

The effect of natal experience on habitat preferences

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Several important problems in ecology, evolution and conservation biology are affected by habitat selection in dispersing animals. Experience in the natal habitat has long been considered a potential source of variation in the habitat preferences displayed when dispersers select a post-dispersal habitat. However, the taxonomic breadth of this phenomenon is underappreciated, in part because partially overlapping, taxon-specific definitions in the literature have discouraged communication. Here, we explore the phenomenon of natal habitat preference induction (NHPI) and demonstrate that NHPI has been observed in a broad range of animal taxa. We consider the potential adaptive significance of NHPI, identify implications of its occurrence for problems in evolution, ecology and conservation biology, and encourage further study of this phenomenon.

The decisions that animals make when selecting a habitat affect both the ecological interactions in which they participate and the selective pressures that shape their phenotypes and those of their descendants. Consequently, individual variation in the behaviors involved in habitat selection is relevant to many larger scale evolutionary and ecological processes. For example, individual variation in habitat preferences can play a role in metapopulation dynamics [1], local adaptation [2] and sympatric speciation [3]. Natal habitat preference induction (NHPI), in which experience with a natal habitat shapes the habitat preferences of individuals, has long been recognized as a potentially important source of individual variation in habitat selection [4]. However, in part because scientists working with different taxa have used different terms to describe this phenomenon [4–6], it is currently unclear how frequently NHPI occurs and what the implications of its occurrence might be.

The terms used in taxon-specific literatures to describe the effect of natal experience on habitat preferences each include particular criteria that make comparisons across species difficult. In the entomological literature, ‘Hopkin’s host selection principle’ [5] implies that experience during the larval period is carried across metamorphosis to influence adult habitat preferences (Box 1). The term ‘habitat imprinting’, which is more often encountered in the vertebrate literature [4], implies that stimuli will have a stronger impact on preferences if encountered during a particular ‘sensitive period’ than if encountered at other

stages of life. However, as Dethier [7] noted in 1982, the mechanisms by which natal experiences affect later preferences are varied and might not necessarily involve sensitive periods. Dethier therefore endorsed the more general term ‘preference induction’ to describe situations in which experience with particular stimuli increases subsequent preferences for those same stimuli.

NHPI is a type of preference induction that occurs in a specific context: experience with stimuli in an individual’s natal habitat increases the probability that the individual will, following dispersal, select a habitat that contains comparable stimuli. The reason for focusing on situations in which natal experience affects the choice of a

Box 1. The timing of natal habitat preference induction

The life stage at which experience affects preference for a post-dispersal habitat has attracted attention in both the insect and vertebrate literatures. In entomology, one of the first hypotheses about the effects of natal experience on host preference (natal habitat preference induction, NHPI) was Hopkin’s host-selection principle [5]. Although not originally stated as such, this principle has been interpreted to mean that the relevant experience must occur during the larval stage of insect development. Empirical support for effects of larval experience on adult habitat preference has been meager (review in [5] but see [25,41]), perhaps because the brain of insects is greatly reorganized during metamorphosis [5]. However, several studies have shown that insect habitat preferences can be shaped by stimuli experienced by adults immediately after emergence from their pupae (Table 1 in main text). Because the habitat experienced by a newly emerged adult is typically similar to the habitat in which that individual developed, the stage at which the relevant experience occurs should rarely matter in terms of the ecological and evolutionary implications of NHPI [5,6].

Traditionally, the term ‘imprinting’ (most often encountered in the vertebrate literature) implies both the existence of a sensitive period during which the individual is susceptible to the influence of experience and that experience occurring after this sensitive period cannot reverse the effect [4]. However, many cases of NHPI, including some of those described as ‘habitat imprinting’, do not satisfy these criteria. For example, the permanence of preferences formed by natal experience varies across species. In some species, exposure to alternative stimuli later in life has little effect on preferences formed through induction in the natal habitat (e.g. [9,13,22]), whereas in others, experience with alternative habitats can reverse the effects of early induction [23]. However, in nature, once dispersers have selected a suitable habitat (e.g. as a result of NHPI), they might have little reason to travel to alternative habitats and hence would be unlikely to undergo the secondary shifts in preference that are generated in laboratory experiments. Generally, one would expect the relative impact of natal versus post-dispersal experience on habitat preferences to vary across species (e.g. as a function of the degree to which individuals remain faithful to the first site they select after dispersing from their natal habitat).

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post-dispersal habitat is that this is a context in which preference induction is likely to have a major impact on evolution and ecology. Note that this definition does not imply that individuals are more sensitive to experience before dispersal than they are later in life. Nor does it imply that individuals always prefer post-dispersal habitats containing the natal stimuli over every alternative habitat, only that they are more likely to select habitats with these stimuli than are individuals that originate from another type of habitat.

To demonstrate that NHPI affects habitat preferences, empirical studies must satisfy three criteria: (i) researchers should control for genetic variation in habitat preferences (e.g. by assigning individuals randomly to alternative natal habitats), (ii) experience with natal environments should occur before the age or ontogenetic stage at which individuals typically disperse from their natal habitat, and (iii) habitat preferences should be tested at ages or ontogenetic stages in which dispersers typically select a new habitat in which to live or reproduce. Using these criteria, we searched the literature and found evidence that NHPI occurs in a broad array of taxa (Table 1).

In addition, a wider search of the literature revealed many other studies that do not demonstrate NHPI *sensu stricto*, but which imply that natal experience in other taxa might affect subsequent habitat preferences. For example,

adult crab spiders (*Misumena vatia*) choose to hunt from the flower species they experienced during their final molt [8], and food preference induction has been demonstrated in arachnids [9], terrestrial snails [10], nudibranchs [11], snakes [12], turtles [13] and several mammals (e.g. [14]).

The adaptive significance of NHPI

Currently, hypotheses for the adaptive significance of NHPI fall into two categories [15]. Habitat cuing hypotheses suggest that preferences for stimuli comparable to those in the natal habitat might help dispersing individuals locate a suitable habitat quickly and efficiently. By contrast, preference-performance hypotheses suggest that successful dispersers enjoy higher fitness if they select a new habitat of the same type as their natal habitat [15].

Habitat cuing: recognizing a suitable habitat in a heterogeneous landscape

After leaving their natal habitats, dispersers are expected to be under strong selection to detect, recognize and quickly settle in suitable habitats. However, in many species, dispersers have difficulty assessing the relative quality of potential habitats accurately. For example, factors that affect habitat quality over the long term might not be apparent during the period when dispersers are selecting new habitats. Furthermore, the sampling

Table 1. Experiments demonstrating natal habitat preference induction^a

Taxonomic group	Species	Choice ^b	Refs
Insects			
Diptera	<i>Drosophila melanogaster</i> (vinegar fly)	H	[24]
	<i>Musca domestica</i> (house fly)	H	[25]
	<i>Rhagoletis pomonella</i> (apple maggot fly)	H	[26]
	<i>Culex quinquefasciatus</i> (mosquito)	O	[27]
Lepidoptera	<i>Spodoptera littoralis</i> (noctuid moth)	O	[28]
Hymenoptera	<i>Tetravormium aculeatum</i> (ant)	H	[29]
	<i>Oecophylla longinoda</i> (ant)	H	[29]
	<i>Pachycondyla villosa</i> (ant)	H	[30]
	<i>Microplitis croceipes</i> (parasitoid wasp)	H	[31]
	<i>Dianarmus basalis</i> (parasitoid wasp)	O	[32]
	<i>Nemeritis canescens</i> (parasitoid wasp)	O, H	[33]
	<i>Eupelmus vuilleti</i> (parasitoid wasp)	O, H	[34]
	<i>Cotesia plutellae</i> (parasitoid wasp)	H	[35]
	<i>Nasonia vitripennis</i> (parasitoid wasp)	O	[36]
	<i>Anagrus nigriventis</i> (parasitoid wasp)	H	[37]
	<i>Aphidius colemani</i> (parasitoid wasp)	H	[38]
	<i>Pachycrepoides vindemiae</i> (parasitoid wasp)	O	[39]
	<i>Trichogramma nr ivelae</i> (parasitoid wasp)	O	[40]
Coleoptera	<i>Euchrychiopsis lecontei</i> (weevil)	F, H	[20]
	<i>Sitophilus granaries</i> (weevil)	F, H	[41]
Fish			
	<i>Amphiprion melanopus</i> (clownfish)	H	[42]
	<i>Amphiprion ocellaris</i> (clownfish)	H	[43]
Amphibians			
	<i>Desmognathus ochrophaeus</i> (dusky salamander)	H	[44]
	<i>Rana temporaria</i> (common frog)	H	[45]
Birds			
	<i>Tyniopygia castanotis</i> (zebra finch)	N	[46]
	<i>Parus ater</i> (coal tit)	H	[47]
	<i>Dendroica pensylvanica</i> (chestnut-sided warbler)	H	[48]
	<i>Acrocephalus melanopogon</i> (moustached warbler)	H	[49]
	<i>Spizella passerine</i> (chipping sparrow)	H	[50]
	<i>Vidua chalybeate</i> (indigobird)	O	[51]
	<i>Cuculus canorus</i> (cuckoo)	H	[21]
	<i>Tyto alba guttata</i> (barn owl)	H, N	[22]
Mammals			
	<i>Peromyscus maniculatus</i> (deer mouse)	H	[52]

^aCases in which: (i) individuals were assigned randomly to different natal habitats to control for genetic variation in habitat preferences; (ii) experience or training was provided to subjects at an age before the typical age of dispersal and (iii) preference was tested at an age at which dispersers would typically select a new habitat.

^bThe type of preference tested: H, habitat; F, food; O, oviposition site; N, nest site

required to assess habitat quality accurately involves time and risk, and energy invested in sampling potential habitats is unavailable to support activities that enhance fitness after settlement, such as establishing a territory and producing offspring [15].

NHPI provides a risk-averse solution to this problem by ensuring that dispersers can quickly and reliably recognize at least one type of suitable habitat that exists in the current landscape at the current time. In particular, habitats comparable to the natal habitat of the individual must be suitable for residency and reproduction because the dispersing individual itself survived to the age of dispersal. A preference for habitats comparable to the natal habitat implies that a disperser might bypass a habitat of higher quality than its natal habitat, but it also reduces the risk of selecting a habitat in which the disperser has a low probability of survival or reproduction.

Generally speaking, habitat cuing is important when dispersers are faced with a range of similar habitats that are difficult to discriminate from one another, when habitat assessment is costly (e.g. because of a high risk of predation while sampling prospective habitats), and when individuals are site-faithful after settlement, so that the initial choice of a habitat has a strong impact on lifetime reproductive success.

Matching preference and performance: finding the right home for you

Classic models of habitat selection by dispersers assume that, in a given landscape at a given time, a particular habitat is equally suitable for all the individuals in that population [15]. However, recent studies have begun to emphasize individual differences in traits associated with fitness, and suggest that individuals differ in terms of the niche that suits them best [16]. When individuals differ in their potential for success in different environments, selection should favor mechanisms that help individuals select and use habitats that best suit their phenotype. If the habitat type that an individual experiences before dispersal is the type to which its phenotype is best suited, NHPI is one such mechanism.

One reason that animals might perform better in habitats of the same type as their natal habitat is that different types of habitat exert different selective pressures on individuals before dispersal. In this situation, selection on eggs, juveniles or other pre-dispersal stages would be expected to weed out phenotypes that are ill adapted to that type of habitat. Indeed, habitat-specific selection could affect phenotype distributions even after dispersers have left their natal habitat (e.g. if ill-adapted phenotypes were in worse condition at departure and, hence, less likely to reach a new patch of habitat). This suggests that, as a result of selection in the natal habitat, immigrants originating from one type of natal habitat would have different phenotypes compared with those originating from a different type of natal habitat. Hence, to the extent that individuals experience the same types of selective pressure in their natal and post-dispersal habitats, individuals from a particular type of habitat might perform better if they recruit to the same type of habitat.

In species with a pronounced metamorphosis (e.g. holometabolous insects), individuals are likely to experience different types of selective pressures as juveniles in their natal habitats and as adults in their post-dispersal habitats. However, NHPI can also be advantageous in this situation if some of the variation in juvenile success in particular types of natal habitat is a result of heritable differences. In that situation, individuals that survived in a given type of natal habitat would be more likely to have successful offspring if they placed them in the same type of habitat.

Adaptive plasticity can also produce a positive correlation between the natal habitat type of an individual and its optimal post-dispersal habitat. Many aspects of the phenotypes of animals are shaped by the environments that they experience before dispersal, making them particularly well suited to those habitats. Adaptive behavioral, physiological and morphological plasticity is common; examples include learning how to recognize, capture and handle food (e.g. [17]), the upregulation of enzymes required to utilize previously eaten foods effectively (e.g. [14]), and the development of appendages that are well suited to the locomotor style favored in a particular habitat (e.g. [18]). These forms of plasticity act to make individuals better suited to life in their natal habitat, often at the expense of the ability to perform well in other types of habitat. For example, in several species of ruminants, individuals unfamiliar with a particular environment spend 20% more time eating, but ingest 40% less food compared with conspecifics with previous experience in the same environment [14]. Therefore, when the natal environment shapes adaptively plastic traits, NHPI will encourage individuals to select the best habitat for their modified phenotype.

Implications of NHPI for ecology and evolution

NHPI has three effects on habitat selection that are particularly relevant to the study of ecology and evolution. First, it is a predictable source of individual differences in habitat preferences. Second, NHPI provides a mechanism by which individuals are more likely to select habitats to which they are best suited, thus encouraging the maintenance of genetic variation in heterogeneous landscapes. Finally, NHPI acts as a mechanism for the extragenetic inheritance of phenotypically plastic traits in which expression depends on the natal environment.

The predictable variation in habitat preferences generated by NHPI is particularly relevant to problems in ecology because ecologists often ignore individual variation in resource and habitat use [16]. For example, if dispersers prefer their natal habitat type, then rates of dispersal between different patches in the same landscape will be influenced by the degree of similarity between them. In turn, biased dispersal will affect source-sink dynamics, patch extinction and rates of colonization of empty patches [1].

NHPI can affect the maintenance of genetic variation in populations by encouraging individuals to select the type of habitat in which they are likely to be most successful. Traditionally, environmental heterogeneity has been thought to play an important role in the

maintenance of genetic variation because different genotypes are likely to be favored in different types of environment. However, random dispersal between different types of habitat will produce gene flow that limits local adaptation and the conditions under which genetic polymorphisms remain stable [2]. NHPI is a behavioral mechanism that generates adaptively non-random dispersal: individuals are more likely to select habitats in which they (or their offspring) are likely to perform well after arrival. Hence, in species with NHPI, environmental heterogeneity might maintain genetic variation despite high rates of dispersal.

NHPI can encourage the extragenetic inheritance of phenotypically plastic traits by providing a comparable natal environment for parents and their offspring. This is because NHPI not only encourages the extragenetic inheritance of habitat preferences, but also the extragenetic inheritance of all traits for which the development is affected by experiential factors in the natal environment. For instance, in species with environmental sex determination (e.g. turtles), all behavioral mechanisms that encourage mothers and offspring to select similar types of environments for reproduction will facilitate the extragenetic inheritance of sex ratios [19].

NHPI and the extragenetic inheritance of habitat preferences might play an important role in the colonization of new habitat types, the expansion of host ranges and the formation of host races [4,20]. Imagine a small group of pioneering individuals that find themselves in a novel habitat in which they manage to reproduce. If habitat preferences are formed independently of natal experience, their offspring would be likely to return to the types of habitat used by the rest of the population. With NHPI, their offspring would be more likely to recruit to the novel type of habitat. Similarly, if individuals of both sexes prefer their natal type of habitat after dispersal, and if mating occurs within preferred habitats, then NHPI can encourage the formation of races. For instance, the formation and maintenance of host races in brood-parasitic cuckoos is a consequence of host fidelity that is driven, at least in part, by NHPI [21]. In extreme cases, the combination of reduced gene flow and local adaptation facilitated by NHPI might lead eventually to speciation [3].

Future directions

At this point, NHPI in the strict sense has been observed in relatively few species (Table 1), so additional studies of this phenomenon are necessary. We hope that the ecologically based definition of NHPI adopted in the current paper will encourage research on this phenomenon in taxa in which NHPI has not yet been investigated.

Additional studies on NHPI are also required to answer broad-scale questions about its adaptive value and evolution. For instance, comparative studies of NHPI in related taxa might help identify the types of ecological factors (e.g. spatial and/or temporal environmental heterogeneity) that favor or disfavor the use of natal stimuli when dispersers are searching for a new habitat. Similarly, further research might uncover general patterns that provide insight into the processes responsible for NHPI. One interesting example is evidence from several taxa of

systematic bias in the effects of natal stimuli on habitat preference, such that natal experience with cues from commonly used environments has a stronger effect on later habitat preference than does experience with cues from rarely used environments. This pattern is observed in the clownfish, *Amphiprion melanopus*, which associates with the sea anemone species, *Entacmaea quadricolor* in the wild. If *A. melanopus* fry have early experience with odors from *E. quadricolor*, they quickly accept them as hosts later in life. By contrast, if they are raised with a non-host anemone (*Heteractis malu*) or with no experience with any anemone, they are slow to accept either anemone host and show no preference between host and non-host anemones [42,43]. This pattern of 'unidirectional' NHPI might represent the product of continued selection on an environmentally induced preference, and therefore provide insight into how such plastic traits evolve.

NHPI has long been considered a potentially important behavioral mechanism, but taxon-specific terminology has led many authors to consider it a mere curiosity

Box 2. Ecological applications of NHPI

Natal habitat preference induction (NHPI) has obvious relevance for problems in applied ecology, including conservation biology, pest management and range management. To date, three basic insights from research on NHPI seem particularly relevant for ecological applications.

Early experience can affect the habitat preferences of adults

An NHPI perspective argues that attempts to reintroduce animals to empty reserves or restored habitats are more likely to meet with success if animals are released in habitats comparable to those in which they were raised. Indeed, much of our understanding of the importance of early experience in conservation has grown out of failed attempts at reintroduction [53]. Similarly, given the evidence that NHPI is important for insect parasitoids, success rates of biological control efforts might be higher if parasitoid wasps are reared on hosts and/or host plants that are similar to those that they are expected to be associated with after release [54].

Habitat preferences can be manipulated via early experience

NHPI might be useful for designing particular habitat preferences for applied purposes. For instance, Provenza and Balph [14] suggest that training young domestic ruminants to use particular types of range might help ranchers expand the types of habitat used by their stock and avoid the overutilization of sensitive areas. Similarly, Djieto-Lordon and Dejean [29] suggest that ant species that form ant-plant mutualisms (where the ants protect the plants from herbivores) might be manipulated via NHPI to build their nests in crop plants in the tropics, thus providing these plants with resident biocontrols. An advantage of using NHPI to manipulate habitat preferences is that if the individuals are successful in their new habitats, then these preferences are likely to be inherited, reducing requirements for additional training in subsequent generations.

Species differ in their propensity to exhibit NHPI

Because species differ with respect to the effects of natal experience on adult habitat preference (e.g. [42,49]), tests for NHPI before release might help reduce the unintended transfer of species to non-target hosts or habitats. For instance, selecting the most effective parasitoid for biological pest control might involve raising prospective parasitoids on intended and non-intended hosts to screen out species that are likely to shift from the former to the latter. Similarly, testing for NHPI might be an important component in the risk assessment of potentially invasive species.

irrelevant to habitat selection in most animals. By generating an ecological definition that focuses on the habitat selection of natal dispersers, and by noting the range of species that satisfy the criteria for NHPI under this definition, we have shown that NHPI might be more common than previously suspected. Given the implications of NHPI for current problems in basic and applied behavior (Box 2), ecology and evolution, we suspect that research into in this phenomenon will continue to accelerate in the near future.

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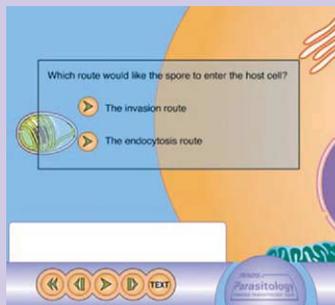
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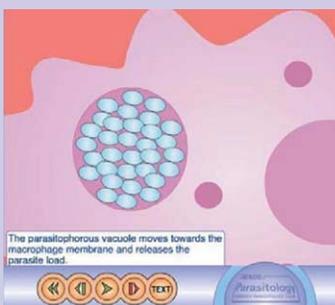
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