

Assortative Mating in an Ecological Context: Effects of Mate Choice Errors and Relative Species Abundance on the Frequency and Asymmetry of Hybridization

Anna Qvarnström,^{1,*}† Thor Veen,^{2,*} Arild Husby,³ Murielle Ålund,¹ and Franz J. Weissing⁴

1. Animal Ecology, Department of Ecology and Evolution, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, 752 36 Uppsala, Sweden; 2. Life Sciences, Quest University Canada, Squamish, British Columbia V8B 0N8, Canada; 3. Evolutionary Biology, Department of Ecology and Evolution, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, 752 36 Uppsala, Sweden; 4. Groningen Institute for Evolutionary Life Sciences, University of Groningen, Nijenborgh 7, 9747 AG Groningen, The Netherlands

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ABSTRACT: The frequency and asymmetry of mixed-species mating set the initial stage for the ecological and evolutionary implications of hybridization. How such patterns of mixed-species mating, in turn, are influenced by the combination of mate choice errors and relative species abundance remains largely unknown. We develop a mathematical model that generates predictions for how relative species abundances and mate choice errors affect hybridization patterns. When mate choice errors are small (<5%), the highest frequency of hybridization occurs when one of the hybridizing species is at low abundance, but when mate choice errors are high (>5%), the highest hybridization frequency occurs when species occur in equal proportions. Furthermore, females of the less abundant species are over-represented in mixed-species matings. We compare our theoretical predictions with empirical data on naturally hybridizing *Ficedula* flycatchers and find that hybridization is highest when the two species occur in equal abundance, implying rather high mate choice errors. We discuss ecological and evolutionary implications of our findings and encourage future work on hybrid zone dynamics that take demographic aspects, such as relative species abundance, into account.

Keywords: mate choice model, unidirectional hybridization, prezygotic isolation, speciation, sexual isolation, discrimination ability.

Introduction

Hybridization is defined as the production of offspring through mating between individuals belonging to genet-

ically distinct populations, subspecies, or species (Barton and Hewitt 1981; Mallet 2007; Abbott et al. 2013). Few processes in nature have such diverse ecological and evolutionary implications as hybridization. Incomplete reproductive isolation between genetically diverged populations can contribute to extinctions of unique evolutionary lineages (Rhymer and Simberloff 1996; Allendorf et al. 2001) or lead to the completion of the speciation process through reinforcement of premating isolation (Liou and Price 1994; Servedio and Noor 2003). Hybridization may also provide a source for novel genetic combinations on which selection can operate and potentially generate novel species (Seehausen 2004; Gross and Rieseberg 2005; Mallet 2007; McFarlane and Pemberton 2019). Since these consequences range all the way from having negative to positive effects on biodiversity, predicting hybrid zone dynamics is a long-standing key scientific question.

Together with the level of genetic divergence between the two hybridizing populations and hybrid fitness, the frequency and asymmetry of mixed-species matings largely set the stage for the various consequences of hybridization. The frequency of hybridization, in turn, depends both on the encounter rate between heterospecific individuals and on the likelihood to accept a heterospecific individual as mate when encountered. The evolution of mate choice aspects that reduce the likelihood of accepting heterospecific individuals as mates (i.e., behavioral isolation) have received considerable theoretical and empirical attention and is considered to be an important component of speciation processes (Liou and Price 1994; Servedio and Noor 2003). In areas of co-occurrence of genetically distinct

* These authors contributed equally to this work.

† Corresponding author; email: anna.qvarnstrom@ebc.uu.se.

ORCID: Qvarnström, <https://orcid.org/0000-0002-1178-4053>; Veen, <https://orcid.org/0000-0002-7862-8944>; Husby, <https://orcid.org/0000-0003-1911-8351>; Ålund, <https://orcid.org/0000-0003-2861-9721>; Weissing, <https://orcid.org/0000-0003-3281-663X>.

populations, behavioral isolation depends either on divergence in both mating signal and preferences for those signals or on matching rules, such as sexual imprinting, that result in a learned mate preference function that favors conspecific mating signals (e.g., Kopp et al. 2018). Mate choice is a cognitive phenotype that depends on the underlying (inherited or learned) preference functions that are expressed or realized in response to mating signals or other features of potential mates (Kilmer et al. 2017). Because of assessment errors, mate choice is not flawless with respect to the preference function, meaning that population divergence in mating signals and in mate preferences need not necessarily ensure perfect assortative mating. Mate choice also depends on the sampling behavior that enables assessment of several potential mates (Jennions and Petrie 1997). Nevertheless, it remains largely unknown how mate choice assessment errors interact with encounter rates between heterospecifics in determining the frequency of hybridization.

Sources of premating isolation that rely on reduced encounter rates between heterospecific individuals—such as divergence in timing of breeding (causing temporal isolation) or divergence in habitat use (causing habitat isolation)—are well recognized in the scientific literature (Alexander and Bigelow 1960; Rice 1987; Coyne and Orr 2004). As populations diverge in timing of breeding or in habitat use, we generally assume a corresponding decline in hybridization as encounters between heterospecific individuals become uncommon. At the same time, it is typically assumed that hybridization should be most common when one of the two hybridizing species is much less abundant (Hubbs 1955; Mayr 1963; Randler 2002), an idea often referred to as the desperation hypothesis. Intuitively, an individual belonging to the less abundant species has a higher probability to end up with a partner of the other species, as there are fewer (or, in the extreme, no) potential partners of their own kind. However, even if individuals have the highest tendency to mate with heterospecifics when conspecifics' abundance is lowest, this does not imply that hybridization on the population level reaches its highest frequencies when one of the species is rare. Since the rare species contributes much less to the total number of matings than the abundant species, its impact on overall hybridization rate is limited. Additionally, the rate of encounters between heterospecific individuals—and hence the opportunity for the formation of mixed-species pairs—is highest when both species are of similar abundance. The outcome of such a scenario illuminates a possible interaction between relative species abundance and mate choice errors. One of our main aims is quantifying how individual-level mate choice decisions affect population-level mating patterns, such as the rate of hybridization.

Asymmetries between the two types of mixed-species matings can affect the evolutionary implications of hy-

bridization in yet another way. Consider a scenario where females of species A frequently mate with males of species B while females of species B rarely mate with males of species A. Females of species A and males of species B are thus most exposed to the costs of hybridization, and if female choice predominates, this would select for increased discrimination ability and choosiness in females of species A, which in turn may modify sexual selection acting on males of species A. The most likely outcome is an observed sexual character displacement of males belonging to species A. An evolutionary change of the display traits of males of species B is expected only if male mating with a heterospecific female results in a reduction of other mating opportunities (i.e., a realized fitness cost for the male) and if a potentially modified display trait would not reduce the attraction of conspecific mates. Low abundance of one of the species has been proposed to explain the often asymmetric mixed-species pair formation in natural hybrid zones (Wirtz 1999; Randler 2002). The reasoning behind this argument is that mixed-species pairs should mostly involve the choosier sex of the less abundant species and the opposite sex of the common species. However, this verbal argument has, to our knowledge, never been formally modeled. It remains unexplored how encountering likelihood and mate choice errors interact in determining asymmetry in the formation of mixed-species pairs.

We present a theoretical mate choice model, based on a scenario with female mate choice, to study how (1) the probability of an individual female to hybridize depends on the relative abundance of conspecific partners and the propensity to make mate choice errors and (2) how this determines asymmetry in the formation of mixed-species pairs and hybridization frequency. We then compare these theoretical insights to an empirical example using two long-term studies of hybridizing passerine bird species, the collared flycatcher (*Ficedula albicollis*) and pied flycatcher (*Ficedula hypoleuca*). As our study populations differ in relative species abundance between areas, this provides an ideal opportunity to test the impact of relative species abundance on hybridization. All code and data necessary to reproduce theoretical and empirical results have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.qnk98sfhd>; Qvarnström et al. 2022).

Theoretical Considerations

A Hybridization Model

Hybrid zones are geographical areas where the distribution ranges of two interbreeding but genetically diverged populations or species co-occur (Barton and Hewitt 1981; Mallet 2007; Abbott et al. 2013). In our model, we assume that divergence in mating signals has occurred and that there are

mate preferences (either inherited or learned) for conspecific mating signals, but we make no assumptions about potential benefits or costs associated with hybridization. We consider a large well-mixed population with female mate choice, in which species A and B coexist in relative abundances $p_A = n_A/(n_A + n_B)$ and $p_B = n_B/(n_A + n_B) = 1 - p_A$. Mate choice is modeled as a sequential process during which each female gets to accept or reject a randomly drawn male, up to a maximum number of sampled males (i.e., n draws). If the female rejects all n males, she subsequently mates with the next male she encounters, regardless of its species identity. Such sequential mate choice with a time limit is a reasonable assumption for species with resource-based mating systems, such as hole-nesting songbirds. Mate choice is not flawless with respect to the preference function since females can make mate assessment errors. From a species assortative perspective, a female can make two wrong choices: reject a conspecific male or accept a heterospecific male. These two errors occur with probability α_i and β_i , respectively, where i stands for either species A or species B (see table 1 for a list of parameters and their definitions). These errors are similar to type I and type II errors in statistical hypothesis testing. For females of species i , the probabilities of mating with a conspecific male (x_i) and of mating with a heterospecific male (y_i) in a single mate choice event are given by

$$\begin{aligned} x_i &= p_i(1 - \alpha_i), \\ y_i &= (1 - p_i)\beta_i. \end{aligned}$$

The probability of remaining unmated (u_i) after n rounds is given by

$$u_i = (1 - x_i - y_i)^n.$$

If a female accepts a male within the first n rounds (probability $1 - u_i$), the probability that she mates with a con-

specific male is $x_i/(x_i + y_i)$. Otherwise, with probability u_i , she will accept the next male she encounters, which will be a conspecific with probability p_i . Combining these two options gives the probability that a female of species i mates with a conspecific (c_i) after n rounds as

$$c_i = (1 - u_i) \frac{x_i}{x_i + y_i} + u_i p_i.$$

The probability that a female belonging to species i mates with a heterospecific male (h_i) is given by $h_i = 1 - c_i$.

Below we evaluate how various degrees of mate choice error and relative species abundances influence hybridization patterns at different levels: (1) an individual female's probability to hybridize, (2) the population-level frequency of hybridization depending on the mate choices made by females belong to a focal species i , and (3) the overall frequency of hybridization at the hybrid zone depending on mate choices made by females of both species. Finally, we evaluate how mate choice error and relative species abundance affects the asymmetry in the formation of mixed-species pairs (i.e., to what extent females of one species are overrepresented among the mixed-species pairs).

Individual-Level Probability of Hybridization

We first use our model to evaluate how mate choice error and relative species abundance influence the probability that an individual female hybridizes. As shown in the supplement PDF, the probability h_i that a female of species i hybridizes with a male of the other species is positively related to the propensity β_i to (wrongly) accept a heterospecific male. Moreover, h_i is negatively related to p_i , the relative abundance of species i . Figure 1 illustrates that both effects are nonlinear. Moreover, the individual hybridization probability is more strongly affected by the relative species abundance p_i than by the error rate β_i . These results are in line with the desperation scenario, a reasoning from the perspective of an individual's mate choice.

Population-Level Hybridization Frequency Driven by Mating Decisions Made by Females of Species i

Next we use the model to evaluate how relative species abundance and mate choice error of females belonging to species i influence the population-level hybridization frequency observed at a hybrid zone. We find that c_i and h_i , which are the individual-level mating probabilities, do not accurately reflect the mating frequencies at the population level, as they do not include the frequency of occurrence of a specific mating event. For example, when conspecifics are rare, a female of species i is likely to end up with a heterospecific male (high individual-level hybridization

Table 1: Model parameters and definitions

Parameter	Definition
n_i	Abundance of species i ($i = A, B$)
p_i	Relative abundance of species i ($p_A + p_B = 1$)
α_i	Type I error probability: probability of rejecting a conspecific male when encountering one
β_i	Type II error probability: probability of accepting a heterospecific male when encountering one
c_i	Probability that female of species i mates with a conspecific male
h_i	Probability that female of species i mates with a heterospecific male ($h_i = 1 - c_i$)
C_i	Relative frequency of conspecific matings involving females of species i ($C_i = p_i c_i$)
H_i	Relative frequency of heterospecific matings involving females of species i ($H_i = p_i h_i$)
R_i	Fraction of heterospecific matings involving a female of species i ($R_i = H_i / (H_A + H_B)$)

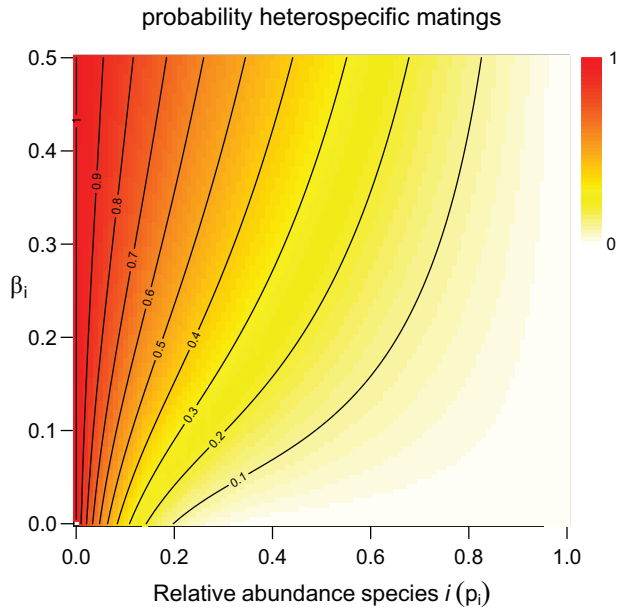


Figure 1: Probability of mating with a heterospecific male from an individual female's perspective. The figure shows the probability h_i that a female of species i mates with a heterospecific male in relation to the relative abundance of species i (p_i) and the error probability β_i . Other parameters: $\alpha_i = 0.05$, $n = 10$.

probability), but the total number of females of species i —and hence occurrence of mixed-species pairings—is low. To obtain the relative frequency of the different types of mating in the population, the individual-level probabilities c_i and h_i have to be multiplied with the relative abundance p_i of species i . The relative frequency of conspecific and heterospecific matings involving a female of species i will be denoted by $C_i = p_i c_i$ and $H_i = p_i h_i$, respectively. Accordingly, $H_{\text{total}} = H_A + H_B$ denotes the relative frequency of heterospecific matings among all matings (the hybridization frequency). The fraction of all heterospecific matings involving a female of species i will be denoted by $R_i = H_i/H_{\text{total}}$.

As a concrete example, consider a situation where there are three times as many females of species B than of species A ($p_A = 0.25$), and the per-female hybridization rates are 20% per mating for a female of species A ($h_A = 0.2$) and 10% for a female of species B ($h_B = 0.1$). Then $H_A = p_A h_A = 0.05$, $H_B = p_B h_B = 0.075$, $H_{\text{total}} = H_A + H_B = 0.125$, and $R_A = H_A/H_{\text{total}} = 0.4$. In words, 5% of all matings are hybridization events involving a female of species A, 7.5% are hybridization events involving a female of species B, 12.5% of all matings are hybridization events, and 40% of these hybridization events involve a female of species A.

The relative frequencies of conspecific and heterospecific matings involving females belonging to the focal species i depend on the species abundances and the assessment error β_i resulting in a heterospecific mating (fig. 2). In line with intuitive expectation, the relative frequency of heterospecific matings involving females of species i (h_i) increases with the assessment error β_i , while the relative frequency of conspecific matings (c_i) decreases with β_i . Furthermore, the relative frequency of conspecific matings involving females of species i increases with the relative abundance p_i of this species (fig. 2A). This can also be shown analytically (supplemental PDF). The relationship between the relative frequency of mixed-species matings with p_i is less straightforward. As shown in the supplemental PDF, for each value of the assessment error (β_i), h_i is a unimodal function that is first increasing and later decreasing with p_i . The maximum frequency of mixed-species pairs involving females of species i shifts to larger values of p_i with an increase in the error rate β_i (fig. 2B). Importantly, the population-level frequency of mixed-species pairings becomes very small when relative species abundance (and hence availability of conspecific males) is very low, which is in sharp contrast with the individual-level hybridization probability (h_i ; see fig. 1), which is close to 1 when few conspecific males are available.

Total Frequency of Hybridization Based on Mating Decisions Made by Females of Both Species

We also used our model to evaluate how mate choice errors made by females belonging to both of the co-occurring species together with relative abundance of the two species affected the total frequency of hybridization at a hybrid zone. The magnitude of the error rates α , α_B , β_A , and β_B have only a limited effect on the total frequency of hybridization $H_{\text{total}} = H_A + H_B$. Figure 3 shows that a 20-fold increase of the β_i values in both species just about triples H_{total} . Asymmetries in errors between the two species affect the relative species frequency at which most hybridization occurs but only slightly affect the maximum value of H_{total} (compare fig. 3A, 3C and fig. 3B, 3D). The shape of the function H_{total} is strongly affected by the values of β_i . If β_A and β_B are very small, both H_A and H_B are strongly skewed unimodal functions with a maximum at a low abundance of the corresponding species. As a consequence, $H_{\text{total}} = H_A + H_B$ is a bimodal function with maxima at those frequency abundances, where H_A and H_B are maximized (fig. 3A, 3B). For larger values of β_i , H_{total} is a unimodal function of the relative species abundances, with a maximum value at intermediate abundances (fig. 3C, 3D). As expected, the maximal hybridization frequency increases with the error rates β_i , while it decreases with the number n of males sampled during the mate choice process (fig. S1).

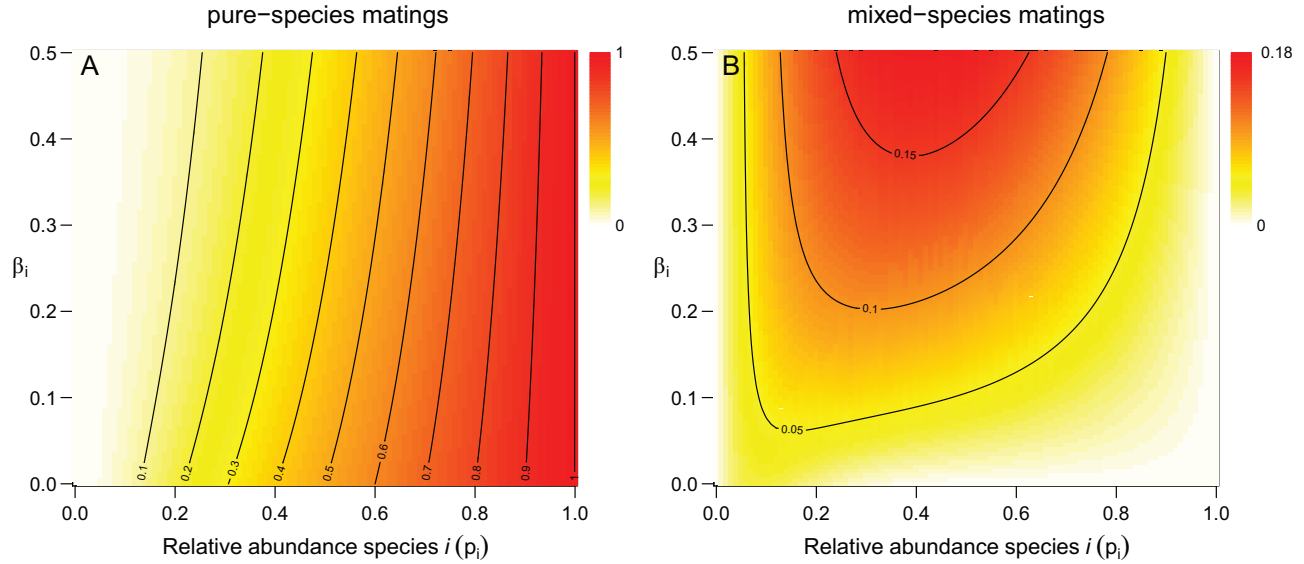


Figure 2: Population-level conspecific and mixed-species matings involving females of focal species i . The figure shows the population-level frequencies of pure species matings C_i (A) and mixed-species matings H_i (B) involving females of species i as a function of species abundance (p_i) and mate choice error (β_i). Other parameters: $\alpha_i = 0.05$, $n = 10$.

Asymmetry of Hybridization

Last, we focus on the relative contribution $R_i = H_i/H_{\text{total}}$ of females of species i to the total frequency of hybridization. Figure S2 shows R_A as a function of relative species abundance p_A for the four scenarios considered in figure 3. The relative contribution of a species to population-level hybridization is strongly asymmetric: R_A is much larger than 50% if p_A is low, and it is much smaller than 50% if p_A is high. The function R_A has a sigmoidal shape for small values of β_i , while it decreases more gradually for large values of β_i . When error rates are symmetric ($\beta_A = \beta_B$), R_A takes on the value 50% at $p_A = 0.5$; if the error rate of species A is higher ($\beta_A > \beta_B$; as in fig. 3B, 3D), R_A is larger than 50% for a broader range of p_A values.

Empirical Hybridization Patterns in *Ficedula* Flycatchers

The Flycatcher Hybrid Zone

Collared and pied flycatchers diverged less than 1 million years ago (Nadachowska-Brzyska et al. 2013) and hybridize regularly (~5%) where they co-occur, despite severely reduced hybrid fertility (Qvarnström et al. 2010, 2016; Saetre and Saether 2010; Cramer et al. 2016). Past experiments indicate that females of both species display strong preferences for conspecific males, while males appear to court females of both species indiscriminately (Dale and Slagsvold 1994; Saetre et al. 1997). The two species are sympatric throughout much of their breeding ranges in

central Europe and on the Baltic islands of Öland and Gotland (Sweden), where the data were collected. This hybrid zone has been subject to long-term studies across woodlots that differ in the relative abundance of the two species, giving us the possibility to quantify the relationship between relative species abundance and hybridization probability and frequencies. Nest boxes used by both species have been installed in many fragmented areas of deciduous forest (hereafter, woodlots), separated from each other by habitat unsuitable for breeding flycatchers (cleared farmland or coniferous plantations). Sites vary in size from 4 to 50 ha (mean = 16.5 ha) and contain 15–357 nest boxes (mean = 98).

Sites were monitored each breeding season (May–June) on Gotland (1980–2007) and Öland (2002–2012), and the species composition of all nest box breeding pairs was recorded. Species identification was based on morphology and vocalizations. All intermediate-looking males and infertile females (potential hybrids) were removed from our analyses. On both Öland and Gotland, the pied flycatcher is the less abundant species, but there is large spatial and temporal variation in the relative abundances of the two species across woodlots. We assume that local mate availability (relative abundance of conspecifics in a woodlot) reflects the encounter rate between heterospecific individuals since female flycatchers rarely move between forest sites when sampling mates (Dale and Slagsvold 1996). Relative abundance of the two species at each site was measured as the ratio of the number of breeding pied flycatcher females divided by all breeding pairs in a given year. This

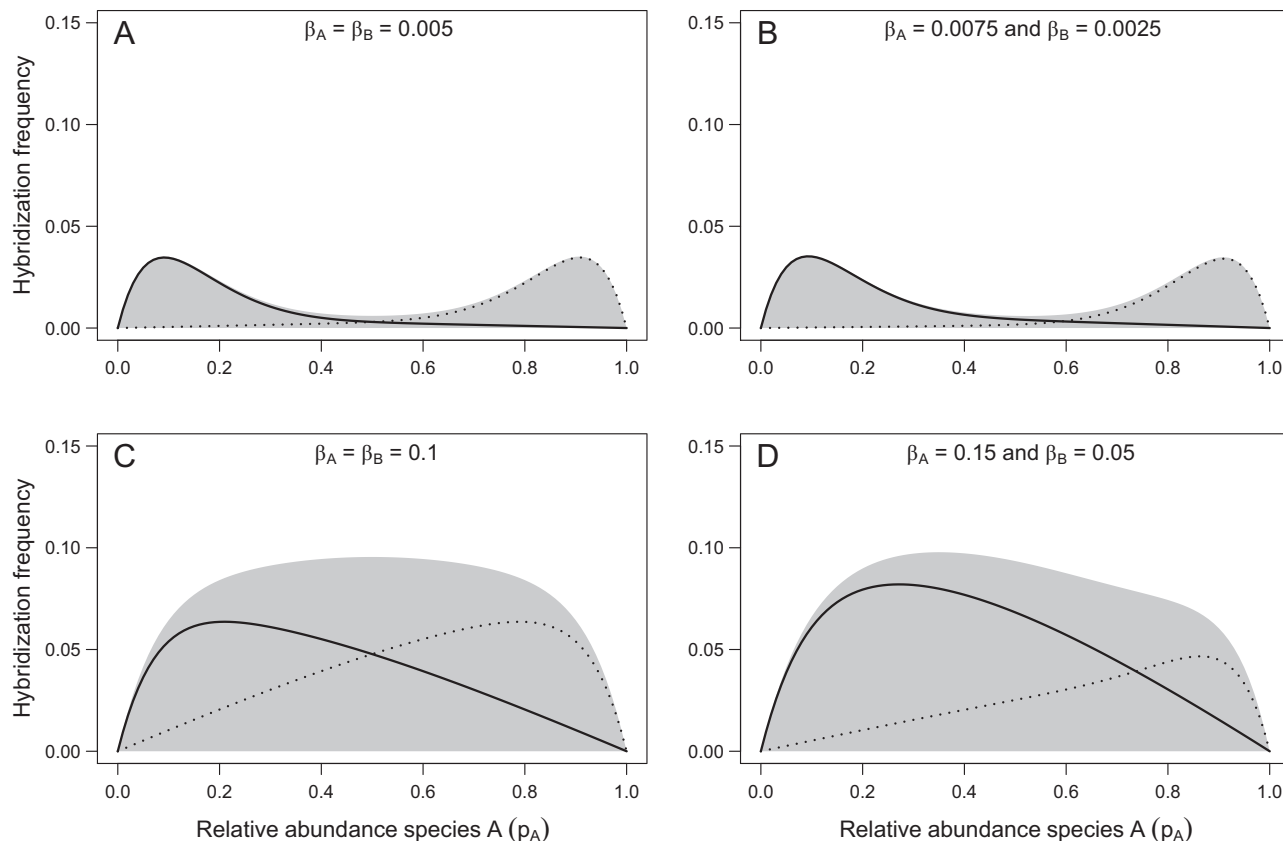


Figure 3: Total hybridization frequency in area of co-occurrence of two species depending on mate choice errors and relative species abundances. The figure shows the population-level frequency of mixed-species matings involving females of species A (H_A ; solid line), mixed-species matings involving females of species B (H_B ; dotted line), and all mixed-species matings (H_{total} ; shaded area) as a function of relative species abundance p_A . A, B, Small mate choice error β_i values ($\beta_i = 0.005$). C, D, Large β_i values ($\beta_i = 0.1$). A, C, Symmetric β_i values ($\beta_A = \beta_B$). B, D, Asymmetric β_i values ($\beta_A \neq \beta_B$). In all cases, $\alpha_A = \alpha_B = 0.05$.

does not include unmated individuals, but data on males caught while displaying at the beginning of the breeding season (two sites on Gotland in 2002, five sites on Öland in 2005) showed a strong correlation between the relative frequency of the two species based on breeding females and based on unpaired males ($r = 0.8$). This suggests that the proportion of breeding birds is a good indicator of relative species abundance. Other estimates of relative abundance (e.g., based on the ratio of collared pairs to pied pairs) were highly correlated with estimates based on females alone ($r = 0.98$, $n = 39$ sites).

Individual-Level Hybridization Probabilities in the Flycatcher Hybrid Zone

We recorded a total of 11,802 pairing events on Öland and Gotland combined, including 10,825 pairings between conspecific collared flycatchers (CF), 624 pairings between conspecific pied flycatchers (PF), and 353 heterospecific pairs

(PF female – CF male = 226, CF female – PF male = 127). To examine the relationship between individual-level hybridization probability and relative species abundance, we fitted a generalized linear mixed model (GLMM) with binomial error structure using the R package lme4 (Bates et al. 2014) and included woodlot as a random effect to account for differences in woodlot size. For each breeding female, we assigned a value of 1 if she mated with a heterospecific and 0 if she mated with a conspecific. The probability of females mating with a heterospecific increases as conspecifics become less abundant (fig. 4). This relationship is significant for both female pied flycatchers ($b = -5.727$, $SE = 0.760$, $z = -7.53$, $P < .0001$; fig. 4A) and female collared flycatchers ($b = 5.720$, $SE = 0.629$, $z = 9.08$, $P < .0001$; fig. 4B). Thus, the probability to mate with a heterospecific is highest for females breeding in sites where their own species is less abundant. This is in qualitative agreement with the results of the theoretical model (fig. 1), although the error rate (β_i) is unknown in this system.

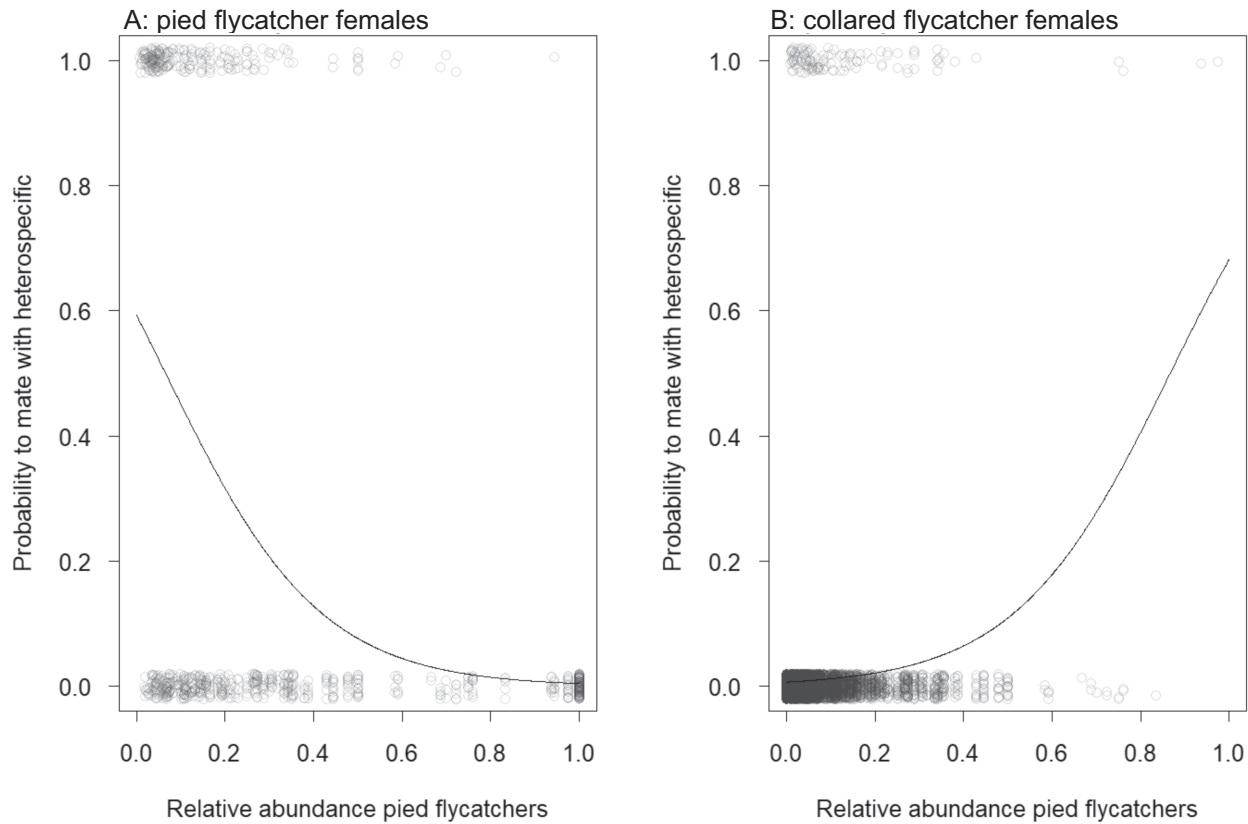


Figure 4: Effect of relative abundance of pied flycatchers on probability to mate with a heterospecific male for pied flycatchers (A) and collared flycatchers (B). Lines show the relationships predicted by GLMMs. Note that random uniform noise (jitter) has been added to the binomial data to facilitate visual inspection of the data.

Frequency of Hybridization

We next examined how population-level hybridization frequency relates to species abundance, first for each species separately and then for both species combined. In each of three analyses, we fitted a GLMM with woodlot included as a random effect and binomial error structure as well as a two-level response variable, including number of heterospecific pairs (involving pied or collared flycatcher females or all mixed species pairings combined) and number of all breeding pairs within each woodlot. Thus, the observed frequencies (proportions) are weighted by the total number of observations in each woodlot. The frequency of heterospecific pairings involving pied flycatcher females mated to collared flycatcher males changed in a nonlinear fashion in relation to the relative abundance of pied flycatchers, with a maximum frequency observed at a relative abundance of about 0.4 (Akaike information criterion [AIC] = 825.13 vs. 897.04 for model with second-order polynomial vs. first-order term; likelihood ratio test: $\chi_1^2 = 73.92$, $P < .0001$; fig. 5A). A similar but weaker nonlinear relationship was found for the frequency of heterospecific

pairings involving collared flycatcher females mated to a pied flycatcher male (AIC = 603.95 vs. 633.01 for model with second-order polynomial vs. first-order term; likelihood ratio test: $\chi_1^2 = 31.05$, $P < .0001$; fig. 5B). The total hybridization rate (involving both types of mixed-species pairings) in relation to the relative frequency of pied flycatchers is also best explained by a second-order polynomial regression (AIC = 1,028.3 vs. 1,134.3 for model with second-order polynomial vs. first-order term; likelihood ratio test: $\chi_1^2 = 108.02$, $P < .0001$) and is largely driven by the patterns observed for heterospecific matings involving pied flycatcher females. The frequency of hybridization is highest when both species occur in roughly equal abundance (fig. 5C). A similar unimodal distribution of the total hybridization rate is predicted by our theoretical model when the mate choice error β is relatively high and the two species do not differ much in their error rate (fig. 3).

Asymmetry of Hybridization

We observed a significant asymmetry in the formation of the two types of heterospecific pairings. Across all years

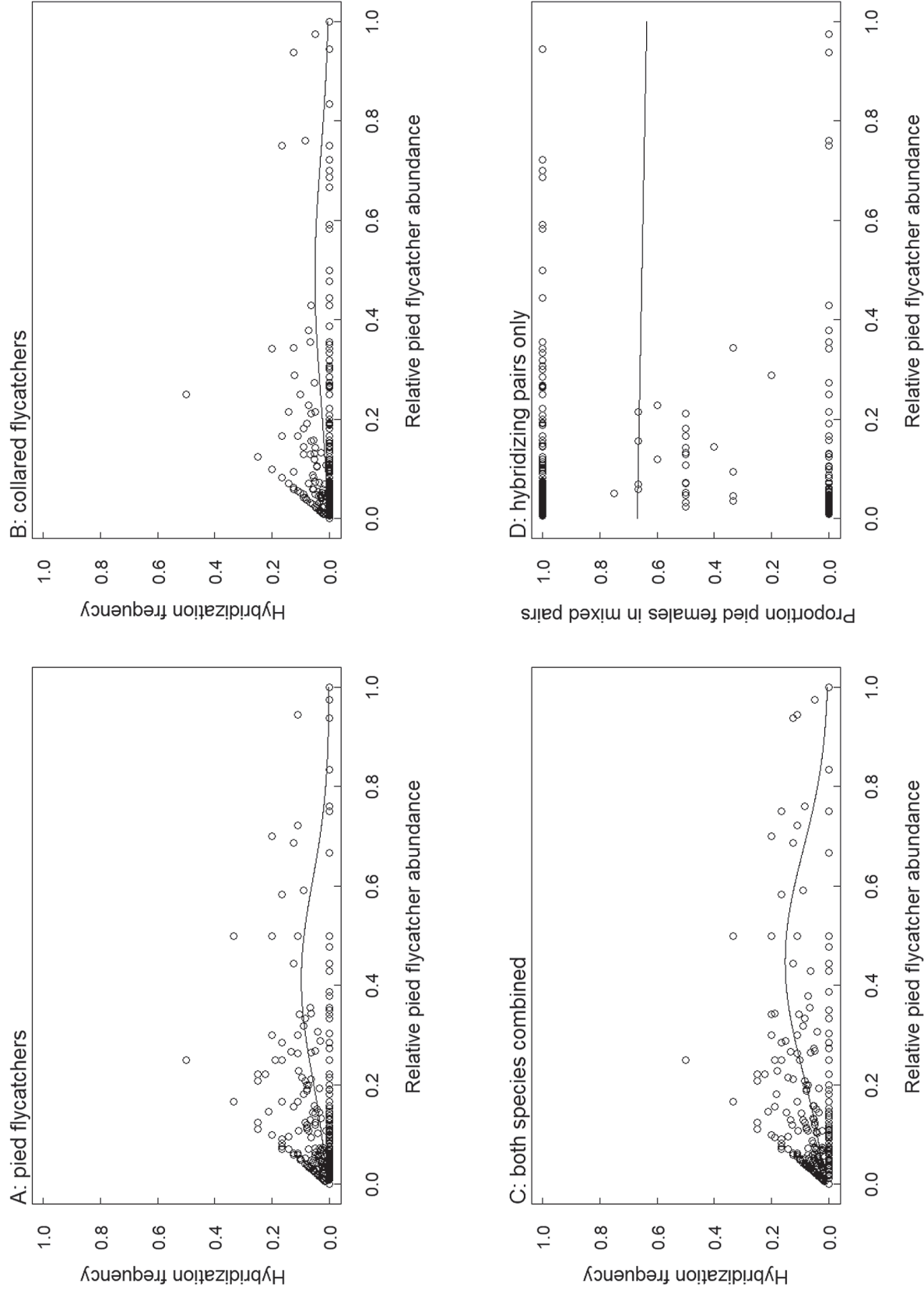


Figure 5: Relationships between relative abundance of pied flycatchers within a woodlot and hybridization frequency involving only pied flycatchers (A), only collared flycatchers (B), and both species (C), that is, total hybridization frequency. There was no significant relationship between the proportion of all heterospecific pairs involving a pied flycatcher female and the relative abundance of pied flycatchers (D). Fitted lines are the back-transformed values as predicted from a GLMM.

and wood lots, 64% of all hybrid pairings involved a female pied flycatcher and a male collared flycatcher (binomial test, $N = 353$, $\chi^2_1 = 54.41$, $P < .0001$). To examine how this asymmetry relates to the relative abundance of pied flycatchers in the population, we fitted a binomial GLMM with the number of heterospecific pairs involving a pied flycatcher female and the total number of heterospecific pairs included as a two-level response variable with relative abundance of pied flycatchers as a fixed effect and woodlot as a random effect. There was no significant relationship between the proportion of all heterospecific pairs involving a pied flycatcher female and the relative abundance of pied flycatchers (AIC = 396.28 vs. 394.84 vs. 394.87 for model with second-order vs. linear term vs. intercept only; likelihood ratio tests: second-order term against first-order term, $\chi^2_1 = 2.564$, $P = .11$; first-order term against model with intercept, $\chi^2_1 = 0.023$, $P = .88$; fig. 5D).

Discussion

Hybridization has important ecological and evolutionary implications, but how hybridization rate is impacted by relative species abundances and mate choice error is largely unknown. We first used a theoretical model to examine how mate choice error and relative species abundance influence hybridization rates and compared these insights with empirical data from a natural hybrid zone. Our theoretical model demonstrates that with relatively low mate choice errors (<5%), the highest frequency of hybridization occurs when one of the hybridizing species is at low abundance, but with relatively high mate choice errors (>5%), hybridization frequency is highest when species occur in equal proportions. The patterns observed at the monitored natural hybrid zone where two species of *Ficedula* flycatchers co-occur are qualitatively similar to the theoretical predictions of the model when mate choice errors are high (>5%). Below we discuss limitations and implications of our findings. Our main conclusion is that although genomic tools facilitate detection of patterns of gene flow at hybrid zones at an increasingly high resolution (Abbott et al. 2013), interpretations are often focused on postzygotic isolation, and the combined effects of mate choice errors and demographic aspects (e.g., relative species abundance) are surprisingly understudied. One important take-home message from our work is that demographic factors could often override mate choice errors in explaining the frequency and asymmetry of hybridization.

Frequency and Asymmetry of Hybridization

The theoretical model evaluates two lines of verbal reasoning about the effects of relative species abundance and mate choice on patterns of hybridization, namely, the des-

peration hypothesis (Hubbs 1955) and the unidirectional hybridization hypothesis (Wirtz 1999), which we will discuss in turn.

The desperation hypothesis assumes that hybridization mainly happens when individuals fail to find mates of their own species (i.e., low abundance of conspecifics) and in desperation pair across species boundaries. Accordingly, our model predicts that the individual probability of heterospecific mating indeed is highest at low species abundance, even when mate choice errors are constant (i.e., in the absence of relaxed discrimination against heterospecifics when conspecifics are rare). However, this does not imply that the population-level hybridization rate is also maximal at the lowest abundance of this species. The population-level hybridization frequency is a unimodal function of species abundance, and the mate choice error rate β determines the skew of this frequency toward the extremes of the relative species abundance range. When mate choice errors are low, the highest frequency of hybridization in either species is associated with a low abundance of conspecifics (fig. 3A). When, however, mate choice errors are higher (>5%), the rate of hybridization is highest when the two species occur at similar abundance (fig. 3D). The empirical results from the natural flycatcher hybrid zone are consistent with this latter situation; the highest frequency of mixed-species pairs is found in areas where neither species occurred in low abundance. Collared flycatchers have almost entirely displaced pied flycatchers from most monitored woodlots on Gotland and from some of the preferred woodlots on Öland through a competitive advantage over nesting sites (Vallin et al. 2012a, 2012b; Qvarnström et al. 2016). The few remaining female pied flycatchers therefore experience high risk of hybridization in such areas, which may speed up extirpation of pied flycatchers (Vallin et al. 2012a). However, we show here that the few hybridizing pairs found in such areas do not contribute much to the overall hybridization frequency. The highest frequency of hybridization is instead found in woodlots close to the edge of the moving hybrid zone on Öland, where the two species occur in fairly equal abundance. In line with these findings, a survey of 40 mixed populations of *Dryopteris* fern also reported maximal hybridization rates at equal abundance of parental species (Hornych et al. 2019).

The unidirectional hybridization hypothesis builds on the same idea as the desperation hypothesis and reasons that patterns of hybridization often are asymmetric because the choosy sex of the less abundant species should be overrepresented in mixed-species pairs (Wirtz 1999). Our theoretical model provides strong support for Wirtz's verbal hypothesis. Even if the two species differ greatly in their discriminatory ability (i.e., in mate choice error), there is still an asymmetry toward females of the less abundant

species rather than toward females with the higher mate choice error (fig. 3). However, this was not observed empirically: the asymmetry toward female pied flycatchers in mixed pairs was not significantly related to this species' relative abundance (fig. 5D). The reason for this is unknown (but see below).

Limitations of the Theoretical Model

Our model is based on a highly stylized view of the mating process, allowing us to draw general conclusions on the basis of a small number of parameters. Obviously, such simplification may lead to inaccurate predictions when the model assumptions are not met. For example, we assumed a sequential mate choice scenario with fixed errors. From sexual selection theory (Kuijper et al. 2012), we know that other mate choice scenarios (e.g., best of n) can strongly affect mating patterns within a species. This may also apply to mate choice patterns between species leading to hybridization. We assumed that the per-encounter error probabilities are the same for all females of the same species and that they are constant in time. However, individual differences in mate choice are often observed (Schuett et al. 2010). In the case of sequential mate choice, it is likely that errors change over time, either becoming smaller (because of experience) or larger (females waiting for a suitable mate becoming less selective with time). Mate choice errors may furthermore depend on the ecological setting and change over time and space (see Schumer et al. 2017). This may be important when pooling data from different areas, with each of them potentially having a different error structure (and, consequently, different functions of H_i). The number of mates sampled may depend on the density of available mates, which may change throughout the season or across habitats. In addition, mate choice errors may depend on species abundance, causing interactions between these two factors in determining patterns of hybridization (see below). Moreover, mate choice in both sexes may cause variation in rates of assortative mating and hybridization over time, as shown by Aubier et al. (2019).

Extensions of the Model

Many of the limitations that we have discussed can be incorporated in future extensions of the model. We focus on one example that we consider particularly relevant on the basis of findings from empirical studies, including previous research on the flycatcher hybrid zone. Studies of *Drosophila* fruit flies (Dukas 2008), *Poecilia* fish (Magurran and Ramnarine 2004), *Mesocricetus* hamsters (delBarco-Trillo and Johnston 2012), and *Calopteryx* damselflies (Svensson et al. 2010) have shown that individuals can reduce their mate choice error after exposure to heterospecifics. Alter-

natively, individuals may increase their error rate when they perceive the chances of finding a conspecific mate as very low (i.e., as predicted by the desperation hypothesis). For example, in naturally hybridizing *Xiphophorus* swordtails, females experiencing delayed encounter of conspecifics increased the time spent with heterospecific males, suggesting an increased mate choice error (Willis et al. 2011). Yet another complicating factor is that males may change the signals they use to attract mates in response to the relative density of heterospecific individuals. Pied flycatchers are known to often copy the song of collared flycatchers (Alatalo et al. 1990; Haavie et al. 2004), a behavior more likely when they experience a high rate of social contact with male collared flycatchers (Svedin et al. 2008), and mixed song dramatically increases the risk of hybridization (Qvarnström et al. 2006). In the flycatcher case, there is hence an indirect link between relative species abundance and mate choice error mediated by a change in male song.

Thus, there are multiple potential sources of direct and indirect interactions between mate choice error and relative species abundance affecting symmetry in the formation of hybridizing pairs. We therefore compared a scenario where mate choice error changes linearly with species abundance with the constant mate choice error in our model (fig. S3A). In comparison to the constant mate choice error (gray line), an error that decreases with relative abundance (blue line) leads to an underrepresentation of species A among mixed-species pairs (fig. S3B). This effect is reverse when mate choice errors increase with the relative abundance of A (red line), which leads to a shallower relationship between R_A and relative abundance. However, even a positive covariance between relative abundance and mate choice error could not explain why the proportion of female pied flycatchers among mixed-species pairs does not change with pied flycatcher abundance (fig. 5). Instead, this pattern could be caused by the mixed singing of pied flycatchers in collared-dominated areas mentioned above, known to increase the likelihood of attracting heterospecific females (Qvarnström et al. 2006). Moreover, competitive asymmetry between males of the two species means that male pied flycatchers are forced to settle in less preferred habitats (Vallin et al. 2012a, 2012b), likely avoided by female collared flycatchers. Areas with a high proportion of collared flycatchers, generally of higher quality, may thus be more attractive as breeding locations to female pied flycatchers than areas with a high proportion of pied flycatchers are to female collared flycatchers. Since we estimated relative species abundance on the basis of breeding individuals rather than unpaired males caught early in the season, it is possible that the relative proportions of unpaired pied flycatcher males were specifically overestimated in areas with higher proportions of breeding collared flycatchers (i.e., if pied flycatcher males are displaced from areas

that pied flycatcher females still are attracted to; see also the supplemental PDF for an extension of the model)

Implications

There are conceptual and practical take-home messages from our findings. First, we discuss the relevance of the population-level frequency of hybridization for making predictions about ecological and evolutionary implications. Second, we discuss some examples illustrating why our findings have implications for studies aiming to interpret patterns of asymmetric genetic transfer between species.

We show that even if the desperation hypothesis in principle is correct, one should not assume that hybridization occurs most frequently on the population level when one of the two hybridizing species is very rare. This insight is important when the aim is to predict ecological and evolutionary implications of hybridization. Whether hybridization should be seen as a threat or an engine of biodiversity is highly debated. This debate is important since hybridization can have extremely variable outcomes both for the short-term ecological dynamics and in the long-term evolutionary perspective, and hence much caution is needed when trying to predict its outcomes. In animals, where hybridization often is associated with reduced fitness (at least initially), there may be a delicate balance between short-term costs and long-term benefits of hybridization (Abbott et al. 2013; McFarlane and Pemberton 2019). A high enough frequency of hybridization is needed to exert enough selection pressure to lead to reinforcement of the speciation process (when there is selection against hybrids; Liou and Price 1994; Servedio and Noor 2003) or to ensure the formation of rare recombinant genotypes of high fitness that could contribute to adaptation either by introgression of single favorable alleles or by the establishment of recombinant genotypes (e.g., Seehausen 2004; Grant and Grant 2019). However, a too high frequency of hybridization may lead to merging of populations or contribute to extinctions (Rhymer and Simberloff 1996). Thus, the frequency of hybridization has crucial ecological and evolutionary implications. The effects of relative species abundance in combination with mate choice error on predicting hybridization frequency (i.e., the degree of assortative mating) and the interplay between these factors in determining hybridization frequency were not fully captured by previous theoretical models and verbal arguments. Our results imply that aspects of demography and ecology on the relative abundance of hybridizing species are important components for future models aiming to understand the determinants of hybridization. Hence, any observed snapshot level of the frequency of hybridization (or degree of species assortative mating) and resulting gene flow needs to be placed not only in an evolutionary context of a speciation

continuum but also in an ecological perspective where relative species abundance plays a central role.

Our findings also have implications for the interpretation of observed patterns of gene flow. Correct interpretations of patterns of gene flow between emerging species are important for studies aiming to provide insights into the process of speciation (Barton and Hewitt 1989; Rice et al. 2011; Butlin et al. 2012; Seehausen et al. 2014; Irwin 2020; Metzler et al. 2021). Asymmetrical introgression of genetic material is often interpreted in light of differences in the strength of pre- or postzygotic barriers to gene flow. While the importance of asymmetric behavioral (or sexual) prezygotic isolation is often acknowledged (e.g., Arthur and Dyer 2015; Semenov et al. 2021), our results show that effects of relative species abundance often override asymmetry in mate choice errors in explaining patterns of asymmetric hybridization. Therefore, studies on the role of behavioral isolation should also take population abundance and the ecological factors influencing population abundance into account. Asymmetric transfer of genetic material is often interpreted in the light of selection in the different genetic backgrounds (i.e., solely in the context of postzygotic isolation). Our theoretical model indicates that future studies should aim to integrate genomic findings revealing patterns of gene flow with information on initial pairing patterns or factors such as levels of mate choice errors and relative species abundances, which in turn can be used to predict the frequency and asymmetry in the formation of hybridizing pairs.

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Statement of Authorship

A.Q., F.J.W., and T.V. designed the study. F.J.W. and T.V. performed modeling work and theoretical simulations.

A.H. and M.Å. performed statistical analyses of the empirical data. A.Q. wrote the manuscript with contributions from all coauthors. A.Q. and T.V. contributed equally to the manuscript.

Data and Code Availability

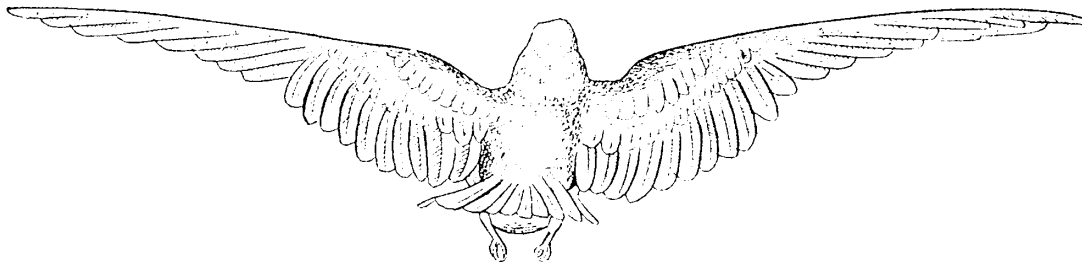
All data files, code, and README files have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.qnk98sfhd>; Qvarnström et al. 2022).

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“In these conditions the whole animal is carried onward in space; all the points of its wing have the same velocity (*vitesse*). The neighboring regions of the body are useful to press upon the air which acts as on a paper kite (*cerf-volant*). The base of the wing also in the bird, is broad and provided with feathers, which form a broad surface on which the air presses with a force and method very efficacious in supporting the bird.” From “The Flight of Birds and Insects” (*The American Naturalist*, 1871, 5:29–33).