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Mate choice based on a key ecological performance trait

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Abstract

Mate preference for well-adapted individuals may strengthen divergent selection and thereby facilitate adaptive divergence. We performed mate choice experiments in which we manipulated male red crossbill (*Loxia curvirostra* complex) feeding rates. Using association time as a proxy for preference, we found that females preferred faster foragers, which reinforces natural selection because poorly adapted males would be less likely to obtain a mate as well as less likely to survive. Although theoretical models predict direct preference for adaptation and performance, to the best of our knowledge this experiment provides the first evidence of individuals directly assessing feeding performance in mate choice. In species where assessing the ecological adaptation of potential mates is possible, females may gain fitness benefits from choosing a well-adapted mate directly or indirectly, promoting the use of information about ecological adaptation in mate choice.

Introduction

The role of divergent ecological selection has been an important focus of studies of speciation (Schluter, 2001). Complementary to such divergent ecological selection, but less recognized, is mate choice based on the level of adaptation of individuals within a group. For example, if individuals are able to choose the best-adapted mate from within their group, sexual selection will reinforce divergent natural selection between groups and increase the level of adaptation and speed of speciation (Schluter, 2001; Lorch *et al.*, 2003). The use of a direct assessment of adaptation in mate choice may be the most powerful way for sexual selection to reinforce divergent natural selection, although more common types of mate choice such as the use of condition-dependent or 'good genes' cues may have a similar evolutionary effect.

Mate preferences that act in concert with divergent natural selection may have facilitated the rapid radiation of call types of red crossbills (*Loxia curvirostra* complex) in North America. Red crossbills are subdivided into groups referred to as 'call types' that are defined by their nonsong vocalizations (Groth, 1993a; Benkman, 1999) and have diverged morphologically within the last 12 000 years (Benkman *et al.*, 2001; Parchman & Benkman, 2002; Parchman *et al.*, 2006). Call types specialize on extracting seeds from the closed or partially closed cones of different and often sympatric conifer species, with variation in bill morphology linked to variation in feeding efficiency and survival (Benkman, 1993, 2003; Benkman & Miller, 1996).

Red crossbills are known to mate assortatively by call type in the wild, with over 99% of the individuals pairing assortatively by call type (Smith & Benkman, 2007; see also Groth, 1993b). This assortative mating is apparently related, at least in part, to mate preferences based on vocalizations (Snowberg & Benkman, 2007). Although calls reflect trophic adaptation in the group, as shown by the repeated pattern of a close fit between the predicted optimal and observed bill structures of each call type (Benkman, 1993, 2003; Benkman *et al.*, 2001), morphology is variable within call types (Benkman, 1993; Groth, 1993a). Previous studies however found that bill morphology is not directly assessed in mate choice (Snowberg & Benkman, 2007). Nevertheless, crossbills could use other cues to choose mates that are well adapted to their group's primary resource. Indeed,

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mating preferences based on a trait that more precisely indicates the degree of trophic adaptation would be beneficial to females. For example, the direct benefits of mating with a faster forager could be considerable because male crossbills feed their mate and offspring during much of the breeding season (Newton, 1972) and the male's ability to provide sufficient food probably affects the timing of breeding (Benkman, 1990). In addition, foraging ability is likely to be a reliable cue of parental care because red crossbills are both socially and genetically monogamous (Kleven *et al.*, 2008; see also Smith & Benkman, 2007).

Previous investigations of how male signals are correlated with parental care have shown the range from the most ornamented males being the best providers (Senar *et al.*, 2002; Siefferman & Hill, 2003) to the worst providers (Badyaev & Hill, 2002; Mitchell *et al.*, 2007) to no relationship (Smiseth *et al.*, 2001; Jawor & Breitwisch, 2006). Traits correlated with parental investment may not ultimately be correlated with adaptation to the environment due to the number of factors that determine condition-dependent traits (Cockburn *et al.*, 2008), as well as trade-offs between life-history traits that may influence allocation to current vs. future reproductive effort (Burley, 1986; Sheldon, 2000; Badyaev & Qvarnström, 2002). Empirical tests are therefore needed to determine whether mate choice reinforces divergent natural selection either through direct assessment of the ecological adaptation of potential mates or through the use of a condition-dependent trait that accurately reflects the level of adaptation of potential mates. Choosing a mate based on adaptation directly should be especially important to mate choice reinforcing natural selection (Kokko, 1998), although choice based on correlated ornaments may be more common.

We hypothesized that female crossbills assess the feeding rates (the rate at which seeds are extracted from a conifer cone) of potential mates and prefer males with faster feeding rates (and therefore a phenotype likely closer to the optimum). Crossbills use the feeding rate of flock mates to assess patch quality (Smith *et al.*, 1999); feeding rate is easy to assess, because when crossbills extract a seed from between cone scales they lift their head and remove the seed coat using characteristic and obvious movements of their mandibles (Benkman, 1997; Fig. 1). Because crossbills flock year round and often choose their mate from within their flock (Newton, 1972), they have plenty of opportunity to assess feeding rates of potential mates. Crossbill feeding rate is largely determined by the interaction between bill morphology and cone structure, as well as the number of seeds in the cone, and reflects resource acquisition ability on a given conifer rather than simply the motivation to forage (Benkman, 1987, 1993). In addition, crossbills do not defend territories (Newton, 1972), eliminating the confounding effect of territory quality on provisioning ability present in many studies.

To determine whether females use foraging ability to assess potential mates, we experimentally manipulated feeding rates of morphologically matched (based on bill depth, the primary morphological determinant of foraging success; Benkman, 1993, 2003) pairs of male crossbills. Females observed pairs of males foraging on what

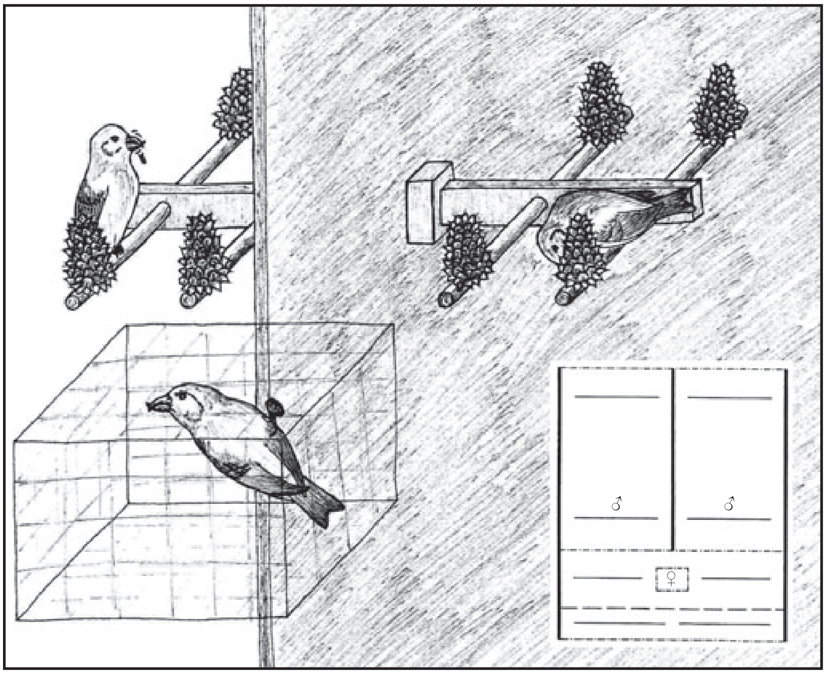

Fig. 1 During each trial two males foraged on four cones attached to the removable artificial branches placed opposite one another. From the female's observation cage, the two branches appeared contiguous despite a solid partition. Cones were visually matched for similar size and shape. The male on the left is husking a seed while the male on the right spreads apart cone scales to reach underlying seeds. The screen along the front of the males' cages and the female's outer cage are not shown. Inset: Schematic diagram of the mate choice arena. Dark solid lines represent solid partitions, dash-dot lines represent mesh partitions, heavy dash lines represent female no-choice barrier, and light solid lines represent perches. Foraging perches were located directly behind and slightly above the front perch in each male's cage.

appeared to be the same resource patch (Fig. 1), but males had dramatically different feeding rates; in previous experiments (Smith *et al.*, 1999) where clusters of cones were divided by a screen partition, the crossbills behaved as if cones on the two sides of the partition were from the same tree. We then removed the food resource and allowed the female to choose a male. We found that females strongly preferred the faster forager. In wild populations, such a preference would reinforce divergent natural selection and increase adaptation to the key resource. Although preference for faster foragers is consistent with the good parent hypothesis (Hoelzer, 1989), our experiment is novel in that we test for a preference for ecological performance rather than a trait correlated with parental investment.

Materials and methods

We captured 13 male and 24 female immature call type 9 or South Hills crossbills in August and September 2004. We used South Hills crossbills because this group has been the focus of considerable research. This call type is involved in a coevolutionary arms race with lodgepole pine (*Pinus contorta latifolia*) in the South Hills, Idaho causing divergent selection (Benkman, 1999, 2003; Benkman *et al.*, 2001) and reproductive isolation between South Hills crossbills and other call types (Smith & Benkman, 2007; Snowberg & Benkman, 2007). We held the crossbills in single sex flocks at the University of Wyoming until we conducted experiments in the spring of 2005, which is when South Hills crossbills pair and begin nesting (Smith & Benkman, 2007). Crossbills were kept on a natural light cycle for the South Hills to allow for hormonal fluctuations caused by changes in the light–dark cycle that trigger breeding in birds. None of these crossbills would have bred previously because they would have been < 5 months old at capture (see Smith & Benkman, 2007). Crossbills received fresh lodgepole pine cones and pine branches to maintain bill condition.

We varied feeding rates by altering the number of seeds in mature serotinous (i.e. remain closed until heated) lodgepole pine cones. Cones were placed in a drying oven to separate cone scales, and then randomly assigned to either the removal or control group. We used tweezers to remove between 3/4ths and 5/6ths of the seeds (these cones average about 63 seeds per cone; Benkman *et al.*, 2001) from half the cones (removal group). We removed one to three seeds from control group cones to ensure that most seeds were full. Cones were then misted with water and stored at 4 °C to re-close the scales. Crossbills typically feed on serotinous cones only after the bonds, which keep the scales closed, weather and scales begin to open. Thus our procedure produced cones that were very similar to those crossbills would forage on in the wild. Indeed, the feeding rates of crossbills on the control cones (median = 0.10 seeds per second, 0.08 and 0.13 seeds per second for the 10% and 90% quantiles respectively, $n = 30$ trials) did not differ from the feeding rates measured of South Hills crossbills foraging on lodgepole pine cones in the South Hills (Kruskal–Wallis test: $\chi^2 = 1.80$, $P = 0.18$; median = 0.11 seeds per second, 0.06 and 0.19 seeds per second for the 10% and 90% quantiles, respectively, $n = 1281$ feeding bouts; Smith & Benkman, 2007). However, the feeding rates for crossbills foraging on the removal group of cones fell significantly below the median feeding rate for crossbills in the South Hills (Kruskal–Wallis test: $\chi^2 = 55.81$, $P < 0.0001$; median = 0.05 seeds per second, 0.04 and 0.07 for the 10% and 90% quantiles, respectively, $n = 30$ trials), but nevertheless were in the range of feeding rates measured in the South Hills. In each trial, we matched removal and control cones for size and shape. Cones thus looked the same externally but contained different numbers of seeds.

Importantly, the variation in feeding rates between the two treatments was not the result of differences in foraging effort but instead the result of variation in the amount of time an actively foraging crossbill spent extracting a seed from the cone. Crossbills foraging on cones from which most of the seeds had been removed still spent time prying apart scales to determine which scales had seeds at their base. To an observer, time spent prying apart scales without seeds is similar to time spent (by a poorly adapted crossbill) unsuccessfully prying apart scales from where there are seeds. Thus, the variation in feeding rates that we created was comparable to the variation we have repeatedly found among individuals differing in bill size within and between call types (e.g. Benkman, 1993, 2003; Benkman & Miller, 1996; Parchman & Benkman, 2002) including within South Hills crossbills (Benkman *et al.*, 2001).

We coloured males with red permanent marker (Sharpie® brand; Sandford Corp., Oak Brook, IL, USA) to avoid any preference based on carotenoid colouration, which is a common sexual signal in passerines including crossbills (Hill & Benkman, 1995; Hill, 2002). We matched pairs of males morphologically (< 0.1 mm difference in bill depth). Bill depth is the primary predictor of foraging success in wild crossbills (Benkman, 2003) and we therefore sought to manipulate foraging rate independent of bill depth to test for female preference for foraging rate itself. Due to constraints in the number of males available for experiments, we used males as both the faster and slower forager in multiple trials with different females. Because the character of interest, feeding rate, was experimentally manipulated, there was no consistent association between foraging rate (fast or slow) and any characteristic of individuals, and differences in preference for the fast or slow groups can be attributed to the foraging rate difference. We confirmed statistically that male identity had no effect on the percentage of time females spent in association with a male (see below).

A trial began when a female was placed in a small observation cage (20 × 15.5 × 15.5 cm) suspended in the centre of her lane (152 × 61 × 122 cm), which ensured that she would be able to observe both males (Fig. 1). After 10 min of acclimation, the lights were turned off to minimize disturbance to the birds, and the males were introduced to their respective lanes (122 × 76 × 122 cm each; Fig. 1 inset).

Soon after the lights were turned on both males began foraging (Fig. 1). Males did not have access to food for 14 h prior to experiments to ensure consistent and high motivation to forage. We video recorded the trials to quantify seed consumption. After 10 min, the lights were turned off. We removed the branches so that available food resources would not bias the female's subsequent decision (females had unlimited access to food prior to the trial) and opened the small observation cage on the side facing the males.

We then turned the lights on so that the female could fly into her lane and move between males or spend time in an area where she could not see either male. We recorded the female's position every 15 s (from video) during the 10-min choice period. We calculated the percentage of time the female spent with each male and used this in our statistical analysis. Physical association or orientation towards an individual is commonly used as a proxy for mate preference (Clayton, 1990; Hill, 1990, 1993; Forsgren, 1992; Enstrom, 1993; Johnson *et al.*, 1993; Hankison & Morris, 2003; Cummings & Mollaghan, 2006; Wong & Rosenthal, 2006; see Byers & Kroodsma, 2009 for a discussion of the superiority of proximity measures over copulation solicitation displays as a measure of mate choice). Moreover, time in association during such mate choice experiments is a good predictor of mating behaviour in captive birds (Clayton, 1990; White & Galef, 1999).

We discarded all trials in which the female failed to fly from the small observation cage within 1 min, one or both males did not forage at least 75% of the foraging period, or a male either sang or clung to the wire opposite the female during the foraging period. The females used in discarded trials were re-tried with different males no more than two times to maximize the number of females that were able to choose. Only one trial per female was used in analyses. A total of 16 trials were discarded due to lack of female response and 12 were discarded because of problems with behaviour of one or both males. This number includes 12 trials involving four females that failed to have an acceptable trial within the allotted maximum of three trials per female, either due to nonresponse by the female or unacceptable behaviour (as defined above) by the males.

We also conducted control experiments to determine whether our measure of mate preference could have been confounded by a preference for the (now gone) food resource. Controls were conducted as above, except in addition to removing the cones we also removed the males during the transition from the foraging to choice periods. We used the 20 females that had demonstrated a preference in the first set of experiments, and we used the same protocol to discard trials.

We used a repeated measures analysis to determine whether foraging treatment (fast vs. slow forager) or male identity had significant effects on the percentage of time a female spent with a male. We arcsin transformed the frequency data and performed separate analyses for the experimental and control trials using R (R Development Core Team, 2007). We tested for differences in the percentage of time a female spent with a male using a mixed effects model with foraging treatment as a fixed effect and the identity of the male as a random effect, and female as a random block effect. Choice trials produce two data points (percentage of time spent with male A and percentage of time spent with male B) that are not independent. This is accounted for by blocking by female in the model. We then used log-likelihood ratio tests to compare the fit of this model to the same model without the fixed effect of foraging treatment and to the same model without the random effect of male identity. The first comparison tests for whether the inclusion of foraging treatment increases the fit of the model significantly and the second tests for whether including male identity increases the fit of the model.

Results

Foraging differences between the faster and slower foraging males were similar between the experimental and control trials. The 'faster feeding' male consumed between 1.3 and 3.4 times (mean = 2.0) more seeds per 10-min experimental trial (Fig. 2a) and between 1.6 and 2.8 times (mean = 2.2) more seeds per control trial (Fig. 2b) than did the 'slower feeding' male.

Seventeen of 20 (85%) females associated preferentially with males having faster feeding rates (Fig. 3). Excluding foraging treatment in the model of association time significantly decreased the fit of the model ($\chi^2_1 = 15.3$, $P = 0.00009$), indicating that foraging treatment was a major determinant of the amount of time a female spent in association with a male. The exclusion of male identity did not significantly worsen the fit of the model ($\chi^2_1 < 0.01$, $P > 0.99$), indicating the use of males in multiple trials had no effect on our results.

In the control experiment, only 40% of the females preferentially associated with the side of the arena where the faster forager had been (Fig. 3). Furthermore, foraging treatment did not significantly affect the association time of females with the sides of the arena that had contained the faster and slower males ($\chi^2_1 = 0.71$, $P = 0.40$). Inclusion of male identity did not significantly improve the fit of the model ($\chi^2_1 = 0.90$, $P = 0.34$). The difference in results between experimental trials, in which the males were not removed with the food, and control trials, in which the males were removed along

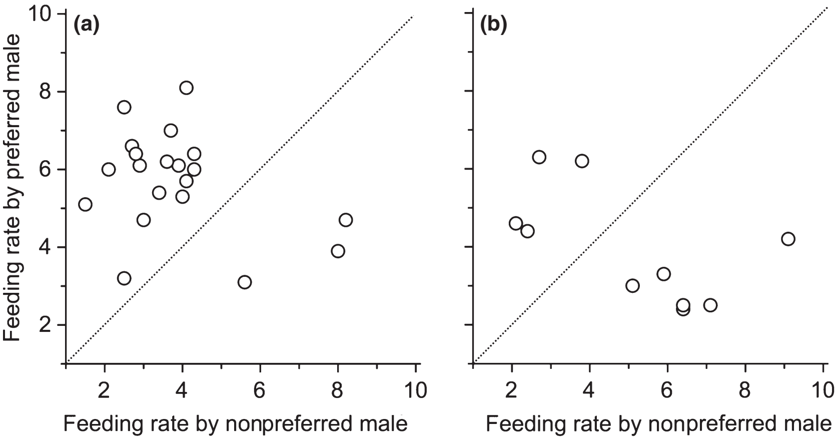

Fig. 2 The feeding rates (number of seeds consumed per minute) of the preferred and nonpreferred males in each experimental (a) and control trial (b). Each trial is represented by a single point. The dotted lines represent equal feeding rates for the two males and points above the lines represent female preference for the faster forager.

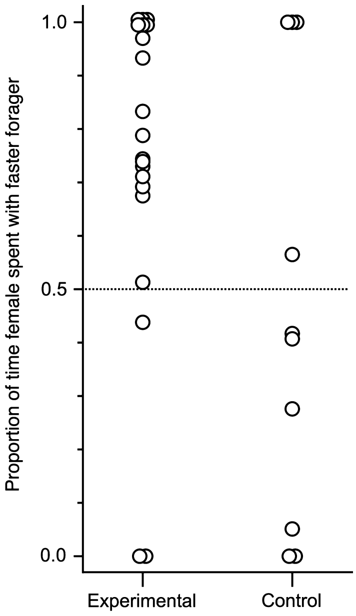

Fig. 3 The proportion of time spent by each female with the faster forager in the experimental (n = 20 females) and control trials (n = 10 females).

with the food, indicates that the female preferred the faster forager, rather than preferring the area where the male had been more successful at foraging.

Discussion

To the best of our knowledge, this is the first experiment that shows females assess levels of ecological adaptation through direct observation and use feeding rate or ability in subsequent mate choice decisions. This result supports the good parent hypothesis (Hoelzer, 1989) in a novel way, as previous tests have been based on signals or signs that less directly reflect parental ability and do not necessarily reflect adaptation. A preference for faster foragers would reinforce both stabilizing natural selection within call types (e.g. Benkman, 2003), especially when only a single conifer is foraged upon as in the South Hills crossbill, and divergent natural selection between call types. Small changes in bill morphology within a call type have dramatic consequences on feeding ability and survival in wild populations of red crossbills (Benkman, 2003), and our results indicate that they may also have even stronger consequences on fitness because poorly adapted individuals are less likely to obtain a mate.

Although assessing feeding rate is a powerful way to choose a well-adapted mate within a call type, simply choosing the faster forager will not lead to assortative mating between crossbill call types. Assortative mating between crossbill call types requires some other preference, such as their preference to pair with individuals producing similar calls (Snowberg & Benkman, 2007). Such a preference also enhances offspring fitness relative to random mating (Snowberg & Benkman, 2007) because calls identify group trophic adaptation (Benkman, 1993, 2003; Benkman *et al.*, 2001). However, individuals that base their mate choice on trophic cues would further benefit because individuals within a call type vary morphologically (Benkman, 1993; Groth, 1993a) and therefore differ in the level of adaptation to their key conifer. In addition, choosing a mate based on feeding rate may be a better way to assess adaptation to key resources than physically assessing bill morphology because, for example, feeding rate varies as a result of variation in traits that cannot be easily detected (e.g. palate structure; Benkman, 1993, 2003).

The selective benefit for females of preferences for faster foragers is straightforward. Female crossbills accrue direct benefits from choosing a well-adapted mate because males provide most of the food to the incubating female and the young (Newton, 1972; Benkman, 1990), and such care is likely critical to the breeding success of the female (Benkman, 1989). Moreover, feeding rates determine the timing of breeding (Benkman, 1990) and faster foragers should be able to nest earlier and potentially more often. Although more tenuous, the possibility remains that females gain indirect benefits by choosing to mate with a faster forager. Bill structure in birds is generally highly heritable (Merilä & Sheldon, 2001) and estimates of narrow sense heritability for bill depth of Scottish crossbills (*Loxia scotica*) are between 0.58 and 0.71 (Summers *et al.*, 2007). In addition, if the variation in foraging ability for a given bill size (Benkman, 1993; Benkman *et al.*, 2001) is also heritable, then offspring may inherit other characteristics that enhance foraging ability and increase indirect fitness benefits. However, the importance of indirect fitness benefits in the evolution of mate choice when direct benefits are present has been questioned (Arnqvist & Kirkpatrick, 2005; Charmantier & Sheldon, 2006; Qvarnström *et al.*, 2006; Kotiaho & Puurtinen, 2007) and the direct benefits females gain from choosing mates with better foraging abilities are likely sufficient to account for the observed preferences.

An individual's feeding rate reflects its level of morphological adaptation and directly influences its physical condition and survival (Benkman, 2003). Thus, choosing a faster forager is a more direct way to choose the better-adapted mate than choice based on a condition-dependent trait, which is potentially influenced by life history tradeoffs (Badyaev & Qvarnström, 2002; Muñoz *et al.*, 2008) and environmental conditions unrelated to ecological adaptation (Cockburn *et al.*, 2008). Nevertheless, theoretical models show that the use of condition-dependent traits in mate choice can lead to more rapid adaptation and may have important consequences for speciation (Lorch *et al.*, 2003). Thus, condition-dependent mate choice, given condition is indicative of ecological adaptation, is likely a general mechanism by which sexual selection reinforces natural selection for exploiting alternative resources.

This study also contributes to our understanding of the role of whole-organism performance in mate choice. Performance has received increased attention in sexual selection research, but links between male performance and female choice have been largely neglected (Lailvaux & Irschick, 2006a). Some exceptions include correlational studies of swimming performance and female choice in guppies (Nicoletto, 1991, 1993) and female choice experiments for sprinting performance in lizards (Lailvaux & Irschick, 2006b). However, our study is unique because a key ecological performance trait under divergent selection was experimentally manipulated and used in mate choice. Importantly, such divergent natural selection on mating cues may enhance ecological speciation, wherein divergent ecological selection causes phenotypic divergence and reproductive isolation between diverging groups (Schluter, 2001).

The ability of female crossbills to choose a mate by directly assessing adaptation may have contributed to the rapid radiation of crossbills into call types that specialize on different species of conifers and to the remarkable morphological fit of the different call types to their respective key resources. Because our experiment involved observation periods of only 10 min, a long observation period (e.g. year-round flocking) may not be necessary for foraging skill to play a role in mate choice. Moreover, the widespread use of public information, through observing the foraging success of other individuals to assess patch quality (Valone, 2007), suggests that assessing ecological adaptation during mate choice may be possible in a wide variety of taxa. Using the level of ecological adaptation of potential mates may also strengthen divergent ecological selection between other groups undergoing ecological speciation. For example, sympatric morphs of Darwin's medium ground finch (*Geospiza fortis*) on Santa Cruz Island, Galápagos, experience divergent selection due to gaps in the resource distribution (Hendry *et al.*, 2009). These morphs mate assortatively by bill dimensions (Huber *et al.*, 2007), and further choice based on the level of adaptation would strengthen the disruptive selection based on survival. Consequently, future research on mate choice in ecological speciation should consider signs or signals that reflect the level of adaptation between individuals and their environment.

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