

Comment on Van Belleghem et al. 2016: Habitat choice mechanisms in speciation and other forms of diversification

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Several mechanisms of habitat choice can contribute to speciation. Empirical studies of habitat choice mechanisms provide important insights into the relative roles of these mechanisms in speciation. A recent paper by Van Belleghem and colleagues characterizes the mechanistic basis of a component of habitat choice—departure behavior—in two salt marsh beetle ecotypes that inhabit different environments. The authors compare the departure behavior between the two ecotypes in response to an environmental cue and find that ecotypes differ in their tendency to depart in response to this cue and that the environment experienced by immature beetles affects the departure behavior of adult beetles. The authors conclude that such plastic behavioral differences between ecotypes should reduce gene flow and thereby facilitate reproductive isolation between ecotypes. We question whether such a mechanism of departure behavior would effectively reduce gene flow between ecotypes. Furthermore, their study highlights the need for some clarification of habitat choice mechanisms and related concepts, as conceptual inconsistencies are common in the literature. Here, we clarify major mechanisms of habitat choice and discuss how each mechanism might facilitate speciation. We emphasize that future empirical work should be guided by careful consideration of the natural history of species under study.

KEY WORDS: Dispersal, habitat choice, habitat preference, matching habitat choice, nonrandom dispersal, *Pogonus chalceus*.

Identifying the sources of reproductive isolation between diverging populations is central to studies of speciation and other forms of diversification (Coyne and Orr 2004). The role of ecologically based divergent selection in driving the evolution of reproductive isolation has been well-studied empirically (Schluter 2009; Sobel et al. 2010). Indeed, there is much empirical evidence to suggest that divergent selection can facilitate the evolution of reproductive isolation (Nosil 2012). However, the role of habitat choice in speciation and other forms of diversification (e.g., polymorphism) has received comparatively less empirical attention.

Progress toward speciation might critically depend on how individuals select habitats. If individuals select habitats randomly as many theoretical models have assumed (e.g., Felsenstein 1981), the evolution of reproductive isolation between diverging populations will be inhibited. In contrast, when individuals select habitats

nonrandomly, the evolution of reproductive isolation between diverging populations can be enhanced—even in the face of gene flow (Maynard Smith 1966; Rice 1984; Diehl and Bush 1989; De Meeûs et al. 1993; Johnson et al. 1996; Kawecki 1996; Fry 2003; Ravnigné et al. 2004; Beltman and Metz 2005; Thibert-Plante and Gavrilets 2013; Berner and Thibert-Plante 2015).

Such nonrandom dispersal can also have other important evolutionary implications. For example, nonrandom dispersal can increase the rate and the degree to which diverging populations are locally adapted (Armsworth and Roughgarden 2008; Edelaar et al. 2008; Holt and Barfield 2008; Edelaar and Bolnick 2012; Bolnick and Otto 2013); can allow populations to ford fitness valleys on the adaptive landscape (Edelaar et al. 2008); and provides one of the most plausible explanations for the unexpectedly abrupt genetic and phenotypic clines that occur in highly mobile

organisms (Bolnick et al. 2009; Urban 2010; Richter-Boix et al. 2013; Richardson et al. 2014).

Although there is much theoretical support for the power of habitat choice to facilitate divergence, most of these studies do not consider how different habitat choice mechanisms could affect the role that habitat choice plays in divergence (but see Berner and Thibert-Plante 2015). In addition, most empirical studies that have assessed the role of habitat choice in divergence (e.g., MacCallum et al. 1998; Cruz et al. 2004; Eroukmanoff et al. 2011) have not identified the underlying mechanisms mediating habitat choice. Indeed, threespine sticklebacks (*Gasterosteus aculeatus*; Jiang et al. 2015; Jiang et al. 2016) and red crossbills (*Loxia curvirostra* complex; Benkman 2017) are currently the only systems for which the mechanisms of habitat choice—and their effects on divergence—are well-characterized.

A recent publication by Van Belleghem et al. (2016) has attempted to add another system to this list. In their paper, Van Belleghem and colleagues characterize the mechanistic basis of departure behavior in the salt marsh beetle *Pogonus chalceus* to assess whether the way in which individual beetles depart from habitats could contribute to reducing gene flow between two sympatric ecotypes. The two ecotypes occupy different hydrological regimes that often occur in a sympatric mosaic: tidal marshes that are connected to the sea and flooded on a daily basis for short periods throughout the year and seasonal marshes that are disconnected from the sea and are completely inundated for several months a year. The authors predict that tidal marshes should favor resident behavior because frequent departure in response to small, daily but ephemeral inundations is costly. In contrast, they predict that seasonal marshes should favor departure to unflooded patches of marsh habitat because less frequent but longer lasting inundations might increase the likelihood of mortality. The authors test these predictions by comparing the departure behavior of tidal and seasonal marsh ecotypes in response to simulated inundations. They find that the seasonal marsh ecotype departed in response to simulated inundations more frequently and departed from simulated inundations more rapidly than the tidal marsh ecotype. In addition, they find that the hydrological regime experienced by the larvae and pupae affects the departure behavior of the adults. Specifically, adults that experience an experimental tidal flooding regime as larvae and pupae have a reduced tendency to depart inundations compared to beetles that are raised in a dry environment, irrespective of the ecotypic origin of their parents. The authors conclude that plastically induced differences in departure behavior between the two ecotypes is a mechanism that could potentially lead to reductions in gene flow, and thereby cause reproductive isolation between tidal marsh and seasonal marsh ecotypes.

We commend the authors for conducting a valuable empirical study of a component of habitat choice in a system that

has become an outstanding model for the study of speciation and adaptation (Dhuyvetter et al. 2004; Dhuyvetter et al. 2007; Raeymakers and Backeljau 2015). We further believe that one of the main conclusions of their article—that the mechanism of departure behavior in the two ecotypes consists of plastically induced behavioral differences—is well supported. However, we call into question their conclusion that such a mechanism of departure behavior would effectively reduce gene flow in *P. chalceus*. More generally, their study highlights the need for some clarification of habitat choice mechanisms and related concepts, as habitat choice mechanisms have been inconsistently conceptualized in the literature over the past decade. Here, we briefly describe and clarify major mechanisms of habitat choice, emphasizing how each is mechanistically distinct. We use the context of the Van Belleghem et al. (2016) study throughout our comment to help clarify the distinctions between habitat choice mechanisms, discuss how different habitat choice mechanisms might contribute to diversification, and highlight why careful consideration of the natural history of species under study is critically important for empirical studies of habitat choice.

Conceptualization of Habitat Choice Mechanisms

The literature on the role of habitat choice in speciation and other forms of diversification has expanded rapidly in recent years (Edelaar et al. 2008; Webster et al. 2012). As a consequence, the terms used to describe habitat choice mechanisms have become correspondingly more complex. However, as the terminology has become more complex, inconsistencies in the use of terms have become more common. In some cases, terms used to refer to specific habitat choice mechanisms by one author are used more loosely by other authors to refer to several habitat choice mechanisms or to outcomes of habitat choice that are agnostic to the underlying mechanism(s). In other cases, different terms have been used to refer to the same habitat choice mechanism. While it is beyond the scope of this comment to clarify the vast language of habitat choice that has developed during recent years, below, we briefly describe three major classes of habitat choice mechanisms—plastic habitat choice, direct genetic habitat choice, and matching habitat choice—emphasizing how each is mechanistically distinct and how each might contribute to speciation and other forms of diversification (Table 1). In doing so, we clarify some terminology and discuss a misunderstanding of matching habitat choice made by Van Belleghem et al. (2016). We would like to stress that Van Belleghem et al. (2016) are not the first authors to confuse these concepts, but that their study provides an excellent context in which to address general misunderstandings of habitat choice mechanisms that have plagued the field in recent years. We finish each section by discussing how relevant each

Table 1. Glossary of key terms.

Term	Definition
Competition-dependent habitat choice	When the strength of competition in a habitat determines the habitat preferences of individuals.
Direct genetic habitat choice	When individuals prefer a habitat because alleles directly induce preference.
Dispersal	The movement and incorporation of individuals between habitats. Dispersal consists of departure, transience, and settlement phases.
Habitat choice	When individuals choose a habitat in which to perform their activities.
Habitat choice mechanism	The proximate means by which individuals choose a habitat in which to perform their activities.
Matching habitat choice	When individuals prefer a habitat as a result of assessment of local performance.
Nonrandom dispersal	When the movement of individuals between habitats depends directly or indirectly on their phenotype.
Plastic habitat choice	When individuals prefer a habitat because of an environmental cue experienced during ontogeny.
Philopatry	When individuals prefer familiar habitat.

mechanism of habitat choice might be in *P. chalcone* based on the study of Van Belleghem et al. (2016) and previous work.

PLASTIC HABITAT CHOICE

Habitat choice is plastic when preference for a habitat is induced by an environmental cue during ontogeny. Thus, “learned habitat choice,” “habitat imprinting,” and “natal habitat preference induction” all constitute forms of plastic habitat choice but differ in the timing and nature of the environmental cue responsible for inducing habitat choice (Maynard Smith 1966; Immelmann 1975; Beltman and Metz 2005; Stamps et al. 2009).

Because plasticity in habitat choice can generate the immediate separation of individuals when individuals experience different environmental conditions, plastic habitat choice is likely most important during early stages of divergence. How strongly plastic habitat choice ultimately contributes to the early stages of divergence critically depends on the reversibility of habitat choice after it has been induced. For example, if habitat choice is induced via imprinting and thereby results in an irreversible preference for a particular habitat, then plastic habitat choice will be effective at reducing gene flow between diverging ecotypes because ecotypes will tend to remain segregated between habitats if their preference does not change. Indeed, most theoretical models that have shown that plastic habitat choice can be one of the most powerful facilitators of diversification among habitat choice mechanisms have generally assumed that habitat choice induced during ontogeny is irreversible (Beltman et al. 2004; Beltman and Metz 2005; Berner and Thibert-Plante 2015). In contrast, if habitat choice induced during ontogeny is not irreversible—that is preference for a habitat can be modified later in life history—then the contribution of plastic habitat choice to reducing gene flow, and thus speciation, will be reduced because some ecotypes would inevitably settle in habitats different from the one in which they were reared, thereby leading to a breakdown in habitat isolation.

Plastic habitat choice can also enhance divergence at later stages by promoting the differential fixation of alternative habitat preferences among diverging populations. The contribution of plastic habitat choice to diversification during later stages is likely affected by the costs of plasticity. For example, when the costs of plasticity are high, plasticity in habitat choice might be lost—and preference for a habitat could become fixed within ecotypes—after populations have diverged enough such that ecotypes rarely experience alternative habitats (Pfennig et al. 2010). Alternatively, if the costs of plasticity are low or if there are no costs, then plasticity in habitat choice could be maintained long after populations have begun to diverge. In such cases, gene flow between diverging ecotypes might be maintained since preference for a habitat is not fixed within ecotypes.

The simulated inundation experiments of Van Belleghem et al. (2016) provide evidence that the decision to depart from a habitat is plastically induced by the habitat in which the pupae and larvae develop. However, whether this mechanism of departure behavior ultimately reduces gene flow between ecotypes is unclear because their experiments do not show whether this tendency to depart (or to not depart) from a habitat is stable throughout the life of an individual. If individuals are capable of modifying their response to inundation later in life (i.e., departure behavior is reversibly plastic), then ecotypes might frequently settle in habitat types different from those in which they developed, thereby increasing gene flow between ecotypes. On the other hand, if responses to inundation are stable throughout the life of an individual (i.e., departure behavior is irreversibly plastic), then ecotypes might remain segregated and, consequently, gene flow would be reduced between ecotypes. However, even if the differences in departure behavior between ecotypes are irreversibly plastic, the efficacy of this mechanism in reducing gene flow depends on the critical assumption that departing individuals selectively settle in more suitable habitat. A number of things could

happen during the transience phase of dispersal that could cause individuals that selectively depart unsuitable habitat to ultimately not settle in suitable habitat. Thus, the extent of genetic divergence that has been documented between *P. chalceus* ecotypes over exceedingly small spatial scales (Dhuyvetter et al. 2007) would most likely arise and be maintained by plastic habitat choice if departure responses to inundation are unchanged throughout life and if departing individuals selectively settle in more suitable habitat.

DIRECT GENETIC HABITAT CHOICE

By direct genetic habitat choice, we refer to habitat choice that is determined by alleles that *directly* induce preference for a specific habitat (Rice 1984; Diehl and Bush 1989; Jaenike and Holt 1991; Fry 2003; Gavrillets and Vose 2005; Ravigné et al. 2009; Thibert-Plante and Gavrillets 2013; Berner and Thibert-Plante 2015). Although all mechanisms of habitat choice ultimately have a genetic basis, we use direct genetic habitat choice to refer solely to cases when the function of alleles that determine habitat choice are to directly facilitate the ability of individuals to seek and settle in specific habitats. Thus, alleles that are responsible for performance in a habitat, which might affect subsequent departure and settlement decisions between habitats, do not make contributions to direct genetic habitat choice (NB: such alleles do make contributions to matching habitat choice; see **MATCHING HABITAT CHOICE**). For example, alleles that function to sense cues emitted by a specific habitat (as in phytophagous insects that might sense the pheromones emitted by their host plant; Matsubayashi et al. 2010) underlie direct genetic habitat choice. In contrast, alleles that determine performance within a habitat (e.g., feeding rate on a specific resource) do not underlie direct genetic habitat choice. It is of course plausible that some alleles will be pleiotropic (i.e., facilitate the ability of individuals to seek and settle in a habitat as well as perform well within a habitat). In such cases, careful empirical work is necessary to determine whether the causes of departure and settlement are predicted more consistently by performance variation between habitats or by variation in the ability to seek and settle in preferred habitat.

Because the ability of direct genetic habitat choice to spatially separate individuals depends on the association of genes that can be disrupted through recombination between populations, direct genetic habitat choice is likely most important during later stages of divergence. How strongly direct genetic habitat choice ultimately contributes to diversification critically depends on the genetic architecture underlying habitat choice. Generally, direct genetic habitat choice will tend to contribute most strongly to diversification when the number of loci determining habitat choice is low because selection is more intense on a per locus basis, thereby favoring more rapid fixation of alternative habitat choice alleles among diverging populations (Berner and Thibert-Plante 2015).

The experiments of Van Belleghem et al. (2016) only examine the departure tendencies of ecotypes. Thus, whether direct genetic habitat choice contributes to diversification in *P. chalceus* is an open question. Direct genetic habitat choice might contribute to diversification in *P. chalceus* if individuals of the two ecotypes could be shown to seek out and settle in different habitats following departure from inundated habitat. To demonstrate direct genetic habitat choice, follow-up work would be needed to determine whether individuals seek specific habitats due to the presence of alleles that influence the ability to locate and settle in preferred habitat.

MATCHING HABITAT CHOICE

Although the term matching habitat choice had been coined a few times previously (Ravigné et al. 2004; Ravigné et al. 2009), Edelaar et al. (2008) were the first to clearly define the term and to clarify how matching habitat choice is mechanistically distinct from other habitat choice mechanisms. Edelaar et al. (2008) use matching habitat choice to describe a mechanism of habitat choice where individuals tend to settle in habitats in which they are best adapted, based on a comparison of local performance by the organism. Edelaar et al. (2008) distinguish matching habitat choice from other habitat choice mechanisms by emphasizing that the outcome of matching habitat choice is an increased match between the phenotypes of individuals and the environment, resulting in increased fitness. Importantly, Edelaar et al. (2008) further propose that matching habitat choice operates independent of other processes that may mediate increases in the phenotype-environment match such as adaptive phenotypic plasticity, natural selection, imprinting, and genetic variation in habitat choice. Thus, matching habitat choice contributes to the adaptive process simply via an indirect effect of ecological traits (although admittedly redundant to call traits ecological [after all, what traits are nonecological?], we use ecological traits as shorthand to refer to traits that mediate performance trade-offs between habitats): because individuals sample multiple environments and assess their performance in these environments, individuals tend to settle in environments that are best suited to their phenotype (Edelaar et al. 2008).

As Edelaar et al. (2008) have noted, several other terms have been used to refer to matching habitat choice. Although a few of these terms (e.g., phenotype-matching habitat selection) appear to be synonymous with matching habitat choice (sensu Edelaar et al. 2008), most other terms (e.g., phenotypic sorting, adaptive habitat choice, phenotype-dependent habitat choice) are either agnostic to mechanism (i.e., reference the increase in fitness or the pattern of phenotype-environment matching irrespective of how it was produced) or have been used to refer to different habitat choice mechanisms by different authors. Because the consequences of habitat choice for diversification critically depend on the

mechanism individuals use to select habitats, we think that progress in the empirical study of habitat choice mechanisms would be greatly aided if authors used terms that were rooted in mechanism rather than agnostic to mechanism. Thus, we agree with Edelaar et al. (2008) that matching habitat choice is the best term to refer to the mechanism of habitat choice they describe because it emphasizes that individuals ultimately disperse to increase fitness.

The conceptualization of matching habitat choice of Van Belleghem et al. (2016) is not consistent with that of Edelaar et al. (2008). According to Edelaar et al. (2008), matching habitat choice occurs if individuals settle in habitats that are best suited to their phenotypes because individuals experience performance trade-offs across environments. Thus, matching habitat choice operates independent of phenotypic plasticity, a conceptually similar but orthogonal process. The authors do not conceptualize matching habitat choice and phenotypic plasticity as orthogonal processes when they state the following: “when exposure to a particular environment involves plastic behavioral or physiological adaptations that enhance survival of nondispersive individuals, matching habitat choice may even instantly result in spatial separation of adults emerging from these contrasting environments (Ravigné et al. 2009; Stamps et al. 2009; Thibert-Plante and Gavrillets 2013; Nonaka et al. 2015) (p. 1905).” However, for matching habitat choice to contribute to the spatial sorting of phenotypes across environments, phenotypic plasticity must not ultimately determine the environments in which individuals settle. In contrast, for matching habitat choice to contribute to the spatial sorting of phenotypes across environments, performance trade-offs across environments (as a consequence of ecological traits) must ultimately determine the environments in which individuals settle. This is not to say that matching habitat choice and phenotypic plasticity cannot act simultaneously. In fact, theoretical work has shown that diversification can be greatly facilitated when matching habitat choice is aided by phenotypic plasticity (Nonaka et al. 2015).

Because of its ability to produce the immediate spatial separation of individuals based solely on their ecological traits, matching habitat choice is likely most important during early stages of divergence. Matching habitat choice will drive diversification most strongly at early stages of divergence when variation in ecological traits and environments is extensive, when individuals are capable of sampling multiple environments (i.e., dispersal costs are low), and when individuals have control over where they settle (i.e., dispersal capacity is high; Edelaar et al. 2008). Matching habitat choice will also contribute more to diversification when individuals can readily assess their performance within habitats and when performance trade-offs between habitats are strong.

Whether matching habitat choice contributes to diversification in *P. chalceus* is an open question, as Van Belleghem et al.

(2016) do not explicitly test for this mechanism of habitat choice in their study. A number of criteria (discussed in Edelaar et al. 2008) would need to be met to convincingly demonstrate matching habitat choice in *P. chalceus*. However, we expect matching habitat choice contributes little to diversification in *P. chalceus* based on several features of its natural history and biology (see *Natural History as a Guide*).

OTHER HABITAT CHOICE “MECHANISMS”

Some authors have considered philopatry, whereby individuals tend to prefer the habitat in which they were reared, to be a distinct mechanism of habitat choice (e.g., Ravigné et al. 2009). However, we argue that philopatry should not be considered a distinct mechanism of habitat choice for two reasons. First, the definition of philopatry is based on the identity of the preferred habitat—and not on the proximate basis of the preference. That is, philopatry simply describes a pattern of habitats selected by individuals rather than the mechanistic processes underlying the pattern. Second, the proximate causes of philopatry can be manifold. For example, a tendency to prefer the habitat in which an individual was reared can be induced by environmental cues (plastic habitat choice), controlled by preference alleles (direct genetic habitat choice), or based on a comparison of local performance by the individual (matching habitat choice).

Some authors (e.g., Berner and Thibert-Plante 2015) have also considered competition-dependent habitat choice to be a distinct mechanism of habitat choice. Competition-dependent habitat choice occurs when individuals base their departure and settlement decisions on the strength of competition in a habitat (Berner and Thibert-Plante 2015). However, we argue that competition-dependent habitat choice is not a distinct mechanism of habitat choice because, like philopatry, competition-dependent habitat choice is agnostic to the proximate basis of preference. Instead, we propose that competition—as well as any selective agent (e.g., predation, parasitism, etc.)—is better viewed as an agent (i.e., an ultimate cause of preference) that can underly several distinct mechanisms of habitat choice. For example, competition can be considered to be a feature of the environment that can affect the performance of individuals in a habitat. Consider that individuals that are inferior competitors (i.e., individuals that would be competitively excluded from habitats in which they would settle if competitors were absent) will rank habitats differently than individuals that are superior competitors in the presence of intraspecific competition. Such variation in how individuals rank habitats will reflect variation in their ecological traits. As a consequence, individuals will vary in performance among habitats depending on their ecological traits and thereby sort among habitats accordingly. Thus, competition-dependent habitat choice can be one way in which matching habitat choice can proceed. We therefore disagree with Edelaar et al. (2008) when they propose competitive

exclusion as an alternative to matching habitat choice. We expect that competition could play an important role in matching habitat choice as a source of habitat variation that could generate performance trade-offs on which matching habitat choice could be based.

Competition might also facilitate plastic habitat choice if the density of competitors functions as an environmental cue that plastically induces a tendency for individuals to bias their departure and settlement decisions on the strength of competition in a habitat. Likewise, competition might facilitate direct genetic habitat choice if, for example, individuals possess alleles that function to sense the density of competitors (e.g., the strength of pheromones emitted by competitors) so that their departure and settlement decisions are biased on the strength of competition in a habitat. Although such mechanisms are conceptually plausible, empirical cases of competition facilitating plastic and direct genetic habitat choice are apparently nonexistent.

Natural History as a Guide

Determining the mechanisms of habitat choice operating in any one system poses a considerable empirical challenge. After demonstrating a habitat choice mechanism, another considerable empirical challenge is posed by estimating the contribution of that mechanism of habitat choice to diversification relative to other processes (e.g., divergent natural selection). Regardless of the mechanism, both demonstrating habitat choice as well as assessing the role of habitat choice in diversification requires study of both the departure and settlement phases of habitat choice. Because Van Bellegem et al. (2016) have not studied the settlement phase of habitat choice, whether the plastic mechanism of departure behavior that they demonstrate results in the sorting of *P. chalceus* ecotypes between habitats, and thereby reduces gene flow between ecotypes, is uncertain. Although ecotypes might sort between habitats if individuals exclusively followed the plastic departure mechanism described in their article, whether such a departure mechanism alone is sufficient to generate sorting, and thereby reduce gene flow between ecotypes, cannot be known until differences in departure behavior are shown to lead to differences in settlement among habitats.

However, daunting addressing these empirical challenges may be, careful consideration of the natural history of species under study is imperative for guiding empirical work on habitat choice mechanisms. For example, species that experience temporally variable environments are primed to experience plastic habitat choice. *Pogonus chalceus* occurs in coastal marshes, which are dynamic habitats that experience substantial temporal variation in waves and tidal currents. Thus, the finding that habitat choice is plastic in *P. chalceus* is consistent with this expectation. On the other hand, species that are highly specialized on a specific

resource, such as many phytophagous insects, or respond strongly to specific cues present in different habitats are primed to select habitats via direct genetic habitat choice. Although possible, whether direct genetic habitat choice contributes to divergence in *P. chalceus* is unclear because there is currently no evidence to suggest that the two ecotypes innately respond to cues specific to different habitats.

Species that are highly mobile, have control over where they settle, experience performance trade-offs between habitats, and are capable of readily assessing their performance are primed to select habitats via matching habitat choice. Matching habitat choice likely contributes little to diversification in *P. chalceus* based on several aspects of its natural history and biology. First, most *P. chalceus* do not appear to sample multiple habitats based on what is known of its dispersal biology. Most tidal marsh *P. chalceus* have small wings and lack functional flight muscles and thus are expected to be incapable of substantial dispersal (Desender 1985). In contrast, most seasonal marsh *P. chalceus* have large wings and functional flight muscles (Desender and Serrano 1999), yet are expected to move infrequently between habitat patches and only in response to inundation (Van Bellegem et al. 2016). Indeed, the authors expect departure costs are high in *P. chalceus* because frequent flights can “impose considerable costs both in terms of energetic investment as well as increased exposure to predators (p. 1905).” Thus, the majority of *P. chalceus* individuals may not sample multiple habitats throughout their lifespans. Second, *P. chalceus* have little control over the habitats in which they settle. As with most carabid beetles, adult *P. chalceus* are clumsy fliers: the wind can play a major role in guiding their movements (Den Boer et al. 1980). Even though the small percentage of tidal marsh *P. chalceus* that have functional flight muscles tend to fly on warm and sunny days when the wind is weak (Desender 1985), the more dispersive seasonal marsh *P. chalceus* is typically not able to fly during such optimal conditions because flight is most often initiated by the exigent need to depart inundated habitat. Thus, the majority of dispersing beetles will tend to have little control over where they settle.

Third, little is known about the strength of performance trade-offs that adult *P. chalceus* experience between occupying tidal and seasonal marshes. The authors indicate that the frequency and duration of inundations is the most important axis of habitat variation that would generate performance trade-offs between tidal and seasonal marsh habitats. However, performance trade-offs that arise from the frequency and duration of inundations may be nonexistent if, for example, responses to inundation that are plastically induced by larval and pupal experiences are modified by subsequent exposure to tidal floods later in life history. This is a moot point: because the departure of individuals is only induced by long-lasting inundations and not by performance assessment in such habitats, the frequency and duration of inundations is not an

axis of habitat variation that could generate performance trade-offs. There may be other independent axes of habitat variation other than the frequency and duration of inundations that have not yet been identified that impose strong performance trade-offs between tidal marsh and seasonal marsh habitats of their own. Furthermore, whether individuals of *P. chalceus* are subject to performance trade-offs as a consequence of other ecological traits on which matching habitat choice can be based is unknown.

Conclusion

Characterizing mechanisms of habitat choice in natural populations can be an empirical nightmare. Indeed, determining the mechanisms underlying habitat choice might not be empirically possible in many systems. This is not to say that nonmechanistic studies of habitat choice in empirically challenging systems are not valuable. In contrast, such pattern-based studies have made invaluable contributions to our understanding of habitat choice and the role it plays in diversification (Schemske 2010). When it is possible however, identifying the mechanisms of habitat choice that are operating in natural populations promises to provide important new insights into how habitat choice contributes to diversification. Although more convincing empirical demonstrations of habitat choice mechanisms would be valuable, future empirical work should strive to go beyond demonstrating that habitat choice mechanisms occur to show that such mechanisms actually contribute to diversification and to assess whether such mechanisms differentially promote progress along the speciation continuum. To answer these questions, it is imperative that habitat choice mechanisms be consistently and accurately conceptualized in the literature and that empirical work be guided by the biology and natural history of species under study.

AUTHORS CONTRIBUTION

C.K. Akcali and C.K. Porter both wrote the manuscript.

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LITERATURE CITED

Armstrong, P. R., and J. E. Roughgarden. 2008. The structure of clines with fitness-dependent dispersal. *Am. Nat.* 172:648–657.

Beltman, J. B., P. Haccou, and C. ten Cate. 2004. Learning and colonization of new niches: a first step toward speciation. *Evolution* 58:35–46.

Beltman, J. B., and J. A. Metz. 2005. Speciation: more likely through a genetic or through a learned habitat preference? *Proc. R. Soc. B Biol. Sci.* 272:1455–1463.

Benkman, C. W. 2017. Matching habitat choice in nomadic crossbills appears most pronounced when food is most limiting. *Evolution* 71:778–785.

Berner, D., and X. Thibert-Plante. 2015. How mechanisms of habitat preference evolve and promote divergence with gene flow. *J. Evol. Biol.* 28:1641–1655.

Bolnick, D. I., L. K. Snowberg, C. Pattenia, W. E. Stutz, T. Ingram, and O. L. Lau. 2009. Phenotype-dependent native habitat preference facilitates divergence between parapatric lake and stream stickleback. *Evolution* 63:2004–2016.

Bolnick, D. I., and S. P. Otto. 2013. The magnitude of local adaptation under genotype-dependent dispersal. *Ecol. Evol.* 3:4722–4735.

Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sinauer, Sunderland, MA.

Cruz, R., C. Villas, J. Mosquera, and C. Garcia. 2004. Relative contribution of dispersal and natural selection to the maintenance of a hybrid zone in *Littorina*. *Evolution* 58:2734–2746.

De Meeüs, T., Y. Michalakis, F. Renaud, and I. Olivieri. 1993. Polymorphism in heterogeneous environments, evolution of habitat selection and sympatric speciation: soft and hard selection models. *Evol. Ecol.* 7:175–198.

Den Boer, P. J., T. H. P. Van Huizen, W. Den Boer-Daanje, B. Aukema, and C. F. M. Den Bieman. 1980. Wing polymorphism and dimorphism as stages in an evolutionary process (Coleoptera, Carabidae). *Entomol. Generalis* 6:107–134.

Desender, K. 1985. Wing polymorphism and reproductive biology in the halobiont carabid beetle *Pogonus chalceus* (Marsham) (Coleoptera, Carabidae). *Biol. Jaarboek* 53:89–100.

Desender, K., and J. Serrano. 1999. A genetic comparison of Atlantic and Mediterranean populations of a saltmarsh beetle. *Belgian J. Zool.* 129:83–94.

Dhuyvetter, H., E. Gaublomme, and K. Desender. 2004. Genetic differentiation and local adaptation in the salt-marsh beetle *Pogonus chalceus*: a comparison between allozyme and microsatellite loci. *Mol. Ecol.* 13:1065–1074.

Dhuyvetter, H., F. Hendrickx, E. Gaublomme, and K. Desender. 2007. Differentiation between two salt marsh beetle ecotypes: evidence for ongoing speciation. *Evolution* 61:184–193.

Diehl, S. R., and G. L. Bush. 1989. The role of habitat preference in adaptation and speciation. Pp. 345–365 *in* D. Otte, and J. A. Endler, eds. *Speciation and its consequences*. Sinauer, Sunderland, MA.

Edelaar, P., A. M. Siepelski, and J. Clobert. 2008. Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. *Evolution* 62:2462–2472.

Edelaar, P., and D. I. Bolnick. 2012. Non-random gene flow: an underappreciated force in evolution and ecology. *Trends Ecol. Evol.* 27:659–665.

Eroukhanoff, F., A. Hargeby, and E. I. Svensson. 2011. The role of different reproductive barriers during phenotypic divergence of isopod ecotypes. *Evolution* 65:2631–2640.

Felsenstein, J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* 35:124–138.

Fry, J. D. 2003. Multilocus models of sympatric speciation: Bush versus Rice versus Felsenstein. *Evolution* 57:1735–1746.

Gavrilets, S., and A. Vose. 2005. Dynamic patterns of adaptive radiation. *Proc. Natl. Acad. Sci. USA* 102:18040–18045.

Holt, R. D., and M. Barfield. 2008. Habitat selection and niche conservatism. *Israel J. Ecol. Evol.* 54:295–309.

Immelmann, K. 1975. Ecological significance of imprinting and early learning. *Ann. Rev. Ecol. Syst.* 6:15–37.

Jaenike, J., and R. D. Holt. 1991. Genetic variation for habitat preference: evidence and explanations. *Am. Nat.* 137:S67–S90.

Jiang, Y., L. Torrance, C. L. Peichel, and D. I. Bolnick. 2015. Differences in rheotactic responses contribute to divergent habitat use between parapatric lake and stream threespine stickleback. *Evolution* 69:2517–2524.

Jiang, Y., C. L. Peichel, L. Torrance, Z. Rivzi, S. Thompson, V. V. Palivela, H. Pham, F. Ling, and D. I. Bolnick. 2016. Sensory trait variation contributes

- to biased dispersal of threespine stickleback in flowing water. *J. Evol. Biol.* 30:681–695.
- Johnson, P. A., F. C. Hoppensteadt, J. J. Smith, and G. L. Bush. 1996. Conditions for sympatric speciation: a diploid model incorporating habitat fidelity and non-habitat assortative mating. *Evol. Ecol.* 10:187–205.
- Kawecki, T. J. 1996. Sympatric speciation driven by beneficial mutations. *Proc. R Soc. B Biol. Sci.* 263:1515–1520.
- MacCallum, C. J., B. Nümberger, N. H. Barton, and J. M. Szymura. 1998. Habitat preference in the *Bombina* hybrid zone in Croatia. *Evolution* 52:227–239.
- Matsubayashi, K. W., I. Ohshima, and P. Nosil. 2010. Ecological speciation in phytophagous insects. *Entomol. Exp. Appl.* 134:1–27.
- Maynard Smith, S. J. 1966. Sympatric speciation. *Am. Nat.* 100:637–650.
- Nonaka, E., R. Svanbäck, X. Thibert-Plante, and G. Englund. 2015. Mechanisms by which phenotypic plasticity affects adaptive divergence and ecological speciation. *The Am. Nat.* 186:E126–E143.
- Nosil, P. 2012. *Ecological speciation*. Oxford Univ. Press, New York.
- Pfennig, D. W., M. A. Wund, E. C. Snell-Rood, T. Cruickshank, C. D. Schlitting, and A. P. Moczek. 2010. Phenotypic plasticity's impacts on diversification and speciation. *Trends Ecol. Evol.* 25:459–467.
- Raeymaekers, J. A. M., and T. Backeljau. 2015. Recurrent adaptation in a low-dispersal trait. *Mol. Ecol.* 24:699–701.
- Ravigné, V., I. Olivieri, and U. Dieckmann. 2004. Implications of habitat choice for protected polymorphisms. *Evol. Ecol. Res.* 6:125–145.
- Ravigné, V., U. Dieckmann, and I. Olivieri. 2009. Live where you thrive: joint evolution of habitat choice and local adaptation facilitates specialization and promotes diversity. *Am. Nat.* 174:E141–E169.
- Rice, W. R. 1984. Disruptive selection on habitat preference and the evolution of reproductive isolation: a simulation study. *Evolution* 38:1251–1260.
- Richardson, J. L., M. C. Urban, D. I. Bolnick, and D. K. Skelly. 2014. Microgeographic adaptation and the spatial scale of evolution. *Trends Ecol. Evol.* 29:165–176.
- Richter-Boix, A., M. Quintela, M. Kierczak, M. Franch, and A. Laurila. 2013. Fine-grained adaptive divergence in an amphibian: genetic basis of phenotypic divergence and the role of nonrandom gene flow in restricting effective migration among wetlands. *Mol. Ecol.* 22:1322–1340.
- Schemske, D. W. 2010. Adaptation and the origin of species. *Am. Nat.* 176:S4–S25.
- Schulter, D. 2009. Evidence for ecological speciation and its alternative. *Science* 323:737–741.
- Sobel, J. M., G. F. Chen, L. R. Watt, and D. W. Schemske. 2010. The biology of speciation. *Evolution* 64:295–315.
- Stamps, J. A., V. V. Krishnan, and N. H. Willits. 2009. How different types of natal experience affect habitat preference. *Am. Nat.* 174:623–630.
- Thibert-Plante, X., and S. Gavrillets. 2013. Evolution of mate choice and the so-called magic traits in ecological speciation. *Ecol. Lett.* 16:1004–1013.
- Urban, M. C. 2010. Microgeographic adaptations of spotted salamander morphological defenses in response to a predaceous salamander and beetle. *Oikos* 119:646–658.
- Van Belleghem, S. M., K. De Wolf, and F. Hendrickx. 2016. Behavioral adaptations imply a direct link between ecological specialization and reproductive isolation in a sympatrically diverging ground beetle. *Evolution* 70:1904–1912.
- Webster, S. E., J. Galindo, J. W. Grahame, and R. K. Butlin. 2012. Habitat choice and speciation. *Int. J. Ecol.* 2012:1–12.

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