

Opinion piece



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Animal behaviour

Habitat choice promotes and constrains phenotypic plasticity

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Habitat choice can either speed up or slow rates of phenotypic evolution, depending on which trait is measured. We suggest that habitat choice plays an analogous, and generally overlooked, role in shaping patterns of phenotypic plasticity. Using our work with an amphibious fish, we discuss two case studies that demonstrate how habitat choice can both promote and constrain expression of plasticity. First, habitat choice during the dry season accentuates adaptive metabolic plasticity and minimizes maladaptive changes to muscle, ultimately increasing survival time out of water. Second, a trade-off between water- and air-breathing drives matching habitat choice, resulting in positive feedback that reinforces respiratory specialization and environmental preference. Overall, these case studies demonstrate that we must consider the interactions between plasticity and habitat choice to fully understand how animals survive in the face of environmental change. Without considering both processes simultaneously, the performance of animals in challenging conditions can be either under- or over-estimated. Finally, because habitat choice shapes the frequency and predictability of environmental changes that animals experience, feedback between habitat choice and expressions of phenotypic plasticity may be an important factor that influences how plasticity evolves.

1. Introduction

Environmental conditions vary predictably and stochastically across space and time. Understanding how organisms cope with this variability is critical for understanding many fundamental biological processes and for predicting responses to anthropogenic influences such as climate change [1–3]. When an environment changes, a common refrain is that animals can change phenotypes (via plasticity or adaptation, depending on timescales), move or die. While this is a useful general framework, the result is that adaptation/plasticity and habitat selection are often considered in isolation. Several recent studies have highlighted, however, that integrating these processes can be critical for understanding evolutionary responses to changing environments (i.e. these studies provide ultimate explanations for why plasticity and habitat choice evolve) [4–7]. Here, we argue that our proximate understanding of organismal responses to environmental variability would similarly benefit from considering phenotypic plasticity and habitat choice in tandem.

Habitat choice allows mobile animals to match the environment to their phenotype [8–10]. In its simplest form, habitat choice occurs when animals assess various environmental parameters and choose to live in a subset of available habitats where fitness is likely maximized [10–12]. Habitat choice can have a genetic basis and can be further refined by an individual's prior experience and expressed phenotype [13,14]. This 'matching habitat choice' occurs when individuals sample and compare different environments and settle in those that best match their phenotype [14–17]. For example, grasshoppers painted

black choose darker environments compared to those painted white, presumably to improve camouflage [18].

Habitat choice directly shapes the selective environment an animal experiences and thus can influence evolutionary processes [8,9,19]. Habitat choice can increase rates of phenotypic evolution by exposing animals to novel environments in which selection can act [20,21] or decrease rates of evolution by 'buffering' the environment that animals experience [22–24]. In some cases, habitat choice does both simultaneously depending on what trait is measured [6,19]. For example, arboreal anole lizards at low elevations perch on tree trunks and branches to avoid overly hot microenvironments, while at high elevations, these typically arboreal lizards thermoregulate by eschewing tree trunks and instead bask on boulders, which are warmer. This habitat selection effectively homogenizes the temperatures the lizards experience across elevations and thus constrains the evolution of thermal physiology, but the differences in preferred substrate cause evolved skeletal changes to maximize locomotor capabilities in each habitat [6]. In this way, matching habitat choice can promote local adaptation [7,13,18]. If individual phenotypic differences and their resulting habitat choices are heritable, then positive feedback between these processes should strengthen each of them and promote local specialization [13,25–27]. While the above processes act over evolutionary timescales, we suggest that analogous processes also occur within the lifetimes of individual animals due to interactions between phenotypic plasticity and habitat choice (figure 1).

Phenotypic plasticity is the ability of an organism to express alternative phenotypes depending on environmental conditions [21,28,29]. In spatially and temporally variable environments, high site fidelity is generally thought to promote plasticity, while habitat selection that minimizes the magnitude of experienced environmental change should blunt plasticity, although these patterns are complex and depend on the scale and tempo of environmental change [4,30]. The thermal physiology of some lizards, for example, exhibits surprisingly little plasticity because behavioural thermoregulation (often resulting from shifts in habitat use) maintains relatively constant body temperature [31,32]. In salamanders, matching habitat choice apparently causes individuals that are better swimmers to occupy faster flowing water than relatively poor swimmers; morphological plasticity then reinforces this phenotypic divergence [33]. However, in general, there has been little explicit consideration of how habitat choice and phenotypic plasticity interact [34].

Here, we discuss two case studies from our own work that highlight the importance of studying both habitat choice and phenotypic plasticity to understand how animals cope with variable environments. These studies have focused on the transition between aquatic and terrestrial habitats in an amphibious fish, the mangrove rivulus *Kryptolebias marmoratus*. Amphibious fishes are excellent models for investigating links between habitat choice and plasticity. The dramatic differences in physical properties between water and air pose many morphological and physiological challenges that are ameliorated using plasticity [35,36], and the discrete boundary between these environments simplifies measurement of habitat choice. In the wild, mangrove rivulus live in small ponds and crab burrows throughout mangrove forests of the tropical western Atlantic [37]. Abiotic conditions in these habitats are highly variable [38,39], and

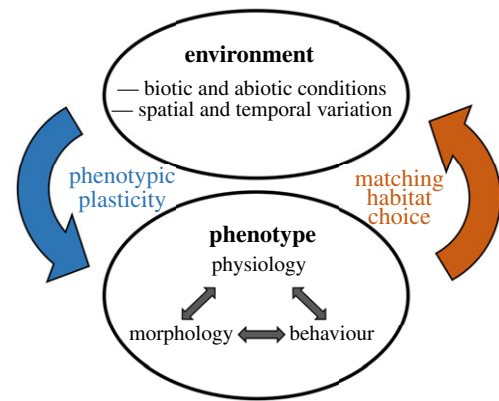


Figure 1. Schematic of possible interactions between environmental conditions and the organismal phenotype. Variation in biotic and abiotic environmental conditions influences the phenotype via plasticity (blue arrow). Phenotypic plasticity often shapes an integrated suite of physiological, morphological and behavioural traits (grey arrows). The expressed phenotype of an animal can also influence the environmental conditions it experiences via matching habitat choice (orange arrow). In this way, phenotypic plasticity and matching habitat choice can influence the strength of the other process via negative or positive feedback. Moreover, patterns of phenotypic plasticity and habitat choice may either be fixed or plastic.

mangrove rivulus often move onto land to cope with the onset of harsh aquatic conditions [39–41]. Water also disappears completely during the dry season [42]. In our first case study, we discuss how habitat choice during the dry season accentuates adaptive physiological plasticity and minimizes maladaptive plasticity to increase survival out of water. Second, we discuss how morphological plasticity and matching habitat choice resulting from performance trade-offs can reinforce each other via positive feedback. Finally, we summarize the importance of integrating habitat choice with plasticity for understanding the environmental tolerances of animals and the evolution of these two processes.

(a) Case study 1: hypoxia-seeking behaviour accentuates metabolic depression

During the dry season, mangrove rivulus must survive in a terrestrial environment for several months [42]. Since these fish are unable to eat on land, like many amphibious fishes, surviving seasonal droughts is dependent on their ability to conserve endogenous energy stores by entering a hypometabolic state [43,44]. Under laboratory conditions, rivulus depress metabolic rate by approximately 40% after three weeks in air [43]. Recently, we discovered that habitat selection in response to prolonged terrestrial exposure accentuates this metabolic plasticity, leading to a suite of potential fitness benefits [44].

The drying of mangrove pools causes rivulus to move into leaf litter or insect tunnels within decaying logs [45]. These logs stay moist long after standing water disappears [42] and are thought to become severely hypoxic owing to the respiratory processes of microbes and insects (as low as 12% air saturation; [46]). Since environmental hypoxia has been reported to depress metabolism in several ectothermic animals (e.g. [47,48]), we hypothesized that rivulus seek hypoxic log microhabitats that in turn accentuate metabolic depression during seasonal droughts. Consistent with this

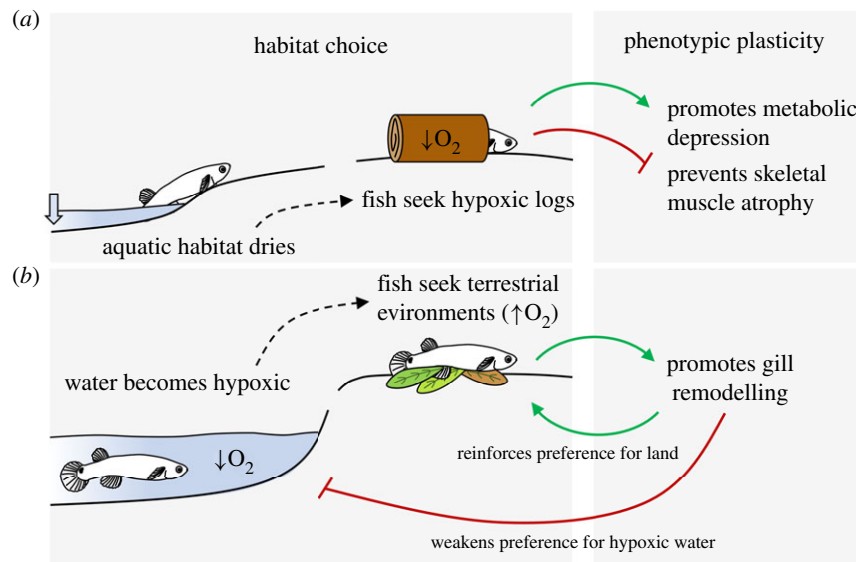


Figure 2. Case studies illustrating how habitat choice can promote and constrain the expression of phenotypic plasticity. (a) Mangrove rivulus seek refuge in moist, hypoxic logs in response to habitat drying [44]. This habitat choice promotes metabolic plasticity and constrains maladaptive skeletal muscle plasticity (i.e. atrophy). (b) Mangrove rivulus escape aquatic hypoxia by moving to land. This habitat choice promotes morphological gill plasticity that impairs respiratory performance in water [38,49,50]. A positive feedback loop may therefore promote fidelity to the terrestrial environment.

idea, we discovered that fish strongly prefer hypoxic terrestrial habitats after three weeks in air [44]. Furthermore, we found that exposure to aerial hypoxia (approx. 9 kPa) accentuated metabolic depression by more than 15%. In a separate experiment, we maintained fish in aerial hypoxia for three weeks and discovered that these fish considerably slowed their use of energetic substrates (e.g. lipid) compared to fish in normoxia, and these energy savings protected muscle protein and, in turn, terrestrial locomotor performance [44]. Taken together, our results show that hypoxic microhabitat selection acts to enhance plasticity in rivulus by accentuating metabolic depression but also blunts maladaptive changes to the structure and function of the skeletal musculature (figure 2a).

Mangrove rivulus is probably not the only ectothermic species that exploits hypoxic habitats during periods of dormancy. Many other fishes [51,52], amphibians [47,53,54] and reptiles [55,56] aestivate/hibernate/brumate within subterranean burrows or beneath the ice of frozen lakes. Is hypoxic habitat selection widespread among dormant taxa? Using the green-striped burrowing frog (*Cyclorana alboguttata*) that aestivates in hypoxic underground burrows, we tested the hypothesis that frogs seek hypoxic microhabitats that in turn accentuate metabolic depression during aestivation. Similar to rivulus, we found that burrowing frogs had a strong preference for hypoxic habitats in response to drying conditions, and when maintained under hypoxic conditions, they had significantly lower metabolic rates at the onset of aestivation [57]. Remarkably, the deeper metabolic depression of hypoxia-exposed frogs was estimated to extend their survival time in an aestivating state by almost 50%, from 180 to 267 days. If climatic changes lead to longer and more severe seasonal droughts, microhabitat selection strategies that help animals economize on endogenous reserves may be critical for their survival. For example, conservation of energy stores is so important for the survival of dormant water-holding frogs (*Litoria platycephala*) that persistence of entire populations is thought to depend on just a few large individuals with enough energy stores to survive extended droughts [58].

(b) Case study 2: positive feedback between respiratory phenotype and habitat choice

Wild mangrove rivulus must often contend with severe aquatic hypoxia that may limit metabolism [38,39]. One solution is to use phenotypic plasticity to increase respiratory performance. Acclimation to aquatic hypoxia involves reversibly increasing gill surface area to maximize oxygen uptake [49] and increasing the concentration and oxygen binding affinity of haemoglobin to aid oxygen transport [59]. Alternatively, amphibious fishes such as rivulus can escape aquatic hypoxia by moving onto land and breathing atmospheric air [40,60]. Increased effective gravity on land, however, imposes other challenges on the respiratory system of amphibious fishes including the collapse of delicate gill lamellae [61,62]. To protect their gills from damage on land, rivulus reversibly fill the spaces between lamellae with a proliferative group of cells known as the inter-lamellar cell mass (ILCM; [63]). Importantly, this adjustment decreases gill surface area via the same mechanism used to increase surface area during acclimation to aquatic hypoxia. Terrestrially acclimated rivulus therefore suffer impaired aquatic respiratory function and are less tolerant of aquatic hypoxia relative to fish acclimated to water [49,50]. Because gill remodelling via ILCM adjustment is a relatively slow process (3–7 days, [63]) and imposes strong respiratory trade-offs between environments, we have hypothesized that gill phenotype may be a strong driver of matching habitat choice [38,49,50]. In turn, matching habitat choice may induce an extreme terrestrial gill phenotype [50,64] that further strengthens habitat choice, resulting in a positive feedback loop that promotes habitat fidelity (figure 2b).

Some of our best evidence to date for positive feedback between habitat choice and phenotypic plasticity comes from a field study of two populations of mangrove rivulus [38]. We compared the respiratory function of fish captured from severely hypoxic crab burrows and a relatively well-oxygenated pond. If rivulus had acclimated or adapted to the aquatic conditions at each site, we would expect improved respiratory

function in crab burrow fish relative to pond fish; instead, we found the opposite result. Aquatic respiratory function was lower in crab burrow fish (i.e. higher critical oxygen tension), and these fish also had reduced gill surface area due to enlarged ILCMs. Next, we tested the possibility that crab burrow fish were avoiding aquatic hypoxia by moving onto land. We discovered that these fish spent almost 90% of their time out of water, more than three times more than pond fish, consistent with hypoxic avoidance. Overall, we hypothesize that crab burrow fish avoided aquatic hypoxia by moving onto land, which caused ILCM enlargement, reduced respiratory function and further increased the tendency to choose terrestrial habitats.

We recently used laboratory experiments to further test the hypothesis that positive feedback can drive extreme phenotypes [50]. First, we found that terrestrially acclimated rivulus were less tolerant of aquatic hypoxia (faster time to loss of equilibrium under severe hypoxia) and were more behaviourally sensitive to aquatic hypoxia than fish acclimated to water [50]. Next, we acclimated fish to severe aquatic hypoxia for 7 days while allowing them access to land. As predicted by our positive feedback hypothesis, and opposite to what we have found in hypoxia-acclimated rivulus that cannot leave water [49], hypoxia-acclimated rivulus developed large ILCMs and decreased hypoxia tolerance relative to rivulus acclimated to normoxic water. In this case, the choice to avoid aquatic hypoxia first promotes phenotypic plasticity, but matching habitat choice then blunts further plasticity that would otherwise be associated with the return to water. This type of feedback loop may have important implications for understanding habitat transitions, as it should both limit the occurrence of habitat switching but also quickly reinforce phenotype–environment matching in a novel environment when transitions do occur.

2. Conclusion

Our view is that the relationship between phenotypic plasticity and habitat choice needs to be considered to fully understand how animals interact with their environments and cope with changing conditions. While the phenomenon of matching habitat choice is starting to be recognized as a powerful force in ecology and evolution [7,14,18], we highlight that habitat choice can also promote and constrain phenotypic plasticity, ultimately influencing subsequent habitat selection strategies (figure 1). Moreover, an animal's tolerance of stressful conditions can be under- or over-estimated depending on our consideration of each process. In case study 1 (§1a), we show how habitat selection accentuates metabolic plasticity in fish and frogs. Failure to consider both these processes simultaneously would lead us to underestimate the tolerance of these animals to dry season

conditions. By contrast, case study 2 (§1b) shows that we would overestimate tolerance of severe aquatic hypoxia under natural conditions if we focus solely on physiological acclimatization to forced hypoxic exposure and neglect habitat choice. Since accurately measuring the environmental tolerances of animals can be important for predicting responses to anthropogenic influences such as climate change [1–3], we encourage researchers to take a wholistic view of how organisms interact with their environment. This includes considering the rate and predictability of environmental variation, as well as understanding how habitat choice and the scope for plasticity change across the life stages of individuals. While our examples focus on our work using amphibious fish, there is potential for feedback between habitat choice and plasticity to occur in diverse mobile organisms, including protists [65] and protostomes [66–68] as well as vertebrates.

Understanding how habitat choice interacts with expressions of phenotypic plasticity may have fundamental implications for how plasticity evolves. In general, plasticity evolves in heterogeneous habitats, but the frequency, magnitude and predictability of environmental change are all important mediating factors [69,70]. For example, plasticity is thought to be favoured in environments that fluctuate relatively slowly and predictably relative to the speed at which animals can respond, but a non-plastic generalist strategy is favoured if conditions change faster than plastic changes can be expressed or if environmental cues are unreliable [30,70,71]. Recent modelling studies also suggest that selection may favour plasticity over habitat choice in variable environments, especially if fluctuations occur temporally [4,5]. Importantly, however, behavioural habitat choice allows animals to directly influence the frequency, magnitude and predictability of the environmental changes that are experienced. Feedback between plasticity and habitat choice has not received much attention to date, but it could be an important factor that influences how phenotypic plasticity evolves in addition to how it is expressed.

Data accessibility. This article has no additional information.

Authors' contributions. A.J.T.: conceptualization, funding acquisition, visualization, writing—original draft, writing—review and editing; G.S.R.: conceptualization, funding acquisition, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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