstract

Hybridization between recently diverged species, even if infrequent, can lead to the introgression of genes from one species into another. The rates of mitochondrial and nuclear introgression often differ, with some taxa showing biases for mitochondrial introgression and others for nuclear introgression. Several hypotheses exist to explain such biases, including adaptive introgression, sex differences in dispersal rates, sex-specific prezygotic isolation and sex-specific fitness of hybrids (e.g. Haldane's rule). We derive a simple population genetic model that permits an analysis of sex-specific demographic and fitness parameters and measures the relative rates of mitochondrial and nuclear introgression between hybridizing pairs. We do this separately for diploid and haplodiploid species. For diploid taxa, we recover results consistent with previous hypotheses: an excess of one sex among the hybridizing migrants or sex-specific prezygotic isolation causes a bias for one type of marker or the other; when Haldane's rule is obeyed, we find a mitochondrial bias in XY systems and a nuclear bias in ZW systems. For haplodiploid taxa, the model reveals that owing to their unique transmission genetics, they are seemingly assured of strong mitochondrial biases in introgression rates, unlike diploid taxa, where the relative fitness of male and female hybrids can tip the bias in either direction. This heretofore overlooked aspect of hybridization in haplodiploids provides what is perhaps the most likely explanation for differential introgression of mitochondrial and nuclear markers and raises concerns about the use of mitochondrial DNA barcodes for species delimitation in these taxa.

Keywords: haplodiploid, hybridization, large X effect, speciation, unisexual inviability, unisexual sterility

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Introduction

Genetic exchange between divergent populations or species (i.e. hybridization) is a widespread and potentially important evolutionary process in both plants and animals (Arnold 1997, 2006; Dowling & Secor 1997; Avise 2004; Seehausen 2004; Bull *et al.* 2006; Mallet 2007; Arnold *et al.* 2012). Possible outcomes of hybridization range from the immediate elimination of unfit hybrids to the formation of novel hybrid species (e.g. Schwarz *et al.* 2005; Mavarez *et al.* 2006; Meyer *et al.* 2006; Mavarez & Linares 2008; Sherman & Burke

2009; Kelly *et al.* 2010). Between these two extremes, hybridization followed by repeated backcrossing can lead to the movement of some genes between species (i.e. introgression). Multilocus studies of hybridizing species demonstrate that the ease with which different genes introgress can vary tremendously. Understanding why these biases exist might yield important insights into the speciation process (Coyne & Orr 2004; Mallet 2005; Hoffmann & Rieseberg 2008; Via & West 2008; Kulathinal *et al.* 2009; Nosil & Feder 2012).

A marked difference in the rates of mitochondrial and nuclear introgression is a common pattern that has been observed across a wide range of organisms (examples compiled in Avise 2004; Chan & Levin 2005; Petit & Excoffier 2009; Toews & Brelsford 2012). Numerous

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hypotheses have been proposed to explain biased introgression of mitochondrial or nuclear genes, and these variously invoke natural selection, genetic drift, behaviour or demography as causal mechanisms (Barton & Jones 1983; Lamb & Avise 1986; Smith 1992; Rieseberg *et al.* 1996; Martinsen *et al.* 2001; Funk & Omland 2003; Ballard & Whitlock 2004; Chan & Levin 2005; Baack & Rieseberg 2007; Currat *et al.* 2008; Petit & Excoffier 2009; Toews & Brelsford 2012). The direction of the bias is taxon dependent and appears to be loosely correlated with sex-determining mechanisms: whereas mitochondrial introgression tends to exceed nuclear introgression in taxa in which males are the heterogametic (i.e. XY or XO) sex, the opposite pattern is more prevalent when females are the heterogametic (i.e. ZW) sex (Avise 2004; Chan & Levin 2005; Toews & Brelsford 2012; but see Petit & Excoffier 2009 for an alternative explanation). This pattern is consistent with Haldane's (1922) rule (Orr 1997; Schilthuizen *et al.* 2011), which, when obeyed, leaves the heterogametic sex absent or sterile and therefore unable to transfer genes from one species to another.

In groups in which males are the heterogametic (i.e. XY or XO) sex, as is the case in mammals, beetles and most dipterans (Bachtrog *et al.* 2014), reduced fertility and viability in hybrid males is expected to lead to biased mitochondrial introgression (Avise 2004). In contrast, when females are the heterogametic (i.e. ZW) sex, as is the case in birds, butterflies and snakes (Bachtrog *et al.* 2014), reduced female fertility and viability should restrict mitochondrial gene flow (Tegelström & Gelter 1990; Funk & Omland 2003; Avise 2004). Although haplodiploid species lack sex chromosomes, Koevoets & Beukeboom (2009) argue that Haldane's rule should be extended to include them because the prevailing explanations for the pattern of male hybrid defects (the dominance, faster-male and faster-X theories) still apply, albeit in modified form. Under this expanded definition, which draws the analogy between hemizygosity and haploidy, hybrid genetic incompatibilities are expected to evolve for haploid males at shorter genetic distances than for hybrid females because males experience all recessive epistatic effects (Breeuwer & Werren 1995). Thus, as in XY systems, this leads to a prediction that in haplodiploid taxa, mitochondrial gene flow should exceed nuclear gene flow across species boundaries, as there is expected to be a deficit of hybrid males relative to hybrid females.

If many speciation events are accompanied by unisexual sterility or inviability in the hybrids, as evidence indicates (e.g. Coyne & Orr 1989, 1997; Coyne 1992; Wu & Davis 1993; Laurie 1997; Sasa *et al.* 1998; Presgraves 2002; Price & Bouvier 2002), Haldane's rule may determine patterns of differential introgression between many, if not most, hybridizing animal species pairs.

Given this potential, we develop a theoretical framework to evaluate sex-specific hybrid fitness as a general explanation for biased introgression in animals with three common sex-determination systems: XY heterogamety, ZW heterogamety and haplodiploidy (either arrhenotoky or paternal genome elimination). The model is simple and sufficiently general to incorporate other hypothesized causes of biased introgression, including prezygotic isolation (Chan & Levin 2005) and sex biases in hybridization rates (Lamb & Avise 1986).

Model and results

We model the introgression of genes from species 1 into species 2. Let n_f and n_m be the number of individuals from species 1 who mate individuals from species 2, which has N_f females and N_m males, with $n_\chi \ll N_\chi$ (where χ can be 'f' or 'm'). If dispersal into the range of species 2 is sex-biased or if prezygotic barriers between the two species are sex specific, then it is likely that $n_f \neq n_m$. Mating produces hybrid offspring, whose fitness (viability and fertility), $v_{i\chi}$, is measured relative to that of species-2 individuals through the first two generations of hybrids. This allows sufficient time to reveal all possible genetic incompatibilities. Let $b_{i\chi}$ be the probability that an i th-generation hybrid backcrosses to species 2. The natural history of the species and their hybrids will influence the value that $b_{i\chi}$ takes, and $b_{i\chi}$ should therefore be understood as a composite of various aspects of behaviour. First, geography can affect this backcross probability. In an allopatric model, hybrids may have no choice but to mate with species 2, which, all other things equal, will only increase $b_{i\chi}$. Second, hybrids may show sex-specific preferences for backcrossing to species 1 or species 2. And finally, species 2 may have sex-specific preferences for mating with hybrids. We assume for simplicity that all later-generation offspring have fitness equal to that of species-2 individuals and that these later-generation individuals backcross to species 2 with 100% probability (i.e. $v_{i\chi} = b_{i\chi} = 1$ for $i \geq 3$).

We focus on two neutral marker loci: A , a nuclear autosomal locus, and M , a mitochondrial locus. Although we limit our analysis to just these two loci, the model and its results are meant to generalize to all neutral loci in the nuclear autosomal and mitochondrial sets. Alleles are given subscripts '1' or '2' to reflect their species of origin. We assume that both loci are unlinked to any genes conferring fitness defects in hybrids. Because the mitochondrial genome is one linkage block, this therefore assumes that mitochondria are not involved in producing hybrid incompatibility. To capture the rate of introgression, we calculate the probability that an allele from species 1 eventually fixes in

species 2 by random genetic drift. We model diploid and haplodiploid systems separately. The transmission genetics for the two genetic systems are depicted schematically in Figs 1–2.

Diploid species

The fixation probability for a species-1 mitochondrial allele, ϕ_M , is equal to the number of M_1 alleles transmitted by hybrid females of the second generation relative to the number of M_2 alleles in females of species 2 (Fig. 1). This probability is:

$$\phi_M = \frac{n_f}{N_f} \cdot v_{1f} b_{1f} v_{2f} b_{2f} \quad \text{eqn 1}$$

By a similar approach, the fixation probability for a nuclear gene of species 1, ϕ_A , is found to be equal to the number of copies of A_1 transmitted by male and female second-generation hybrids relative to the total number of copies of A_2 in species 2. This gives:

$$\phi_A = \frac{1}{2} \cdot \frac{n_f + n_m}{2N_f + 2N_m} \cdot (v_{1f} b_{1f} + v_{1m} b_{1m})(v_{2f} b_{2f} + v_{2m} b_{2m}) \quad \text{eqn 2}$$

The relative likelihood of these two events is given by their ratio:

$$R = \frac{\phi_M}{\phi_A} = \frac{2n_f}{n_f + n_m} \cdot \frac{2N_f + 2N_m}{N_f} \cdot \frac{v_{1f} b_{1f} v_{2f} b_{2f}}{(v_{1f} b_{1f} + v_{1m} b_{1m})(v_{2f} b_{2f} + v_{2m} b_{2m})} \quad \text{eqn 3}$$

If there are no asymmetries between the sexes for fitness or mating behaviour in either generation ($v_{if} = v_{im}$

and $b_{if} = b_{im}$) and if there is no sex ratio bias in the hybridizing migrant pool ($n_f = n_m$) or in species 2 ($N_f = N_m$), equation (3) shows, as expected, that mitochondrial and nuclear genes have equal probabilities of introgressing. In the absence of any of these symmetries, biases arise. For example, if the hybridizing migrant pool contains an excess of males ($n_f < n_m$), there will be a bias for nuclear introgression (Fig. 3). If Haldane’s rule is in effect for a species pair, then the model predicts a mitochondrial bias for XY species (because $v_{1f} > v_{1m}$) and a nuclear bias for ZW species (because $v_{1f} < v_{1m}$) (Fig. 4). Finally, if female hybrids are more likely to backcross to species 2 than hybrid males are ($b_{if} > b_{im}$), a mitochondrial bias is recovered (Fig. 5). These predictions for diploids are consistent with predictions from previous hypotheses that cite sex-specific behaviour and fitness as causes of biased introgression (Avice 2004; Chan & Levin 2005; Toews & Brelsford 2012).

Haplodiploid species

Because haploid males inherit only a maternally derived genome, the first brood of male offspring born to the hybridizing migrant females will have a parental—not hybrid—genotype. Regarding terminology, when we refer to a ‘first-generation hybrid’, we mean an individual whose genotype is 50% species-1 and 50% species-2 alleles, with respect to nuclear genes; the genotype of a ‘second-generation hybrid’ is 25% species-1 and 75% species-2 alleles, with respect to nuclear genes. Confusion may arise because, for instance, some second-generation hybrid males do not appear until five

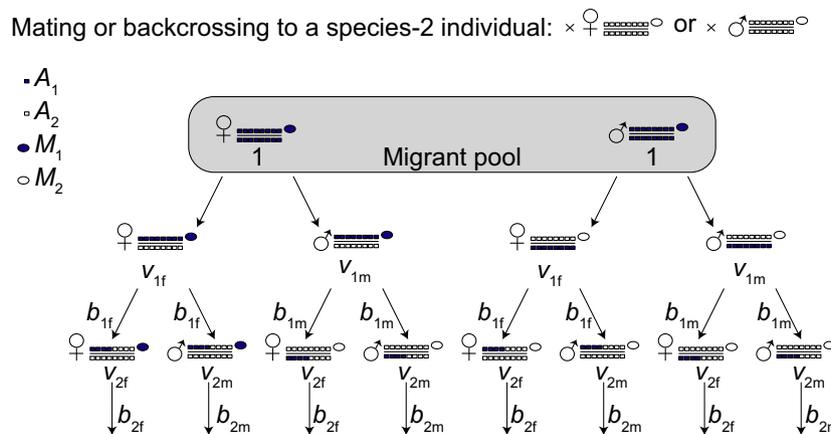


Fig. 1 A schematic diagram of inheritance and selection for diploid hybridization. A single autosome and mitochondrion are depicted for migrants and the hybrid offspring they produce. Each migrant and hybrid individual shown has been crossed to an individual with a pure species-2 genotype. The probability of these backcrosses is given by the b_{ix} for the hybrids. Species 1 has blue alleles and species 2 has white alleles at both nuclear and mitochondrial loci. The viability of each hybrid individual, v_{ix} , is depicted below its genotype with subscripts denoting the generation postmigration (i) and the sex of bearer (x). The number of species-1 alleles can be collected after these two generations, and the total will determine the probability of fixation in species 2 (equations 1 and 2).

Mating or backcrossing to a species-2 individual: $\times \text{♀} \text{---} \text{♂}$ or $\times \text{♂} \text{---} \text{♀}$

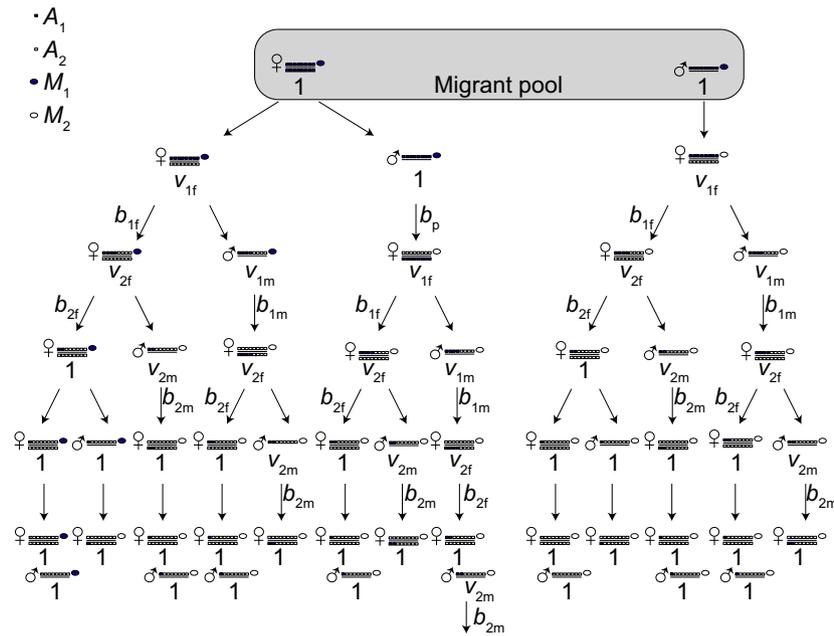


Fig. 2 A schematic diagram of inheritance and selection for haplodiploid hybridization. Inheritance is different in haplodiploids relative to the diploid case (Fig. 1), and first- and second-generation hybrids continue to appear through five generations. As before, species 1 has blue alleles and species 2 has white alleles at both nuclear and mitochondrial loci. Each migrant and hybrid individual shown has been crossed to an individual with a pure species-2 genotype. The probability of these backcrosses is given by the b_{ix} for the hybrids. The viability of each hybrid individual, v_{ix} , is depicted below its genotype. Males develop from unfertilized eggs and transmit their entire genome to daughters. Because of haplodiploid transmission genetics, it takes five generations before all males have $\geq 75\%$ species-2 genomes. At the end of these five generations, the number of species-1 alleles can be counted, and the total will determine the probability of fixation in species 2 (equations 4 and 5).

temporal generations after an interspecies mating (Fig. 2). To give all hybrids the chance to experience selection, we do not calculate the number of species-1 alleles in the range of species 2 until after this fifth generation posthybridization (Fig. 2).

As before, we let hybrid males and females have a probability of backcrossing, b_{ix} , to species 2, but we include a special parameter, b_p , for those parental-genotype males born to migrant females. Their probability of backcrossing to species 2 (i.e. hybridizing) is presumably quite low, as hybridization is assumed to be rare, but, as is the case for b_{ix} , the geography of the hybrid zone is also a factor.

The probability, ϕ_M , that M_1 fixes in species 2 by drift is equal to the number of M_1 alleles transmitted by hybrid females of the fifth generation relative to the number of M_2 alleles in species-2 females:

$$\phi_M = \frac{n_f}{N_f} \cdot v_{1f} b_{1f} v_{2f} b_{2f} \quad \text{eqn 4}$$

For a nuclear autosomal gene of species 1, the probability of introgression, ϕ_A , is simply the expected number of copies of A_1 transmitted by hybrids of the fifth

generation relative to the number of copies of A_2 in species 2:

$$\phi_A = \frac{1}{4} \cdot \frac{n_f + n_f b_p + n_m}{2N_f + N_m} \cdot (v_{1f} v_{2f}) \cdot (b_{1f} b_{2f} + v_{1m} b_{1m} b_{2f} + b_{1f} v_{2m} b_{2m} + v_{1m} b_{1m} v_{2m} b_{2m}) \quad \text{eqn 5}$$

The ratio of the probabilities in (4) and (5) simplifies to

$$R = \frac{\phi_M}{\phi_A} = \frac{4n_f}{n_f + n_f b_p + n_m} \cdot \frac{2N_f + N_m}{N_f} \cdot \frac{b_{1f} b_{2f}}{b_{1f} b_{2f} + v_{1m} b_{1m} b_{2f} + b_{1f} v_{2m} b_{2m} + v_{1m} b_{1m} v_{2m} b_{2m}} \quad \text{eqn 6}$$

This ratio will be shown to lack several of the built-in symmetries found in equation (3). If we start by assuming no asymmetries between the sexes for hybrid fitness or backcross probabilities in any given generation ($v_{if} = v_{im}$ and $b_{if} = b_{im}$) and further assume a 1:1 sex ratio in the hybridizing migrant pool ($n_f = n_m$) and in species 2 ($N_f = N_m$), we still find two possible sources

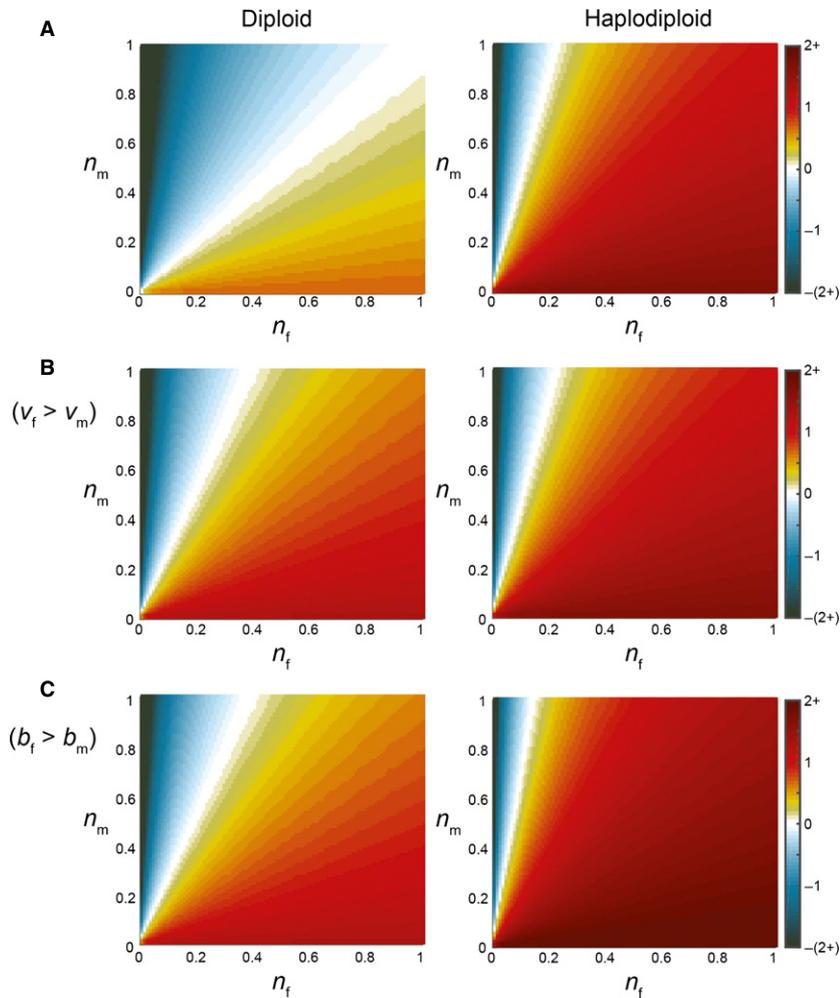


Fig. 3 Impact of sex-biased dispersal on biased introgression under diploidy and haplodiploidy. R , the ratio of mitochondrial to nuclear introgression rates, is shown in colour as a function of female and male migrant numbers (the log of R is depicted). To generate these results, we made the following assumptions: first- and second-generation hybrids have equal fitness and backcross probabilities within a sex ($v_{1\chi} = v_{2\chi} = v_{\chi}$, $b_{1\chi} = b_{2\chi} = b_{\chi}$); sons born to migrant females in the haplodiploid model have zero probability of backcrossing to species 2 ($b_p = 0$). In (A), we equalize fitness and backcross probabilities across the sexes ($v_m = v_f$, $b_m = b_f$). In (B) and (C), we relax one or the other of these symmetries. (A) A fully symmetric parameterization: female and male hybrids have equal fitness ($v_f = v_m = 0.5$); female and male hybrids have equal probabilities of backcrossing to species 2 ($b_f = b_m = 0.5$). An excess of female hybridizing migrants produces a mitochondrial bias in both diploids and haplodiploids. (B) Increased hybrid female fitness (here, $v_f = 1$, $v_m = 0.5$) increases the degree of mitochondrial bias in diploid but not haplodiploid taxa. (C) Mitochondrial bias increases in both diploid and haplodiploid taxa when female hybrids have a higher backcross probability than male hybrids ($b_f = 1$, $b_m = 0.5$).

of a mitochondrial introgression bias. First, if $b_p < 1$, which seems reasonable for most hybrid zones, the ratio R will be >1 (Fig. 6). Second, if male hybrids show any fitness defect (i.e. if $v_{im} < 1$), R will again be >1 (Fig. 4). It would seem therefore that a mitochondrial bias for introgression is assured in haplodiploid species. In fact, there are only two ways for a nuclear bias to be achieved in haplodiploids, both of which occupy a relatively small corner of parameter space: either the hybridizing migrant pool must be heavily enriched for males ($n_f < n_m$) (Fig. 3) or the backcross probability for hybrid females must be considerably less than that of hybrid males ($b_{if} < b_{im}$) (Fig. 5). And when either of these two possibilities is operating, its effect must still be strong enough to counter the opposing bias introduced by having $v_{im} < 1$ (Fig. 4) and $b_p < 1$ (Fig. 6).

Notably absent from the foregoing analysis of equation (6) is any mention of the fitness of hybrid females. This is because the ratio of mitochondrial to nuclear introgression is unaffected by the fitness of hybrid females: female fitness drops out of the equation

entirely. The only exception to this is when $v_{if} = 0$, in which case there is no introgression of any kind. Hybrid female fitness, whether greater or less than hybrid male fitness, has no bearing on the ratio of mitochondrial to nuclear introgression (Fig. 4).

Discussion

Before exploring the implications, it is worth highlighting the main results of the two models above. The diploid model recovers results that are consistent with intuition and with previous explanations for biased introgression. Namely, when an excess of one sex participates in hybridization, a bias ensues: more hybridizing females cause a mitochondrial bias; more hybridizing males cause a nuclear bias (Fig. 3). When Haldane's rule is observed between species pairs, the direction of the bias depends on the sex-determining mechanism (Fig. 4): species with male heterogamety (XY or XO systems) are predicted to show a mitochondrial bias, and species with female heterogamety (ZW)

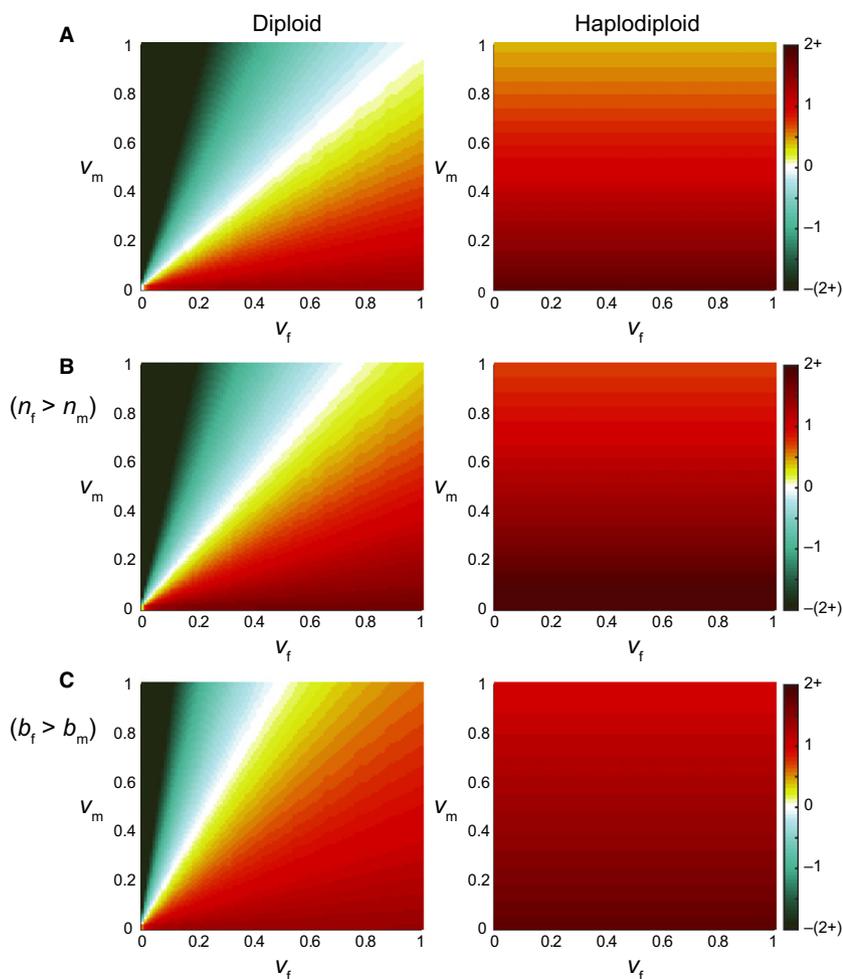


Fig. 4 Impact of sex-biased fitness on biased introgression under diploidy and haplodiploidy. R , the ratio of mitochondrial to nuclear introgression rates, is shown in colour as a function of female and male hybrid fitness (the log of R is depicted). Assumptions are as described in Fig. 3. In (A), we equalize the number of hybridizing migrants and backcross probabilities across the sexes ($n_m = n_f$; $b_m = b_f$). In (B) and (C), we relax one or the other of these symmetries. (A) A fully symmetric parameterization: the number of hybridizing migrants of each sex is equal ($n_f = n_m$); female and male hybrids have equal probabilities of backcrossing to species 2 ($b_f = b_m = 0.5$). Hybrid male fitness defects ($v_f > v_m$) increase mitochondrial bias in both diploids and haplodiploids. Hybrid female fitness defects ($v_f < v_m$) produce nuclear-biased introgression in diploids but not haplodiploids. (B) Mitochondrial introgression bias increases in both diploid and haplodiploid taxa when the hybridizing migrant pool is enriched for females ($n_f = 2 n_m$). (C) Mitochondrial introgression bias increases in both diploid and haplodiploid taxa when female hybrids have a higher backcross probability than male hybrids ($b_f = 1$, $b_m = 0.5$).

are predicted to show a nuclear bias. If hybrid mating behaviour differs between the sexes, this can also introduce biases. For example, if female hybrids are more likely than their male counterparts to backcross to members of species 2—because of the mate preferences of hybrids or species 2 (*sensu* Chan & Levin 2005)—there are predicted to be relatively more opportunities for mitochondrial introgression than nuclear (Fig. 5).

In contrast to the diploid model, the haplodiploid model produces results that were not anticipated. The haplodiploid system ensures that the arrival of male hybrids always lags one generation behind the arrival of female hybrids. This quirk of their transmission genetics has two consequences, both of which encourage mitochondrial-biased introgression. First, although hybridizing migrant females mate with males from another species, their sons will nonetheless possess a pure parental—not a hybrid—genotype. Assuming we have two good species, these sons are presumably unlikely to engage in heterospecific mating, thereby stanching one entire avenue of nuclear gene flow between species after a hybridization event (Figs 2 and 6).

Second, all i th-generation hybrid males have an i th-generation hybrid mother. Thus, for nuclear introgression to keep up with mitochondrial introgression, these sons must be, on average, as fit as their mothers. This is not to say they must be as fit as their mother's class of hybrid—that is, it is not that v_{im} must equal v_{if} . The condition is more restrictive. These males must be as fit as their own mothers, who are the fortunate subset of i th-generation hybrid females that actually survived and reproduced. Thus, unless hybrid male fitness is exactly equal to 1—which, if we are dealing with two good species, seems an unlikely prospect—there will be a bias in favour of mitochondrial introgression. Simply put, if interspecific hybridization is relatively rare and if hybrid males suffer any sort of reduction in fitness, then our model predicts that introgression will be biased towards mitochondria in haplodiploid species pairs. The same cannot be said of diploid species pairs. We consider this to be a uniquely haplodiploid phenomenon, which, to our knowledge, has been overlooked thus far as an explanation for biased introgression in haplodiploid taxa.

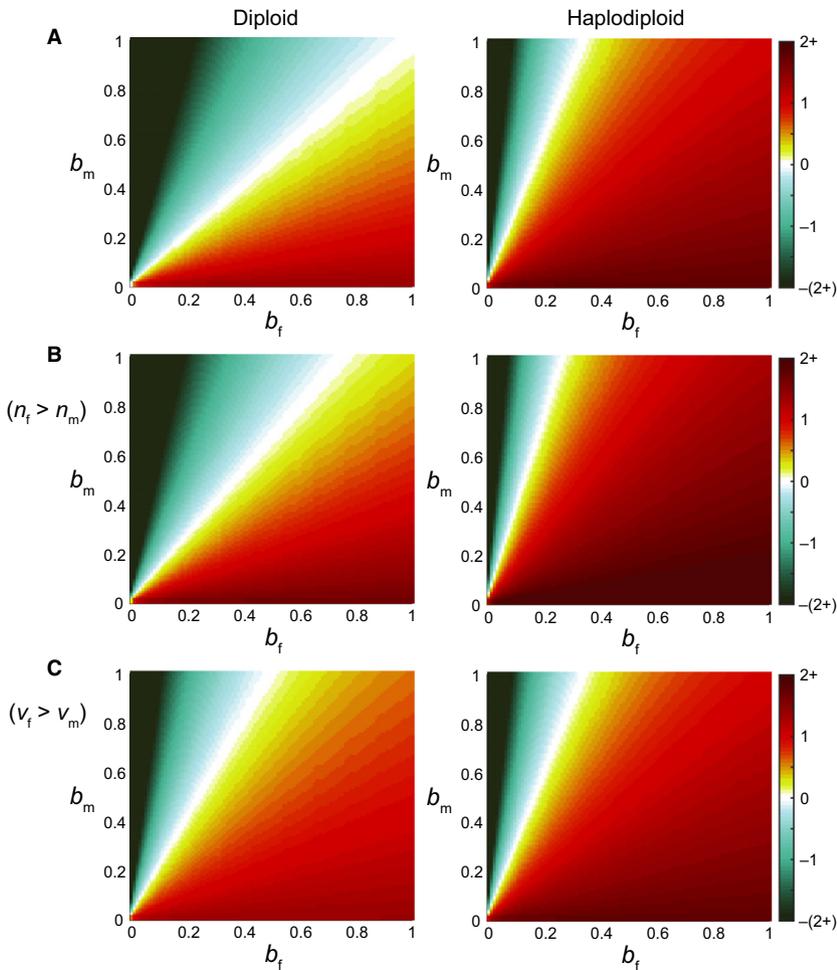


Fig. 5 Impact of sex-biased backcross probabilities on biased introgression under diploidy and haplodiploidy. R , the ratio of mitochondrial to nuclear introgression rates, is shown in colour as a function of female and male hybrid backcross probabilities (the log of R is depicted). Assumptions are as described in Fig. 3. In (A), we equalize the number of hybridizing migrants and fitness across the sexes ($n_m = n_f$; $v_m = v_f$). In (B) and (C), we relax one or the other of these symmetries. (A) A fully symmetric parameterization: the number of hybridizing migrants of each sex is equal ($n_f = n_m$); female and male fitnesses are equal ($v_f = v_m = 0.5$). An increased probability for female hybrid backcrossing causes a mitochondrial bias in both diploids and haplodiploids. (B) Mitochondrial introgression bias increases in both diploid and haplodiploid taxa when the hybridizing migrant pool is enriched for females ($n_f = 2n_m$). (C) Increased hybrid female fitness ($v_f = 1$, $v_m = 0.5$) increases mitochondrial bias in diploid but not haplodiploid taxa.

In contrast, an older explanation in the literature for biased introgression is Haldane's rule (Avice 2004), which contributes to biased introgression by eliminating one sex of hybrid. In fact, this idea is so widely accepted that the observation of biased introgression has been used as indirect evidence for the existence of sex-specific hybrid defects (e.g. Carling & Brumfield 2008). Haplodiploids lack sex chromosomes but should nonetheless be sensitive to the genetic causes thought to underpin Haldane's rule in heterogametic taxa (Wu *et al.* 1996; Koevoets & Beukeboom 2009; Schilthuisen *et al.* 2011). Haplodiploids might be especially vulnerable to hybrid male inviability, owing to the complete hemizygoty of the genome in males (Breeuwer & Werren 1995; Koevoets & Beukeboom 2009). Where XY species have large sex chromosomes, unisexual sterility and inviability have been found at shorter genetic distances (Turelli & Begun 1997), suggesting that the bias for introgression of mitochondria might be proportional to the fraction of the genome that is hemizygous or haploid. Indeed, this motivated our initial comparison of diploids and haplodiploids. The thinking was as

follows: if XY species are somewhat vulnerable to mitochondrial biases, then haplodiploids should be extremely vulnerable owing to their entirely hemizygous males. Although we recovered the expected Haldane's rule result in our model for diploids (by setting $v_{1m} < v_{1f}$ in equation 3), we did not obtain a similar result for haplodiploids. In fact, we found that no matter the relationship between v_{if} and v_{im} —even if $v_{if} < v_{im}$ —we should expect a mitochondrial bias for introgression in haplodiploids. The magnitude of mitochondrial bias will be greater, however, whenever hybrid male fitness is absolutely low, as can be seen by inserting small values of v_{im} in equation (6).

Our finding that mitochondrial bias can occur in haplodiploids even when hybrid males are fitter on average than hybrid females, although at first unexpected, nevertheless has an intuitive explanation: hybrid males cannot form without hybrid females. An equally unexpected result was revealed via simulation of introgression during colonization (Currat *et al.* 2008). Specifically, Currat *et al.* found that introgression into the colonizing species is biased towards markers with low

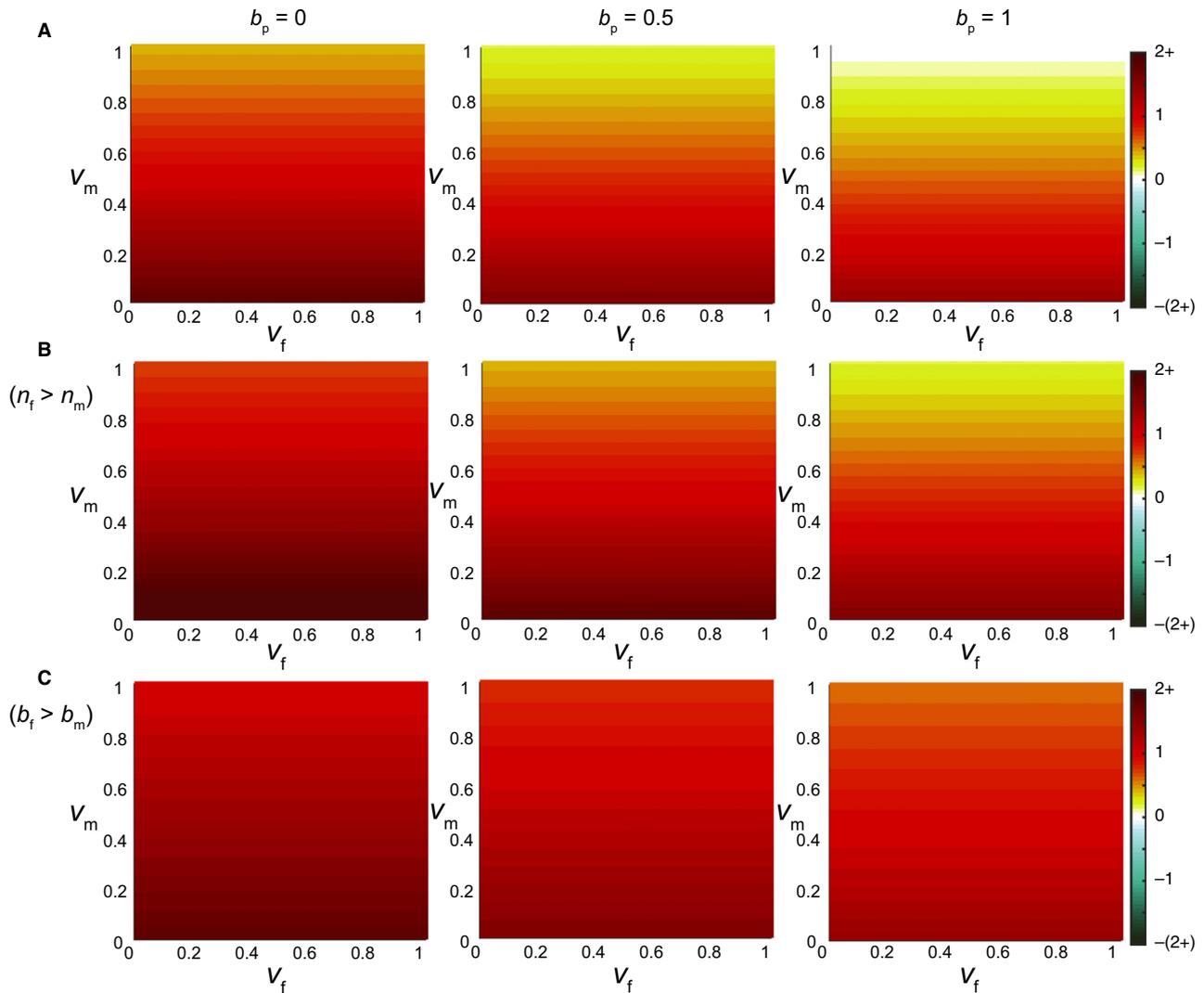


Fig. 6 Impact of parental-genotype male backcross probabilities on biased introgression under haplodiploidy. R , the ratio of mitochondrial to nuclear introgression rates, is sensitive to b_p ; the probability in the haplodiploid system that sons born to migrant females will backcross to species 2. R is shown in colour as a function of female and male hybrid fitness (the log of R is depicted) for three values of b_p . Assumptions are as described in Fig. 3. In (A), we equalize the number of hybridizing migrants and backcross probabilities across the sexes ($n_m = n_f$; $b_m = b_f$). In (B) and (C), we relax one or the other of these symmetries. (A) A fully symmetric parameterization: the number of hybridizing migrants of each sex is equal ($n_f = n_m$); female and male hybrids have equal probabilities of backcrossing to species 2 ($b_f = b_m = 0.5$). Increased values of b_p decrease the mitochondrial introgression bias, but there is a bias in favour of mitochondria for all $b_p < 1$. (B) Mitochondrial introgression bias increases when the hybridizing migrant pool is enriched for females ($n_f = 2 n_m$). (C) Mitochondrial introgression bias increases when female hybrids have a higher probability of backcrossing than male hybrids ($b_f = 1$, $b_m = 0.5$).

dispersal rates in the colonizing species. They explained that, for low-dispersing markers, introgression from the resident to the colonizing species is less likely to be swamped by gene flow among populations of the colonizing species. Their result is seemingly at odds with our finding that introgression is biased in the direction of the sex with *increased* dispersal (greater n_χ). The most salient difference between the two models—and probably the source of this apparent contradiction—is that they assume rather different demographic scenarios.

Whereas Currat *et al.* (2008) simulated a range expansion with gene flow in the colonizing species, our model depicts rare hybridization followed by introgression into the resident species, thus disregarding the colonizing species' gene pool. Our model is more in line with the Hubbs effect (Hubbs 1955), which posits that hybridization occurs most often when one of the species is greatly outnumbered by the other, which is captured in our model by assuming $n_f + n_m \ll N_f + N_m$. That theoretical models can yield unexpected insights highlights

their utility for understanding introgression bias. And their seemingly incompatible results only emphasize the need for further theoretical development and empirical testing.

In terms of theoretical work, the framework we produce here could be extended to a number of other interesting areas. One could explore sex-linked markers in diploids, the possibility of weak selection against the markers or linked loci, the possibility of hybrids mating with one another and a wider range of demographic scenarios (e.g. population structure in the migrant and/or recipient species). From an empirical perspective, there are now several non-mutually-exclusive explanations for observed patterns of biased introgression (Rieseberg *et al.* 1996; Avise 2004; Chan & Levin 2005; Petit & Excoffier 2009), and some of the hypothesized mechanisms provide discriminating predictions. For example, while both the Haldane's rule mechanism and Chan & Levin's prezygotic (2005) mechanism rely on an under-representation of one sex or the other, the former deals with deficits of one sex of hybrids in a pattern predicted by genetic sex determination; the latter deals with deficits of one sex from the hybridizing migrant pool with no predicted difference between genetic systems with different sex determination patterns. Currat *et al.*'s invasion scenario (2008) predicts that if a group shows male-biased dispersal, mitochondria are more likely to introgress. Consistent with this idea, taxa in which male-biased dispersal has been demonstrated or inferred show mitochondrial-biased introgression and taxa where female-biased dispersal has been demonstrated or inferred show nuclear-biased introgression (but see Toews & Brelsford 2012). However, most of the examples Petit & Excoffier present (2009; their Table 1) show higher dispersal of the heterogametic sex, such that only a few instances offer a discriminating test between sex-biased dispersal and Haldane's rule as general explanations of biased introgression. Therefore, it might not be possible to decide whether Haldane's rule or sex-biased dispersal is a more general explanation of these observed patterns. Moreover, seeking general explanations might not reward the effort, as the genetics of speciation and the demography of hybrid zones are likely to differ from one species pair to the next.

However, our model provides a rebuttal to such pessimism: owing simply to their transmission genetics, haplodiploid taxa are poised for a considerable bias in favour of mitochondrial introgression under almost any hybrid fitness or demographic scenario (right panel of Figs 3–5). For example, Haldane's rule can be upheld ($v_{1f} > v_{1m}$) or violated ($v_{1f} < v_{1m}$), and hybridizing migrant males may even outnumber females to some degree ($n_f < n_m$), but a mitochondrial bias for introgression

ensues nonetheless. Consistent with this prediction, Linnen & Farrell (2007) documented extensive mitochondrial introgression across an entire clade of pine-feeding sawflies (Hymenoptera: Diprionidae). Moreover, using coalescent-based isolation-with-migration models, they demonstrated that mitochondrial gene flow rates were consistently higher than nuclear gene flow rates across 120 pairwise species comparisons. While Linnen & Farrell (2007) suggested that this bias may be due to features of sawfly biology that are conducive to Chan & Levin's (2005) prezygotic mechanism, our model indicates that this bias would occur even in the absence of such features. To date, too few haplodiploid taxa have been evaluated for introgression bias to draw strong conclusions regarding the prevalence of mitochondrial introgression under this sex-determination mechanism. Taxa harbouring variation in sex-determining mechanisms, such as scale insects (Normark 2003; Ross *et al.* 2010), would be especially informative with respect to the contribution of transmission genetics to introgression patterns. Should the impact of transmission genetics be as strong as our models predict, one practical implication would be that mitochondrial DNA barcodes, which are widely employed in Hymenoptera (Smith *et al.* 2008; Jansen *et al.* 2009; Fernández-Flores *et al.* 2013; Ueda *et al.* 2015), may be especially prone to misidentifications in hybridizing haplodiploid taxa (e.g. Nicholls *et al.* 2012).

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Data accessibility

There are no data associated with this study.