# Mating with the wrong species can be right

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**The evolutionary importance of interspecific hybridisation has been a controversial issue for quite some time. Some view mating between different species as a maladaptive process; others stress the adaptive value of choosing heterospecific mates under ecological conditions that favour hybrids. A recent paper by Pfennig is the first study to make *a priori* predictions of how adaptive choice between con- and heterospecific partners should vary with ecological conditions, and then testing these predictions experimentally.**

## Paradigms of hybridisation

The debate over whether hybridisation in nature is adaptive or maladaptive traditionally occurred between botanists and zoologists. The division arose from the, on average, higher number of successful hybrids in plants than in animals [1,2]. With the application of molecular tools, scientists increasingly came to realise that, in both kingdoms, interspecific hybridisation (see Glossary) is very unequally distributed among and within taxa, and in some animals the rate of hybridisation even exceeds that in plants [2–4]. This shifted the debate from a specific comparison between plants and animals to a more general question: what traits and environmental conditions separate groups with frequent and successful hybridisation from those where it does not occur in the first place (prezygotic isolation) or leads to unviable or less fertile offspring with no or little chance to pass on their genes (postzygotic isolation)?

In several taxa, the extent of hybridisation increases with increasing similarity between the species in colouration, size, shape or courtship display [4–6]. This suggests that many heterospecific matings might simply represent mistakes which arise from a lack of clear species-specific signals in one sex and/or insufficient discrimination abilities in the other. This interpretation is supported by the poor species discrimination abilities of many evolutionarily young taxa and of individuals from allopatric populations or populations with a short history of sympatry. In these groups, not enough time might have passed to allow reproductive character displacement to be selected for and reinforced [5,7]. Related to this historical explanation is the hypothesis that preference for heterospecific over conspecific partners can result from an ancestral sensory bias for bigger, brighter or other more conspicuous traits, if the other species happens to exhibit such traits [8,9]. Alternatively, mating with heterospecifics might not reflect mistakes but represent a 'best-of-a-bad-job strategy' under circumstances where chances of finding conspecific

partners are low. Such circumstances might occur at times when operational sex ratios are strongly skewed (e.g. late in the season) and in areas where population density of conspecifics is low (e.g. at the fringe of the geographic distribution area) [1,10,11]. In such areas, hybrid matings are usually between the females of a rare species and the males of a common species, but not vice versa. This is to be expected because the higher parental investment of females should make them more choosy than males, so that they only accept fertilisations by heterospecific males in the absence of conspecific males [12].

## Adaptive hybridisation in spadefoot toads

In a recent paper, Karin Pfennig [13] suggests that, under certain environmental conditions, mating with heterospecifics might represent an adaptive choice, rather than an accident. Her suggestion arises from a mate choice experiment with two American spadefoot toad species, *Spea bombifrons* (BB) and *Spea multiplicata* (MM). The experiment was motivated by previous field and laboratory studies by the author and her coworkers [14,15]. The major results from these studies are summarised in Table 1. Where the two species live in sympatry, they hybridise, but the proportion of hybrids varies locally from 0 to 40%, with higher values in shallow ponds that tend to desiccate than in deeper and more permanent ponds [13,15]. Hybridisation between BB females and MM males (leading to BM

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**Table 1. Relevant results from previous studies on hybridisation between *Spea bombifrons* (BB) and *S. multiplicata* (MM)**

| | Pure species BB♀ X BB♂ | Hybrid BB♀ X MM♂ | Hybrid MM♀ X BB♂ | Pure species MM♀ X MM♂ | Refs |
|---|---|---|---|---|---|
| Proportion of hybridisation | N.A. | 0.582[a] | 0.165[a] | N.A. | [15] |
| Offspring fecundity and fertility | 1.0 | Females: 0.5 Males: 0.0 | Females: 0.5 Males: 0.0 | 1.0 | [15] |
| Size at metamorphosis | Equal | | Smaller | Larger | [15] |
| Probability of surviving to metamorphosis | Equal | | Lower | Higher | [13,15] |
| Time to metamorphosis in the laboratory | Longer | Shorter | Longer | Shorter | [13,15] |
| Speed of development in the laboratory within 16 days | Lower | Higher | N.A. | | [13,15] |
| Probability of metamorphosing in drying pools | Lower | Higher | N.A. | | [13,15] |

[a]The proportions of hybridisation were calculated from the total number of heterotypic pairs observed in natural breeding aggregations. The proportions do not add up to 1, because other heterotypic mating types were found as well (e.g. various hybrid X pure species combinations).
Orange cells denote worse performance and blue cells better performance when hybrids are compared to pure-species offspring of the maternal species. N.A. = not applicable.

offspring) is much more frequent than hybridisation between MM females and BB males leading to MB offspring [15]. Hybrid offspring of both types (BM, MB) are viable, but result in sterile males and 50% less fecund females. Hence, all other things being equal and assuming a sex ratio of 1:1, hybrid offspring fitness will be only 25%, compared to pure species offspring.

Moreover, when life-history traits are compared between hybrid and pure species offspring of the maternal species, MB hybrids perform significantly worse than MM offspring in all studied traits (Table 1). By contrast, BM larvae are only slightly (and not significantly) inferior to BB larvae in terms of survival to and size at metamorphosis. Importantly, in terms of time to metamorphosis, they even do better: they develop about 2 days faster and, as a result, are more likely to metamorphose before ponds dry up (Table 1).

Given the low fertility and fecundity of both hybrid types, selection should favour the evolution of pre-mating mechanisms that prevent hybridisation and reinforce reproductive isolation. The low proportion of hybrids in deep ponds is in line with this prediction. The strength of reinforcement, however, could differ between the two species. This is because for BB females in shallow, desiccating ponds, the fitness costs from hybridisation are, to some extent, compensated by faster development and more successful metamorphosis of BM compared to BB larvae, whereas for hybridising MM females and their MB offspring, no such advantage exists (Table 1). This expected asymmetry is supported by the much higher proportion of BM than MB hybrids in nature [15].

These previous results led Pfennig to predict that *S. bombifrons* females will more likely choose *S. multiplicata* males in shallow than in deep ponds (prediction 1). She also predicted that this mate choice response to water level should increase with decreasing female body condition (prediction 2). This second prediction was based on another previous finding, namely that the tadpoles' chances for successful metamorphosis decrease with decreasing body condition of their mothers [13,15]. Hence, benefits from an acceleration of larval development through hybridisation should be higher for females in poor than for those in good body condition.
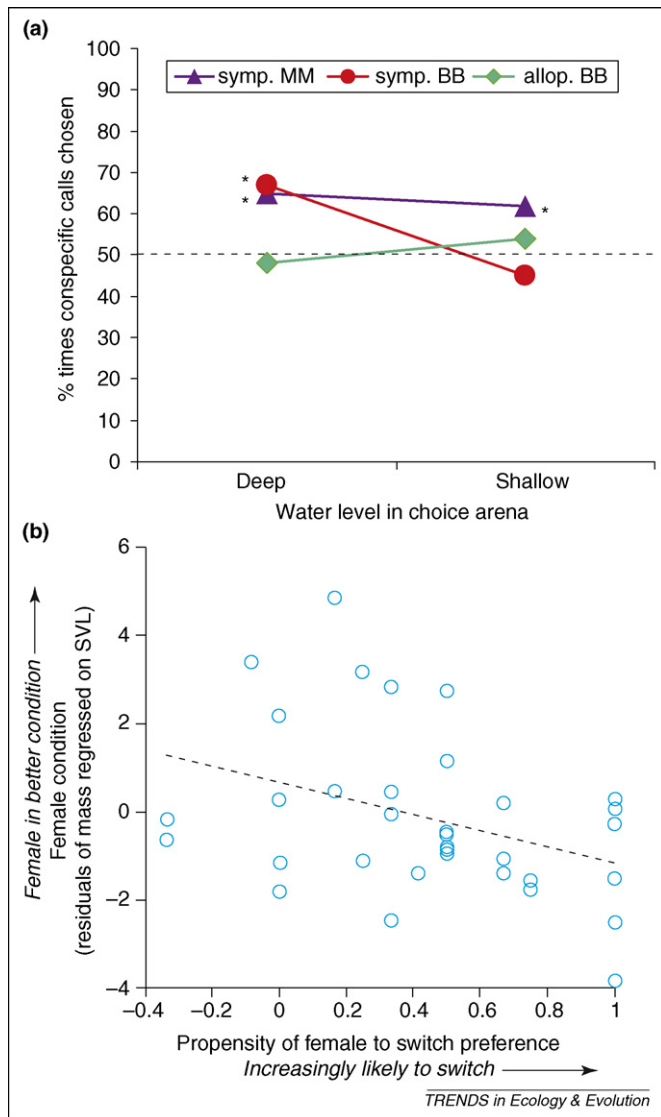
To test these two predictions, Pfennig exposed females to male calls of the two species in a choice arena with 30 cm deep and 6 cm shallow water. *S. multiplicata* females

preferred conspecific over heterospecific calls, regardless of water level (Figure 1a). The result agrees with the expectations, because this species does not benefit from hybridisation under any water depth; on the contrary, MB offspring perform significantly worse than MM offspring in all measures (Table 1). By contrast, *S. bombifrons* females preferred conspecific calls only in deep water (Figure 1a). Under shallow water conditions, the preference disappeared and choice of heterospecific calls became relatively more frequent (Figure 1a). Although *S. bombifrons* females did not actually prefer heterospecific calls in shallow water, the observed shift was consistent with the first prediction. Results of the experiments also agreed with the second prediction: the propensity of *S. bombifrons* females to shift preferences toward *S. multiplicata* calls increased with decreasing body condition (Figure 1b).

The preference for conspecific calls and the tendency to shift mate choice toward heterospecific males in response to decreasing water level appear to have evolved in sympatric populations. *S. bombifrons* females from allopatric populations, where the costs and benefits of hybridisation do not apply, neither discriminated between con- and heterospecific calls, nor adjusted their response to the water level (Figure 1a).

### Questions and implications

This is neither the first study addressing environmental causes of individual variation in mating preferences [16] nor the first one to stress the adaptive value of choosing heterospecific mates when ecological conditions favour hybrids [4,17]. However, the vast majority of previous studies only provide post hoc explanations for the observed patterns. The strength of Pfennig's investigation is that it uses previous data to make specific predictions of how choice between con- and heterospecific partners should vary with ecological conditions and then tests these predictions experimentally. Although the results from the experiment are consistent with the initial predictions, more investigations are needed before we can firmly conclude that *S. bombifrons* females really adjust their mate choice in an adaptive way, even to the point of choosing males of another species, and that this facultative choice lies behind the variability of hybrid frequencies observed in nature. Accordingly, the following four questions are meant to stimulate further investigations (not only on toads), rather than to criticise the present study.

**Figure 1**. Change of mate preference in females of two spadefoot toad species in relation to **(a)** two water depths and **(b)** body condition, expressed by the residuals of mass regressed on snout-vent length (SVL). In (a) the dotted horizontal line illustrates a random expectation of 50% under the assumption of no discrimination. *Spea bombifrons* females from allopatric populations (allop. BB, green) do not discriminate among conspecific and heterospecific male calls. In females from sympatric populations, preference for conspecific calls significantly exceeds random expectations (*) at both water depths in *S. multiplicata* (symp. MM, blue) and under deep water conditions in *S. bombifrons* (symp. BB, red). (a) modified from data in [13]; (b) reproduced from [13] (with permission from *Science*).

*Are there alternative explanations for the results?*
For *S. bombifrons* females as a group, the decrease in water level did not actually reverse mate choice but only led to a shift from toads prefering conspecific calls to not discriminating (Figure 1a). Hence, it could be argued that females lost their mating motivation under shallow water conditions and just happened to approach one loudspeaker or the other while moving around the choice arena, rather than directly responding to the playback. Such a demotivating effect of shallow water should be less visible in prospective mothers of fast-developing tadpoles, that is, *S. multiplicata* females and *S. bombifrons* females in good body condition. The choice results agree with this prediction (Figure 1a,b). Yet, loss of mating motivation is unlikely to fully explain the results. Across trials, individual

females chose the same stimulus 76% of the time [13]. This significant consistency in preference suggests that most females in this study maintained their interest in males, even under shallow water conditions. Moreover, adaptive hybridisation does not necessarily require the females to prefer heterospecific males *per se*. Selection might simply favour weaker discrimination between conspecifics and heterospecifics when, in some environments or for certain individuals, hybridisation is advantageous.

*To what extent can a preference shift toward heterospecific males compensate for the negative effects of hybridisation?*
The answer to this question depends on the relative magnitudes of negative hybridisation effects (arising from the reduction in fertility) and positive effects (resulting from faster development). Although the negative effects might be more or less constant, the positive effects depend on a whole suite of factors. For example, the benefits depend on how often and at what time of the year the shallow ponds dry up and, hence, favour rapid development. They also depend on whether the dry spells occur regularly and can be predicted by the toads at the time of mating. Furthermore, the benefit of hybridisation depends on the extent to which an average acceleration in development of 2 days improves escape from drying ponds which, in turn, depends on desiccation speed. Finally, faster larval development usually comes at the expense of smaller body size at metamorphosis; hence, the benefits from hybridisation will also depend on the relative importance that time to and size at metamorphosis have on future survival and reproduction. We need data on all these factors before we can decide whether, and under what conditions, increased hybrid survival can compensate for the four times lower reproductive rate of hybrid tadpoles.

*What genetic mechanisms would allow the evolution of facultative mate choice?*
An allele that prompts BB females to mate with MM males will find itself in BM hybrids. To achieve a net increase in frequency, it must return to the maternal species (BB) through backcrossing. BM x BB backcrosses do indeed occur. But not only is their average proportion very low (2%), which might be a direct result of the poor hybrid fitness, it is even lower than that of BM x MM backcrosses (3.5%) [15]. Hence, the allele will more often be lost in *S. multiplicata* than return to *S. bombifrons*. It is therefore difficult to imagine how a facultative preference of BB females for MM males could spread and evolve via the hybrid route. By contrast, the observed shift from conspecific preference in deep water to no preference in shallow water might appear if *S. bombifrons* populations living in sympatry with *S. multiplicata* are experiencing gene flow from allopatric *S. bombifrons* populations inhabiting shallow water. Because species discrimination is lacking in allopatry (Figure 1a), such gene flow would erode the reinforcement of reproductive isolation in sympatry (see e.g. Ref. [18]). Assuming some linkage between alleles for mate choice and those for habitat preferences, we would then expect to see lack of species discrimination in shallow water but not in deep water. This hypothesis is by no

means better supported than the assumption that facultative mate choice in *S. bombifrons* females was selected for, and it is only presented here as a speculation to illustrate that presently we lack a genetic explanation for the choice results.

*Will a change in female preference really affect relative mating frequencies in nature and, hence, explain the pond-to-pond differences in hybrid proportions?*

In several anurans, female choice measured in twofold choice experiments cannot be realised in mating assemblies in natural ponds, partly because the acoustic environment is too complex to allow unambiguous discrimination and partly because female choice is overrun by competition among indiscriminately mating males [19–21]. Moreover, shallow and deep ponds are likely to differ in many more ways than just in the risk of desiccation. Variation might occur in population density, species ratios and sex ratios, abiotic factors and food resources, as well as in the surrounding community of competitors, predators and parasites. All these factors can, directly or indirectly, affect the ratio of conspecific versus heterospecific mating combinations and the proportions of surviving BB, BM and MM offspring.

Pfennig and her collaborators seem to have already collected most of the ecological, demographic, life-history and genetic data needed to answer a few of these questions [13–15]. It would be interesting to see all data combined and incorporated into a mathematical model. This could allow a quantitative test whether the cost/benefit ratio from hybridisation can really select for facultative mate choice, with a preference for heterospecific mates in ephemeral ponds. Whatever the outcome, the present study adds exiting new insights into sexual selection and the role of adaptive hybridisation.

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**Letters**

# Animal-borne imaging takes wing, or the dawn of 'wildlife video-tracking'

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Moll and colleagues [1] presented a timely review of the use of animal-mounted video cameras for basic and applied ecological research. We welcome the authors' attempt to unveil the scientific potential of this emerging technology, but wish to highlight new research opportunities arising from the latest work with bird-mounted cameras.

For about two decades, marine biologists have used animal-borne video cameras on seals, sharks, whales

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