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Jean-Michel Gaillard

Universite Lyon, gaillard@biomserv.univ-lyon1.fr

Mark Hebblewhite

University of Montana - Missoula, mark.hebblewhite@umontana.edu

Anne Loison

Universite de Savoie

Mark Fuller

US Geological Survey, Forest and Rangeland Ecosystem Science Center

Roger Powell

North Carolina State University at Raleigh

See next page for additional authors

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Authors

Jean-Michel Gaillard, Mark Hebblewhite, Anne Loison, Mark Fuller, Roger Powell, Mathieu Basille, and Bram Van Moorter

Review

Habitat–performance relationships: finding the right metric at a given spatial scale

Jean-Michel Gaillard^{1,*}, Mark Hebblewhite², Anne Loison³,
Mark Fuller⁴, Roger Powell⁵, Mathieu Basille^{1,6}
and Bram Van Moorter¹

¹*Unité Mixte de Recherche CNRS-Université Lyon 1 N° 5558 ‘Biométrie et Biologie Evolutive’,
Bâtiment Gregor Mendel, 43 boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France*

²*Wildlife Biology Program, College of Forestry and Conservation, University of Montana,
Missoula, MT 59812, USA*

³*Unité Mixte de Recherche CNRS-Université de Savoie N° 5553 ‘Laboratoire d’Ecologie Alpine’,
Université de Savoie, 73370 Le Bourget du Lac, France*

⁴*US Geological Survey, Forest and Rangeland Ecosystem Science Center, 970 Lusk Street,
Boise, ID 83706, USA*

⁵*Department of Zoology, North Carolina State University, Raleigh, NC 27695, USA*

⁶*Centre d’Étude de la Forêt and Département de Biologie, Université Laval, Sainte-Foy,
Québec, Canada G1V 0A6*

The field of habitat ecology has been muddled by imprecise terminology regarding what constitutes habitat, and how importance is measured through use, selection, avoidance and other bio-statistical terminology. Added to the confusion is the idea that habitat is scale-specific. Despite these conceptual difficulties, ecologists have made advances in understanding ‘how habitats are important to animals’, and data from animal-borne global positioning system (GPS) units have the potential to help this clarification. Here, we propose a new conceptual framework to connect habitats with measures of animal performance itself—towards assessing habitat–performance relationship (HPR). Long-term studies will be needed to estimate consequences of habitat selection for animal performance. GPS data from wildlife can provide new approaches for studying useful correlates of performance that we review. Recent examples include merging traditional resource selection studies with information about resources used at different critical life-history events (e.g. nesting, calving, migration), uncovering habitats that facilitate movement or foraging and, ultimately, comparing resources used through different life-history strategies with those resulting in death. By integrating data from GPS receivers with other animal-borne technologies and combining those data with additional life-history information, we believe understanding the drivers of HPRs will inform animal ecology and improve conservation.

Keywords: density dependence; fitness; global positioning system; habitat selection; individual heterogeneity; scaling

1. INTRODUCTION

Studies based on long-term monitoring of recognizable individuals have reported larger than expected variation in life-history traits among individuals. Besides well-known differences of traits according to sex (Short & Baladan 1994), age (Charlesworth 1994) or cohorts (Beckerman *et al.* 2003; Gaillard *et al.* 2003), individuals within a given population still exhibit contrasting life histories in relation to their ability to acquire and allocate resources (Van Noordwijk & De Jong 1986). Identifying the sources

of variation in resource acquisition and assessing its link with variation in individual performance are thus required to understand major biological processes such as population dynamics of, or trait selection in, free-ranging populations. Within this framework, an increasing number of empirical studies have focused on the relationship between performance and habitat at various spatial scales. The questions to be addressed, as well as the metrics used for measuring performance and habitat, are expected to differ markedly depending on the spatial scale considered in a given study. For instance, at a broad scale, several works have looked for identifying the factors determining the presence of a given species at a given location (Hirzel *et al.* 2001; Brotons *et al.* 2004; Segurado & Araujo 2004) to define Hutchinson’s (1957) ecological

* Author for correspondence (gaillard@biomserv.univ-lyon1.fr).

One contribution of 15 to a Theme Issue ‘Challenges and opportunities of using GPS-based location data in animal ecology’.

niche and provide habitat suitability models. At the population scale, spatial variation in habitat features has been included in analyses of population dynamics to account for observed variation in population abundance (Fuller *et al.* 1995), survival (Holmes *et al.* 1996) or reproduction (Donovan *et al.* 1995). Lastly, at the finer scale of patches within an individual home range, changes of food intake with changes of availability and/or quality of food items have been quantified in the context of the optimal foraging theory (Stephens & Krebs 1986; Owen-Smith *et al.* 2010). However, performance and habitat are often measured independently of the spatial scale at which the study takes place. For instance, the proportion of forest cover can be used when studying species distribution, home-range distribution or habitat distribution within a home range. Thus, a clear definition of the terms ‘performance’ and ‘habitat’ is often lacking. Imprecise terminology has prevented reliable comparisons across studies that should be required to get an overall understanding of how animal performance is influenced by variation in habitat use. We aim here to propose a general approach for studying habitat–performance relationships (called HPR hereafter) in a framework matching the scales of the study and the metrics used.

2. HABITAT, HABITAT USE AND HABITAT SELECTION

(a) *The habitat concept, problems and definitions*

We recognize two fundamentally different, but complementary, uses of the term ‘habitat’ that span a gradient from the classic niche to the food resource consumed. The niche-based definition of habitat is rooted in Hutchinson’s (1957) seminal work and has been exemplified by Sinclair *et al.* (2005) and others (Block & Brennan 1993; Hall *et al.* 1997) who define habitat as the suite of resources (food, shelter) and environmental conditions (abiotic and biotic) that determine the presence, survival and reproduction of a population. In this definition, resources and conditions are the items that animals select (hence the term ‘resource selection’), which lead to a given performance. The advent of niche-based modelling (which we return to below) has encouraged recent interest in this definition of habitat (Pulliam 2000; Soberon 2007; Hirzel & Le Lay 2008). Because this conceptualization of habitat can be functionally linked to performance, we call this *N*-dimensional space the ‘functional’ habitat definition.

In contrast, using the perhaps more common-sense resource-based definition, habitat is defined as a set of physiognomically distinct categories of vegetation communities (Hutto 1985). This is often thought to be synonymous with particular forage or vegetation resources, or entities that exist in space independent of their use or selection by an animal, including trees, nests, vegetation or communities (Hutto 1985). Under this restricted and descriptive definition, there can be aspen, oak forest and riparian habitats, some of which might be generally good or bad wildlife habitat. The limitations with this definition are that,

while it depends on classification of often continuous resources or conditions into discrete categories, habitat is not species-specific, it is insensitive to the spatial and temporal scales and its quality to the animal is difficult to measure. We call this dimension space the ‘structural’ definition of habitat, and recognize that despite its problems, it corresponds to the definition considered when developing legislation or policy to protect endangered species in geographical space.

Despite these two definitions (‘functional’ and ‘structural’), we argue that as long as one takes a multi-scale view of habitat and recognizes the definition with which one is working, both provide complementary insights to the ecology of habitat selection. At small spatial and temporal scales, animals select different ‘structural’ habitats (i.e. local resources or conditions) in a way that is intended to increase performance. As both spatial and temporal scales increase, these individual behavioural decisions to select resources result in the survival and reproductive performances at the levels of individuals and populations. Over evolutionary time, these habitat choices contribute to the species’ environmental niche or ‘functional’ habitat.

The acknowledgement that the two commonly used definitions of habitat (resource type, i.e. the structural meaning, and niche, i.e. the functional meaning) correspond to different scales of investigation helps us address certain inconsistencies in studies of habitat use and selection. This multi-scale gradient from structural to functional habitat used as conceptual frameworks matches processes of habitat selection that are also multi-scale, from the selection of a food item by a given individual to the selection of an ecological niche by individuals of a given species. In many studies, one of the goals of studying habitat use is to assess the structural habitats (resources, conditions) that are ‘important’ for the performance of the focal species. Such information also can be useful for identifying the functional habitat (niche). Thus, in many applications, these habitat concepts are mixed, and both definitions occur in the examples we present.

Johnson (1980) recognized four main hierarchical levels of selection, which he defined as a process in which an animal actually chooses a component. The four levels are: selection for a distribution range (first-order selection), selection for a home range (second-order selection), selection for a patch within a home range (third-order selection) and selection for a site (e.g. nest) or item (e.g. food; fourth-order selection). Of course, these levels of selection are only landmarks belonging to a continuum from very fine to very coarse spatial scales (Kie *et al.* 2002; Mayor *et al.* 2009), and reflect the above-mentioned gradient from the niche to food. However, Johnson’s designation of selection levels has a strong heuristic value by explicitly demonstrating that habitat selection is likely to differ among spatial scales, so that the spatial scale at which the analysis has been performed is of prime importance when interpreting studies of habitat selection. This needs to be kept in mind when conducting comparative analyses of habitat selection among species or study sites. Global positioning system (GPS) devices can be used to track animals during natal dispersal, when they establish a

home range and during site use. GPS technology is especially useful for remote study of site use and site selection because of the location accuracy and precision it allows, especially after appropriate corrections (Frair *et al.* 2010). It also is a valuable technique for tracking continuum of use and selection behaviours and the survival of individuals.

(b) *Habitat use versus habitat selection*

Habitat use generally refers to the way in which an individual or species chooses habitat resources or conditions to meet its life-history needs. Habitat use therefore can be directly described from observations of how the animal interacts with habitat features, or it can be inferred from association of habitat features with the presence of individuals of the focal species. Locations obtained from GPS receivers on animals allow establishing more accurate, fine-scaled associations, and thus more realistic estimates of habitat use than previous techniques (Cagnacci *et al.* 2010). Ultimately, it is the pattern of habitat use that matters to performance of an animal.

Habitat selection is a complex, hierarchical process of behavioural responses and choices. Johnson (1980) defined habitat usage to be *selective* if components are used disproportionately to their availability. Availability refers to a component being present and ready for immediate use; it must be the accessible or obtainable by an animal (Hall *et al.* 1997). However, rather than availability, what biologists often quantify is the *occurrence*, that is, the existence or the abundance of components in the animal's environment. These components might not be actually *available* for the animal to use (Johnson 1980; Manly *et al.* 2002; see also Beyer *et al.* 2010 for alternative definitions of available versus accessible). Nevertheless, available is the term commonly used as a synonym with occurrence in much of the literature we cite. Some of this literature includes analytical methods for which selection refers to disproportionate use relative to availability of resources, which is in fact the quantity of the resource within a specified area and period of study.

Thus, habitat selection encompasses mechanisms by which a given pattern of use is obtained, and provides the link between structural habitat and the resulting functional habitat for the individual or population. Habitat selection cannot be simply deduced from field observations but must be calculated by measuring the relationship between factor occurrence or availability and factor use. Either absolute (i.e. calculating the difference between availability and use; Hall *et al.* 1997) or relative (i.e. calculating the ratio between use and availability as in compositional analyses; Aebischer *et al.* 1993) measures of habitat selection can be used.

In recent years, a growing number of procedures for analysing habitat selection have been proposed (Kneib *et al.* 2007). Two main types can be recognized. One type includes methods based on the ecological niche and involves measuring the difference between the multi-dimensional space of structural habitat components corresponding to recorded locations of animals (i.e. habitat use) and the multi-dimensional

space of structural habitat components corresponding to the entire set of available locations. Although these designs have been referred to as 'presence-only' designs, analyses still involve comparisons between used locations with availability so that non-recorded presence is confounded with absence. Since the publication of the original ecological niche factor analysis (ENFA) by Hirzel *et al.* (2002), other methods such as the Mahalanobis distances factor analysis (MADIFA; Calenge *et al.* 2008) or the factor analysis of the niche taking the environment as the reference (FANTER; Calenge & Basille 2008) have recently emerged, all together forming a general framework: the general niche-environment system factor analysis (GNESFA; Calenge & Basille 2008). All these multivariate analysis methods provide useful and reliable description of the multivariate niche, and are most often used to map the habitat required for a population or species at broader spatial and temporal scales in a manner consistent with the niche-based definition of habitat. The high number of variables included to assess habitat components does not affect the results, but explicit testing of selection for individual resources or conditions cannot easily be performed using this approach. It is therefore difficult to compare among studies performed in different study sites. Moreover, it is difficult to link the multivariate description of habitat that results from niche-based models to performance, because it is not possible to evaluate the contribution of individual resources to performance.

A second approach for evaluating habitat involves testing for disproportionate use of structural habitat components; that is, testing for selection. Typically, the use of a given habitat component is regressed against its occurrence or availability in the environment using a used–unused design, either with logistic, count (Poisson) or more advanced generalized linear models like zero-inflated Poisson models (e.g. Manly *et al.* 2002). Assuming that the null model of no selection corresponds to a proportional relationship between use and availability, one can statistically test whether a given habitat component is selected for, selected against or not selected. This statistical definition of selection might not correspond to actual biological preference because several factors other than absolute availability may constrain resource use and selection. For instance, a high risk of predation or competitive interactions at intra- or interspecific level might lead a highly preferred habitat to be used less than expected from its availability. The resource selection function (RSF) is the most commonly used method (Boyce & McDonald 1999; Manly *et al.* 2002; McLoughlin *et al.* 2009). This approach allows comparing coefficients of selection among studies, but problems of collinearity among independent variables (i.e. non-independence in the availability of different habitat types) set a limit to the number of habitat variables to include in the analysis. RSF-type models provide an approximation of functional habitat for an individual or species because the contribution of individual structural habitat components to performance can be measured. A third, and important, variant on these two approaches is the comparison of

used–unused resources that, when adjusted for sampling probability or detection probability, can be used to model occupancy (MacKenzie *et al.* 2005). However, whatever the type of approach for investigating habitat selection, they all overlook the correlation between occurrence and performance.

(c) *A theory for fitness-based habitat selection*

Assuming that a given animal should select the habitat that increases its fitness, and that increasing fitness of a given individual should decrease fitness of others (Fisher 1930), individuals should ideally distribute themselves among habitat types with the result that all individuals in the population have the same fitness (ideal free distribution, or IFD; Fretwell & Lucas 1969). We thus expect habitat selection to be density-dependent (Rosenzweig 1981; Morris 1989). Under density dependence, animals select habitats based on the intrinsic quality (perceived) of the habitat, yet experience realized fitness that is lower because of competition with conspecifics. Individual fitness is expected to vary with changes of density in all habitat types, but both the total amount of resources available and the density-dependent function linking fitness and density are expected to vary among habitats. Models of density-dependent habitat selection such as the isodar theory (Morris 1990) thus predict an equilibrium situation at which all individuals will have identical expected fitness because the negative influence of high density should at some point exactly counterbalance the positive influence of abundant resources and *vice versa*. While of great heuristic value, the IFD models only represent idealized abstractions that usually fail to account for observed distributions of animals (Tregenza 1995). Indeed, animals in free-ranging populations are not omniscient, not free to settle anywhere and generally face marked environmental stochasticity that can change the relative value of habitat or prevent expected fitness from being realized. For instance, recent empirical tests using large herbivores have led to reject the IFD model for roe deer (*Capreolus capreolus*; Pettoelli *et al.* 2001), red deer (*Cervus elaphus*; McLoughlin *et al.* 2006) and Soay sheep (*Ovis aries*; Jones *et al.* 2006), although in all cases measures of performance showed that density-dependent responses and habitats varied substantially in the amount of resources available. Although few recent studies have ever explicitly tested for the effects of density on habitat selection (McLoughlin *et al.* 2009), it is difficult to assess the importance of density dependence in habitat selection. A better match between classic density-dependent theory and animal ecology is thus required.

(d) *Assessing habitat quality*

While the measure of habitat quality is scale-specific, one can look for HPR at any spatial scale. However, because the problem of assessing habitat quality has been investigated mainly at the home-range scale in relation to Darwinian fitness, we will restrict our presentation to this scale. Empirical evidence available so far indicates that there is spatial variation in individual fitness in most populations (e.g. McLoughlin *et al.*

2007 for a study case on roe deer). Within a given population, some animals will perform much better in some habitats than in others. As habitats most often vary in terms of population density, amount of resources available and animal performance, one may wonder whether some habitats have higher intrinsic quality (as measured in terms of individual fitness in the focal population) than others. In the simple case where population density, amount of resources and animal performance positively covary among habitat types, one can safely conclude, in contradiction to the concept of IFD, that habitats with the highest population density, largest amount of resources, highest average individual fitness and, thereby, highest population growth rate are the best habitats, whereas habitats with the lowest population density, smallest amount of resources, lowest individual fitness and, thereby, lowest population growth rate are the worst. However, the situation is more complex in most cases, and there have been numerous approaches for assessing habitat, which is sometimes a highly controversial issue.

Using a single proxy of habitat quality, such as density, does not seem to provide a reliable assessment. In her seminal paper, Van Horne (1983) argued that using population density as a measure of habitat quality can be misleading, and recommended instead using measures based on animal performance, such as survival or reproductive success. Although population density might reliably indicate differences in habitat quality at broad spatial scales (see Bock & Jones 2004 among populations of birds), it cannot be used at finer spatial scales, especially within populations in which animal distribution does not follow an IFD (see Mosser *et al.* 2009 for a detailed analysis of lions, *Panthera leo*, within the Serengeti). Furthermore, the most heavily used or selected habitat types are not necessarily the habitat associated with the highest individual fitness. Likewise, although some measures of carrying capacity, such as density after population growth has ceased, have been shown to correlate positively with recruitment (see Lin & Batzli 2001 for a study case on voles), carrying capacity should not be used in general to assess the relative value of a given habitat type, as recently shown for black rhinoceros (*Diceros bicornis*; Morgan *et al.* 2009). Using animal performance as recommended by Van Horne (1983) or Mosser *et al.* (2009) might be better.

Another approach for studying habitat quality is to test for a difference in fitness associated with sites at which habitat features differ. For example, Wightman & Fuller (2006) found that nest sites with certain habitat characteristics were used more consistently by peregrine falcons (*Falco peregrinus*) than sites with other characteristics, and that through time the sites that were used most consistently were associated with higher, less variable productivity than other sites. This suggests that these sites provide a good-quality habitat. However, such an assessment of quality is confounded by factors not related to habitat, such as the genetic or phenotypic quality of the individuals that used the nest sites. GPS now could be used to track individuals and relate their reproductive

performance and survival to nest site characteristics and other habitat features.

While physical attributes of habitat are emphasized in most structural definitions (see above), the place where an animal lives is much more than simply the type of landscape, the elevation, the slope and the level of exposure. In addition to the density and amount of physical resources and food noted above, other biotic factors such as predation pressure, competition, risks of diseases and human disturbances obviously can affect animal behaviour and performance. These ‘non-habitat-related phenomena’ (sic) (e.g. Jones 2000) need to be accounted for in a functional approach of the habitat to interpret more fully observed patterns of habitat use and selection.

3. MEASURING INDIVIDUAL PERFORMANCE IN HPR

(a) *Linking habitat and fitness: a range of proxies for fitness*

As a ‘black-box’ concept (*sensu* Brommer 2000), fitness is inherently difficult to measure. At the individual level, Darwinian fitness is usually measured as the lifetime reproductive success (Clutton-Brock 1988) or as the individual rate of increase (McGraw & Caswell 1996). Yet both measures share a common drawback of being absolute quantities, while fitness is definitely a relative concept (Fisher 1930). Only a few long-term studies based on observations of recognizable individuals monitored over their entire life have assessed the direct link between lifetime reproductive success and habitat use or selection (e.g. Newton 1985).

The long-term monitoring of red deer on the Rum Island in Scotland has revealed a clear positive relationship between the strength of females’ selection for *Agrostis/Festuca* vegetation type and lifetime reproductive success, with a decreasing fitness value associated with using *Agrostis/Festuca* at increasing density (McLoughlin *et al.* 2006). Likewise, the long-term study of roe deer at Trois Fontaines (France) showed that females including meadows in their home range had a lifetime reproductive success three times higher than females that did not include meadows in their home range (McLoughlin *et al.* 2007). Examples of other studies successful at linking habitat and fitness used 40 years of data for pike (*Esox lucius*) in northwest England (Haugen *et al.* 2006) or lions in the Serengeti (Mosser *et al.* 2009). In long-lived species such as large herbivores, more than 20 years of intensive monitoring generally will be required to assess HPR by using lifetime reproductive success as a measure of fitness. The ‘de-lifing’ statistics to partition individual contributions to the population growth (Coulson *et al.* 2006) could provide a useful practical way to assess differences of fitness among individuals on a relative scale and might offer a relevant metric to assess HPR. However, all of these measures require the complete monitoring of individuals from birth to death, which is generally lacking in habitat studies. Survival during a critical life-history stage, annual reproductive success, phenotypic quality and predation or hunting mortality risk have been the

Table 1. A selected set of fitness indices used to assess the relationship between habitat use/selection and performance in studies of vertebrate populations (only one reference is provided as an illustration).

fitness index	reference
lifetime reproductive success	McLoughlin <i>et al.</i> (2006)
apparent survival	Dugger <i>et al.</i> (2005)
adult longevity	Morris (1989)
mortality risk	Nielsen <i>et al.</i> (2006)
pregnancy rate	Miyashita <i>et al.</i> (2008)
proportion of adults in breeding condition	Morris (1989)
reproductive rate	Dugger <i>et al.</i> (2005)
litter (or clutch) size	Forsman <i>et al.</i> (2007)
litter (or nest) success	Muller <i>et al.</i> (2005)
litter (or nest) predation risk	Fontaine & Martin (2006)
young survival	Van Moorter <i>et al.</i> (2009)
number of recruits per litter	Morris (1989)
success at recruiting at least one offspring to adulthood	Lin & Batzli (2001)
daily nest survival	Chalfoun & Martin (2007)
seasonal reproductive success	Chalfoun & Martin (2007)
litter (or clutch) mass	Chalfoun & Martin (2007)
body size at birth (or hatching)	Brown & Shine (2004)
date of first egg	Forsman <i>et al.</i> (2007)
birth (or hatching) date	Forsman <i>et al.</i> (2007)
density after population growth has ceased	Lin & Batzli (2001)

most commonly used proxies of fitness in empirical studies (table 1).

Many studies have focused on proxies such as the influence of birth site selection on fitness components in a large range of vertebrate populations. In most cases, strong evidence for a close relationship between birth site and offspring performance has been reported. For example, changes of habitat structure accounted for habitat-related differences in growth of coral-dwelling fishes (*Gobiodon histrio* and *G. brochus*; Munday 2001). There is also strong empirical evidence that nest site selection by birds is important for fitness, especially in response to predation risk. For instance, Fontaine & Martin (2006) found a causal relationship between habitat selection and nest predation risk from their analysis of eight passerine birds; Muller *et al.* (2005) showed that better camouflaged nest produced more fledging in red-backed shrikes (*Lanius collurio*); and Thomson *et al.* (2006) reported that both habitat selection and reproductive success of flycatchers (*Ficedula hypoleuca*) were influenced by the presence of breeding sparrowhawks (*Accipiter nisus*), an efficient predator of flycatchers. The influence of predation risk on birth site selection is not limited to birds. Freshwater turtles (*Chrysemys picta*) have been reported to avoid predation risk by red foxes by selecting sites with suboptimal incubation

conditions, suggesting that factors affecting female survival rather than offspring survival may ultimately drive nest birth selection (Spencer 2002).

Likewise, bed site selection of most ungulates with hiding young (*sensu* Lent 1974) is strongly influenced by predation risk (Caro 2005), although young ungulates might only do the best of a bad job because their survival is more strongly influenced by the availability of good bed sites within the maternal home range rather than by the young's selection among available bed sites (Van Moorter *et al.* 2009). Likewise, songbirds (*Dendroica coronata*, *Dendroica striata* and *Zonotrichia albicollis*) did not enjoy any fitness benefit of nest site selection despite a clear association between nest site characteristics and nest success (Dalley *et al.* 2008), and sage grouse (*Centrocercus urophasianus*) did not always select for nesting habitats that enhance chick survival (Aldridge & Boyce 2008). For conservation or management purposes, one should strive to enhance habitats that increase average individual fitness, and thereby population growth rate, rather than only habitats selected by animals.

Other factors than predation may drive nest site selection in vertebrates. In tropical snakes (*Tropidonophis mairii*), selection of moist substrates leads to increased body size at hatching, a trait under positive selection (Brown & Shine 2004). Likewise, both the reproductive rate and the apparent survival of northern spotted owls (*Strix occidentalis occidentalis*) increased with increasing proportion of old-growth forest around nest sites (Dugger *et al.* 2005). Interspecific interaction is another factor that can markedly influence the fitness value of breeding habitats, and asymmetry in the response of interacting species can occur. Where great tits (*Parus major*) are sympatric with flycatchers, they show costs of coexistence in several reproductive traits (such as clutch size or number and condition of nestlings), whereas the reproductive performance of flycatchers is not affected (Forsman *et al.* 2007). Flycatchers seem to use tits as information on good nest site locations.

The key role of habitat features for shaping individual fitness can occur at any life-history stage. Adult white-footed mouse (*Peromyscus leucopus*) females have longer residence times in old fields, leading mice occupying this habitat type to have higher fitness (Halama & Dueser 1994) and higher adult survival in forests than in other habitats (Morris & Davidson 2000). The length of forest edge within the maternal home range mostly determined pregnancy rates of sika deer (*Cervus nippon*): all females with a home range including more than 80 m ha⁻¹ of forest edge were pregnant, whereas only half of females with a home range including less than 50 m ha⁻¹ were pregnant (Miyashita *et al.* 2008). Besides the effects of resource-related differences of habitat quality on individual fitness, mortality risk from predation or human-related causes is increasingly assessed as a main driver of spatial variation in individual fitness in several vertebrate populations. For instance, Nielsen *et al.* (2004) found that human access, water and edge features were all associated with an increasing mortality risk of grizzly bears (*Ursus arctos*). Likewise,

wolf (*Canis lupus*) predation caused a higher than expected mortality to occur in mixed deciduous and coniferous forest, whereas caribou (*Rangifer tarandus*) mortality was lower than expected in open-conifer areas (McLoughlin *et al.* 2005). Such case studies support the concept of 'landscape of fear' (Laundre *et al.* 2001). However, mortality risk does not provide a reliable indicator of individual fitness in all cases because, depending on the life-history strategy, compensation can (Jones *et al.* 2008) or cannot (Nielsen *et al.* 2006) occur. Moreover, ecological traps, often anthropogenic in nature, affect many endangered species, and occur when the perceived fitness payoff for a habitat is decoupled from the realized fitness and animals select bad habitats (Robertson & Hutto 2006). Including measures of recruitment is thus required for reliable interpretation of the 'landscape of fear' or ecological traps in terms of fitness.

Despite these problems, this brief review of HPR in vertebrate populations clearly indicates that commonly used proxies of fitness in empirical studies are the rule rather than the exception to assess HPR. The dependence of individual fitness on habitat has led to defining the 'habitat fitness potential' (Wiens 1989a) that measures the fitness value associated with a given habitat, which also was used as a generalization in the habitat suitability index (HSI) models used in the early 1980s (Schamberger *et al.* 1982). However, HSI models were only based on assessing the relative occupancy, use and/or amount of resources of habitat types, and did not include fitness components. Therefore, the value of HSI models for conservation or management is questionable.

All of these studies were based on survival or reproduction, but did not include an overall measure of fitness. As fitness components do not consistently show positive covariation, assessing the habitat fitness potential based only on one or two fitness components might be risky.

We found two papers about northern spotted owls in Oregon and California that provided explicit estimates of habitat fitness potential, using the natural rate of increase (λ) as a metric for fitness. The territory-specific λ estimated for 97 territories varied between 0.29 and 1.09, with an average of 0.86, indicating a declining population (Dugger *et al.* 2005), whereas a previous analysis on 94 territories reported higher values (from 0.74 to 1.15 with an average of 1.105; Olson *et al.* 2004). Interestingly, λ was consistently less than 1 when less than 40 to 50 per cent of old-forest habitats occurred near the territory centre. In addition to average habitat-specific fitness, the variance of individual fitness within a habitat type should be a variable of interest as well. Franklin *et al.* (2000) reported that the fitness variation of northern spotted owls in poor habitats was higher than that observed in good habitats, suggesting that, in addition to a higher average recruitment in good than in poor habitats, a 'buffering effect' (*sensu* Pfister 1998) contributed to increase the difference in average individual fitness between good and poor habitats. Such changes of individual variation in fitness are expected to lead to differential selective pressure on life-history traits among habitats (Coulson & Tuljapurkar 2008).

By accumulating high-quality data on individual trajectories of life histories across contrasted habitats, such analyses should become widespread in the near future (Morales *et al.* 2010). New technologies that integrate with location data from GPS can even render possible studies on hard-to-study species (e.g. Meyburg & Meyburg 2007; Schofield *et al.* 2009).

(b) Linking habitat and fitness: different responses at different scales?

As pointed out by Wiens (1989*b*), observed patterns of habitat use at a given spatial scale can simply result from constraints of habitat selection at other spatial scales (Beyer *et al.* 2010). GPS technology is useful for studying movements that inform us about the dynamics of space use. Edwards *et al.* (2008) used GPS to obtain grizzly bear (*U. arctos*) locations and found that individuals moved to different home ranges over time. The bears remained philopatric to a region, but the annual range shifted, which they interpret as an ‘adaptive strategy of space use for low-density populations in regions of low productivity where quality habitats are spatially and temporally heterogeneous’. Godvik *et al.* (2009) tracked red deer (*C. elaphus*) with GPS and learned that the animals’ habitat selection varied with behaviour and time of day by using pastures with abundant forage during night time while feeding, and spending inactive time in the cover of forests, during the day. Furthermore, habitat selection varied in association with availability; selection of pastures increased when availability was lower and decreased when there was more pasture land in the home range.

GPS provides location accuracy for assessing habitat use during movements at a variety of scales. For example, Ryan *et al.* (2004) used GPS receivers and data loggers to obtain locations during foraging trips and then relate the birds’ broad-scale movements to environmental conditions during trips, foraging site fidelity and spatial segregation of foraging areas among nesting colonies. Also using GPS and data loggers, Trathan *et al.* (2008) tracked the fine-scale foraging of king penguins (*Aptenodytes patagonicus*) in a patchy marine environment where they altered their behaviour in areas of warmer surface temperatures and warmer water at the bottom of the penguins’ dives. Applying logic similar to Wiens (1989*b*), we can expect HPR to vary across spatial scales. Using GPS and other methods, Falcucci *et al.* (2009) found that within a regional distribution of brown bears (*Ursus arctos marsicanus*), there were areas of population sinks in which greater bear mortality occurred in conjunction with various human activities.

In their case study analysis on radio-tracked woodland caribou in central Saskatchewan, Rettie & Messier (2000) found that female habitat selection was aimed to avoid predation by wolves at the broad spatial scale corresponding to the seasonal range, whereas females selected for available forage at the fine spatial scale corresponding to daily range. They then proposed the hypothesis that animals should select for the factors most limiting fitness at broader

spatial scales. Empirical tests of that hypothesis received mixed support. For instance, the results of Dussault *et al.* (2005) were in agreement with the ‘avoidance of limiting factors at broader scale’ hypothesis when finding, using GPS telemetry, that moose (*Alces alces*) indirectly selected against wolves by avoiding areas with the lowest snowfall at the landscape scale and selected for areas with abundant food at the home-range scale. In contrast, Aldridge & Boyce (2008) did not find any difference between spatial scales in habitat selection by sage grouse; at both patch and area scales, birds selected for sagebrush cover. There are several processes that could account for deviations from the ‘avoidance of limiting factors at broader scale’ hypothesis. First, assessing what is the most limiting factor in a given population is far from a simple task. As well known from demographic analyses, the demographic parameter (and thereby the factor causing its variation) leading to the highest potential change in the average fitness (as revealed by prospective perturbation analyses *sensu* Caswell 2000) often is not the same parameter that accounts for most observed variation in fitness among the individuals (as revealed by retrospective analyses). Temporal variation in demographic parameters thus makes a difference (Gaillard *et al.* 2000) and spatial variation will lead to the same outcome (see Ezard *et al.* 2008 for a case study on Soay sheep). Differences in spatial heterogeneity of the most limiting factor among different scales should thus shape habitat selection. For instance, even strong predation risk will not drive habitat selection at a landscape scale if spatial variation of the risk is low (Hebblewhite & Merrill 2009). When food resources are more patchily distributed at broad than at fine spatial scales and mortality risk is more heterogeneous at fine than at broad spatial scales, we should expect animals to select for food resources at broad spatial scales and to select against mortality risk at fine spatial scales, the opposite of the hypothesis by Rettie & Messier (2000). A second cause of deviation involves the temporal variation observed in the most limiting factor. As the most critical demographic parameter is likely to change across density variation over time within a population (Coulson *et al.* 2005), the most limiting factor should change accordingly. In highly stochastic environments, we do not expect animals to be able to track habitat at broad spatial scales to minimize the negative fitness consequences of the most limiting factor. We thus propose that Rettie & Messier’s hypothesis of the avoidance of limiting factors at larger scale is more likely to be supported in predictable environments (e.g. highly seasonal environments like those found in arctic or mountain ecosystems), and when spatial heterogeneities are balanced among limiting factors and across spatial scales (e.g. Hebblewhite & Merrill 2009).

4. ASSESSING HPR: FINDING THE RIGHT METRIC FOR MEASURING FITNESS AT DIFFERENT TIME AND SPATIAL SCALES

Activities of vertebrates such as feeding, moving or reproducing take place at different spatial scales and

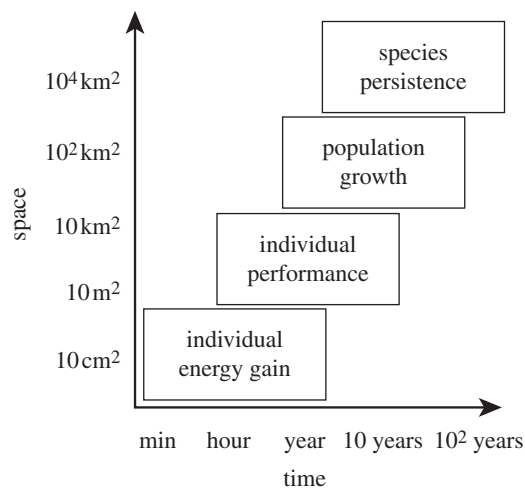


Figure 1. Correspondence among scales and metrics in HPR studies. Temporal and spatial scales positively covary so that the reference area increases from a square metre in which a food item is located at a given second to a hundred square kilometres in which a given species can be found. The metric for measuring performance should vary along this continuum of spatio-temporal dimension. At fine scales, the relevant metric will be some unit of energy gain, whereas at the very broad scale of species geographical distribution, the probability of extinction will provide the most suitable metric. The metric corresponding to Darwinian fitness can only apply at intermediate scales.

habitat selection is thereby expected to differ across spatial scales (Johnson 1980). Also, most vertebrates move throughout their home range or migrate over prolonged periods, and as they encounter different components and mixtures of features of their habitats they also make different selections on temporal scales. Defining a spatial scale thus leads to defining a temporal scale. Bailey *et al.* (1996), Godvik *et al.* (2009) and others clearly showed that decisions made by individual herbivores vary along a continuum of spatio-temporal dimensions. Thus, at the spatial scale of the food item (i.e. bite), intervals between decisions occur within a few seconds, whereas at the spatial scale of home-range occupancy, intervals between decisions occur within some hours, months or years. We can extend the spatio-temporal continuum beyond the individual level to encompass the population and species levels of biological organization. The spatio-temporal dynamics at the species level is played over hundreds of square kilometres during millions of years, while the spatio-temporal dynamics at the population level involves a few square kilometres during several years (figure 1). HPR can be studied at any point on the continuum, but the fitness measure will differ across the continuum. At the fine scale, the appropriate measure of performance—for example, of selecting a given food item—might be energy gain. Energy and many of the other commonly used proxies of fitness (table 1) are measures of short-term benefits, but will not be informative about Darwinian fitness. At the intermediate scale, measures of Darwinian fitness such as lifetime reproductive success, individual λ or individual contributions to future generations can provide the relevant metric. Lastly, the probability of extinction of a given

species in a type of landscape will provide the appropriate measure of performance for assessing HPR at the broadest scale (figure 1). Studies of HPR should thus be performed using the appropriate matching among the variables shaping the three scales in an evolutionary sense (Brown & West 2000)—that is, the spatial scale, temporal scale and metric of fitness measure—and ideally at several spatial scales to maximize the chance that important variables driving the HPR are measured.

5. CONCLUSIONS

There are an increasing number of case studies of habitat selection thanks to the development of new technologies such as GPS tracking and associated telemetry and data logging (Tomkiewicz *et al.* 2010). However, our understanding of HPR is still limited. One of the major problems is the lack of standardization that prevents comparative analyses or meta-analyses from being performed in a straightforward way. To do that in the near future, problems we reviewed in the use of the terms habitat use, habitat selection and habitat quality must be resolved. In addition, the measure of fitness has to be carefully selected to match the spatio-temporal scale of the study, and clearly defined so that results can be correctly used in meta-analyses. While the advent of GPS technology will allow ecologists to develop more sophisticated and rigorous habitat use and selection models, unless ecologists spend increased effort in linking these same GPS data to fitness components, ecologists will be no closer to understanding the basis for the habitat–fitness correlation across species.

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