

Using body size to predict perceptual range

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We examined the relationship between body size and perceptual range (the distance at which an animal can perceive landscape elements) for a group of forest-dwelling rodents. We used previously published data on orientation ability at various distances for three sciurid species (gray squirrel, fox squirrel and chipmunk) and one murid species (white-footed mouse) to build a predictive model. We found a significant positive relationship between perceptual range and body mass. Although this model was built using a 15.5 m high horizon, we used this relation to predict the perceptual range of root voles (3.9–4.3 m) orienting towards a 0.5 m high horizon which was consistent with other empirical work suggesting a value of something less than 5 m. This model illustrates a relationship between perceptual range and body size and can be used to develop starting points for future investigations of perceptual range for similar organisms.

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The spatial and temporal scales of disturbance are important in determining a species' response to habitat fragmentation. While investigations of the influence of temporal scale require long-term studies (Fahrig 1992, Urban et al. 1987, Wiens 1989), spatial processes can be examined with studies that are more logistically feasible. Such studies have revealed that the response of species to habitat fragmentation is influenced by a variety of ecological factors (Lord and Norton 1990, Levin 1992, Gustafson and Gardner 1996, Zollner and Lima 1997) and is dependent upon the spatial scale of the fragmentation (Urban et al. 1987, Krohne and Burgin 1990, Doak et al. 1992, Fahrig 1992, Crist 1994, Davies et al. 2000). For example, at a given level of fragmentation, a species' response will be determined in part by the scale at which it perceives the landscape (Lord and Norton 1990, Levin 1992, Zollner and Lima 1997).

Many life history and behavioral traits will affect how species respond to habitat fragmentation (Lima and Zollner 1996, Andrén et al. 1997, Bolger et al.

1997, Henein et al. 1998). For example, simulation models show that habitat generalists should have longer persistence times in fragmented landscapes than habitat specialists (Henein et al. 1998) and empirical work demonstrates that generalists are better at crossing and using matrix habitat (Laurance 1990). Behaviors, such as gap crossing, have been shown to be important in theoretical models (Fahrig 1988, Dale et al. 1994) and have been suggested as possible mechanisms underlying the differential distribution of some organisms in fragmented landscapes (Zollner 2000). For example, Grubb and Doherty (1999) found that for non-migratory birds the likelihood of crossing gaps within a home range increased with increasing body size. Understanding the influence of characteristics like these on the response of species to fragmented landscapes should allow us to better predict the consequences of changing landscape patterns (Wolff 1999).

Perceptual range, defined by Lima and Zollner (1996), is the range at which an animal can perceive a landscape element as such. This definition has two

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important implied aspects: first, the landscape element must be important to the animal, and second, the perceptual distance will depend on the species. Intuitively, for any set of species with similar habitat requirements, the scale at which the organism uses the landscape will be a function of the perceptual distance (Wiens 1989, Doak et al. 1992, Crist 1994, With and Crist 1996). Species that have short perceptual ranges (e.g. white-footed mice; Zollner and Lima 1997) will be more sensitive to habitat fragmentation than species with long perceptual ranges (e.g. fox squirrels; Zollner 2000). For animals that use vision as a primary mechanism to perceive distant habitat, perceptual range should scale with the height of the animal's eye from the ground and possibly with eye size. Eyes that are higher above the ground should logically provide longer perceptual ranges, and eye size has been shown to affect the distance at which an animal can perceive predators (Smith and Litvaitis 1999). For animals with similar body forms, eye size and height will depend on body size. Furthermore, visual acuity has been shown to scale with body size for both birds and mammals (Kiltie 2000). Thus, we expect that perceptual range, as defined above, should scale with body size (Gillis and Nams 1998) similar to other ecologically important life history traits such as dispersal distance (Sutherland et al. 2000), home range size (Kelt and Van Vuren 1999), basal metabolic rate, physiological parameters, and litter size (Peters 1983).

Our goal is to quantify the relationship between body size and perceptual range. Specifically, we test the hypothesis that perceptual range, and therefore the spatial scale at which an individual will respond to fragmentation, depends on body size. We also develop a model to predict the effects of body size on perceptual range and validate this model using the data of Andreassen et al. (1998) on the perceptual range of root voles (*Microtus oeconomus*).

Methods

We used previously published data on four small mammal species to test for a relationship between perceptual range and body size. The general protocol for collecting these data was to translocate woodland-resident small mammals distances of at least 5 km and release them in barren agricultural fields where they have no previous experience, at different distances from a wooded edge and assess the orientation of their movement paths as indicative of perception. This methodology relies on a critical assumption that these woodland-dwelling small mammals will want to leave the vegetation-free fields where they were released and move to the cover of their preferred forested habitat as quickly as possible. This assumption is supported by the failure to detect any

statistical tendency for homing in any of these studies. The details of these experiments are described in the papers cited below. We used data from Zollner (2000) on the perceptual ranges and orientation ability of three sciurid species: eastern chipmunk (*Tamias striatus*), gray squirrels (*Sciurus carolinensis*), and fox squirrels (*S. niger*) and data on the perceptual abilities of the white-footed mouse (*Peromyscus leucopus*) from Zollner and Lima's (1999a) 'twilight-informed' mice. This experiment involved providing these nocturnal mice with a view of the local landscape during twilight and releasing them after the onset of darkness. We used this data set because the perceptual range of white-footed mice was greatest under these conditions.

Because of the limited number of release distances for each species and because the V-tests used in these previous publications classified species as significantly or not significantly oriented towards the woods from a given distance, we did not use perceptual range as defined by the V-tests directly in our model. Instead, we used the angular divergence, which is different from the orientation angles given in Zollner and Lima (1999a) and Zollner (2000). Angular divergence (Conradt et al. 2000) was defined as the angle from the release point to a critical point along the animal's trail with the direction from the release site to the nearest forest edge defined as zero degrees. Thus, angular divergence ranged from a minimum value of zero degrees for animals headed directly towards the woods to 180 degrees for those headed directly away from it. For these analyses we defined the critical point as the location along the animal's movement path where its net displacement away from the release point was 1 m less than the distance from the site where it was released to the nearest point in the woods. This ensured that we did not falsely attribute orientation to animals that reached the woods because of random movements (Goodwin et al. 1999). For those animals that did not successfully get farther than this critical distance away from the release mechanism within the limits of our tracking ability we used the last known location of the animal to assess angular divergence.

To determine each species' ability to orient across a range of distances, we regressed angular divergence against release distance using standard linear regression. For animals that are perfectly oriented toward the forest angular divergence is expected to be zero, while for animals not oriented toward the forest angular divergence is expected to be randomly and uniformly distributed between 0° and 180° and therefore will have a mean of 90°. This assumes that a smaller average angular divergence relates to a better ability of the species to correctly orient toward the forest. Therefore, we predict that this regression will have a positive slope for each species indicating less accurate orientation as the release distance increases. For white-footed mice, chipmunks and fox squirrels, there were data from

multiple years. Because each year had slightly different conditions (Zollner and Lima 1999a, Zollner 2000), we calculated separate regressions for each species each year. From each of these regressions, we obtained a slope estimate and associated variance. Note the slope is an estimate of how orientation towards the woods varies with release distance and thus is a good surrogate of perceptual range. Due to the large variation in the data, we accepted an alpha-level of 0.1 for this analysis. We then used a weighted regression to predict the relationship between species' body mass and the species-specific slope estimates of perceptual range for those regressions with slopes significantly different from zero. We did not log-transform body mass because this relationship is most likely due to eye-height rather than body mass per se. Local body mass estimates were obtained from Mumford and Whitaker (1982) and are given in Table 1. The inverse of the variance of the slope estimate was used as the weight because this leads to a BLUE (best linear unbiased estimator) for the final regression (SAS 1989). All analyses were performed using SAS (SAS 1996).

Results

Estimates of perceptual range are given in Table 1. Our regressions of angular divergence against release distance varied depending on the species and year. For white-footed mice, the regression was significant (at the $\alpha = 0.10$ level) in 1996 but not in 1995 (Table 2). Likewise, for chipmunks the regression was significant in 1997, but not in 1996 (Table 2). For fox squirrels, the 1997 data showed a significant regression, while the 1998 data did not (Table 2). Gray squirrels, for which we only had one year of data, showed a significant regression (Table 2). For all significant regressions, the intercept parameter was not significantly different from zero.

Relating the species-specific regressions of perceptual range to previous analyses using V-tests, we found that perceptual distances became non-significant (based on V-tests) when the predicted angular divergence was between 63° and 69° (Table 1). In addition, for those

years that did not have a significant regression, the release distances did not span the perceptual range as defined by the V-tests (Table 1 and 2). That is, when all releases were performed at distances less than the maximal distance at which an animal can perceive the landscape, there is no relationship between release distance and angular divergence. The exception to this observation is the fox squirrel data. The 1998 fox squirrel data has a maximum release distance of 500 m, which is larger than the maximal perceptual range (Table 1). However, based on the estimated slopes, it is most likely very near the maximal perceptual range for fox squirrels and, given the limited number of releases in this data set, there is probably too much variation to obtain a significant slope. Note, however, that while the slope for the 1998 fox squirrel data is not significant it is very similar to the slope of the 1997 data.

The weighted least squares regression of the slope of perceptual range against body mass resulted in a significant relationship ($p = 0.0020$) with a very high R^2 ($R^2 = 0.99$; Fig. 1). This indicates that perceptual distance is a function of body size. The scaling-power (slope of the line) of the allometric relationship is -0.00052 . The predictive equation for the slope of the perception line is

$$S = 0.53839 - 0.00052M \quad (1)$$

where S is the predicted slope (°/m) of the species regression and M is the mass of the species in grams. To predict a specific perceptual range, we convert the slope estimated from above to a perceptual distance (D) in meters for any given horizon height (H) in meters using the formula

$$D = (AD_{crit} \div S)(H \div 15.5) \quad (2)$$

AD_{crit} is the critical angular divergence value for perceptual range (63° to 69°). The 15.5 is the approximate height (in meters) of the forest used by Zollner (Zollner and Lima 1999a, Zollner 2000), which allows for correction for the height of the horizon (i.e. landscape element) when dealing with grassland or other non-forest-dwelling species. Note this assumes a zero inter-

Table 1. Perceptual ranges and average predicted angular divergence for the four species studied.

Species	Body mass (g)	Distance (m)	V-test result*	Predicted angular divergence
White-footed mouse	21	90	Sig	63.7°
		120	NS	78.8°
Chipmunk	111	120	Sig	53.3°
		180	NS	82.0°
Gray squirrel	510	300	Sig	45.0°
		400	NS	74.2°
Fox squirrel	787	400	Sig	56.0°
		500	NS	68.8°

* Significance/non-significance of V-tests given by Zollner and Lima (1999a) and Zollner (2000).

Table 2. Regression results of angular divergence (y) against release distance (x). Release distances are the distances from which 20 animals were released. Therefore, each regression has 20 independent y-values (angular divergence) for each release distance.

Species	Year	Release distances (m)	Regression equation	R ²	P
White-footed mice	1995	30, 60, 90	y = 71.466 - 0.233x	0.08	0.469
	1996	60, 90	y = 18.200 + 0.505x	0.01	0.080
Chipmunks	1996	60, 120	y = 19.268 + 0.1967x	0.01	0.616
	1997	60, 120, 180	y = -4.1689 + 0.4787x	0.20	0.004
Fox squirrels	1997	300, 500, 800	y = 4.7397 + 0.1282x	0.18	0.003
	1998	300, 400, 500	y = -6.1249 + 0.165x	0.07	0.229
Gray squirrels	1998	300, 400, 500	y = -42.424 + 0.2916x	0.15	0.044

cept, which is not unreasonable because none of the significant relationships had an intercept significantly different from zero.

To validate our model, we used the data presented by Andreassen et al. (1998). The root voles they released had an average mass of 44.9 g (H. Andreassen, pers. comm.) with an artificial 0.5 m horizon. Using this mass in eq. (1), we estimated that the slope of the regression between angular divergence from the woods and release distance would be 0.52°/m. Using eq. (2) and 63° and 69° as critical angular divergence values (see above) we determined the perceptual range of root voles to be 3.95–4.32 m for a 0.5 m horizon.

Discussion

The individual regressions have different slopes that, for significant regressions, tend to be steeper for smaller-bodied species (Table 2) and there is relative agreement between V-test results and average angular divergence (Table 1). This indicates that a simple linear regression of angular divergence against release distance may be sufficient to predict a maximum perceptual range for any species. Note these regressions all have low R²-values (Table 2). This is due to two factors. First, the inherent noise in this type of data caused by many animals not traveling towards the woods results in a large amount of variation. Second, when release distances are small, animals can have a fairly large angle of divergence and still be oriented towards the woods because at close release distances the woods cover a larger portion of the horizon than at longer release distances. Even with these caveats, this method has certain advantages over Zollner's (Zollner and Lima 1997, 1999a, Zollner 2000) method because there is no need for circular statistics and, more importantly, the releases can be conducted at more release distances with fewer replicates per release distance. However, our analyses indicate that this regression approach is only practical when animals are released both well within and well beyond perceptual range as confirmed using V-tests. Thus, we suggest a combination of these two approaches for evaluating perceptual distances in the future.

Comparing our model to the work by Andreassen et al. (1998), we found our predicted perceptual distance to agree closely with their observed perceptual distance. Andreassen et al. suggested that root voles had a difficult time perceiving 0.5-m high patches at 5 m distances. Our model predicts a perceptual range of 3.9–4.3 m for a 0.5-m high patch, a surprisingly close match with Andreassen et al.'s results. Furthermore, Andreassen et al. (1996) showed that 4-m long gaps in corridors of 0.5-m high vegetation limit the movement of male root voles. This is consistent with our predictions because these gaps would be close to the edge of the root vole's perceptual range.

Our analysis suggests that for visually oriented rodents moving under optimal conditions, perceptual range does depend on body size (Fig. 1). We should emphasize, however, that this relationship might arise due to correlates to body size such as eye size and limb length (therefore eye height), which may be more important in perceptual range than body size per se. The validation of our model against the independently conducted perceptual range experiments on root voles provides additional support for this conclusion and

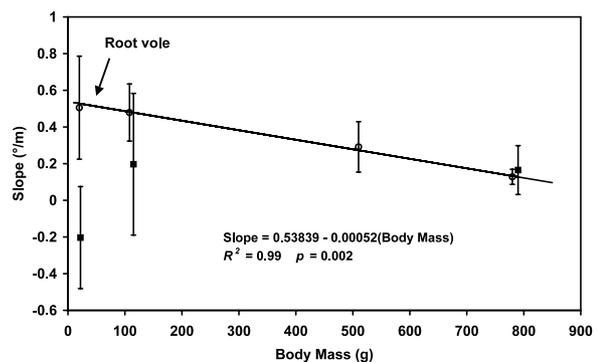


Fig. 1. Weighted regression of perception slope (slope of the lines from Table 2) against average body mass for each species. Circles indicate the slope of statistically significant species-specific regressions. Squares indicate the same values from statistically non-significant species-specific regressions. Bars indicate the error terms around each slope estimate. For the regression through the circles, each data point was weighted by the inverse of the variance in the slope estimate. The arrow indicates the predicted slope for root vole perceptual range.

demonstrates how this model might be applied to other species. However, we wish to stress that we have defined this relationship for a group of ecologically and morphologically similar species. We suspect that similar relationships will exist for other groups of animals, but that the shapes of these relationships may be very different and dependent upon the life history of the taxa in question. The model we are providing should not be applied to species other than visually oriented rodents with body mass between 15 and 800 grams moving under conditions that maximize perceptual range (i.e. open habitat). Also, because this model uses a linear rather than a log-linear relationship, no extrapolation beyond the body masses used here should be attempted. When applied to appropriate species this model will be most useful as a tool in designing field experiments to define perceptual range rather than as a means to parameterize simulations in the absence of confirming empirical data. Recall that our model is based on a 15.5-m horizon height and all calculations should be adjusted accordingly, as given in equation (2) and our validation using Andreassen et al.'s (1998) data demonstrated.

When good relationships can be defined between body size and perceptual range we may learn the most by examining species that are exceptions to the predicted patterns. Several factors might cause a species not to conform to this expected relationship. For example, the perceptual ranges we estimated for squirrels may be underestimates of the effective perceptual range that these arboreal species can experience by climbing trees (Zollner 2000). Alternatively, species that have had a long term evolutionary history within fragmented landscapes should have been selected to either increase their perceptual abilities to an appropriate scale for their environment or to develop mechanisms such as systematic search strategies (Conradt et al. 2000, Zollner and Lima 1999b) that can be used to compensate for limited perceptual abilities. By examining the life history traits of species that do not fit these expected relationships we may gain important insight into their current circumstances and, more generally, the response of animals to fragmented landscapes.

Although the influence of body size on the response of species to habitat fragmentation is ambiguous at the population level (Davies et al. 2000 and references therein), we would argue that, to a large extent, the effects of habitat fragmentation on individuals could be predicted by the body size of the animal. This is due to several factors. First, body size affects perceptual range (this experiment) and perceptual range affects an individual's ability to respond to habitat fragmentation (Crist 1994, Doak et al. 1992, Wiens 1989, With and Crist 1996). Therefore, what a smaller animal would perceive as a barrier, a larger bodied animal would not. Second, body size is associated with home-range size (Kelt and Van Vuren 1999, Peters 1983). If the animal

can only use specific habitat types, habitat fragmentation may reduce the useable habitat below their requirements for a minimum home range, resulting in a negative impact. However, if the animal can perceive usable habitat outside its normal home range, it may expand its home range to include this other habitat (Grubb and Doherty 1999); this is similar to landscape supplementation as described by Dunning et al. (1992). Third, body size is positively associated with how much animals move per day (Fragoso 1999, Garland 1983). Thus, larger animals should be familiar with larger landscapes (Danielson and Anderson 1999) independent of what they can perceive or require. Overall, these results suggest that larger bodied animals will be less affected by habitat fragmentation, and we propose that the effect of body size on perceptual range is one possible mechanism for this effect.

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