

DEFINING AVAILABILITY AND SELECTING CURRENCIES OF USE: KEY STEPS IN MODELING RESOURCE SELECTION

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Abstract: Resource availability and resource use are two key concepts in studies of resource selection. Availability refers to abundance as modified by accessibility, is affected by considerations of scale, and is an assumption against which use can be compared. Accessibility can be affected by physical location with a habitat, by distance from an animal within a specified time frame, and by social constraints that animals face. Although animals generally optimize their fitness via behavior, it is not always clear to the researcher what constrains the animal's behavioral choices. For spatially distributed resources, the animal's home range is a frequent basis for quantifying availability. Within the home range, the animal is assumed to be able to gain access to all resources or those within a specified distance of its position or route of travel – the “choice set” of resources an animal could use. How many sample points a researcher must use to characterize availability within such an area depends upon environmental heterogeneity – the more heterogeneous the environment, the more sample points required. New analytical approaches, including discrete choice modeling and polytomous logistic regression, help address some of the issues with defining availability. A currency of use is a measure of the investment made by an animal in securing resources, avoiding loss of resources, or otherwise optimizing fitness. Common fitness currencies used by researchers include time spent, distance traveled, use of event sites (e.g. nest sites, den sites), or amounts of different kinds of foods consumed. Less common, but potentially useful, are such currencies as energy expended or predation or other risk incurred. A simulation of animal movements through habitat types shows that choice of a currency of use strongly influences inferences about resource selection. We argue that perhaps the most informative currency of use would be overall risk incurred by an animal. Although fairly simple conceptually, such application of risk assessment tools faces formidable empirical challenges and is a worthy goal for the next generation of researchers of animal resource selection.

Key words: availability, currencies of use, discrete choice analysis, resource selection, risk assessment.

Several concepts are fundamental to understanding and studying resource selection in animals: use, availability, and selection. Selection refers to behavioral choices made by animals. Intuitively, resources might represent matter ingested by and assimilated into the bodies of animals. But, resources can be construed as a much broader range of objects (e.g., a log) and conditions (e.g., water temperature) that influence use of resources and ultimately affect animal fitness. As an example, steep slopes are important to bighorn sheep (*Ovis canadensis*) because their proximity reduces risks of predation (Lawson and Johnson 1982). Likewise, slow current is important for stream fish because it allows them to minimize locomotor energetic costs (Facey and Grossman 1992). Windy ridges and areas downwind from large bodies of water allow caribou (*Rangifer rangifer*) to avoid harassment by insects (Moerschel and Klein 1997). In each case, some environmental condition reduces a negative factor – exposure to predators, expenditure of energy, and harassment by insects, respectively. Thus, a resource can include the presence of something that affects fitness positively, or the absence of something negative, perhaps something as intangible as wind. Many resources used by free-ranging animals are arranged heterogeneously across the landscape so that resource selection is closely linked to use of space. But, a spatial component need not be present in resource selection problems. Resources of captive animals might include various food types placed in open containers separated by a few centimeters; here the spatial component of resource selection is of little interest, but salient issues of defining use and availability remain.

By definition, used resources are a subset of available ones. Likewise, used resources and unused but available resources are mutually exclusive. Because comparing resources used with available ones involves comparing a part with the whole, such a comparison will be less likely to reject H_0 : no difference between use and availability than an otherwise similar comparison of used with unused resources. Yet, distinctions between what is used and what is available are strongly influenced by semantics and scale. Johnson (1980) considered resource selection to be a

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spatially hierarchical set of choices. First-order selection, at the broadest scale, relates to the choice of the geographic range by a taxon, second-order selection results in choice of a home range within the geographic range, third-order selection pertains to use of a habitat component within the home range, and fourth-order selection refers to a specific resource within a habitat component (Johnson 1980). So, each level of selection is conditional: given that the geographic range is specified, what resource selection is apparent from the selection of home ranges? In this scheme, what is used (e.g. an animal's home range) at a large scale defines what is available at a smaller one. The same is true of other resources with less of a spatial component. For example, for a wolf, available food can be defined as sympatric vertebrates. Assuming that to be true, certain species (e.g. moose) might be selected over others (e.g. hummingbirds). Among moose, certain sex, age, and vulnerability classes might be selected over others. Once killed, certain body parts (e.g., viscera) may be selectively ingested over others (e.g., skin and fur). Once ingested, certain tissue types (e.g. epithelia and muscle) are digested and assimilated into the tissues of the wolf; others (e.g. bone, hair) are egested. For this system, as for spatially distributed resources, what is selected can only be specified after what is available is assumed.

Another general assumption in resource selection studies is optimization of fitness via behavior, but several factors can alter our understanding of the fitness consequences of behavioral choices related to resources. The first is ignorance of the fate of the animal studied. In most cases we do not know whether behavioral choices made by the animal in fact optimized fitness, only that animals have an evolutionary predisposition to choose correctly within certain constraints. The second is the temporal context of choices an animal makes. If an animal moves toward, finds, consumes, and moves away from food, we may infer that the behavior was motivated by the proximal need for nutrients, and we will probably be correct. However, if an animal spends time near the boundaries of its territory where food resources are scarce, that may not mean that it is a poor forager or that its behaviors are maladaptive. The animal may be motivated by a need for territorial defense; its presence at the territory edge may be to behave in ways that protect the territory from inroads by conspecific neighbors. Thus, the fitness consequences of the animal's behavior might need to be understood in a broader temporal context than for a hungry animal seeking food. The third factor is the set of constraints within which animals make choices. For example, an animal's home range, or a site of resource use within the home range might be located not where resources are most abundant, but where the animal can live with the least conflict, given the locations and social dominance of sympatric conspecifics. Low social status might restrict an animal to suboptimal habitats, from which it selects optimally. Therefore, uncertainties about the fates of study animals and the temporal and social context for behavior are important considerations in making any assumptions about fitness consequences of behaviors.

Here, we define and discuss concepts related to availability and use, describe how availability and use are characterized and quantified in the wildlife literature, and show that availability and use can both be defined and estimated in multiple ways that affect inferences about resource selection. We propose alternative approaches to studying resource selection that allow availability to be more easily defined, especially for studies that allow frequent locations of animals at non-independent points.

RESOURCE AVAILABILITY

A key element of resource selection studies is what and how much the biologist decides to include as available. Manly et al. (2002:1) defined the availability of a resource as “the quantity accessible to the animal (or population of animals) during that same period of time.” Similarly, Johnson (1980:66) defined “the availability of that (resource) component is its accessibility to the consumer.” Samuel and Fuller (1994:400) noted that “availability represents the amount of area of each habitat type that is available for use by the population or an individual animal.” With each definition, there is an assumption, either stated or implied, that availability considers the amount and accessibility of a set of resources to the animal or population under study.

To assess selection of spatially explicit resources, the investigator must place spatial bounds around what is available. Availability can be defined at the level of the population, the individual animal, or both. Normally, the largest spatial domain that is considered available to an animal or population is the study area. Often, the study area is defined by political boundaries (e.g., a park boundary), although a more biologically meaningful definition might be used (e.g., a watershed). The study area is commonly used when inference regarding home range placement within the study area is of interest (i.e., Johnson's [1980] second order selection). At a finer scale, group home ranges might be used to delineate resource availability for the population. For example, Miller et al. (2000) defined resource availability in their Wild Turkey (*Meleagris gallopavo*) study by combining the outer boundaries of all 95% polygon home ranges of turkeys. Use of a population home range limits availability to sites that one or more of the sampled animals used. Thus, analyses consider selection within habitats already known to be occupied. Animal home ranges commonly define the boundaries of what is available for individual animals (i.e., third order selection;

Johnson [1980]). Many researchers justify the use of the home range because it is the area known and normally used by the animal. Given knowledge of the home range, researchers assume an animal could traverse to any portion of the range if it decided to do so. At the finest scale, a “choice set” consisting of all resources the animal could have sampled along a travel path might be used to delineate the extent of resource availability (Cooper and Millspaugh 1999, 2001). A simple choice set would be a circle bounding all possible paths between an animal’s initial and final locations, given the time between observations, and movement rates of that animal. For example, Arthur et al. (1996) and Cooper and Millspaugh (1999) used successive observations and projected travel rates to define choice sets in their studies of polar bear (*Ursus maritimus*) and elk (*Cervus elaphus*) resource selection, respectively. Choice sets can be variable in size and shape, and can overlap spatially and temporally. Use of choice sets offers maximum flexibility in defining the boundaries of what is available for each point of use.

The decision of which boundary to use depends on what order of selection (Johnson 1980) is of interest, characteristics of the study animal, and the aims of the study. Often, and consistent with the recommendations by Johnson (1980), researchers define availability at more than one scale. A multi-scale approach is useful in evaluating selection of habitat types at broad to fine scales. Study area definitions are sometimes considered biologically inappropriate, but might be appropriate in coarse-scale evaluations (e.g., Erickson et al. 1998). When using an animal’s home range to define availability, the researcher should acknowledge that some level of selection has already taken place (White and Garrott 1990). Use of choice set boundaries allows for a refined definition of resource availability. Often, choice sets ensure accessibility to all habitats within the set boundary. To be useful, the researcher must have detailed observations to compute a choice set. Researchers will encounter problems if animals are located infrequently, because the size of the choice set will increase nonlinearly with the time between observations (Cooper and Millspaugh 2001). Beyond some point in time, which is species-specific, the choice set would quickly exceed the size of the animal’s home range and of the study area.

Once the spatial limits have been established, the availability of a resource is often computed as the abundance of each resource within the assigned boundary. In the case of habitat type studies (e.g., χ^2 analyses), the proportional occurrence of habitat types within the boundary is computed. When exact calculation is unachievable, a random or systematic sample of points placed within the boundary is used to estimate the proportion of each habitat type (Marcum and Loftsgaarden 1980). Use of such a sample provides an estimate of the proportion of each habitat type, rather than a true value without associated error. If resource maps with appropriate information, resolution and accuracy are available, geographic information systems (GIS) are useful in sampling resource availability.

When using multivariate procedures, such as logistic regression, resource attributes associated with available (or non-used) points are often used to assess the availability of resource features. Placement of available points within the landscape may be achieved in several ways. Simple random sampling is common; however, spatial stratification of available points has also been used. For example, one could make the number of available points within various habitats conditional on the number of points observed to be used in those habitats (e.g., if 10% of the telemetry observations occurred within forested wetlands, 10% of the available points would be located within forested wetlands [Kolowski and Woolf 2002]). In the Kolowski and Woolf (2002) study, placement of available points within habitats proportional to use points permitted site-level inference within previously used sites. Sometimes available or non-used points are paired with used points (Arthur et al. 1996; Cooper and Millspaugh 1999, 2001). That is, associated with each use point is one to many points that define availability. Pairing helps evaluate finer scale resource selection patterns and helps ensure that available resources were accessible. Use of paired available points is particularly advantageous when resource availability changes through time (Arthur et al. 1996). For example, in studies of resource selection by riverine fish, the availability of aquatic resources is dynamic. As water levels shift, available resources could be paired with used locations to assess what was available at each point of use. In this case, availability should be measured at the time use was observed to accurately depict what was available. A GIS would be useful only in assessing resources that did not change, although a different layer could be generated for each time at which use was observed.

The number of random points needed to define resource availability depends on the heterogeneity of the area to be sampled, with more diverse environments requiring more random points. When deciding on the number of points to use, adequate coverage of the area is most important. A common misconception states that the number of used and available points must be equal; they need not be. Logistic regression is particularly robust to differences between the number of used and available points (Hosmer and Lemeshow 2000) and can cope with rather dissimilar use and availability samples. Importantly, however, the effective sample size is closer to the smaller sample size than the larger. For some procedures, general guidelines have been established; Cooper and Millspaugh (1999, 2001) recommended a 5:1 ratio of available:used points for discrete choice analysis. Nielsen et al. (this volume) found no improvement when > 10,000 available points were used to define availability at the study-area

scale. Using GIS, a large number of available points can be obtained, essentially producing a census of the available area.

To determine how availability is quantified in wildlife habitat selection studies, we characterized measures of availability in 179 Journal of Wildlife Management papers published 1990-2002. Of these, 140 were concerned with habitat. We divide our review into 2 different types of habitat selection studies: (1) selection of cover types and (2) studies of site-specific resource selection (e.g., nest site, denning site). Studies of food or other resource selection differed in sufficient respects to warrant excluding them here, although we do consider them in our section on currencies of use.

Of the 140 articles that estimated habitat availability, 57% were site-selection studies and 43% were habitat resource-selection studies. Of the site selection studies, 53% used the study area, 40% specified available points within some specified distance of the focal site, 6% used study area and another measure (e.g., study area and home range), and 2% used home range exclusively to define availability. In 45% of the habitat selection studies researchers used the study area, 22% used individual home ranges, and 7% used a group or population home range. The remaining 37% of the studies used a multi-stage approach; 11% used a study area and group range, 23% used the study area and home range, and 3% used the group home range and individual home ranges.

We now turn our attention to accessibility, the second component in defining resource availability. It is assumed that all resources within the spatially explicit boundary are equally accessible at all times. For example, when computing the proportional occurrence of resources within a home range, there is an implicit assumption that all habitat types within the boundary are equally available. This ideal free distribution (Fretwell and Lucas 1969) of available resources is often not met when defining available resources at large scales, such as the study area. Even techniques that refine the definition of resource availability, such as discrete choice modeling, must carefully consider accessibility when quantifying shape and size of the choice set. Moreover, this assumption may prove unreasonable for central-place foragers (i.e., nesting animals; Rosenberg and McKelvey 1999). Further, consider the case when the study area delimits resource availability. Are all resources equally accessible even to those animals that only reside within a small region of the study area? One might argue that a multi-stage design, as proposed by Johnson (1980) and Aebischer et al. (1993) that uses the study area boundary offers insight into home range placement within the study area. However, there are a few problems with this logic (Garshelis 2000). For one, animals likely did not have equal access to all habitats within the study area boundaries when defining their home range (Garshelis 2000). For example, territoriality might constrain juvenile animals to sub-optimal areas for their home ranges. Also, many species, such as white-tailed deer (*Odocoileus virginianus*), establish a home range in association with the natal territory (Porter et al. 1991). Thus, given these biological constraints on establishing a range within the study area, a researcher might not be able to assess the selection of home ranges within their study site.

Even at smaller spatial scales, such as the home range, regions at the periphery of the range, or even some areas contained within the range might not meet the assumption of equal accessibility. Although for some species, such as territorial animals, it might be easy to delineate home range boundaries, for others, the periphery of the home range is used less than the center. To evaluate this possible problem, an RSF might include distance from the home range center as a predictor. And, estimating home range boundaries is problematic in studies that have few peripheral observations. Further, some home range techniques, such as the adaptive kernels, might overestimate home range size when there are not enough sample points (< 30) to delineate the home range (Seaman et al. 1999). Thus, inclusion of peripheral areas as "available" could be an artifact of the sampling and analytical procedures used to estimate the boundaries of the home range. One might argue that given that the animal has prior knowledge of resources within the home range, it could theoretically choose to move to any portion of it. However, if observations are collected close in time, relative to expected travel distances, the researcher could reasonably assume that not all portions of the range were equally accessible. For example, assume that an animal's home range covers 5,000 ha. On day 1, the animal was located in the extreme northeast corner of its range; 24 hr later, it was located only 0.25 km away. Although the animal had prior knowledge of its home range, its position at time t and time $t + 24$ hr would suggest that all portions of the range were not equally sampled when the choice at $t + 24$ hr was made. Instead, these successive locations indicate that in all likelihood, the animal's set of choices at $t + 24$ hr was from an area smaller than its home range.

Many other biotic and abiotic factors influence the accessibility of resources to animals, but are rarely considered. Geographic conditions, namely terrain and slope, might limit access to resources within the study area or home range. The presence of conspecifics might either promote or restrict accessibility. For gregarious animals, such as elk, the presence of other elk might enhance accessibility through attraction. Although accessibility to a habitat might be enhanced in an elk herd, at a finer scale certain age groups might not have access to specific resources. For example, an adult and young elk might find a certain meadow accessible, despite the risk of

predation, if other elk are present. However, the young elk might be excluded from some parts of the meadow because of competition with older animals, thus making some resources within the meadow inaccessible. These intraspecific interactions might have profound influences on the accessibility of resources, and the placement of individual ranges within the study area.

Several analytical developments, specifically discrete choice modeling (McCracken et al. 1998, Cooper and Millspaugh 1999, 2001), help address some of the assumptions about accessibility. These techniques also help deal with problems when availability changes. Cooper and Millspaugh (1999, 2001) and McCracken et al. (1998) first proposed the use of discrete choice modeling, a common approach to assess human purchasing choices, to study wildlife resource selection. Discrete choice is also commonly called “brand choice modeling”, “McFadden’s choice” among others in the economics literature (McFadden 1974). Although not called discrete choice, techniques such as paired logistic regression (Compton et al. 2002) are discrete choice models. If one assumes that Arthur et al.’s (1996) selection index (w_k) is equal to $\exp(B'X_{Aj})$, that the amount of habitat is incorporated into the selection index, and that the selection index errors were distributed as a Type I Extreme Value, then one obtains the multinomial logit discrete choice model (Cooper and Millspaugh 1999). The data necessary to estimate the resource selection function from the multinomial logit form of the discrete choice model are similar to data required for standard logistic regression (Cooper and Millspaugh 1999). The general form of the discrete choice model is quite similar to the logistic model (Cooper and Millspaugh 1999, 2001); both consider continuous and categorical variables; the model fitting procedures are also identical.

A benefit of discrete choice analysis is the ability to define resource availability separately for each animal observation (Cooper and Millspaugh 1999, 2001). This desirable attribute helps researchers narrow the definition of availability should the study objectives and the available data suggest that availability change. As a result, we are able to address the previously discussed problem of constant availability. Further, a finer-scaled measure of resource availability implies that we will be more likely to meet the assumption of equal accessibility. The boundaries of these choice sets must be determined based on the researcher’s knowledge of the system and the biology of the animal in question. The main assumption in defining choice set boundaries is that the individual could choose every resource within the choice set at that particular time and place (Cooper and Millspaugh 1999, 2001). For this reason, the definition of choice sets in discrete choice analyses may be different, and often, much smaller in scale than what is allowed available when using other analytical techniques. The real utility of discrete choice modeling might be in studies that use global positioning systems to record animal positions. In such cases when observations are collected close in time, the assessment of fine scale choices might be modeled using discrete choice analysis.

Other procedures, such as polytomous logistic regression (North and Reynolds 1996), might also prove useful in some studies by assuming there is a continuous probability of use within an animal’s home range. North and Reynolds (1996) first proposed polytomous logistic regression in the context of wildlife resource selection studies. They quantified the number of radio-marked bird locations in each habitat patch throughout their study area. Patches were defined by forest stand attributes. Based on the total percent of observations observed in each patch, they assigned each used patch a categorical ranking of low, medium, or high use. In this way, no inference was made to patches in which no observations were recorded. Instead, inference was restricted to used sites only, thus avoiding problems with delimiting resource availability. Polytomous logistic regression was used to generate a resource selection function that predicted the proportional probability of use (low, medium, and high) throughout the landscape. As described by North and Reynolds (1996), the polytomous approach is beneficial because as used in their study, it did not require them to define availability. Instead, environmental attributes associated with different use intensities (low, medium, high) are compared. Rittenhouse et al. (2003) extended this approach by using kernel density estimates to refine use intensity categories. Both procedures provide an RSF that predicts use intensity. Both procedures require that resource patches be defined and that use-intensities throughout the animal’s home range be ordinated. In the Rittenhouse et al. (2003) procedure, the boundary of the kernel estimate defines the spatial extent within which animals can choose resources (i.e., availability). The primary distinction though between the PLR procedure and a typical use v. availability study is that a comparison of resources associated with differing levels of use is made instead of comparing attributes of used and available points that were sampled from within the home range boundary. In this way, Rittenhouse et al. (2003) assumed that there is some quantifiable probability of use within all resource patches within the animal’s range. They further assume that this probability can be estimated, through use of a kernel density estimate, in areas where locations were not observed. This requires an appropriate sampling strategy for the animal being studied.

CURRENCIES OF USE

Whereas discussions of the multiple meanings and ways of quantifying resource availability are fairly common in the wildlife literature, analogous discussions of quantifying use are rare. A currency of use is a measure of investment by an animal in reaching, finding, or using a resource. It is an expression of resources expended to acquire resources, to minimize loss of resources, or to otherwise maximize fitness. Selection of food types can be characterized in this way. The space within an animal's digestive tract is limited. The allocation of that space to different food types, measured in weight or volume of each, is an expression of investment of a limited resource (gut space) in the various food types. Other currencies of use important to us here are time spent within or to reach a spatial resource, distance traveled within or to reach a resource, and events related to use that can be counted. We discuss the conceptual framework for using other currencies of use – not commonly used – that are related to risks that an animal that is behaving optimally must manage: energy expended in or to reach a resource, and predation or other risk of a violent death incurred to acquire a resource. An intuitive analogy for multiple currencies of use can be found in the realm of marketing, referred to above. Assume that a store manager wishes to quantify customer use of various product types. The manager might tally the sales of each item in dollars, or count the number of items of each type sold. Another measure might be the number or proportion of shoppers that buy a product type. Further, the manager might want to measure use in terms of the weight of each product type sold, or even by the profit generated from the sale of each product type. The manager might be interested customer interest in various items that they don't buy, and tally the numbers of customers removing items from shelves and examining the package closely. Lastly, the manager might be interested in use of floor space in the store and tally the number of shoppers in each aisle at various times. Each of these approaches would produce a measure of use, but they could lead to highly divergent inferences about selection of items by customers.

The same is true of studies of resource selection by free-ranging animals. To determine how use is quantified in the wildlife literature, we characterized currencies of use in the same 179 articles dealing with resource selection in the *Journal of Wildlife Management* (1990-2002) reviewed above. We found that articles dealing with resource selection composed 13% of those published during the period. In 53% of the cases (some articles used >1 currency) time was the currency of use, in 35% event sites were the currency, in 4% food types were the currency, in 3% feeding marks were the currency, in 2% distance traveled was the currency, and in 2% presence-absence or density, measured at the level of the population, was the currency of use. Here we discuss the most common and problematic of these currencies, as well as others that did not appear in our literature review, but appear in other journals or are potentially useful to researchers:

Common Currencies

Time.--Time is the operative currency of use if the researcher samples presence of animals in various habitats on a systematic or random temporal basis, for example once daily. Most commonly, this is accomplished by means of telemetry, but also can be done using visual scans or other sampling approaches that place animals in habitats through time. Time spent in a habitat may be informative about thermal energetic costs and predation risks, because these kinds of investments tend to accrue through time, and also may be informative about foraging success where searching for or handling food is time-intensive. Time is not a highly informative currency of use regarding rare events, such as visiting watering sites or mineral licks, or seeking females during breeding; these events may consume relatively little time over an animal's life, but have disproportionately large fitness consequences.

Event sites.-- These sites are defined around dens, nests, leks, beaver dams, or other places that animals use intensively, or where they accomplish important life functions. They can represent large investments as measured by multiple currencies of use (e.g., time and energy), or can be fairly trivial and non-limiting (defecation sites). Because they tend to be localized, distance traveled is not a currency of use that relates well to event sites. Event sites are appealing to wildlife researchers because they tend to be discrete units (e.g. trees, logs, stream segments) that are intuitive and easy to sample, and may represent large investments by animals in resources that are rare in the environment. As a disadvantage, event sites may tend to overemphasize the importance of events that lack fitness implications (e.g., defecation with no scent-marking function) or resources that are not limiting (e.g., perching sites for passerine birds). The use of event sites will have maximum utility if chosen to have a clear and direct relationship to some fitness-limiting life function. This could include thermal protection during energetically stressful times, protection of vulnerable young against opportunistic predators, storage of food, or some combination of functions.

Distance.--Distance traveled is a highly intuitive, although seldom encountered (2% of studies surveyed) currency of use in studies of free-ranging animals, important primarily in studies of habitat selection. The assumption here is that the distance traveled within a spatial resource (e.g. habitat type) is a measure of the investment by the animal in that resource. Micro-scale data can result from tracking animals in snow, where the placement of each foot can be recorded; movement distances can also be inferred from intensive telemetry studies with brief sampling intervals, or from global positioning system transmitters, which can sample animal locations at brief intervals. Distance is an informative currency of use because movement is related to foraging effort, locomotor energetic costs, and predation risks (to the extent that movement increases risk over staying stationary). However, distance is not an informative currency as related to life functions that occur in areas too small to be recorded as movement (e.g. at nests and dens, resting sites, and concentrated resource patches). Further, distance traveled typically is assigned to the habitat in which the movement occurs, when the movement may in fact be motivated by, and towards or away from a different habitat. So, an animal might move through 3 km of low quality habitat to gain access to a resource patch that is 100 m in diameter. In this case the low quality habitat receives the greatest use (distance traveled); inferring habitat quality from this distance would be misleading. Indeed, movement speed may be inversely proportional to habitat quality; habitats that contain dense resources and have small predation risks may evoke slow movement speeds, causing the researcher using distance as the currency of use to incorrectly infer habitat value. Conversely, habitats that have sparse resources and high predation risks may induce animals to cross them quickly, generating high movement speeds and an incorrect inference of high habitat value.

Uncommon Currencies

Energy expended.--While uncommon in the literature, and not found in our review of the Journal of Wildlife Management, energy expenditure is a potentially highly informative currency of use. Energy is a currency closely linked to fitness for many free-ranging vertebrates (Calow and Townsend 1981), methods of estimating energy expenditure in free-ranging vertebrates are available (Speakman 1997), and these methods have been used to estimate differences across broad geographic areas in energy expenditure within species (e.g., forest tits [Paridae], Carlson et al. 1993). Still, the demands of estimating these costs on a much smaller per-habitat-type basis seem prohibitive; models based on estimates of habitat-specific locomotor costs or resting energetic costs may be one of the few approaches possible. Understanding how much energy an animal was willing to invest in a habitat type, or to find and consume some other, non-energetic resource would be a powerful tool for wildlife researchers. The means available to us for accomplishing that are currently quite limited.

Predation risks incurred.--The risk of being killed by a predator (or interspecific competitor) is one of the major fitness consequences of behavioral decisions made by most mobile animals (Lima and Dill 1990). Risk of being killed by a predator can vary with time of day, phase of the moon, weather, snow cover, physical structure of habitat, and the local sympatry of predators or competitors (Lima 1998). Although survival rate has been estimated for many animal species over long time intervals, for few species has predation risk, adjusted for time in habitat, been estimated on a habitat-specific basis. Kunkel and Pletscher (2000) showed that two levels of predation-risk effects can be measured. The first is the effect of predation risk on habitat selection; the second is the risk of being killed by a predator given the predation-influenced pattern of habitat selection. Importantly, animals should weigh predation risks against potential fitness gains of an action in the context of its fitness condition; an animal that is well-nourished, well-sheltered, and pregnant might tolerate little additional predation risk. However, an animal that is poorly nourished, in an anomalous habitat, or seeking scarce breeding opportunities may accept much higher apparent predation risks in order to maximize its individual fitness.

Simulation

We demonstrate how the choice of a currency of use affects inferences about resource selection using the following simulation. Fig. 1 shows the hypothetical movement paths of an animal through 3 habitat types on 3 consecutive days. Given that the animal is inactive during 1800-0600 daily, and assuming that the animal moves at a constant rate while active, movement paths and times of activity can be used to derive habitat selection data (Fig. 2). Further, by assuming energy expenditure while active is 4 \times that while resting (Gorman et al. 1998), energy expenditure for each habitat can be estimated (Fig. 2). Lastly, we assumed that predation risk while active was 4 \times that while resting and that, while active, predation risk was influenced by habitat, with risks in habitat B 0.3 \times those in habitat A, and those in habitat C 3 \times those in A. Using a simple selection ratio (U/A), we show that selection for habitat types is strongly affected by choice of currency of use (Fig. 3). Using time as our currency of use, habitat B is preferred, habitat C is avoided, and habitat A is used in proportion to availability. Using distance as our currency

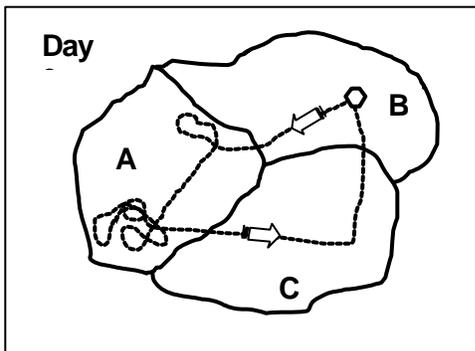
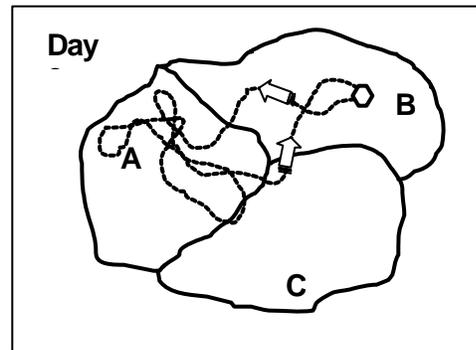
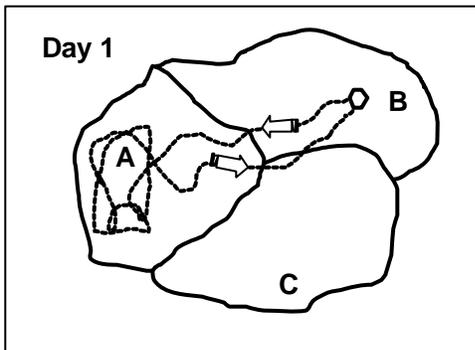


Fig. 1. Movement paths of an animal through three habitat types of equal availability on three consecutive days. On each day, the animal leaves its resting site (hexagon) at 0600, and returns to it at 1800. Movement rate is constant while traveling.

of use, habitat A is selected for and habitats B and C are selected against. Patterns for energy expended and predation risk incurred track distance more closely than they do time, because we assumed that animals expended more energy and were more exposed to predation while moving than while resting. These assumptions seem reasonable generally.

The problems of calculating the fitness tradeoffs associated with dissimilar currencies of use are considerable. Use of a particular habitat type might be characterized by higher distance traveled, lower time spent, higher energy expended per unit time, but lower predation risk per unit time, relative to another habitat. In theory, the most informative, integrative measure of investment by an animal in using a resource is the risk of lost fitness that it accepts to do so. A behaviorally optimizing animal that accepts simultaneously high predation risks, high risks of energy loss, and high risks of conflict with conspecifics must perceive very large potential marginal gains in fitness from using a resource. A risk assessment approach that allows us to integrate these various currencies of use into a single one – risk – should be a goal of the next generation of resource selection studies. Returning to the example of the prudent store manager, the manager should optimize the business's chance of success by minimizing overall risk of failure – including trading-off various kinds of risk. Thus, the manager might choose between closing the store early in the evening and losing sales to competitors vs. staying open all night and risking higher insurance costs because of increased chances of being robbed. Enlarging the store might allow a wider range of items to be displayed and increase customer traffic, but reducing the size of the store might lower rental and heating costs, leaving more money in reserve. Leaving potholes in the parking lot unrepaired might leave more money in reserve, but also might increase the risk of being sued. The business strategy of the manager, to be successful, must minimize overall risk of failure, not a single kind of risk. Therefore, any increased risk taken by the manager must be for the purpose of a perceived potential gain – a commensurate or greater reduction in another kind of risk. In this sense, the marginal increase in perceived risk resulting from a resource selection decision is the clearest measure of perceived potential gain from using the resource, and is the metric that we believe is of ultimate value in studies of animal use of resources. Developing metrics of animal risk will require considerable empirical development.

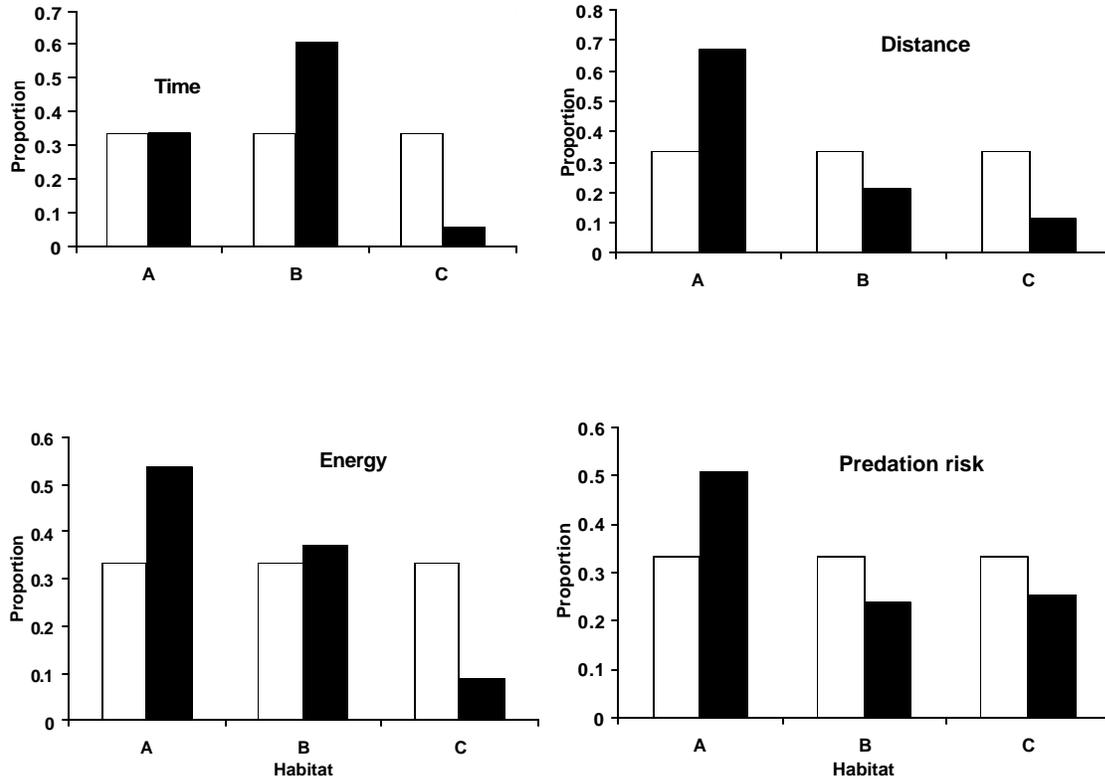


Fig. 2. Apparent selection of three habitat types (A-C) of equal availability (cross-hatched bars) for an animal over three consecutive days (Fig. 1) using four currencies of use (solid bars): time spent, distance traveled, energy expended, and predation costs incurred. Time spent assumes the animal leaves its resting site at 0600 and returns at 1800 on each day. Energy expended assumes energetic costs while traveling are 4 \times those at rest (Gorman et al. 1998). Predation risk assumes risk of predation while traveling is 4 \times that while resting, with a

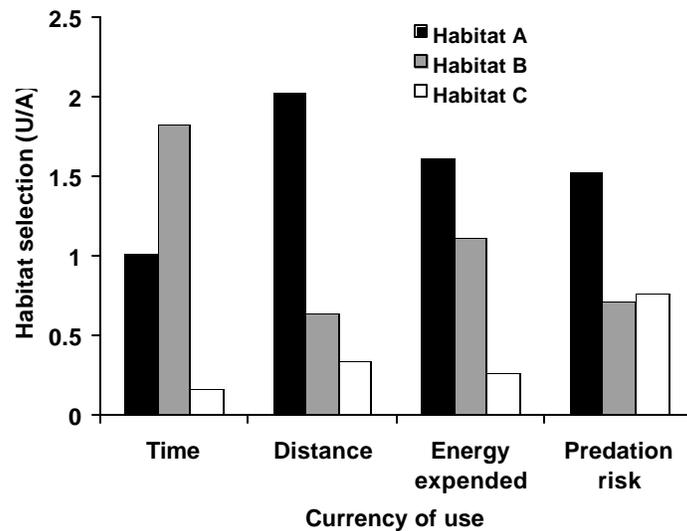


Fig. 3. A habitat selection index (use/availability [U/A]) for four currencies of use (time, distance, energy, predation risk) based on data in Figs. 1-2. U/A for a single habitat type (B) varies from 0.7 to 1.8, depending on the currency of use employed, showing how choice of a currency of use affects inferences of resource selection.

CONCLUSIONS

Defining availability and choosing a currency of use are two important steps in addressing a resource selection problem. Availability is defined in terms of abundance as modified by accessibility; what is available is not so much measured as it is assumed. For highly spatial resources such as habitat types, availability can be defined at the level of the population or the individual animal and requires placing spatial bounds on what habitats can be reached by the animal in question during the time interval under study. Often and appropriately, availability is defined at multiple scales. After spatial bounds on availability are set, various means of characterizing resources within the available area are used: random and stratified sampling, and pairing of available sites with used ones. The choice depends on the study objectives. Analytical procedures that refine our definition of availability, such as discrete choice analysis, are beneficial when data are collected at short time intervals.

Use can be quantified using various currencies, and the choice of appropriate currencies affects inferences about resource selection. What is an available resource at one scale (e.g. an animal's home range) can define used resources at a different scale. Understanding what motivates the behavior of an animal is important to understanding the fitness implications of its patterns of resource use. Common currencies of use in the wildlife literature on resource selection are time spent and distance traveled. Event sites – places where animals expend multiple use currencies and accomplish important life functions – are also common currencies of use. Currencies that are less common in the literature, but potentially valuable to the animal ecologist, include energy expended and predation risk (or other risk of violent death) incurred. The means to estimate these currencies are just starting to become available now. An estimate of composite risk incurred by an animal to use a resource should be a goal of the next generation of students of resource selection. Only by understanding how animals manage and trade off dissimilar kinds of risk can we begin to understand the importance of resource selection decisions.

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