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DISPERSAL DISTANCE OF MAMMALS IS PROPORTIONAL TO HOME RANGE SIZE

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Abstract. We tested the prediction that home range area and dispersal distance in mammals are related when considered independently of body size. Regression of log-transformed data demonstrated that more variance in maximum dispersal distance could be explained by home range area (74%) than could be explained by body size (50%). The relationship between maximum dispersal distance and home range size was isometric (slope = 1) when the square root of home range area (i.e., linear dimension of home range) was used. Thus, maximum dispersal distance was related to home range size by a single constant of 40. A linear relationship remained between these two variables after the effects of body size were removed ($F = 31.6$, df = 1, 32, $P = 3.2 \times 10^{-6}$, $R^2 = 0.50$). A similar isometric relationship with home range size was found for median dispersal distance (related by a multiple of 7). This isometric relationship between dispersal distance and home range size was tested using a second data source: maximum movements made by mammals after translocation, which also was linearly related to home range area ($F = 94.5$, df = 1, 23, $P = 1.3 \times 10^{-9}$, $R^2 = 0.81$). The slope and intercept of this relationship were not different from those of the relationship between maximum dispersal distance and home range area. We suggest that the vagility of mammals affected both home range size and dispersal distance (or movement after translocation) independently of body size, such that these movements could be predicted by home range area better than by body size alone. The resulting isometric relationship between dispersal distance and home range size has potential as a useful scaling rule for ecological practitioners.

Key words: allometric; dispersal distance; home range; homing; isometric; mammal; relocation; scale; scaling; simulation model; translocation; vagility.

INTRODUCTION

Dispersal is an important process that has profound effects on the structure of populations. For example, spacing patterns (Krebs et al. 1969), habitat colonization (Bowman et al. 2001*a*), allelic frequencies (Landry and Lapointe 1999), extinction thresholds (Fahrig 2001), dispersion (Shaw 1995), and demographics (Krohne and Hoch 1999) are all affected by dispersal. One of the important attributes of dispersal is the distance traveled by dispersers, which constrains the ability of a species to colonize an empty habitat patch (Bowman et al. 2001*a*). As such, dispersal distance is an important parameter in many population and conservation models (e.g., Henein et al. 1998).

Although the distance traveled by dispersers is an important aspect of population biology, it also is challenging to study, and therefore is often poorly known. Difficulties in predicting when and where an organism is going to disperse create serious logistical problems in collecting these data. There are a number of theoretical models that attempt to generalize the distribution of dispersal distances, but there remain relatively few empirical data (Peles et al. 1999). This lack creates a problem for ecologists and conservationists attempting to formulate hypotheses or build models using information about dispersal distance.

Recently, there have been some advances in our knowledge of how dispersal distances vary across mammal species. Wolff (1999) and Sutherland et al. (2000) have demonstrated that dispersal distance in mammals is linearly related to body size when both variables are expressed on a $\log_{10}$ scale. One could use this relationship to predict the expected median or maximum dispersal distance for a mammal of a given body size (e.g., Sutherland et al. 2000). The predictive ability

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of this relationship is limited, however, because some species disperse much farther than expected for a given body size, whereas other species disperse a shorter distance than expected. Wolff (1999) has advocated using these residuals as a behavioral model system (BMS) for landscape ecology studies.

The home range area of mammals also is related to body size when both variables are expressed on a $\log_{10}$ scale (Harestad and Bunnell 1979, Lindstedt et al. 1986). As with dispersal distance, there is variability in the home range area vs. body size relationship, such that some mammals have larger or smaller home ranges than expected for a given body size.

Dispersal distance and home range size should covary across mammal species because both are related to body size. However, these two measures of movement also quantify an animal's vagility, or inherent ability to move. We suggest that the residual variance in both the home range area vs. body size and the dispersal distance vs. body size relationships represent differences in vagility that are independent of body size. Thus, dispersal distance and home range size also should covary across mammal species after the effects of body size are removed. For example, species with home ranges larger than expected for a given body size also should disperse farther than expected. Knowledge of such a relationship would improve both our understanding of the process of dispersal and our ability to accurately predict dispersal distances. Here, we test the prediction that home range area and dispersal distance in mammals are related when considered independently of body size.

METHODS

We obtained data on home range area for North American mammals, averaged across sexes, from Harestad and Bunnell (1979). Other sources of home range data exist, but we sought simplicity and transparency in our approach. Thus, we chose the Harestad and Bunnell (1979) data, which are well known to ecologists and have been reanalyzed recently (Kelt and Van Vuren 1999). We obtained median and maximum natal dispersal distances for mammals from Sutherland et al. (2000). By cross-referencing these two data sets, we established a set of 33 data points containing both home range area and maximum dispersal distance, and nine data points containing both home range area and median dispersal distance. We added to this one data point for dispersal of the red-backed vole (*Clethrionomys gapperi*) that was available (Bowman et al. 2001*b*) at a later date than the Sutherland et al. (2000) data. This gave us sample sizes of 34 (maximum dispersal distance and home range area) and 10 (median dispersal distance and home range area). The two data sets (Harestad and Bunnell 1979, Sutherland et al. 2000) used different sources for estimating body size. A Pearson correlation analysis of the two log-scale body size data sets for our subset of mammals, averaged across sexes, demonstrated a correlation of $r > 0.99$ ($n = 34$, $P < 0.00001$). Thus, we chose to use the Harestad and Bunnell (1979) body size data for all analyses.

We used least squares regression to relate $\log_{10}$-transformed variables according to the power law equation:

$$Y = aX^b \tag{1}$$

where Y is a response variable; X is an independent variable; a is a scaling constant derived from the regression intercept, but corrected for different units of measure; and b is a constant equal to the regression slope.

We first regressed each home range area and maximum dispersal distance for all mammals against body size. We were interested in exploring a pattern across the class Mammalia, so we did not split up trophic groups. All variables were on a $\log_{10}$ scale and we followed the suggestions of Sprugel (1983) to correct for bias associated with logarithmic transformations. The relationships between home range area and body size and between dispersal distance and body size are already known from Harestad and Bunnell (1979) and Sutherland et al. (2000). However, because we were using a subset of the data from these previous analyses, we required an appropriate standard for comparison. Next, we regressed log-scale maximum dispersal distance against log-scale home range area. Multiple linear regressions were then used to partition the variance in maximum dispersal distance that could be uniquely explained by home range area and body size. To further assess the relationship between maximum dispersal distance and home range area independently of body size, we used residuals of the $\log_{10}$ (home range area) vs. $\log_{10}$ (body size) regression and from the $\log_{10}$ (maximum dispersal distance) vs. $\log_{10}$ (body size) regression. We then regressed this residual maximum dispersal distance against the residual home range area. These steps were repeated for the smaller data set ($n = 10$) containing median dispersal distance and home range area.

Our next step was to assess the validity of our empirically derived relationship between dispersal distance and home range area. This was difficult, given that Sutherland et al. (2000) had been thorough in their review of natal dispersal distances. However, we found that reports of translocations were a second good source of long-distance movement data. Of course, movements after translocation are qualitatively different than natal dispersal movements, but if maximum movements have a behavioral or physiological basis, we thought that they should be related. We reviewed literature for reports of the maximum distance moved by

TABLE 1. Maximum long-distance movements after translocation for some North American mammals.

Species	Distance (km)	Return to home?	Reference
Canis latrans	48	yes	Danner and Fisher (1977)
Canis lupus	282	yes	Henshaw and Stephenson (1974)
Canis lupus	302	no	Fritts et al. (1984)
Clethrionomys gapperi	0.60	yes	Bovet (1980)
Felis concolor	494	no	Ruth et al. (1998)
Lepus americanus	4.83	yes	Keith and Waring (1956)
Lepus californicus	1.61	yes	Lechleitner (1958)
Martes americana	158	no	Slough (1989)
Martes pennanti	163	no	Roy (1991)
Microtus pennsylvanicus	1.20	yes	Ostfeld and Manson (1996)
Peromyscus maniculatus	3.22	yes	Murie and Murie (1931)
Procyon lotor	23.40	yes	Tabatabai and Kennedy (1989)
Procyon lotor	29.50	no	Tabatabai and Kennedy (1989)
Scapanus townsendii	0.14	yes	Giger (1973)
Sciurus carolinensis	4.49	yes	Hungerford and Wilder (1941)
Sylvilagus bachmani	0.16	yes	Chapman (1971)
Sylvilagus floridanus	7.65	yes	Applegate (1977)
Sylvilagus floridanus	19.32	no	Bowers (1954)
Tamias striatus	0.55	yes	Seidel (1961)
Tamiasciurus hudsonicus	1.61	yes	Hamilton (1939)
Thomomys talpoides	0.79	no	Vaughan (1963)
Ursus americanus	99	yes	Rutherglen and Herbison (1977)
Ursus americanus	179	no	Payne (1975)
Ursus arctos	258	yes	Miller and Ballard (1982)
Vulpes vulpes	56.35	yes	Phillips and Mech (1970)

mammals after translocation. Many of these were ‘‘homing’’ studies, in which animals were released at successive distances until they no longer returned to their home range. Others were reports from relocations in which animals dispersed from a release site. Our review was limited to species that were included in Harestad and Bunnell (1979). This gave us a set of 25 data points containing both maximum distance moved after translocation and home range area (Table 1). None of these translocation movements was from the same author or study site as the data in Sutherland et al. (2000). We analyzed the translocation data in the same manner as the maximum dispersal data and predicted that slopes and intercepts should be the same for both data sets. This analysis was conducted as a test of the relationship between maximum dispersal distance and home range area.

RESULTS

When all variables were expressed on a $\log_{10}$ scale, both home range area ($F = 47.8$, df = 1, 32, $P = 7.9 \times 10^{-8}$, S.E.E. [standard error of the estimate] = 1.17) and maximum dispersal distance ($F = 31.6$, df = 1, 32, $P = 3.3 \times 10^{-6}$, S.E.E. = 0.76) had linear relationships with body mass for the sample of mammals common to both Harestad and Bunnell (1979) and Sutherland et al. (2000) (Fig. 1A, B). Maximum dispersal distance had a significant linear relationship with home range area ($F = 92.7$, df = 1, 32, $P = 5.7 \times 10^{-11}$, S.E.E. = 0.55) (Fig. 1C). We found that more of the variation in maximum dispersal distance was explained by home range area than was explained by body mass (Fig. 1). Multiple regression analyses demonstrated that 49% of the variance in dispersal distance was shared by body size and home range area, 1% was uniquely explained by body size, 25% was uniquely explained by home range area, and 25% remained unexplained.

The slope of the relationship between $\log_{10}$ (maximum dispersal distance) and $\log_{10}$ (home range area) was 0.50, a result that has important implications. When solving the power law Eq. 1, a slope of 0.50 becomes an exponent of 0.50, which is equivalent to the square root of home range area. Because dispersal distance is a linear measure and home range area is a square of a linear measure, taking the square root of home range area places both terms on the same linear scale. Thus, maximum dispersal distance was related by a single constant to the linear dimension of the home range (i.e., the square root of the home range area). Solving Eq. 1 for the relationship between maximum dispersal distance and home range area gave the isometric equation:

$$\text{maximum dispersal distance} = 40(\text{linear dimension of home range}). \qquad (2)$$

When body size effects were removed from both max-

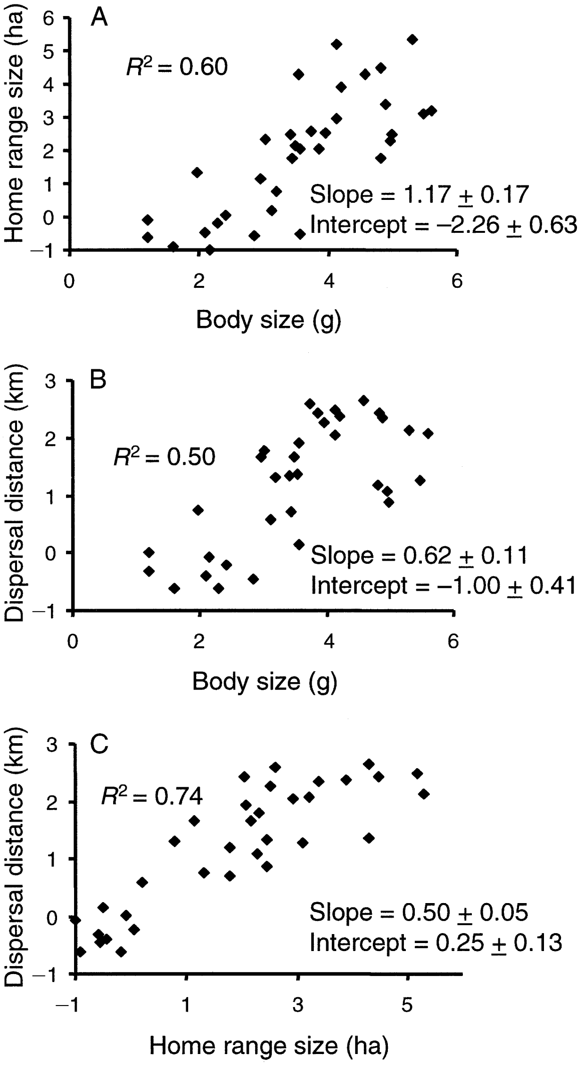

FIG. 1. Relationships between (A) home range area and body size, (B) maximum natal dispersal distance and body size, and (C) maximum natal dispersal distance and home range area for 34 North American mammal species. All variables are on a $\log_{10}$ scale. Slope and intercept values are expressed as mean ± 1 SE.

imum dispersal distance and home range area, the residual dispersal distance had a linear relationship with residual home range area (F = 31.6, df = 1, 32, $P = 3.2 \times 10^{-6}$, S.E.E. = 0.54). The slope of this relationship was not significantly different than 0.50 (Fig. 2).

Median dispersal distance also was linearly related to home range area (F = 28.6, df = 1, 8, P = 0.0006, S.E.E. = 0.55). As was the case for maximum dispersal distance, the slope of this relationship (0.46 ± 0.07; mean ± 1 SE) was not significantly different than 0.50, whereas the intercept was −0.48 ± 0.24. Assuming that the slope of this relationship was equal to 0.50, and using the same steps outlined previously to solve the power law Eq. 1, resulted in an isometric relationship:

$$\text{median dispersal distance} = 7(\text{linear dimension of home range}). \quad (3)$$

When expressed on a log scale, maximum distance moved by North American mammals after translocation was linearly related to body size (F = 47.6, df = 1, 23, $P = 5.0 \times 10^{-7}$, S.E.E. = 0.64; Fig. 3A). Maximum post-translocation movement also was linearly related to home range area (F = 94.5, df = 1, 23, $P = 1.3 \times 10^{-9}$, S.E.E. = 0.50; Fig. 3B). Just as with dispersal movements, more variation in maximum post-translocation movement was explained by home range area than was explained by body size (Fig. 3). A multiple regression was used to partition the variance in distance moved after translocation that could be explained by these two covariates. We found that 67% of the variance in distance moved was shared by body size and home range area, whereas 0% was uniquely explained by body size and 14% was uniquely explained by home range area. Only 19% of the variance was unexplained.

The slopes and intercepts of the relationships between maximum dispersal distance and body size and maximum post-translocation movement were not significantly different (Figs. 1C and 3B). Thus, maximum distance moved after translocation also could be related to the linear dimension of home range by Eq. 3, which gave:

$$\text{maximum distance moved after translocation} = 40(\text{linear dimension of home range}). \quad (4)$$

Again, as for maximum dispersal distance, when body

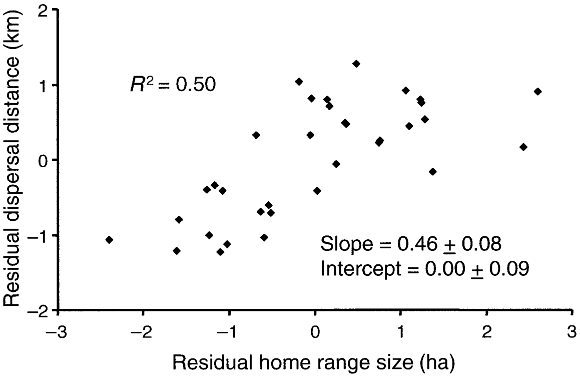

FIG. 2. Relationship between residuals of maximum natal dispersal distance (after effects of body size are removed) and residuals of home range area (after effects of body size are removed) for 34 North American mammal species. All variables are on a $\log_{10}$ scale. Slope and intercept are expressed as mean ± 1 SE.

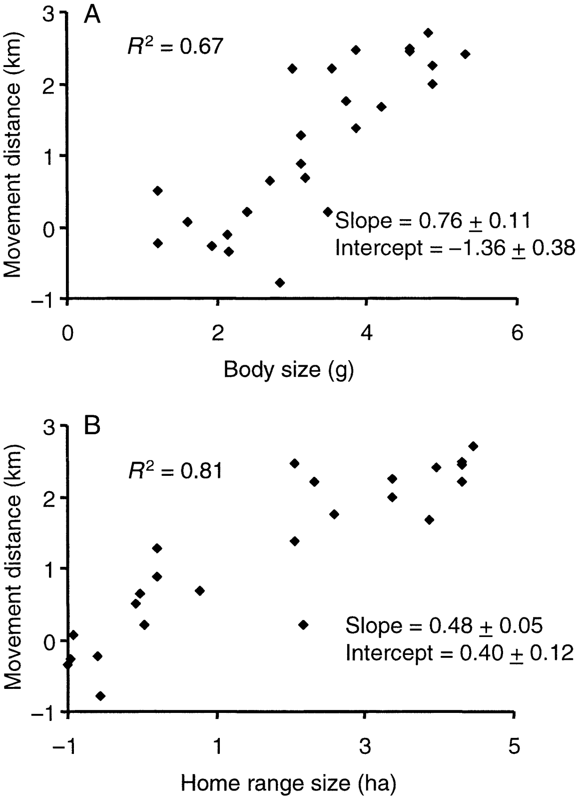

FIG. 3. Relationships (A) between maximum distance moved after translocation and body size, and (B) between maximum distance moved after translocation and home range area (n = 25). All variables are on a $\log_{10}$ scale. Slope and intercept are expressed as mean ± 1 SE.

size effects were removed, residual maximum post-translocation movement was linearly related to residual home range area (F = 16.2, df = 1, 23, P = 0.0005, S.E.E. = 0.49). The slope of this relationship was not different than 0.50 (Fig. 4).

DISCUSSION

As we predicted, dispersal distance of mammals was related to home range size when the effects of body size were removed (Fig. 2). This also was true when we replaced dispersal distance with distance moved after translocation (Fig. 4). Variance partitioning demonstrated that a model of dispersal distance explained by body size could be improved by adding home range size; however, a model of dispersal distance explained by home range size could not be improved by adding body size. These results show that, for mammals, home range size is a better predictor of dispersal distance than is body size. We suggest that this is because the vagility of mammals affects both home range size and dispersal distance, independently of body size. Thus, mammals with small home ranges (for a given body size) also will disperse a shorter distance than we would expect based on body size alone.

It was intriguing that the slope of the relationship between dispersal distance and home range area was 0.50. Because home range area (X) is a squared value, when solving for the power law Eq. 1, $X^{0.50}$ becomes $\sqrt{X}$, which becomes the linear dimension of the home range. This allowed dispersal distance to be related to home range size by a single constant value: 40 for maximum dispersal distance and 7 for median dispersal distance (Eqs. 2 and 3). This simplicity is useful because the home range size of many mammals is well documented, whereas information about dispersal is harder to obtain and the process is poorly understood (e.g., Peles et al. 1999). To provide an example, neither median nor maximum dispersal distance of cotton mice (*Peromyscus gossypinus*) was included in the review of Sutherland et al. (2000), but the mean home range of cotton mice can be estimated as $\sim$0.6 ha, using a review by Stickel (1968) of seven studies. The linear dimension of this area is 77 m, so we estimate the median dispersal distance of cotton mice as 7×77 m $= 539$ m and the maximum as 40×77 m $= 3080$ m. Our result also suggests that simulation models can be parameterized such that the distribution of dispersal distances for a species is the same relative to cell size (where cell corresponds to home range), regardless of the scale of the model. This is a useful circumstance, suggesting that some kinds of simulation results can be generalized across scales.

Because maximum distance moved after translocation could be predicted by home range area using the same parameter values used to predict maximum dispersal distance (Figs. 1 and 3), it seems plausible that

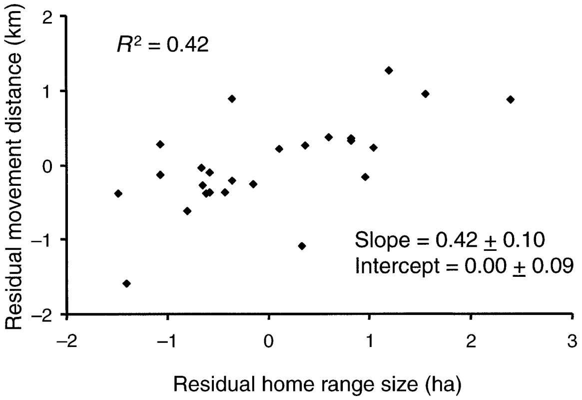

FIG. 4. Relationship between residuals of maximum distance moved after translocation (with effects of body size removed) and residuals of home range area (with effects of body size removed); n = 25. All variables are on a $\log_{10}$ scale. Slope and intercept are expressed as mean ± 1 SE.

a similar combination of body size and vagility affects the maxima for both movement types. Many of the post-translocation movements were ''homing'' studies (Table 1). Our results suggest that the distance over which a mammal can home and the distance over which a mammal can disperse are under similar behavioral and physiological constraints. Some mechanisms for homing that should have such constraints, and thus are consistent with our findings, have been suggested, e.g., prior knowledge of the terrain (Robinson and Falls 1965) and the critical distance model (Bovet 1995).

We recognize that there are trophic differences and possible nonlinearities in the relationships between either dispersal distance or home range area and body size (Harestad and Bunnell 1979, Lindstedt et al. 1986, Kelt and Van Vuren 1999, Sutherland et al. 2000). These effects do not necessarily translate to the relationship between dispersal distance and home range area, and this is one reason why the relationship has potential as a scaling tool. For example, there was an apparent nonlinearity between maximum distance moved after translocation and body size (Fig. 3A) which corresponded to the 100-g body size that Brown et al. (1993) suggest might be optimally efficient for mammals. However, this nonlinearity disappeared when movement was regressed against home range area (Fig. 3B). A mammal with an optimal body size may have a smaller home range area than that expected by a linear relationship. This animal also will travel after translocation (or will disperse; Fig. 1B) a shorter distance than expected on the basis of its size. Presumably this is for the same underlying energetic reasons suggested by Brown et al. (1993).

In summary, we found that, in mammals, both dispersal distance and distance moved after translocation could be predicted as a simple multiple of the linear dimension of home range size. We suggest that the vagility of mammals affected movement independently of body size, such that dispersal distance (or distance moved after translocation) was better predicted by home range size than by body size. Consequently, this relationship has the potential to be a useful scaling rule for ecological practitioners.

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