HABITAT QUALITY: A BRIEF REVIEW FOR WILDLIFE BIOLOGISTS

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Abstract. Understanding habitat quality for wildlife is extremely important for biologists, but few papers have explored the pros and cons of how to measure it. In this review, I clarify terminology and distinguish habitat quality from related terms, differentiate habitat quality from animals' and wildlife managers' perspectives, and describe different ways of measuring habitat quality in the field. As is feasible, biologists concerned with habitat quality should emphasize demographic variables while recognizing that reproduction, survival, and abundance may not be positively correlated. Animal distribution can also reveal habitat quality (e.g., through patterns of habitat selection), but biologists should first investigate how closely their subjects follow ideal distributions because numerous ecological factors can lead animals to select poor, and avoid rich, habitats. Lastly, measures of the animals' body condition can provide convenient measures of habitat quality, but variation in body condition may not result in differential animal fitness among habitats. Biologists should use caution before relying on shortcuts from more labor-intensive demographic work.

TRANSACTIONS OF THE WESTERN SECTION OF THE WILDLIFE SOCIETY 41:31–41; 2005

Key words: body condition, demography, distribution, habitat preference, habitat quality, habitat selection, habitat suitability.

The loss and degradation of habitat are the largest threats to wildlife (Fig. 1). Therefore, the maintenance of high-quality habitat is fundamentally important for wildlife biologists. Indeed, for many biologists, "wildlife management is habitat management." This is especially true in California, where the average human population density is >8 times higher than in the other 10 western states, and concomitant native habitat loss is intense (U.S. Census Bureau 2000).

It is no surprise, then, that biologists have long recognized the need to identify, conserve, and manage habitats for wildlife. Limited funding requires prioritizing habitats based on their value for particular management objectives, which often revolve around focal species such as game species and species of special conservation concern. But how can habitats be judged for their importance to animals; how can good, marginal, and poor habitats be distinguished? That is, how can biologists assess the *quality* of habitats for particular animals?

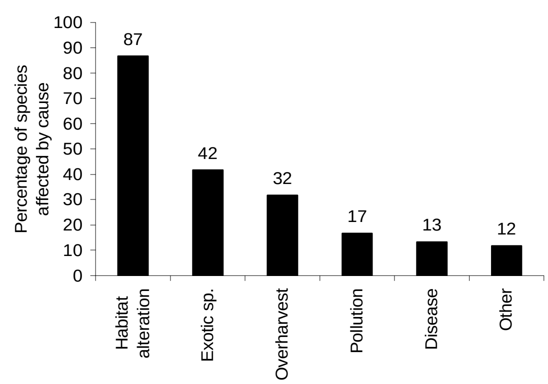

Fig. 1. Causes of endangerment of non-fish vertebrate species listed as threatened and endangered in California. A species can have more than 1 cause of endangerment. Note that habitat alteration–which includes habitat loss, degradation, and conversion–is by far the greatest threat, followed by interactions with exotic species, which often invade following habitat alteration. The data in this figure were obtained from the Federal Register and cover all species listed or proposed for listing as of 31 July 2005.

Van Horne (1983) provided one of the first formal treatments of habitat quality, and she cautioned that the density of animals in a habitat

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can, in some cases, be a misleading indicator of habitat quality. Since the publication of her influential and oft-cited paper, biologists recognize that robust measures of habitat quality require a thorough unraveling of habitat-specific measures of demography (i.e., density, reproduction, and survival measures in each habitat considered). Time and money constraints, however, rarely allow these measures to be obtained. Therefore, biologists often rely on other measures to help distinguish rich and poor habitats, spawning related terms and concepts such as habitat carrying capacity, habitat preference, and habitat occupancy. In many cases, habitat quality is taken to be a somewhat vague concept that enables habitat patches to be ranked, often eroding into an index ranging from 0 to 1, as in the U.S. Fish and Wildlife Service's "habitat suitability index" (HSI) models (Schamberger et al. 1982). Despite its importance to the discipline and the myriad recognized ways it can be measured, there have been few reviews of habitat quality and how it can be quantified by wildlife biologists (but see introductions of James 1971, Bernstein et al. 1991, Block and Brennan 1993, Lin and Batzli 2001, Sergio and Newton 2003). Herein, I describe ways of conceptualizing and measuring habitat quality. Specifically, I have 3 objectives: (1) clarify terminology and distinguish habitat quality from related terms; (2) differentiate habitat quality from animals' and managers' perspectives; and (3) outline different ways of measuring habitat quality in the field, recognizing methods that emphasize demographic, distributional, and individual condition variables.

TERMINOLOGY

Hall and her colleagues (Hall et al. 1997, Morrison and Hall 2002) argued that some of the confusion surrounding habitat's role in wildlife ecology stems from inconsistent and imprecise use of terms, which is, in part, understandable given habitat's long history in ecology (Grinnell 1917, MacArthur et al. 1962, James 1971, Whittaker et al. 1973). Hall et al. (1997:175) sought to provide standards and defined habitat as "the resources and conditions present in an area that produce occupancy, including survival and reproduction, by a given organism." They consider habitat quality as the ability of the environment to provide conditions appropriate for individual and population persistence. This is an intuitive and attractive operational definition, but much is masked by considering habitat quality to relate to both individual and population-level perspectives. For example, consider 2 habitats: Habitat A has relatively few high-quality resources and Habitat B has abundant lower quality resources (Fig. 2). The details of the resources are unimportant; for example, they could be nest sites for songbirds or forage for deer. Habitat A offers the higher intrinsic rate of population growth (r) and Habitat B has a higher carrying capacity (K).

Which habitat is best? From an individual animal's perspective, Habitat A is better in many cases because it provides the animal with access to high-quality resources that maximize chances for survival and reproduction. However, from the perspective of a population, Habitat B may be better because it supports a larger persistent population. This tradeoff in quality and quantity of resources was explored by Hobbs and Hanley (1990), and it underscores the necessity to distinguish habitat quality between different perspectives of individual animals and wildlife managers.

Wiens (1989*a*) and Orians and Wittenberger (1991) emphasized the importance of considering temporal and spatial scales in animal habitat ecology, which extends to measures of habitat quality. A habitat's quality can change rapidly for a given species, and care must be taken to understand when resources are most limited and when consequences of rich and poor habitats most influence an individual's fitness. Spatially, an animal's use of the landscape can vary dramatically, with some areas (even within its home range) nearly ignored while others receive the most intense use (Manley et al. 2002). Therefore, fine scales of habitat selection (e.g., Johnson's 2nd and 3rd orders, 1980) must be understood to fully reveal nuanced patterns of habitat quality. Moreover, some animals may not achieve adequate fitness unless multiple habitats are juxtaposed in ways that enable them to meet all of their life history requirements, further underscoring the importance of considering spatial scales of habitat quality (Pulliam 2000). Nonetheless, biologists can learn much by focusing on the consequences of habitat occupancy (i.e., demographic and other indicators of habitat quality) because they manifest in population dynamics. In the end, well-managed habitats should yield well-managed wildlife populations.

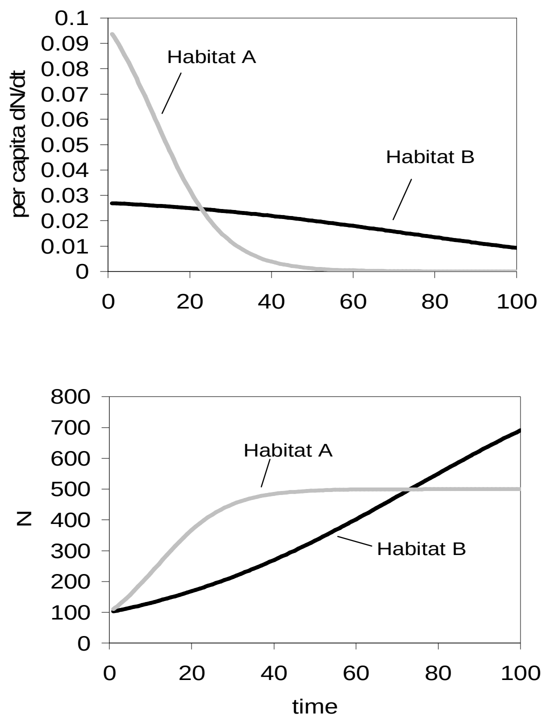

Fig. 2. Logistic population growth curves for animals in 2 hypothetical habitats. Habitat A has relatively few high-quality resources and Habitat B has abundant lower quality resources, resulting in a higher intrinsic rate of population growth in A (r_A = 0.12, r_B = 0.03) and a higher carrying capacity in B (K_A = 500, K_B = 1000). Both populations were simulated with initial population sizes of 100 and run for 100 time intervals. If habitat quality is considered purely from an individual animal's perspective, then Habitat A is the better habitat until time 23, after which point Habitat B offers the higher average per capita dN/dt. In contrast, if habitat quality is measured as the current population size, then Habitat A remains better until time 74. If habitat quality is considered the maximum sustained population size, as may be the perspective of many wildlife mangers, then Habitat B is always best because it has the higher carrying capacity.

HABITAT QUALITY FROM ANIMALS' AND WILDLIFE MANAGERS' PERSPECTIVES

Habitat quality is easiest to conceptualize with regard to individual animals. Individual organisms occupying habitats that maximize their lifetime reproductive success will produce the most progeny. Natural selection, therefore, favors individuals that distinguish between high- and low-quality habitats based on the habitats' potential to confer fitness on their inhabitants. Habitat quality from an individual animal's perspective is, therefore, simply the per-capita rate of population increase (per capita dN/dt) expected from a given habitat.

For a wildlife manager, what constitutes high-quality habitat varies depending on objectives. For example, in the 2-habitat scenario proposed above, the habitat with the higher carrying capacity (Habitat B) is the higher quality habitat when a premium is placed on population size, as may be the case for game species or species vulnerable to pitfalls of small populations. However, the habitat with higher quality resources and higher rates of increase is best when wildlife managers are seeking the healthiest individuals possible, such as for trophy species or critically endangered species whose populations need to be enhanced. Which perspective should we emphasize? Clearly, the appropriate perspective on habitat quality will depend on the management objective. Ideally, one should consider both perspectives simultaneously because identifying discrepancies between the two will reveal the prioritizations individual animals make over populations (Bernstein et al. 1991), although accomplishing this will rarely be feasible in the field. Nonetheless, prioritizing habitats based on their value *to individual animals* will rarely yield unwanted results. In addition, the individual animal's perspective is theoretically preferable because natural selection operates more strongly on individuals than on populations—it is individual animals, not wildlife managers, that select among habitats. Therefore, throughout the remainder of this paper, I consider habitat quality from the individual animal's perspective.

MEASURING HABITAT QUALITY

Basic Approaches

There are 2 basic approaches to conceptualizing how to measure habitat quality. We can either assess habitat quality directly by measuring attributes of the habitats themselves, or we can measure variables for animals and populations in different habitats to reveal variation in habitat quality. In measuring habitats directly, we should, of course, be concerned with critical resources, such as food and nest sites, but habitat is far more than the vegetation and resources surrounding an animal. Equally important are the ecological constraints that may limit the use of those resources, such as risk of predation, intensity of competition, and/or physical accessibility of resources. Indeed, habitat is defined by not only the resources necessary for survival and reproduction, but also by the conditions that constrain its use (Morrison et al. 1998).

Relatively few studies that directly measure habitat attributes are done in an attempt to explicitly measure habitat quality. That is not to say that few studies measure vegetation and resources in an attempt to describe habitat. To the contrary, the wildlife literature is rife with studies relating animal distribution or demography to aspects of habitat, especially vegetation (Morrison et al. 1998, Scott et al. 2002), but few of these studies consider vegetation metrics to be measurements of habitat quality. Instead, they rank the quality of habitats based on the abundance, distribution, or performance of the animals inhabiting them and use statistical associations with habitat measurements to identify features potentially contributing to a habitat's quality. This descriptive approach to examining wildlife–habitat relationships is of limited use (Morrison 2001), and hypotheses relating habitat quality to features that humans can potentially influence, such as vegetation cover, forest-stand characteristics, and habitat fragmentation, have not been fully tested.

Nonetheless, the features hypothesized to govern habitat quality are feasibly quantified in some systems, allowing habitat quality to be measured directly. For example, McCorquodale (1991) evaluated habitat quality for elk (*Cervus elaphus*) in Washington by quantifying metabolizable energy available in major summer forage grasses. Barnes et al. (1995) measured habitat quality for northern bobwhite (*Colinus virginianus*) by quantifying grass forage quality, food (insect) abundance, and availability of cover. Goss-Custard (1995) documented food availability and competition to quantify habitat quality for oystercatchers (*Haematopus ostralegus*). These approaches assume we understand (or can learn) what the animals actually need in order to quantify habitat quality. In these well-studied species, and a few others, researchers have worked toward this goal. However, we simply do not know enough about most wildlife species to follow this approach. Instead, it may be more efficient to assess habitat quality by studying animals in different habitats, using variation in the animals' demographics or performance to reveal variation in habitat quality.

Let Animals Reveal Habitat Quality

Most studies take the second conceptual approach by quantifying animal abundance, distribution, and/or performance among different habitats to reveal variation in habitat quality. Few studies can measure all of these potential indicators simultaneously, and it is not always clear which measure is most appropriate. Here, I describe the strengths and limitations of various measures of habitat quality. I classify these animal-based indicators of habitat quality into 3 categories—demographic, distributional, and individual condition measures.

Demographic Measures.—As explained earlier, habitat quality is best defined from an individual animal's perspective as the per-capita rate of population increase (per capita dN/dt) expected from a given habitat. Therefore, the roots of the concept are demographic, and habitat-specific measures of density, reproduction, and survival offer some of the best measures of habitat quality (Franklin et al. 2000, Lin and Batzli 2001, Wheatley et al. 2002, Pettorelli et al. 2003, Persson 2003, Franken and Hik 2004). The major disadvantage of using demographics to indicate habitat quality is that they are difficult to measure. Therefore, researchers rarely measure density, reproduction, *and* survival, and if these measures are not tightly correlated, any of them can be misleading. Van Horne (1983) outlined scenarios in which density can be high where reproduction is low, although Bock and Jones (2004) suggest that density is usually roughly correlated with habitat quality for breeding birds. Habitat conditions favoring survival and reproduction may not be the same (Franklin et al. 2000), which could lead to misleading measures of habitat quality if only 1 parameter is used to rank habitats.

Distributional Measures.—The Ideal Free and Ideal Despotic Distribution models provide the theoretical backdrop for how animal distribution may reveal variation in habitat quality (Fretwell and Lucas 1970, see Parker and Sutherland 1986 for modifications). In these models, the highest quality habitats are occupied first, and as they fill and diminish in quality because of competition, lower quality habitats are occupied in sequence (Bernstein et al. 1991). Fretwell and Lucas (1970) distinguished cases in which all animals were equal competitors, were free to choose among habitats, and achieved equal fitness from cases in which dominant individuals (despots) occupied the best habitats and relegated subordinate individuals into lesser habitats. The models share the assumption that all animals have complete knowledge of habitat options and select the habitat that maximizes individual fitness.

Numerous measures of animal distribution can be used to indicate habitat quality based on these models. The disproportionate use of a habitat relative to its availability (i.e., habitat selection) can indicate high-quality habitats, and the field and analytical methods to investigate habitat selection are well described (Morrison et al. 1998, Manley et al. 2002). For example, Hunt (1996) used patterns of habitat selection to evaluate habitat quality for American redstarts (*Setophaga ruticilla*) breeding along a successional gradient in New England. In addition, Nicholson et al. (1997) used habitat selection to assess habitat quality in migratory mule deer (*Odocoileus hemionus*), and Rittenhouse et al. (2004) used selection of substrate habitat to infer habitat quality for spotted salamanders (*Ambystoma maculatum*).

The principal weakness in using distribution to reveal habitat quality is that many different scenarios, such as incomplete information (Shochat et al. 2002, Stamps et al. 2005), ecological traps (Battin 2004), time lags and site fidelity (Davis and Stamps 2004), strong despotic distributions (Parker and Sutherland 1986), and a lack of high quality habitat (Halpern et al. 2005) can lead to “non-ideal” distributions (i.e., animals selecting poor, and avoiding rich, habitats). Therefore, researchers should first establish how well a given system adheres to patterns of ideal habitat selection before using animal distribution to reveal variation in habitat quality (Pulliam 2000, Morris 2003).

Habitat selection models predict that, relative to low-quality habitats, high-quality habitats should be occupied for longer periods within a season and more consistently over years. Consequently, many researchers have used timing, duration, and frequency of habitat occupancy as measures of habitat quality (Sergio and Newton 2003). For example, Ferrer and Donázar (1996) found habitat occupancy related to both resource availability and reproduction for imperial eagles (*Aquila heliaca*) in Spain. This approach has the advantage that simple occupancy is usually far easier to quantify than intensive demographics, and it could be very useful for populations in heterogeneous landscapes and for which not all habitats are occupied every year. However, using occupancy as a measure of habitat quality usually requires data covering multiple seasons, and conclusions can be clouded by changes in population size or landscape features. Moreover, site fidelity and social constraints or other forms of “time lags” (Wiens 1989*b*) can cause poor-quality habitats to remain occupied, even when better habitats become available, and good habitats to remain unused, decoupling the link between habitat occupancy and quality (Pulliam 2000). In addition, for animals whose home ranges encompass numerous patches of potentially very different habitats, it may be difficult to ascribe quality based on occupancy without understanding which patches within the home range are most critical.

If animals distribute among habitats with respect to their quality, then habitats used for parts of the annual cycle should be occupied in sequence from best to worst and abandoned in sequence from worst to best. Therefore, dates of arrival in and departure from particular habitats can be used as measures of habitat quality, especially for migratory animals (Alatalo et al. 1986, Marra 2000, Marra and Holmes 2001). For example, Lanyon and Thompson (1986) found that arrival patterns of painted buntings (*Passerina ciris*) correlated with reproduction and habitat quality, and Smith and Moore (2005) confirmed that early arriving American redstarts chose better habitats and achieved higher reproductive output than later arrivals. This approach has the advantage of being easily measured in the field for some systems, and arrival date can potentially reveal information relevant to the previous phase of the annual cycle (Gill et al. 2001, Norris 2005). However, as with all distributional measures, animals may not have complete information on available habitats (Stamps et al. 2005), and, indeed, may use each other as indicators of where to settle (Muller et al. 1997), causing the initial settling period to be highly dynamic and not strongly associated with spatial variation in habitat quality.

The despotic distribution model predicts that dominant individuals should settle disproportionately in the highest quality habitats. Therefore, the ratio of behavioral classes among habitats (e.g., adult vs. young, male vs. female, etc.) could reveal variation in habitat quality. For example, Rohwer (2004) used age ratio of warblers to infer survival and habitat quality, and Marra (2000) found that ratios of dominant to subordinate age and sex classes were strongly associated with patterns of habitat quality for wintering American redstarts. This approach can be convenient in the field, but it requires that dominant and subordinate individuals be easily distinguished (e.g., by age-specific plumage or body size) and relies on a well-established despotic distribution. Moreover, precisely when age ratios are determined is important. For example, post-breeding age ratios are often used as an index of reproduction with the opposite prediction–the best (most productive) habitats should have a low ratio of adult:young (Flanders-Wanner et al. 2004).

Individual Condition Measures.—Nearly all the measurements of habitat quality reviewed so far require measuring populations of animals, often over extended breeding or non-breeding periods. These approaches can be problematic when wildlife are difficult to observe or capture and when animals use habitats briefly, such as migratory species. As an alternative, some researchers have used measures of individual animals' physical condition as an indicator of habitat quality.

We can distinguish variables that rely on external visible and measurable features, called morphological condition measures, from variables that rely on analysis of sampled tissues (especially blood), called physiological condition measures. Regardless, all measures of body condition share 2 requirements to be useful as indicators of habitat quality. First, variation in condition must be a consequence (rather than a cause) of differential habitat use. That is, variation in habitat attributes such as food supply and predation risk must lead to variation in the animals' condition. Although this may often be partially true, in some systems, it is also likely that preexisting differences in the animals' condition lead them to use different habitats. For example, lean individuals might choose food-rich but risky habitats while fat individuals might choose food-poor but safer habitats (e.g., Moore and Aborn 2000). If this were the case, body fat and local food supply would be inversely related, and good body condition would not necessarily be an indicator of food-rich habitats. Second, using measures of body condition as indicators of habitat quality assumes that differences in condition ultimately manifest in differential fitness. This has been confirmed in a number of species (Bety et al. 2003, Reading 2004, Johnson et al. in press). Nonetheless, statistically significant variation in body condition among habitats does not guarantee variation in reproduction and or survival.

It is also important for researchers to match the temporal scale over which measures of body condition change to the temporal scale over which habitat quality is to be judged. For example, horn growth in mountain goats (*Oreamnos americanus*) reflects the quality of habitats the goats occupy over several years (Cote et al. 1998), whereas body mass in roe deer (*Capreolus capreolus*) changes seasonally, reflecting annual variation in habitat quality (Pettorelli et al. 2002), and blood metabolites in songbirds change hourly, reflecting the feeding and fasting behavior of the birds occupying habitats over very short time frames (Jenni-Eiermann and Jenni 1994). This variation both enhances and detracts from using measures of body condition as indicators of habitat quality. On one hand, dynamic measures of body condition are potentially much more sensitive to variation in habitat quality than other measures, such as demographics, and they may enable biologists to quantify habitat quality for animals occupying habitats only briefly. On the other hand, these measures may be too subject to temporal variation to reveal lasting variation in habitat quality. For example, fat stores in wintering songbirds may reveal more about recent weather patterns than about the quality of winter-occupied habitats (Rogers et al. 1994). Measures of body conditions that change more slowly may be useful for ranking habitats occupied over long periods, but, for mobile species, they may not reflect local habitat quality. For example, the body mass of a deer on its fawning grounds may be more dependent on the habitats it has occupied in the previous months than on its current habitat conditions. Researchers must seek to understand which periods of the season are most critical, and optimize their sampling of body condition accordingly.

Many different body condition measures have been considered indicators of habitat quality. Common morphological measures include: body mass (Pettorelli et al. 2002); body size (often based on multiple morphometrics); mass corrected for body size (Latta and Faaborg 2002); fat stores (Strong and Sherry 2000, Brown et al. 2002); various measures of pigmentation, especially the prominence of ultraviolet wavelengths (Siefferman and Hill 2005); and fluctuating asymmetry (Lens et al. 1999), the latter based on the notion that high-quality habitats enable symmetric morphological development. Physiological measures are less commonly used, but endocrinological indicators of stress (e.g., concentrations of corticosterone in blood) have increasingly been used to assess habitat quality (Marra and Holberton 1998, Homan et al. 2003). More recently, workers have suggested that concentrations of blood metabolites, especially triglycerides and ß-hydroxy-butyrate (Jenni-Eiermann and Jenni 1994, Williams et al. 1999), can indicate short-term patterns of foraging and fasting, and therefore provide a measure of habitat quality. With all of these methods, researchers should first confirm that the measures indicate habitat quality by comparing data in habitats known from independent work to be high and low in quality.

CONCLUSIONS

Animal distribution is dependent on the fitness conferred by selected habitats (Fretwell and Lucas 1970), which provides the theoretical underpinnings for conceptualizing and measuring habitat quality for wildlife (Franklin et al. 2000). When we know what resources and ecological constraints govern fitness and can measure them, measuring habitat quality directly is advisable but in reality is rarely practical.

When using animals' abundance, performance, or condition in habitats to reveal habitat quality, biologists should emphasize demographics whenever feasible, recognizing that reproduction, survival, and abundance may not be positively correlated. Emphasizing demographics when measuring habitat quality is appropriate because the root of the concept is in demography (Block and Brennan 1993, Hall et al. 1997), and demographic measurements suffer from few limitations except their difficulty to obtain in the field. In addition, for wildlife managers to effect change on the landscape, they must work to identify on-the-ground variables that affect animal demography.

When quantifying variables related to the distribution of animals as a measure of habitat quality (e.g., habitat selection, presence/absence, habitat occupancy), biologists should first investigate how closely their subjects follow ideal distributions because a variety of ecological factors can lead animals to select poor, and avoid rich, habitats. Lastly, measures of animals' body condition can provide convenient measures of habitat quality, but the link between body condition and habitat-specific fitness has been confirmed in relatively few systems. Biologists should use caution before relying on shortcuts from more labor-intensive demographic work.

ACKNOWLEDGMENTS

I thank B. Kristan, A. Strong, and the Humboldt State University Advanced Habitat Ecology classes for stimulating discussion of this topic. B. Garrison, D. Van Vuren, and 2 anonymous reviewers provided helpful suggestions on an earlier version of this manuscript.

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