variation, including novel mutations, affect the probability of which colors become established in populations. However, selection sorts among the variants, and pan-selection arguments are certainly possible. For example, the yellow crown in the hybrid manakin species may be favored over the structurally produced colors in parentals because of some special feature of the environment this species is found in.

The persistent challenge will be to circumscribe the range of possible variants, and how they may be differentially favored. In 1983 Maynard-Smith stated that, although we have a strong theory of evolution, we have no comparable theory of development [10]. That sentiment is changing, at least with respect to color. As the underlying genetics (e.g., in the red canary) and reconstructions of the past (e.g., in the manakins) improve, we feel we are at the beginning of a research program whereby selection and developmental biases can be united into a more complete theory. Some of the seemingly arbitrary distribution of color in the animal world is likely a result of developmental biases, whereby very general selection pressures (e.g., for brightness) are solved. To understand why animals are the colors they are, we must pay close attention not only to their ecology and environment but also their evolutionary history and the underlying developmental mechanisms.

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Forum

An Alternative to Adaptation by Sexual Selection: Habitat Choice

Cody K. Porter[1,2,*] and Christopher K. Akcali[3,4]

Adaptation in mating signals and preferences has generally been explained by sexual selection. We propose that adaptation in such mating traits might also arise via a non-mutually exclusive process wherein individuals preferentially disperse to habitats where they experience high mating performance. Here we explore the evolutionary implications of this process.

Mating Performance as a Driver of Habitat Choice

Although selection is a main cause of adaptation, it has long been recognized that habitat choice can also contribute to adaptive correlations between phenotype and environment, especially when choice reflects an individual's local performance variation across habitats [i.e., matching habitat choice (MHC)] [1]. As originally described [1], MHC occurs when individuals disperse between habitat patches and preferentially settle in those environments that their '**ecological traits**' (see Glossary) are better suited for because they experience higher fitness in preferred habitats over non-preferred ones. To date, biologists have focused primarily on how variation in ecological traits (e.g., traits involved in foraging activities, predation deterrence, and thermoregulation) among individuals combined with ecological performance tradeoffs between environments can influence individual **dispersal** decisions such that individuals preferentially use habitats to which their ecological traits are well suited [1–3]. Conversely, there has been little consideration of how variation in mating signals and preferences (hereafter '**mating traits**') combined with mating performance tradeoffs between environments can influence individual dispersal decisions (but see [4]). We term this process **'sexual MHC' (SMHC)** to contrast it with **'natural MHC' (NMHC)**, or MHC as defined by Edelaar *et al.* [3] (Figure 1). We name these two types of MHC natural and

Glossary

Dispersal: the movement and incorporation of individuals between habitat patches; comprises departure, transience, and settlement phases.
Ecological trait: phenotype involved in activities other than mate acquisition that could mediate performance tradeoffs between habitats.
Magic trait: a trait subject to divergent selection that also contributes to reproductive isolation.
Mating trait: phenotype involved in mate acquisition that could mediate mating performance tradeoffs between habitats.
Natural matching habitat choice (NMHC): when individuals prefer a habitat due to assessment of local ecological performance.
Sexual matching habitat choice (SMHC): when individuals prefer a habitat due to assessment of local mating performance.

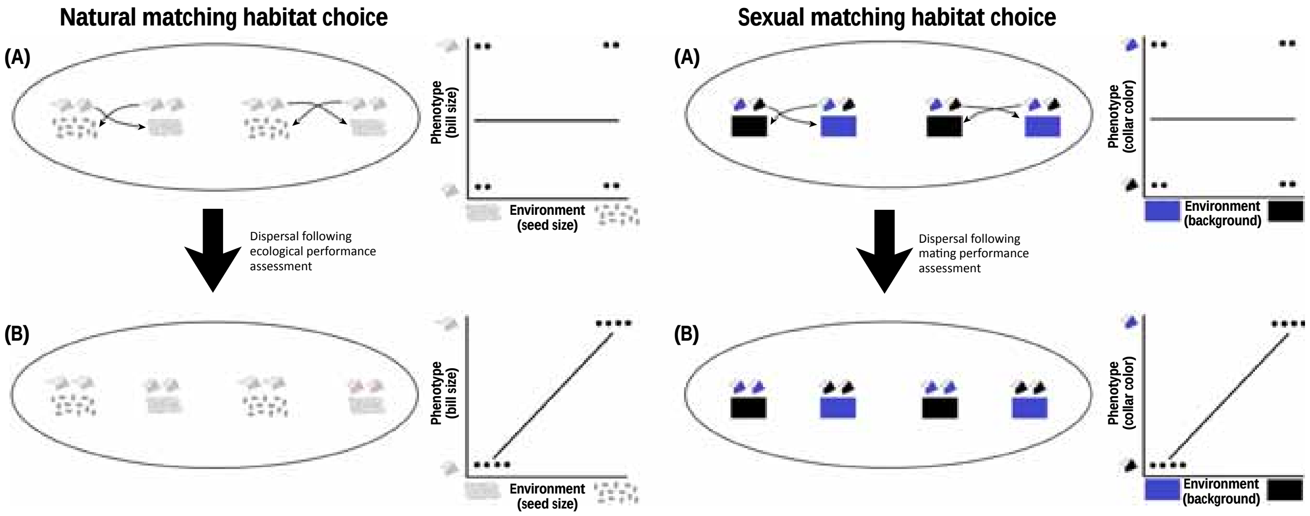

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Figure 1. An Idealized Representation of How Natural Matching Habitat Choice and Sexual Matching Habitat Choice Lead to Local Adaptation. Individuals are phenotypically variable and sample different environments in their dispersal range. However, phenotypes do not perform equally among environments. As individuals continuously assess their performance by monitoring some aspect of their well-being, some individuals depart to different environments. The process continues until individuals settle in environments to which they are better suited, resulting in a stronger correlation between phenotype and environment, thereby increasing performance and, presumably, fitness. In our example of natural matching habitat choice, birds that vary in bill size sample different environments with different-sized seeds. Large-billed individuals perform better on large seeds and small-billed individuals perform better on small seeds. By assessing their ecological performance via foraging rate, (A) nonlocally adapted large-billed birds depart from environments with small seeds and nonlocally adapted small-billed birds depart from environments with large seeds. (B) Large-billed individuals settle in environments with large seeds and small-billed individuals settle in environments with small seeds, increasing the correlation between environment (seed size) and phenotype (bill size) and thereby increasing ecological performance. In our example of sexual matching habitat choice, birds comprise males that vary in the coloration of a sexual ornament (a collar). Males with blue collars are most attractive to females in black environments where they are most conspicuous, whereas males with black collars are most attractive to females in blue environments where they are most conspicuous. Males assess their mating performance by the attention they receive from females. As a consequence of mating performance assessment, (A) nonlocally adapted blue-collared males depart from environments with a blue background and nonlocally adapted black-collared males depart from environments with a black background. (B) Blue-collared males settle in environments with a black background and black-collared males settle in environments with a blue background, increasing the correlation between environment (background) and phenotype (collar color) and thereby increasing mating performance. Although not shown, sexual matching habitat choice could also occur in females if females prefer environments where they perceive a higher density of preferred males.

sexual after natural and sexual selection, given that we expect that SMHC could provide unique insights into the role of MHC in adaptation much as sexual selection has for the role of selection in adaptation. The definition of NMHC proposed by Edelaar *et al*. [3] is identical to our definition of SMHC, except we substitute ‘mating traits’ for ‘ecological traits’ and treat competition as a possible driver of MHC [5]. Although for convenience we primarily focus throughout this Forum on how mate choice can mediate SMHC, we note that competition for mates could also drive SMHC (Box 1). Below, we outline a hypothetical example of how mate choice could mediate SMHC.

Consider fish occupying a deep lake. In many fish species, males develop bright coloration during breeding, and females generally prefer males with more conspicuous coloration [6]. As with most traits, males within a population often vary extensively in nuptial coloration. Importantly, habitats at different depths in a lake tend to have different ambient light environments, with deeper habitats tending to be more redshifted than shallower habitats in turbid water. Thus, the conspicuousness of a given male’s nuptial coloration (and the extent to which he is able to attract a mate) can heavily depend on water depth, with redder males contrasting more with the environment in shallow water and less-red males contrasting more with the environment in deep water [6]. If males sample habitats that vary in depth and ambient light and can assess their ‘mating performance’ in each environment (perhaps by evaluating female responses to courtship displays), males should factor variation in mating performance across environments and settle in environments that best match their phenotype. The end result of these individual-level dispersal decisions at a population level is a correlation between variation in mating signals and variation in environmental characteristics that tends to maximize signal transmission efficiency and thus the fitness of individual males. An analogous process could occur in

Box 1. The Other Major Mechanism of SMHC: Reproductive Competition

We expect that SMHC arises mainly via two mechanisms: mate choice (Figure 1) and reproductive competition. Below, we outline how reproductive competition could mediate SMHC.

The mating performance of individuals can often be inhibited by intraspecific interactions given that conspecifics interact frequently and often directly for access to mates. If reproductive competition between conspecifics is sufficiently strong, competitive interactions might even result in reproductive exclusion. Such intraspecific reproductive competition can be an agent that could mediate performance tradeoffs underlying SMHC, since competition for mates might differentially affect the performance of individuals in a habitat.

Consider that individuals that are inferior reproductive competitors (i.e., individuals that would be reproductively excluded from a habitat in which they would settle if competitors were present) will rank habitats differently than individuals that are superior reproductive competitors in the presence of intraspecific reproductive competition. Such variation in how individuals rank habitats will reflect variation in their mating traits. As a consequence, individuals will vary in performance among habitats depending on their mating traits and thereby sort among habitats accordingly. Thus, intraspecific reproductive competition could play an important role in SMHC by generating tradeoffs in mating performance among habitats. These ideas also apply to the role of resource competition and ecological performance in NMHC (see [5]).

The hypothesis that intraspecific reproductive competition can mediate mating performance tradeoffs underlying SMHC leads to the predictions that: (i) dispersal decisions should be responsive to the strength of intrasexual reproductive competition; and (ii) dispersal decisions should vary among individuals and should be correlated with traits associated with reproductive competitive ability. Although some studies have established a link between dispersal and intraspecific reproductive competition, most of these studies have not established whether variation in dispersal is related to variation in mating performance (but see [12] for an exception). Future empirical work should focus on measuring mating performance in different habitats to determine whether performance variation predicts dispersal decisions.

females if females vary in their ability to perceive male signals in different environments [6]. Furthermore, although this example highlights how variation in the detectability of male mating signals in different environments could influence habitat choice, variation in other traits (e.g., those involved in intraspecific reproductive competition for mates) could also be associated with variation in mating performance across environments and thus mediate SMHC (Box 1).

That such a process has been largely neglected in the literature is somewhat surprising, given that there is evidence for the predicted outcomes of this process in nature. First, there are hundreds of cases of variation in mating traits correlated with variation in certain environmental characteristics both within and across species [6]. Second, these patterns of mating trait–environment correlations are as predicted based on studies demonstrating that variation in mating traits is associated with high expected mating performance in occupied habitats and low performance in unoccupied habitats [6]. These patterns have generally been explained through a process in which different habitats facilitate divergent sexual selection on mating traits such that mating performance is optimized in each habitat [7], much as adaptive ecological trait–environment correlations have traditionally been explained by natural selection. However, most studies that have demonstrated such mating trait–habitat correlations are in species that are sufficiently mobile to both sample multiple habitats and have control over habitat settlement. Thus, variation in mating traits and performance tradeoffs between habitats might influence individual dispersal decisions, potentially generating such phenotype–environment correlations.

Below, we discuss the implications of SMHC for several important evolutionary processes; namely, local adaptation, sensory drive, and speciation with gene flow.

Rate and Degree of Local Adaptation

One implication of NMHC is the rate at and degree to which populations can become locally adapted, especially when migration between populations is high, contrary to traditional expectations [1]. SMHC should be equally effective at promoting rapid and substantial local adaptation of mating traits. However, because MHC can be mediated by both sexual and ecological performance tradeoffs that might oppose or promote each other, several outcomes are theoretically possible. Below, we outline how MHC could both constrain and promote local adaptation.

Local adaptation by NMHC occurs because individuals with similar ecological traits cluster together through directed movement. Thus, finding that mobile organisms with similar ecological traits fail to cluster together among habitats despite experiencing performance tradeoffs between habitats might lead to the conclusion that individuals do not select habitats via NMHC. However, jumping to this conclusion overlooks the possibility that the lack of an ecological trait–environment correlation could also be explained by an interaction between SMHC and NMHC (Figure 2). Interactions between SMHC and NMHC can arise if mating and ecological performance tradeoffs are negatively correlated across habitats. When mating and ecological performance tradeoffs are negatively correlated, ecological and mating performance could become poor predictors of habitat settlement because mean performance might not vary across habitats. Thus, although individuals continue to assess performance in multiple habitats, MHC does not lead to a strong correlation between traits and environments (i.e., MHC occurs, but local adaptation does not increase).

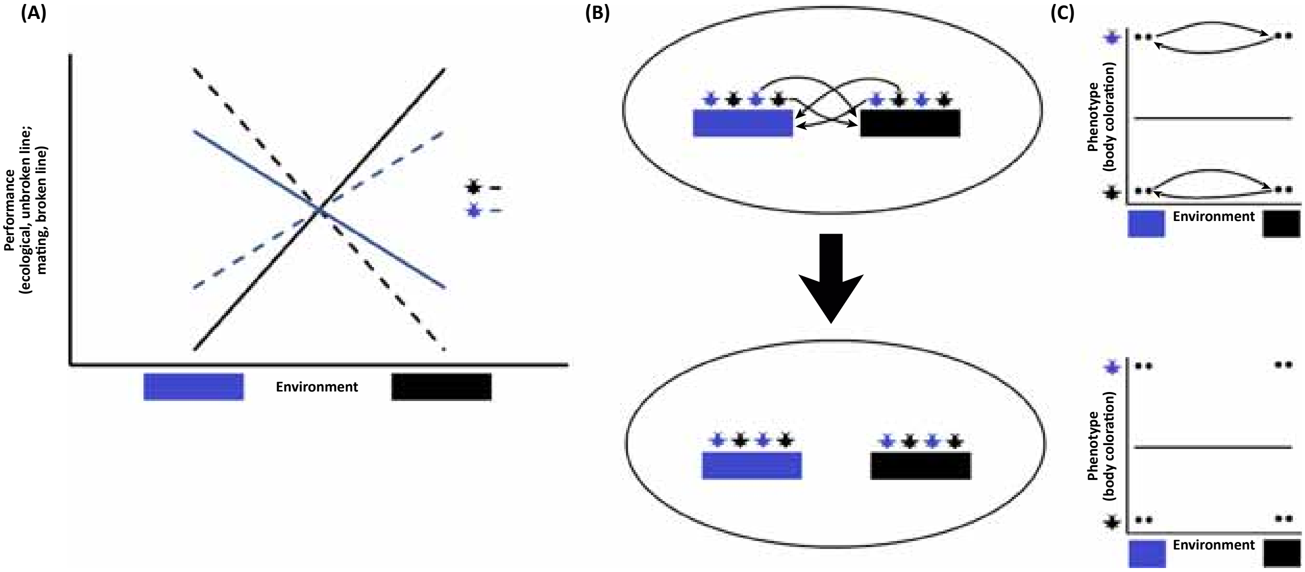

Figure 2. An Idealized Representation of How Natural Matching Habitat Choice and Sexual Matching Habitat Choice Might Interact to Constrain Local Adaptation. Insects that vary in body coloration sample different environments: one with a blue background and one with a black background. Body coloration is a pleiotropic trait and affects both ecological performance (ability to evade predation via camouflage) and mating performance (ability to attract mates via conspicuous coloration). However, ecological and mating performance are negatively correlated. (A) Blue individuals avoid predation better in blue environments but attract more females in black environments, whereas black individuals avoid predation better in black environments but attract more females in blue environments. As a result, (B) performance becomes a poor predictor of habitat settlement and (C) matching habitat choice does not lead to a correlation between phenotype and environment.

Interactions between SMHC and NMHC can also have the opposite effect wherein local adaptation is enhanced substantially more than could be achieved by either SMHC or NMHC alone. Such interactions between SMHC and NMHC can arise if mating and ecological performance tradeoffs are positively correlated across habitats, as might occur when mating traits are condition dependent [8]. When mating and ecological performance tradeoffs are positively correlated, net fitness tradeoffs across habitats might exceed mating and ecological performance tradeoffs across habitats alone. Thus, ecological and mating performance both become strong predictors of habitat settlement and MHC leads to a strong correlation between traits and environment.

We would like to stress that we have highlighted only a few of the possible ways in which SMHC and NMHC might interact. Currently, we feel there is no sufficient framework for predicting which interactions are most likely in general. Ultimately, how SMHC and NMHC interact in any one system will depend on the details of the ecology and breeding biology of the focal species.

Reinterpreting the Sensory Drive Literature

The term 'sensory drive' was coined to describe the process by which the direction of selection and thus signal evolution is driven by sensory systems and sensory conditions (e.g., the environment that signals are both advertised and received in). There are now hundreds of studies that document correlations between signal and environmental variation and interpret these patterns as evidence for sensory drive, given that signals are associated with environments in which they transmit most effectively [6,7]. Sensory drive is no doubt a potentially widespread and important evolutionary process. However, we suggest that SMHC offers an alternative, non-mutually exclusive hypothesis for the processes underlying mating trait–environment correlations. Just as the direction of signal evolution can be biased by environmental conditions that affect signal performance, so too can individual dispersal decisions. If individuals assess variation in their signal performance across environments and base dispersal decisions at least in part on this variation, correlations between signals and environmental conditions can be generated without any evolutionary change via sexual selection. Thus, SMHC could help to explain patterns of mating trait–environment correlations across small spatial scales (e.g. [6]), much as NMHC has been invoked to explain ecological trait–environment correlations over small spatial scales that would require unrealistically high levels of divergent selection [2]. Going forward, a major challenge for empiricists is to quantify the relative importance of MHC, selection, and other processes to adaptive phenotype–environment correlations [1]. We suggest that expanding this effort to include mating trait–environment correlations would be a fruitful avenue for future research.

Speciation with Gene Flow

Evolutionary biologists have long debated the likelihood of speciation with gene flow. Perhaps the greatest impediment to speciation with gene flow is that gene flow and subsequent recombination between diverging lineages breaks down associations between the loci under divergent natural selection and those promoting assortative mating [9]. NMHC can effectively circumvent this issue: if individuals with similar ecological traits tend to use and breed in similar habitats, assortative mating is automatically generated and there is no potential for recombination to break down linkage disequilibrium between loci, as only ecological traits diverge [1]. Thus, NMHC can result in ecological traits acting as **magic traits** [1], wherein ecological differences directly lead to reproductive isolation through differences in the habitats in which breeding occurs.

SMHC might be similarly capable of promoting speciation with gene flow, but in a manner distinct from NMHC. Just as variation in ecological traits and performance across environments leads directly to assortative mating during NMHC, variation in mating traits and performance across environments leads directly to assortative mating during SMHC. Furthermore, under this scenario, SMHC, unlike NMHC, should directly facilitate the development of linkage disequilibrium between male signals and female preferences, which is a major difficulty for models of speciation with gene flow via sexual selection [9]. In this way, SMHC can soften theoretical objections to sexual selection playing a leading role in speciation with gene flow. Of course, SMHC ultimately depends on environmental heterogeneity and promotes habitat isolation between diverging lineages, so ecology will still play a critical role in speciation with gene flow, as most models indicate is necessary [9]. In contrast to most of these models, however, variation in mating traits might play an important role in initiating ecological divergence, rather than emerging as a byproduct of ecological divergence.

Finally, we also note that SMHC might be more likely than NMHC to automatically result in assortative mating. In many closely related, sympatric taxa, ecological divergence associated with resources that impose strong performance tradeoffs is generally most pronounced in non-breeding periods when resources are scarce, whereas the breeding season is marked by ecological convergence on abundant resources that are easily accessible to a range of phenotypes [10]. Similar observations coupled with the extreme breeding habitat specificity of birds led Mills [11] to suggest that sexual selection generally might play an important role in determining what constitutes a suitable breeding habitat (and, by extension, in the evolution of habitat isolation). Thus, the scenario of NMHC promoting clustering of ecologically similar individuals during breeding is likely to be restricted to systems where breeding is marked by ecological divergence between lineages (e.g., many phytophagous insects). Conversely, performance tradeoffs associated with mating traits across environments necessarily occur during breeding and might thus be more likely to promote assortative mating generally.

Concluding Remarks

The study of SMHC and NMHC is currently in much the same state as the study of sexual and natural selection was during Darwin's time: the concepts have explanatory potential but a strong empirical foundation is lacking. Basic studies that document the performance of individuals in different habitats and the movement of individuals among habitats are needed to advance our understanding of MHC beyond this incipient stage. We encourage more empirical studies with more species, particularly in the field, to address basic questions about SMHC and NMHC (see Outstanding Questions). We also welcome theoretical studies to explore the various assumptions, predictions, and implications of these MHC processes.

Outstanding Questions

How common are NMHC and SMHC in nature?

Do NMHC and SMHC interact? If so, do NMHC and SMHC more often interact to facilitate or impede local adaptation?

Is SMHC mediated more commonly by mate choice or reproductive competition?

Can SMHC facilitate speciation by sexual selection?

How effective is SMHC at facilitating assortative mating relative to NMHC?

What is the relative importance of MHC, selection, and plasticity in driving phenotype–environment correlations?

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