

# Metrics for Studies of Resource Selection

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## Abstract

Resource availability and resource use are 2 key concepts in studies of resource selection. Although equal accessibility to resources is one component defining resource availability, we rarely know what restricts access to resources. Consequently for spatially distributed resources, the animal's use of space in association with the occurrence of resources is a frequent basis for inferring resource use and testing for resource selection. For many resources, occurrence can be defined for the population or the individual animal and requires that researchers specify the spatial extent of resources an animal might use during the time interval of study (e.g., the "choice set"). Often the occurrence of resources is defined at multiple scales, which facilitates understanding hierarchical selection patterns. We discuss numerous factors and criteria that should be considered when delineating the area an animal might use during a period of interest. New analytical approaches to resource selection, including resource utilization functions (RUF) and discrete choice modeling, help address some of the issues of defining availability and dealing with the behaviors associated with resource use. 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 currencies used by researchers include time spent or distance traveled in a cover type, use of event sites (e.g., nest sites, roosting sites, den sites), or amounts of different kinds of foods consumed. Less common, but potentially highly informative, are such currencies as energy expended or predation risk or other risk incurred. Simulation of animal movements interspersed with diel resting periods, through habitat types with activity-dependent energy expenditure and habitat-specific predation risk showed that choice of a currency of use strongly influences inferences about habitat selection. We argue that perhaps the most informative currency of use would be increased risk to fitness accepted by an animal. Although fairly simple conceptually, such application of risk assessment faces formidable empirical challenges and is a worthy goal for the next generation of researchers of animal resource selection. (JOURNAL OF WILDLIFE MANAGEMENT 70(2):358–366; 2006)

## 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, the matter assimilated into the bodies of animals might represent resources used. But resources can include a much broader range of objects (e.g., a log) with which animals associate and conditions (e.g., water temperature) that influence use of places and ultimately affect animal fitness. For 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 reduces 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 be matter that is taken up by an animal and affects fitness positively, or the absence of something negative, perhaps something as intangible as wind. Many resources used by free-ranging animals occur heterogeneously across the landscape so that resource selection is closely linked to use of space. Resource selection is affected by the abundance and diversity of resources in an animal's 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 close to each other; here the spatial component of resource selection is of little interest, but salient issues of defining use, availability, and selection 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. At the same time, comparing used with unused resources (nonoverlapping subsets of the choice set of available resources) involves comparing 2 nonoverlapping but nonindependent groups (Jones 2001). Distinctions between what is used and what is available are strongly influenced by semantics and scale. Johnson (1980) considered resource selection to be a 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 use area (e.g., home range) within the geographic range, third-order selection pertains to use of a habitat component within the use area, 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 might 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 dead, certain body parts (e.g., viscera) may be selectively ingested over others (e.g., skin and fur). Once ingested,

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certain tissue types (e.g., epithelia and muscle) are well-digested and assimilated into the tissues of the wolf; others (e.g., bone and hair) pass through the digestive tract largely unassimilated. For the simple system of wolf foods, as for spatially distributed resources like habitats, what is selected can only be specified after available resources are defined or assumed.

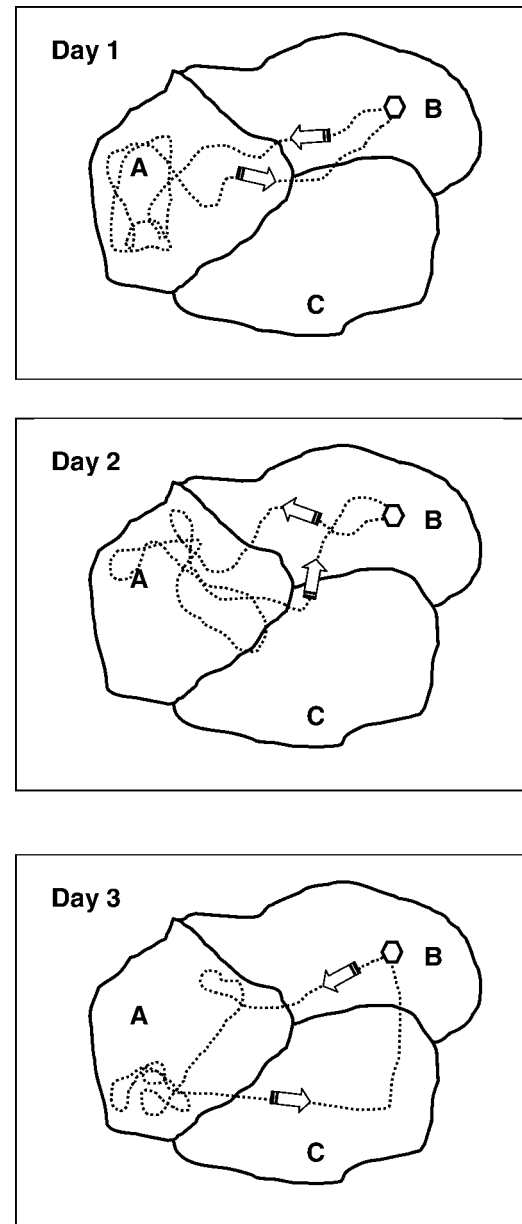
Another important assumption in resource-selection studies is optimization of fitness via behavior, but several factors can alter our understanding of the fitness consequences of behavioral choices related to resources. The first is ignorance of the fate of the animal studied. In most cases we do not 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 (Jones 2001). The second is the temporal context of choices an animal makes. If an animal moves toward, finds, consumes, and moves away from food or water, we may infer that the behavior was motivated by the hunger or thirst, and we will probably be correct. However, if an animal spends time near the boundaries of its territory where food resources are scarce, we may be incorrect to infer that it is a poor forager or that its behaviors are maladaptive. The animal may be motivated by instinctive territorial defense; its presence at the territory edge may be to 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 forage with the least conflict, given the locations and social ranks of sympatric conspecifics (Rosenberg and McKelvey 1999). 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 contexts for behavior are important considerations in reaching any conclusions about fitness consequences of behaviors.

Here, we define and discuss concepts related to resource availability and resource use, describe how availability and use are characterized and quantified in the wildlife literature, and show that availability and use can 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 nonindependent points.

## Methods

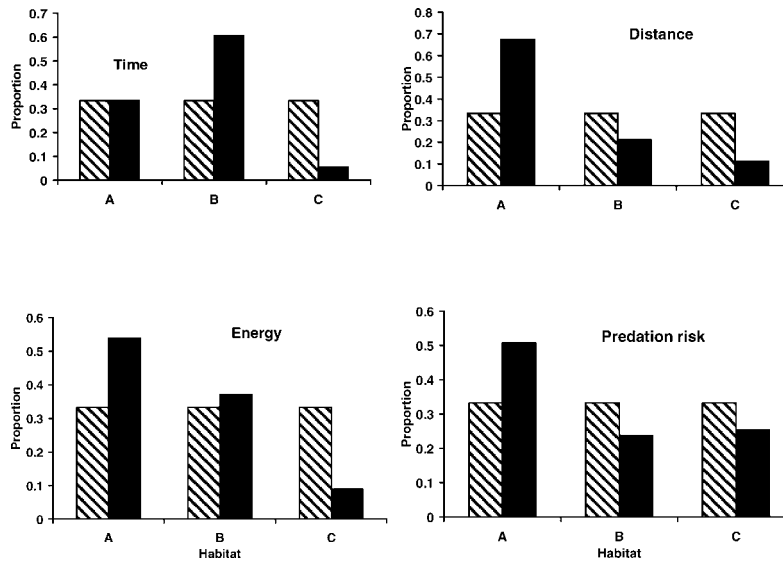
To determine how availability is quantified in wildlife habitat selection studies, we characterized measures of availability in 239 articles published in *The Journal of Wildlife Management* during 1990–2004. Of these, 208 were concerned with habitat. We divide our review into 2 different types of habitat-selection studies: 1) selection of cover types, and 2) site-specific resource selection (e.g., nest site, denning site). We characterized currencies of use for all 239 articles.

We tested how the choice of a currency of use affects inferences about resource selection using a simulation of animal movements across habitat types for 3 consecutive days (Fig. 1). The simulation



**Figure 1.** Movement paths of a hypothetical animal through 3 habitat types of equal availability on 3 consecutive d. On each day, the animal leaves its resting site (hexagon) at 0600 hr, and returns to it at 1800 hr. Movement rate while traveling is constant.

assumed that the animal was inactive during 1800–0600 hours daily and moved at a constant rate while active. Foraging was concentrated in habitat A, resting in habitat B. Movement paths and times of activity were then used to derive habitat-selection data (Fig. 2). Further, by assuming energy expenditure while active was 4 times that while resting (Gorman et al. 1998), energy expenditure for each habitat was estimated (Fig. 2). Last, 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. We used a simple selection ratio, proportional use divided by proportional availability ( $U/A$ ), to express selection for each habitat type.



**Figure 2.** Apparent selection of 3 habitat types (A–C) of equal availability (cross-hatched bars) for an animal over 3 consecutive days (Fig. 1) using 4 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 hr and returns at 1800 hr 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 habitat multiplier while traveling of 1 for habitat A, 0.3 for habitat B, and 3 for habitat C.

## Results

### Literature Review

We found that the 239 articles dealing with resource selection comprised 15% of those published during the period. Of the 172 articles that estimated habitat availability, 52% were site-selection studies and 48% were habitat resource-selection studies. Of the site-selection studies, 51% used the study area, 43% specified available points within some specified distance of the focal site, 5% used study area and another measure (e.g., study area and home range), and 1% used home range exclusively to define availability. In 48% of the habitat selection studies, researchers used the study area, 21% used individual home ranges, and 5% used a group or population home range. The remaining 36% of the studies used a multistage approach; 9% used a study area and group range, 26% used the study area and home range, and 1% used the group home range and individual home ranges.

Of the 239 articles (some used >1 currency), 52% used time as the currency of use; 31% used event sites as the currency; 6% used presence–absence, relative density or absolute density as the currency; 5% used food types as the currency; 2% used feeding marks as the currency; and 2% used distance traveled as the currency of use.

### Simulated Animal Movements

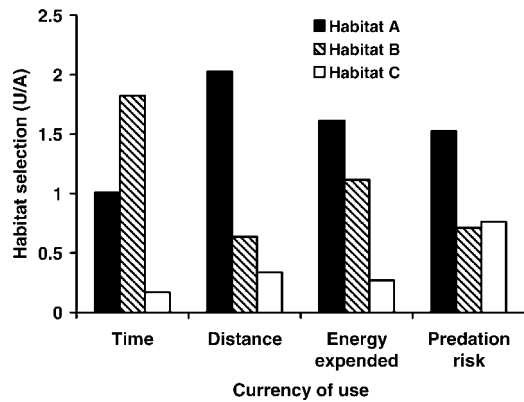
Using time as the currency of use, habitat B was preferred, habitat C was avoided, and habitat A was used approximately in proportion to availability (Fig. 3). Using distance as our currency of use, habitat A was preferred, and habitats B and C were avoided. Patterns for energy expended and predation risk incurred tracked distance more closely than they did time because we assumed that animals expended more energy and were more exposed to predation while moving than while resting.

## Discussion

### 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.” Fuller et al. (2005) noted that “resource availability represents the amount of area of each habitat type (e.g., meadow, forest) that is accessible for use by the population or individual animal.” With each definition, there is an assumption, stated or implied, that availability considers the amount and accessibility of a set of resources to the animal or population under study. However, few investigators study what is accessible, and instead the comparison becomes one of proximity or use of a resource to only the occurrence of the resource at the specified spatial and temporal scales. In many instances, particularly those that define availability at a large scale, it is likely that the resource quantity that occurred was not that actually available to the animal. Consequently, the selectivity calculated might be erroneous, and thus, so might be any importance we assign to the resource for the animal. Therefore, defining and estimating resource availability is critical to inferences about resource selection.

To assess selection of spatially explicit resources, the investigator must estimate the maximum area that an animal could move within during a specified period, or limit the area of consideration based on other criteria, such as a refuge boundary. The potential area of use 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 (e.g., park or refuge) boundaries or an ecological unit such as a watershed. The study area is commonly used when inference regarding home



**Figure 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.

range placement is of interest (i.e., Johnson’s [1980] second-order selection). At a finer scale, space use by a sample of individuals could be used to delineate potential resources for a 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 wild turkeys. Use of a collective ‘home range’ limits availability to sites that 1 or more of the sampled animals used. However, delineating an area near a population is likely to result in the inclusion of area that might not result in equal access of all resources to all animals, perhaps due to social interactions among individuals. 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, but this definition is affected by the observational methods and sampling design used. However, what is contained within the boundary can vary substantially depending on the assumptions and techniques used to describe the area (Seaman et al. 1999). Given knowledge of the home range, researchers assume an animal could use 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). The resources in the choice set might be used and selected if they are available to the animal.

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 study more than 1 scale. Study area definitions are sometimes considered biologically arbitrary, but might be appropriate in coarse-scale evaluations (e.g., Erickson et al. 1998) or be useful because they reflect the circumstances in which the results can be applied. 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 occurrence. Often, choice sets help ensure accessibility of all habitats to an individual within

the set boundary, but unknown factors, including social interactions, could complicate matters. Ideally, the researcher should have detailed observations to estimate choice set boundaries.

Once the spatial limits have been established, the occurrence of a resource is often computed as the abundance of each resource within the boundary. In the case of habitat-type studies (e.g.,  $\chi^2$  analyses), the proportional occurrence of habitat types within the boundary is computed. When exact calculation is unachievable, a random or systematic sample of points 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 sampling error. If resource maps with appropriate information, resolution, and accuracy are available, Geographic Information Systems (GIS) are useful for sampling resource abundance.

When using multivariate procedures such as logistic regression, resource attributes associated with the area or with nonused points are often used to assess the selection of resource features. Samples of points within the landscape may be achieved in several ways. Simple random sampling is common; however, spatial stratification of points has also been used. For example, one could make the number of 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]). Spatial stratification permits site-level inference within previously used sites, where that is a study objective. Sometimes available or nonused points are paired with used points (Arthur et al. 1996; Cooper and Millspaugh 1999, 2001). That is, 1 to many points of resource occurrence are associated with each point of use. 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 the occurrence of resources changes through time (Arthur et al. 1996). For example, in studies of resource selection by riverine fish, the availability of aquatic resources is highly variable through time. As water levels shift, available resources could be paired with used locations to assess resource occurrence at each point of use. In this case, availability should be measured at the time use was observed to accurately depict what 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 sample resource distribution and abundance depends on the heterogeneity of the area to be sampled, with more heterogeneous environments requiring more 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 samples of used and random 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. The standard errors of the estimated coefficients in a logistic regression are generally smaller with similar than dissimilar numbers of used and available points. However, this requires the intercept be corrected to reflect the true population proportions (Hosmer and

Lemeshow 2000). Importantly, however, where sample sizes for used and available points are highly dissimilar, the effective sample size is closer to the smaller than larger sample size. 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. Nielson et al. (2003) found no further improvement when >10,000 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.

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 multistage design, as proposed by Johnson (1980) and Aebischer et al. (1993), that uses the study area boundary, provides insights into home range placement within the study area, but this argument has weaknesses. First, animals likely did not have equal access to all habitats within the study area boundaries when defining their home ranges (Garshelis 2000); territoriality might constrain juvenile animals to suboptimal areas. Second, species such as white-tailed deer (*Odocoileus virginianus*) establish home ranges in association with their natal home ranges (Porter et al. 1991). Given these biological constraints on establishing a home range within the study area, a researcher might not be able to assess selection of home ranges as a series of independent events.

Even at smaller spatial scales, such as within the home range, areas might not be equally accessible. For territorial animals, home-range boundaries might be clear, but for other taxa, the periphery of the home range might be used less than the center (Rosenberg and McKelvey 1999). To evaluate this possible problem, a resource-selection function (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 methods for delimiting home-range boundaries, including adaptive kernels, overestimate home-range size when sample size is small (<30; Seaman et al. 1999). Thus, identifying areas as “available” may be confounded by sampling and other methods used. One might argue that home-range occupants have knowledge of the home range and can choose to move to any portion of it (Garshelis 2000). However, if observations are collected close in time, the researcher might find that not all portions of the range were equally

accessible. For example, assume that a large 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. Therefore, resource accessibility also is a function of animal movement rate.

Many other biotic and abiotic factors influence the accessibility of resources to animals but are rarely considered. Topography, for example, 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, particularly discrete choice modeling (McCracken et al. 1998, Cooper and Millspaugh 1999, Ramsey and Usner 2003), help address the assumptions about accessibility. These techniques also help address problems when availability changes. Discrete choice is also known as “brand choice modeling,” “McFadden’s choice,” and other terms in the economics literature (McFadden 1974). Paired logistic regression (Compton et al. 2002) is analogous. If one assumes that Arthur et al.’s (1996) selection index ( $w_k$ ) is equal to  $\exp(B'X_{Ai})$  (an exponential function of a linear combination of parameters and covariates), 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 those required for standard logistic regression. The general form of the discrete choice model is quite similar to the logistic model; both consider continuous and categorical variables; the model fitting procedures are identical.

A desirable attribute of discrete choice analysis is the ability to define resource availability separately for each animal observation (Cooper and Millspaugh 1999, 2001). Further, a finer-scaled measure of resource availability implies that we will be more likely, although not guaranteed, 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 every item in the choice set is equally accessible. For this reason, the definition of choice sets in discrete choice analyses may be different, and often, much

smaller in scale than what is defined as available using other analytical techniques. The real utility of discrete choice modeling might be in studies that use Global Positioning Systems (GPS) 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 the resource utilization function (RUF) approach (Marzluff et al. 2004, Millspaugh et al. 2006) and polytomous logistic regression (PLR; North and Reynolds 1996) might also prove useful because both focus on differences in intensity of use of available resources. Marzluff et al. (2004) first proposed the RUF in a wildlife context. Their approach relies on a probability density function surface (i.e., a utilization distribution), which is constructed from radiotelemetry data. These utilization distributions are then regressed on continuous and categorical resource variables to estimate a RUF. The RUF coefficients specify how resources relate to variation in the underlying utilization distribution. It is important to note that the kernel analysis induces a correlation between the deviations in neighboring pixels that must be adjusted when inference is intended for an individual animal or locations are pooled across animals, because standard errors will usually be biased low (Neter et al. 1996). To address spatial autocorrelation, a regression model can be fit to the UD with spatial correlation considered as a function of the distance between the pixels using the Matern correlation function (Handcock and Stein 1993, Marzluff et al. 2004). Using PLR, North and Reynolds (1996) also compared the intensity of use of available resources as a categorical measure (i.e., low, medium, high). Using their procedure, no inference was made to patches in which no observations were recorded. Instead, inference was restricted to used patches, thus avoiding problems with delimiting resource availability. The PLR was used to generate a RSF that predicted the proportional probability of use (low, medium, high) throughout the landscape. As described by North and Reynolds (1996), PLR was useful because it did not require them to define availability. Instead, environmental attributes associated with different use intensities were compared. Rittenhouse (2003) combined the Marzluff et al. (2004) and North and Reynolds (1996) procedures by using kernel density estimates to refine use intensity categories throughout an animal's range. The Rittenhouse (2003) technique maintains many of the advantages of UD-based approaches discussed by Marzluff et al. (2004) and North and Reynolds (1996), but uses use-intensity categories throughout the animal's home range instead of assuming that UD estimates are error-free. More work is needed to understand how error in UD estimates influences resource-selection analyses. A review of utilization distribution procedures for estimating resource selection is provided by Millspaugh et al. (2006).

### **Currencies of Use**

Discussions in the literature of how to quantify resource 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, volume or frequency of occurrence

of each food type 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. Other currencies of use—not commonly used—are related to risks that an animal that is behaving optimally must manage: energy expended within or traveling to 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 economics, referred to above. Assume that a store manager wishes to quantify customer use of various products. The manager might tally the sales of each product in dollars or count the number of items of each product sold. Another measure might be the number or proportion of shoppers that buy a product. Further, the manager might want to measure use in terms of the weight of each product sold, or even by the profit generated from the sale of each product, overall or per unit sold. The manager might be interested in customer interest in various products not purchased, and tally the numbers of customers who remove items from shelves and examine the packages. Last, the manager might be interested in use of floor space in the store and tally the number of shoppers in each aisle over time. Each of these approaches would produce a measure of use by customers, but could lead to highly divergent inferences about selection of items.

The same is true of studies of resource selection by wildlife. The most common and problematic of these currencies, as well as others that did not appear in our literature review, but that appear in other journals or are potentially useful to researchers, follow:

**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 hourly, daily, or weekly. 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 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 mates 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 spent and energy expended), or can be fairly trivial and nonlimiting (defecation sites that do not serve as territorial marks). Because they tend to be localized, event sites tend not to be well-characterized by distance traveled. Event sites are appealing to wildlife researchers because they tend to be discrete units that can be counted (e.g., trees, logs, stream segments), that are intuitive and easy to sample, and that may represent large investments by animals in resources that are rare in the environment. Again, 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 informative power if chosen to have a clear and direct relationship to some fitness-limiting life function. Such functions could include thermal protection during energetically stressful times, protection of vulnerable young against 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 habitat selection. The assumption here is that the distance traveled within a spatial resource (2-dimensional habitat types in all cases we observed) is a measure of the investment by the animal in that resource. Microscale data can result from tracking animals in snow, where the placement of each foot can be inferred; movement distances can also be inferred from intensive telemetry studies with brief sampling intervals, particularly from GPS receivers. 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, 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. Thus, an animal might move through 3 km of low-quality habitat to gain access to a resource patch 30 m in diameter. In this case, the low-quality habitat receives the greatest use (long distance traveled); inferring habitat quality from this distance would be misleading. Indeed, movement speed may be inversely proportional to habitat quality; patches that contain dense resources and have small predation risks may evoke slow or imperceptible movement, causing the researcher using distance traveled as the currency of use to infer habitat value completely incorrectly. 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. Clearly, distance traveled is a currency of use that must be interpreted cautiously.

**Energy expended.**—While 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 variation in energy expenditure across broad geographic areas, within species (e.g., forest tits [Paridae], Carlson et al. 1993). Still, the demands of estimating these costs on a much smaller per-habitat basis may be prohibitive; models based on estimates of habitat-specific locomotor costs or resting energetic costs broaden the approaches possible. Understanding how much energy an animal invests in acquiring a resource, or in occupying a habitat type, can be a powerful tool for wildlife researchers. The means available to us for gathering such information currently are limited; telemetry of heart rate may provide a coarse estimate of metabolic rate over short periods.

**Predation risks incurred.**—The risk of being killed by a predator (or interspecific competitor) is 1 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 2 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, optimizing animals should weigh predation risks against potential fitness gains of an action in the context of its fitness condition. For example, an animal that is well-nourished, well-sheltered, and pregnant might tolerate little increase in predation risk. However, an animal that is poorly nourished, in an anomalous habitat, and seeking scarce breeding opportunities may accept large additional predation risks in order to maximize its individual fitness (Houston and McNamara 1999).

The problems of calculating the individual fitness tradeoffs associated with dissimilar currencies of use are considerable. An animal's 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 energy expenditure, and high risks of conflict with conspecifics must perceive very large potential marginal gains in fitness from engaging in some resource-related behavior. A risk assessment approach that allows us to integrate these various currencies of use into a single 1—risk—should be a goal of the next generation of resource-selection studies. Returning to the example of the prudent store manager, she 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 need to 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, reducing overhead, and increasing profit margins. Leaving potholes unrepaired in the parking lot might leave more money in reserve, but might also increase the risk of being sued. The business strategy of the manager, to be successful, must minimize overall risk of failure, not minimize a single kind of risk. Therefore, any increased risk taken by the manager should 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 by a free-ranging animal is the clearest measure of perceived potential gain from using the resource, and is the currency of use that we

believe is of ultimate value in studies of wildlife resource selection. Quantitative approaches to optimizing risk are developed to varying degrees in the financial (Bouchard 2000) and environmental management (Environmental Protection Agency 1997) fields, but are just emerging in behavioral ecology (Houston and McNamara 1999). Developing metrics of composite risk to animals from multiple sources will require considerable conceptual and empirical effort.

## Conclusions

Delineating the area within which resources are to be associated with an animal's behavior and choosing a currency of use are 2 important steps in addressing a resource-selection problem. Availability must be defined in terms of abundance as modified by accessibility. If availability cannot be determined, an animal's association with, or use or selection of resources should be based on occurrence of the resources in the area. For resources with strongly spatial attributes, such as habitat types, occurrence 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 of study. The area in which an animal moves at one scale, such as home range, limits the resources at the next lower scale. Often and appropriately, resource associations are studied at multiple scales. After spatial bounds are set, various means of characterizing resources within the available area are used: random and stratified sampling, and pairing of nonused sites with used sites. The choice depends on the study objectives. Analytical procedures that refine our delineation of the area, 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. Understanding what motivates the behavior of an animal is important to understanding the fitness implications of patterns of resource use. Common currencies of use in the wildlife literature on resource selection are time spent and distance traveled. Event

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sites—places where animals expend time and energy, risk predation, and accomplish important life functions—are also common currencies of use. Currencies that are less common in the literature, but potentially valuable to the wildlife biologist, include energy expended and predation or other risk incurred. Some means to estimate these currencies are available now; others are being developed. 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.

## Management Implications

Management decisions based on resource-selection analyses must consider how availability is defined and what currencies of use are used. Resource-selection analyses, even using the most advanced inferential and modeling methods, are not assumption-free, but require carefully defining or assuming what is available, and identifying currencies of use and how they affect inferences. Evolving analytical methods improve compliance with assumptions that are often violated, including the assumption that resources are equally available across a frame of reference (e.g., home range or study area) and throughout a study. In the future, students of resource selection will need to consider composite currencies of use that consider dissimilar risks that animals must trade-off to maximize individual fitness.

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