Published by Associazione Teriologica Italiana
Hystrix, the Italian Journal of Mammalogy
Volume 24 (2): 181–186, 2013

Available online at:
`http://www.italian-journal-of-mammalogy.it/article/view/8746/pdf`
doi:10.4404/hystrix-24.2-8746

Research Article

Ecological correlates of dispersal distance in terrestrial mammals

Luca Santini[a,*], Moreno Di Marco[a], Piero Visconti[a], Daniele Baisero[a], Luigi Boitani[a], Carlo Rondinini[a]

[a] *Global Mammal Assessment program, Department of Biology and Biotechnologies, Sapienza Università di Roma, Viale dell'Università 32, 00185 Rome, Italy*

Keywords:
allometry
body size
dispersal
ecological correlates
home range
mammals
metapopulation
non-linearity
power law
scaling
sensitivity analysis
vagility

Article history:
Received: 24 January 2013
Accepted: 07 May 2013

Acknowledgements
We thank Luigi Maiorano, Paolo Ciucci and Alessio Mortelliti for their comments and suggestions on the analyses. Louise Sutherland and Stephen Mallon helped with the editing. We would also like to acknowledge all the scientists who shared their data and publications on dispersal making this publication possible.

Abstract

Dispersal distance in mammals is a fundamental information for several ecological and conservation applications. Although dispersal can depend on many intrinsic and extrinsic factors, in recent years many studies have shown that it scales with body size and home range area. However, the role of further ecological correlates to distance travelled is still unclear and the predictive models proposed so far have suffered from small sample size and lack of error estimates. This reduces the practical relevance of the models for ecological and conservation applications. We conducted a comprehensive meta-analysis on 327 studies on the dispersal of 164 mammal species, and performed linear and non-linear regression analyses to explore the relationships of body size and home range area with dispersal distance. We tested the effect of various life history traits and ecological factors on the relationships and performed a sensitivity analysis to evaluate the robustness of the models to sample size. The linear relationships of both home range and body size with dispersal distance were influenced by various life history traits and ecological factors. We developed allometric functions to estimate species dispersal distance based on different predictors and life history traits. Linear models representing the relationship between dispersal distance and body size or home range area received good support; however logistic models better approximates both relationships. Despite receiving less support than a logistic curve, a linear model between dispersal and home range is a good approximation for applicative purposes. Sensitivity analysis showed that our results are robust to subsampling of the original dataset until a sample of 40 species. Our empirical models have the potential to improve theoretical and applied population biology studies by extending the applicability and improving the accuracy of dispersal distance estimation to a large number of mammals.

Introduction

Dispersal behaviour plays a determinant role in a number of ecological processes and is considered a key element in biogeography (McDowall, 2004) and conservation biology (Macdonald and Johnson, 2001). It can be defined as a one-way movement of an individual to a new home range, non-overlapping with the previous one (Stenseth and Lidicker, 1992). Dispersal can occur during the whole life span of an animal, yet it is more common in juveniles (i.e. natal dispersal) (Morris, 1982), and it is generally sex biased (Greenwood, 1980; Johnson and Gaines, 1990). Dispersal distances are highly heterogeneous even within the same species and their frequency in a given population is typically represented by a positively skewed leptokurtic distribution: where most of the animals move short distances and a few of them make long distance movements. Short distance (SDD) and long distance dispersers (LDD) have different effects on metapopulation dynamics: SDDs affect resource use, recruitment patterns, small scale metapopulation dynamics, and species coexistence, whereas LDDs are the major factors responsible for spatial spread and colonization rates which affect both ecology and evolutionary trajectory (Nathan et al., 2003). Moreover, dispersal can determine the spatial pattern of metapopulations (Doebeli and Ruxton, 1998) as well as their genetic structuring (Ibrahim et al., 1996) and diversity (Hastings and Gavrilets, 1999).

The approximate distance that animals can disperse is therefore an important piece of information for multiple ecological and conservation purposes. Unfortunately, the dispersal distance of very few species have been investigated to date. Such studies are in fact extremely challenging (Nathan et al., 2003) and long distance movements are often missed (Koenig et al., 1996). However, given the increasing rate of biodiversity loss, conservation biologists are often forced to make decisions without having sufficient information to provide conclusive answers (Soulé, 1985). In this respect, the development of tools that allow the estimation of unknown parameters can be extremely important (Macdonald and Johnson, 2001; Blaum et al., 2011). Allometric scaling allows for the detection of ecological patterns and, if performed with a representative sample, the estimation of unavailable data from other and more easily recordable data.

Allometry between body size and dispersal distance has been proven in various taxa (Paradis et al., 1998; Van Vuren, 1998; Sutherland et al., 2000; Jenkins et al., 2007; Bradbury et al., 2008; Stevens et al., 2012). A relationship between home range area and dispersal distance was first suggested by Macdonald and Bacon (1982), followed by Trewhella et al. (1988) and more recently by Bowman et al. (2002).

This study aims to improve allometric relationships for applicative studies. Power laws on mammals from Sutherland et al. (2000) and Bowman et al. (2002), which have been widely applied in ecology and conservation biology, performed their regression analyses on a limited sample [28 medians and 63 maximum dispersal distances (Sutherland et al., 2000); 10 medians and 34 maximum dispersal distances (Bowman et al., 2002)], leaving open questions on their applicability.

In addition, non-linearity in the relationship between ecological variables has been found by some authors (Silva and Downing, 1995; Kelt and Van Vuren, 2001; Iriarte-Dìaz, 2002; Clarke et al., 2010). If dispersal distance relationships are non-linear, predictions based on power laws may be biased.

Here we develop power laws with a larger sample, testing the sensitivity of the models' outputs to the size and composition of the training datasets, and therefore the dataset suitability for stable regression mod-

---

[*] Corresponding author
Email address: `luca.santini@uniroma1.it` (Luca Santini)

© 2014 Associazione Teriologica Italiana
doi:10.4404/hystrix-24.2-8746
3rd January 2014

els. We also test the linearity of the relationships between dispersal distance and the two known predictive variables, body size and home range, comparing linear and non-linear models.

We test several ecological hypotheses using categorical factors. First, we expect to detect no difference between the average dispersal distance of the two sexes because a male bias related to distance has been found only in a minority of mammal species and female sex bias has also been rarely found (Greenwood, 1980). Second, we expect to find differences in dispersal distance due to locomotion type as a consequence of movement speed, energetic costs involved and different limitations to dispersal. Third, we expect to find a significant effect of diet on the relationship between dispersal distances and body size (Sutherland et al., 2000) but not home range, since the latter already accounts for variation in diet among species of the same size (McNab, 1963; Harestad and Bunnel, 1979; Jetz et al., 2004). Fourth, we expect territorial species to travel farther than non territorial ones (Greenwood, 1980) as the probability to settle in a new home range will be constrained by the presence of other conspecific individuals. Moreover, within territorial species, we expect gregarious species to travel shorter distances than solitary species, since social behaviour should affect the probability to be accepted in a new territory. Fifth, we expect specialist species to disperse less than generalists, showing a stronger "boundary response" (Fahrig, 2007). Sixth, we expect tropical species to disperse less than temperate ones owing to higher resource density but a generally lower population density (Damuth, 1987). Lastly, we expect to find differences among taxonomic groups due to their shared evolutionary history and adaptations to specific landscape features and behavioural responses to environmental cues and risks (Fahrig, 2007).

Methods

Data collection

Dispersal distances from 329 studies on non-volant terrestrial mammals were collected (see Tab. S1 in Supplemental Information). Bats (i.e. Chiroptera) and aquatic species (i.e. Cetacea, Sirenia, Pinnipedia) were excluded from the analysis because of their particular locomotion, and in the case of bats, for the potential passive dispersal (Hayman, 1959). Records of dispersal by terrestrial mammals in aquatic environment were also ignored.

Distances were collected only when reported as straight line distances (euclidean distance between the start and the end point). Given our interest in dispersal abilities more than in the cause of the process, juvenile, secondary and breeding dispersal distance were all treated together. We are not aware of any study that has extensively analysed possible different distances covered during different life stages. Data from homing studies and dispersal after translocation were also collected.

We included studies that measured dispersal distance through various methods. These included trapping, radio tracking and parent son distance identified through genetics. Studies considering genetic distances expressed as F statistics were excluded since they do not report absolute distances between natal and adult home range.

Published studies report distances as means, median or maximum value recorded for each sex or without sex specification. Thus, all mean, median and maximum dispersal records reported were collected and grouped by sex whenever possible, and were treated separately. If these parameters were unreported and raw data were available (i.e. dispersal distance covered by individual animals), mean, median and maximum distances for each sex were calculated, excluding distances shorter than the mean radius of the species' home range. Whenever means were reported for different subsamples (e.g. grouped by year or location), a mean (weighted on sample size) among subsamples was performed. In a few cases, data were deduced from published figures (see Tab. S1). For species having more than one measurement, the largest maximum reported distance was selected for each sex. Mean and median distance for each species was averaged across studies by calculating the arithmetic mean within and between sexes. Subspecies were pooled to species level.

Overall, data on 165 species from 13 mammal orders were collected. These included: mean dispersal distance for 75 species (67 ♂, 61 ♀) from 114 studies, median distances for 62 species (52 ♂, 47 ♀) from 89 studies, and maximum distances for 156 species (102 ♂, 93 ♀) from 329 studies (see Tab. S1).

Life history data on species for which dispersal data were available were also collected. We used the PanTHERIA database (Jones et al., 2009), scientific literature (Appendix S2) and IUCN Red List of threatened species (www.iucnredlist.org, version 2011.2) as the data source on body size, home range, locomotion type, diet, habitat breadth, territorial and social behaviour. For four species with dispersal but no home range data available, the home range area from congeneric species of similar weight were used (see Tab. S1). We extracted the mean latitude of species' geographic ranges from the IUCN Red List of Threatened species (IUCN 2011).

Following analogous publications (i.e. Sutherland et al. 2000; Kelt and Van Vuren 2001) species were considered carnivorous if animal matter composed more than 90% of their diet volume, omnivorous for values between 10% and 90% and herbivorous with less than 10%. Locomotion types were differentiated in terrestrial, arboreal, fossorial and semi-aquatic; the mix category "semi-arboreal" was considered in two cases (*Peromyscus leucopus* and *P. gossypinus*). Species were considered to be either territorial or non territorial and either solitary, living in pairs, or gregarious. Those species living both as solitary and in social groups were considered as semi-social. Habitat breadth was considered on the basis of the species-habitat relationships reported by Specialist Groups of the IUCN-SSC and collected by Rondinini et al. (2011). Species were assigned to forest, shrubland, grassland, bare and artificial land cover classes. Species assigned to more than one of these land cover macrocategories were considered habitat generalists, the others were considered habitat specialists. Species having the geographic range mean latitude between 23°26′16″N and 23°26′16″S were considered tropical, the others were considered temperate. Taxonomic orders were also treated as categories to identify groups that generally behave differently from the rest of the sample.

Analyses

In order to linearise the relations and to homogenise the variance over the entire range of the variables, dispersal distance (km), home range (km^2) and body size data (kg) were transformed to base 10 logarithms. A generalized additive model (GAM) was used to assess linearity in the relationships between dispersal distance measures (Mn=mean, Med=median, Max=maximum) and either home range (HR) or body size (BS) as independent variables. Since the GAM function suggested a sigmoid shape of the relationships, a four parameter logistic nonlinear regression was compared to a linear regression. We used the Akaike Information Criterion (AIC) to compare the linear and the nonlinear models. Shapiro test was used to test normality of the regression residuals. For each dataset used for linear regressions, we identified the outliers having a Cook's distance greater than 4/n (Max-HR=6; Med-HR=6; Mean-HR=2; Max-BS=9; Med-BS=3; Mean-BS=4) and we excluded them from the analyses following Cook (1977). Analysis of covariance (ANCOVA) was performed to test the effect of the categorical factors (i.e. sex, taxonomic orders, locomotion, diet, geographic range mean latitude, habitat breadth, territorial and social behaviour) on the regressions and Scheffe's post hoc test was used to test differences among subcategories (Ruxton and Beauchamp, 2008). Since the BS - dispersal distance relationships differed significantly between trophic levels, two regressions were conducted: one for carnivores and one for herbivores and omnivores. We used both simple and multiple regression to develop power laws for predictions. We also performed a quantile regression (see Tab. S7) to estimate the conditional quantiles of the response variable distribution in the linear models, these may be used for identifying prediction boundaries or developing modeling scenarios.

We checked for multicollinearity between predictor variables with variance inflation factors (VIFs), both body size and home range had a VIF <10.

Table 1 – F statistics for the two factors tested in ANCOVA analysis conducted on the six datasets used in linear regressions. Max = Maximum distance; Med = Median distance; Mn = Mean distance; BS = Body size; HR = Home range; *** = $p < 0.001$. Dispersal type factor stands for natural vs human-induced dispersal.

	Max-BS	**Med-BS**	**Mn-BS**	**Max-HR**	**Med-HR**	**Mn-HR**
Dispersal type	0.16	2.74	0.19	0.93	0.36	0.27
Sex	0.81	0.82	0.78	1.77	1.51	1.36
Diet	18.21 ***	10.54 ***	14.54 ***	0.88	2.08	0.79
Locomotion	2.39	0.41	0.30	3.09 *	0.36	0.40
Territoriality	0.36	0.58	0.45	0.20	0.26	1.73
Social behaviour	2.84 *	5.18 **	1.59	0.54	0.93	0.68
Habitat breadth	2.28	0.01	0.66	3.71 *	3.59	0.58
Latitude	3.91 *	1.39	3.01	2.77	0.98	1.25

Table 2 – Power laws for the estimate of dispersal distance (km) based on home range (km^2) or body size (kg) and summary of the statistics of regression analyses. CF = correction factor; α = intercept; β = slope; df = degree of freedom; SEE = Standard Error Estimate of the regression; C = Carnivores; H = Herbivores; O = Omnivores; ** = $p < 0.01$; *** = $p < 0.001$.

	Power law	**CF**	α	β	F**-statistic**	**df**	**adjusted** R^2	**SEE**
Maximum distance~HR+BS (O+H)	$13.11\times BS^{0.34}\times HR^{0.27}$	1.13	1.06(±0.18)	W 0.34(±0.14) HR 0.27(±0.11)	150.9 ***	107	0.73	0.49
Maximum distance~Home Range	$29.38\times HR^{0.5}$	1.17	1.40(±0.10)	0.50(±0.05)	365.40 ***	148	0.71	0.56
Maximum distance~Body size (H+O)	$5.97\times BS^{0.6}$	1.14	0.72(±0.10)	0.60(±0.08)	245.30 ***	108	0.69	0.52
Maximum distance~Body size (C)	$34.81\times BS^{0.63}$	1.22	1.45(±0.24)	0.63(±0.20)	40.92 ***	35	0.53	0.64
Median distance~HR+BS (O+H)	$1.68\times BS^{0.43}\times HR^{0.14}$	1.10	0.18 (±0.05)	W 0.43 (±0.23) HR 0.14 (±0.19)	57.33 ***	39	0.73	0.44
Median distance~Home Range	$5.60\times HR^{0.5}$	1.09	0.71(±0.11)	0.50(±0.05)	239.40 ***	56	0.81	0.41
Median distance~Body size (H+O)	$1.06\times BS^{0.55}$	1.10	-0.01(±0.13)	0.55(±0.10)	111.80 ***	40	0.73	0.43
Median distance~Body size (C)	$6.50\times BS^{0.49}$	1.11	0.77(±0.35)	0.49(±0.27)	14.39 **	17	0.43	0.45
Mean distance~HR+BS (O+H)	$5.78\times BS^{-0.03}\times HR^{0.19}$	1.10	0.72(±0.18)	W -0.03(±0.18) HR 0.62(±0.19)	101.20 ***	45	0.81	0.43
Mean distance~Home Range	$5.22\times HR^{0.54}$	1.11	0.67(±0.11)	0.54(±0.06)	332.80 ***	70	0.82	0.45
Mean distance~Body size (H+O)	$1.07\times BS^{0.68}$	1.20	-0.05(±0.17)	0.68(±0.14)	89.09 ***	49	0.64	0.60

To evaluate the robustness of our models (i.e. their dependence on sample size and composition) we performed a sensitivity analysis on the six major datasets used in our regressions (Max-HR, Med-HR, Mn-HR, Max-BS, Med-BS, Mn-BS). The datasets were subsampled from 90% down to 10% of the full dataset of dispersal distances available, by 10% decrements. For each decrement level we extracted 1,000 random subsamples. Each subsample was then used to regress dispersal distance against BS and HR. Using the results from each decrement's subsample (consisting in 1,000 intercept and 1,000 slope coefficients), we calculated: 1) the mean absolute difference from the original model coefficients (based on the full dataset); 2) the frequency of subsample coefficients that fall within the 95% CI of the original model; 3) the 95% confidence intervals associated with each decrement's subsample.

Biases in the power laws due to log transformation were corrected by multiplying the intercept value by a correction factor based on the standard error estimates of the regression (Sprugel, 1983; Wood, 1986).

All statistical analyses were performed in R statistical language v. 2.11.1 (R Development Core Team, 2010). We used the package `mgcv` to perform generalized additive models (GAM). GIS analyses were performed in PostgreSQL v.8.4 database with the PostGIS library v.2.0 (The PostgreSQL Global Development Group, 2012).

Results

Regression residuals were normally distributed for all regressions performed (Shapiro test: $p > 0.05$). Natural and human induced dispersal distances (homing studies and post release dispersal) did not reveal any significant difference in the linear relations with home range or body size (Tab. 1), thus data from both kind of studies were grouped together for further analyses.

According to the Akaike Information Criterion (AIC), the generalized additive models and the four parameter logistic models are comparable and both perform better than linear models, especially for the body size - dispersal distance relationships (Tab. 3). This indicates that an S-shaped logistic function is a good approximation of dispersal distance relationships with home range and body size. Both in linear and non-linear models, home range was the best predictor of dispersal distance (Tab. 2; Tab. 3). However, the performance of home range and body size as predictors depends on the sample considered. In multiple regression the variance uniquely explained by body size in herbivores and omnivores vary between 0.03-12.87%, whereas it vary between 0.01-0.3% in carnivores. In contrast, the variance uniquely explained by home range vary between 1.99-22.40% in herbivores and omnivores and between 8.42-23.11% in carnivores.

The hypothesis of a generalized sex-bias in dispersal, with males dispersing on average more than females was not supported. Arboreal species dispersed significantly less than terrestrial species only in the regression between home range and maximum dispersal distance, however they had a lower intercept in all regressions except one. All linear relationships between dispersal and body size were significantly affected by diet (Tab. 1). Post hoc tests revealed no significant difference between herbivores and omnivores (Sheffe's post hoc test: all cases $p > 0.05$) while both of them significantly differed from carnivores (Sheffe's post hoc test: all cases $p < 0.001$; Fig. 1d-f). On the contrary, diet did not affect any relationship between home range and dispersal distance. Territorial behaviour did not significantly affect any linear regression, however social structure significantly affected two of the three relationships between body size and dispersal distance, but none between home range and dispersal distance. Species habitat breadth significantly affected only two regressions with home range as independent variable. Latitudinal geographic range significantly affected only the regression between body size and maximum dispersal distance, however we found that tropical species had constantly a lower intercept than temperate species (Tab 1). Small sample size may have

Table 3 – Akaike Information Criterion (AIC) comparison between the linear regression, the four parameter logistic non-linear regression and the Generalized Additive model (GAM).

	Linear model	**Logistic model**	**Generalized Additive model**
Med-HR	98.08	96.53	96.52
Mn-HR	122.45	116.31	117.29
Max-BS	326.18	314.93	315.42
Med-BS	109.76	106.36	105.01
Mn-BS	165.81	155.93	152.34

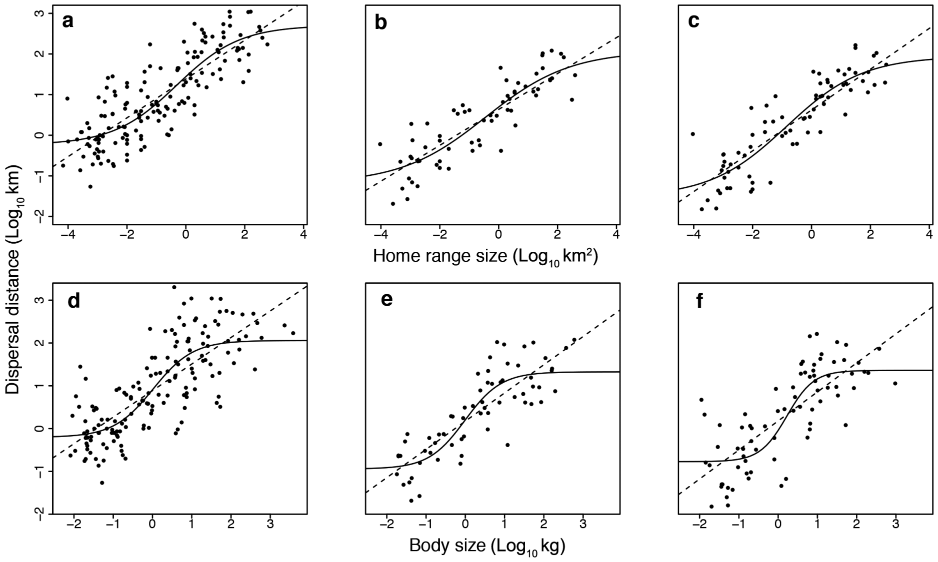

Figure 1 – Linear and logistic non-linear regressions between home range (Log_{10} km^2) and maximum (a), median (b) and mean dispersal distance (c) and between body size (Log_{10} kg) and maximum (d), median (e) and mean (f) dispersal distance (Log_{10} km). Solid lines = Logistic non-linear model; Dashed lines = Linear model.

affected the significance of some of these relationships (see Tab. S3a-b in supplementary materials for mean residual comparisons among categories). Taxonomic order had a highly significant effect on the relationships between mean, median and maximum dispersal distance and body size, whereas only maximum distances were affected by taxonomy when regressed against home range size (Tab. 1; see Tab. S2).

Even with low sample size the relationships described by the regression models remained stable and there was little difference between the subsample coefficients and those from the original models. The frequency of subsample slope coefficients falling within the confidence interval of the original model was consistently high until 40% of the full sample; errors were therefore acceptable until a sample size of 31±18.8 SD for slope and of 43±38.7 SD for intercept coefficients (i.e. frequency of subsample coefficients within models' coefficients 95% CI > 0.95; Fig. 2; see also Tab. S4-6).

Discussion

Predictive value of body size and home range size

Our data collection included 164 species of terrestrial mammals from 13 orders, with a wide range of body sizes and multiple locomotion types, diet and social systems. Although the sample distribution of the two predictive variables, home range and body size, is biased toward large bodied species of terrestrial mammals, they encompass the whole range of weights recorded for terrestrial mammal species (see Figs. S1 and S2).

The relationships of dispersal distance with both body size and home range are better fitted by a logistic model than a linear model. The fitted logistic curves of home range relationships are extremely flat and approximates the linear relation. In contrast, the logistic curve of body size relationships diverge considerably from a straight line, and this difference is likely to be a direct consequence of the non-linearity between body size and home range (Kelt and Van Vuren, 2001). Asymptotes of the logistic curve should not be seen as constraints but rather, as a breakdown of the linear relationship, since dispersion data around them is wide, and there are few dispersal observation data in this part of the curve (Fig. 1).

There might be several reasons why the relationships are better fitted by a logistic model. A less steep relationship for small species may be due to a methodological bias: because the further the animals disperse, the easier it is to lose them in dispersal studies. As a consequence, species with a small dispersal distance could be more accurately estimated than species with large dispersal distance. The reduction in the slope for larger species can be explained by three possible (non-mutually exclusive) reasons. First, the energetic tradeoff between costs and benefits of dispersing may be reached sooner by larger species. Second, beyond a certain distance the probability of missing a good place to settle may reduce while mortality and the chance to encounter an obstacle may increase with the distance travelled. These three factors combined can make it extremely unlikely for an animal to travel as much as its physical and physiological characteristics could allow. The third possible reason is the same bias proposed for smaller species, since the probability of detecting long distance movements decreases with distance travelled by animals, therefore long distance dispersers are more likely to be missed in dispersal studies (Koenig et al., 1996).

However, the right asymptote appears when species are considered altogether. In fact herbivores and omnivores, which cover a shorter range of distances, show a more linear relationship when they are treated apart, non-linearity becomes apparent on the right part of the relationships when carnivores are included.

As a consequence, when species are considered altogether, body size is a poorer predictor of dispersal distance than home range. In fact, dispersal distance significantly varies with diet, given that home range area mostly depends on body size and diet (McNab, 1963; Harestad and Bunnel, 1979; Jetz et al., 2004), it already accounts for this variation and it is consequently more strictly related to dispersal distance. In addition, species of the same size may be more or less vagile for reasons unrelated to diet, and this affects both their home range and dispersal distance (Bowman et al., 2002). Finally, the relationship between body size and dispersal distance appears to be less linear than the relationship between home range and dispersal distance.

However, while in carnivores the proportion of variance explained by body size is negligible, when omnivores and herbivores are treated apart, body size uniquely explain a considerable part of the variance. This is possibly due to a major variance in vagility among carnivores.

For all the above reasons, estimation of dispersal distance with home range data should always be preferred in carnivores, whereas estimation through multiple regression with body size and home range should be preferred in herbivores and omnivores, alternatively, body size alone can be used.

Factors affecting dispersal distance

Intercepts and/or slopes of regressions for males were always higher than those for females, although the differences were not significant. Most mammal species are in fact male biased for dispersal distance and tendency to disperse (Greenwood, 1980; Johnson and Gaines, 1990), yet female biased dispersal does exist in few species (Greenwood, 1980) and females are often potentially equally able to disperse as males.

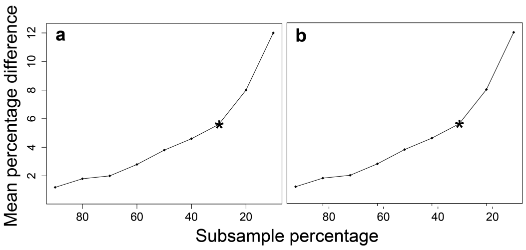

Figure 2 – Absolute distance percentage of slope coefficients of maximum dispersal distance vs. HR (a) and BS (b) at each 10% subsampling decrement. * = indicates the subsampling percentage at which the frequency of subsample coefficients run below 0.95 of the CI of the coefficients of the model based on the full sample.

Consequently the presence of exceptional female dispersal records together with the small sample size of most studies could have prevented the detection of significant differences.

Arboreal species seem to disperse less than terrestrial ones, this could be due to the discontinuity of the canopy that can limit their dispersal, as well as the differential energy expenditure between different locomotion types and in different habitat layers.

We confirm Sutherland's et al. (2000) results: given an equal weight, carnivores disperse farther than omnivores and herbivores, while the latter two do not show significant differences.

We haven't found differences between territorial and non-territorial species, however, such classification is problematic since territoriality behave more as a continuous variable rather than boolean one. Consequently it is possible that we overestimated the weight of this trait preventing the detection of significant differences in the analysis.

Sociality was on the contrary highly influential in the height of the linear relationship between home range and dispersal distance. Gregarious species disperse less than solitary species; this could be explained by the higher probability that gregarious species have to be accepted in new areas by conspecifics and to find a mating partner. However, sociality had no effect on the relationships between body size and dispersal distance, which suggests that sociality has an effect on the relationship between body size and home range. Social species have on average smaller home range than solitary species, and this imply that solitary species, having lower densities, need to move more than gregarious species to avoid inbreeding.

Habitat specialist species seem to travel shorter distances than generalist species, the formers in fact have a stronger habitat boundary response and consequently a lower probability to cross the matrix (Tischendorf et al., 2003). This can limit considerably their dispersal distances in fragmented habitats. Finally, tropical species seem to travel shorter distances than temperate species, probably owing to the higher resource density in the lower latitude. A greater biomass productivity in tropical environments may reduce the distance that individuals need to travel to find suitable new areas to settle in. In addition, in the tropics population density is generally lower than in temperate areas (Damuth, 1987), and this means that a positive density-dependent effect is potentially involved. However, the density dependence of dispersal distance is still unclear in vertebrates and studies investigating this mechanism in mammals are contradictory (Matthysen, 2005).

Taxonomic order affects the relationship between dispersal distance and body size more strongly than the relationship between dispersal distance and home range size. It is possible that this is in part a consequence of the similarity in the diet of related species.

The more represented taxonomic orders in the datasets (i.e. rodents and carnivores) had obviously a stronger influence on the regressions than less represented orders and the analysis of the residuals clearly show a general pattern where some groups disperse significantly less than others (see Tab. S3a-b).

For most of the above factors, the limited sample of some categories in the dataset probably made the comparison statistically significant just for few of the regressions, residuals comparison between categories and among various regressions offer a better picture for evaluating those differences (see Tab. S3a-b and Appendix S1).

It is important to note that intrinsic factors are not the only determinants of dispersal distance, local extrinsic factors can also substantially affect it (Fahrig, 2007). Therefore the accuracy of dispersal distances estimated through allometric equations can vary across space.

Dispersal kernel implications

Median and maximum dispersal distances are in a constant ratio with the home range diameter (i.e. slope coefficient ~0.5; assuming a circular home range area). In fact, although dispersal kernel is highly dependent on the interaction between landscape structure and species' settlement rules, innate dispersal behaviour has probably a considerable influence in the final distance travelled. Therefore, regardless of the suitable areas they encounter, innate behaviour can contribute to the general positive leptokurtic shape of the dispersal kernel.

Compared to median and maximum dispersal distance linear relationships that are parallel, the slope of mean dispersal distance linear relationship is steeper. This suggests that the mean dispersal distance is generally lower than the median in small species, but higher in large species. This may imply that the larger the species, the more skewed to the right the shape of the dispersal kernel is, because long distance dispersal events are more frequent. The allometric relationships presented here suggest that the dispersal kernel may conserve its general shape among populations of the same species, because it is in some way dependent on intrinsic factors, however, this point needs to be further investigated.

Caveats

Since the dispersal of different species is generally investigated with different methods, data used in the analyses may suffer of different biases. For instance, the trapping method, which is much more common for small species, may allow the collection of large samples but it generally misses long distance dispersers (Koenig et al., 1996).

Intrinsic factors are not the only determinants of dispersal distance, local extrinsic factors (Fahrig, 2007) and behavioural response to environmental clues (Bakker and Van Vuren, 2004) can also substantially affect it. Therefore the accuracy of dispersal distances estimated through allometric equations can vary across space. In fact, dispersal distance is an extremely variable character and predictions through allometric formulas should be intended a mean of the distribution of dispersal distances for a given body size or home range size. However, results from quantile regression (see Tab. S7) can be used to predict dispersal distance at different conditional quantiles of its distribution, this may be useful to identify prediction boundaries and to develop modeling scenarios.

Finally, home range - dispersal distance relationships are well approximated by a linear relationship. The same cannot be said for body size - dispersal distance relationships where linear relationship diverge considerably from the logistic curve and the error in prediction can be substantial for very small or very large species.

Model sensitivity and its application

The sensitivity analysis shows that even a relatively small sample size (n>40) allows a stable linear regression to be performed. In fact, from these results it can be inferred that bigger and more diverse samples would have not yielded significantly different regressions, and therefore our datasets were generalizable to other groups. Sample sizes used to perform previous regressions on dispersal distance for terrestrial mammals (except for the Max-BS in Sutherland et al. 2000), although relevant for theoretical ecology, were not suitable for predictions in applied ecology.

Power laws proposed so far have been applied in models without having any measure of uncertainty in their estimations. Our power laws, combined with the residual correction substantially improve the accuracy of predictions.

Dispersal distance can be integrated in several ecological models. Dispersal distance is included in various functional connectivity metrics and adopted to set a fixed critical distance after which a species probability of dispersal is assumed to decline rapidly (Keitt et al., 1997; Bunn et al., 2000; van Langevelde, 2000; Urban and Keitt, 2001; D'Eon et al., 2002; Fagan and Calabrese, 2006; van Teeffelen et al., 2006). Knowing how far a species generally (i.e. median distance) and potentially (i.e. maximum distance) disperse allows to make assumptions about metapopulation structure and to make predictions about sink patch occupancy (e.g. Swihart et al. 2003). Dispersal distance is a determinant factor to take in account when evaluating different spatial designs of protected area expansion projects in order to promote metapopulation persistence (Van Vuren, 1998; Cabeza and Moilanen, 2003; Moilanen et al., 2005; van Teeffelen et al., 2006). Finally, since dispersal affects the probability that dispersing individuals will contribute to population recruitment, it has also been suggested as an important factor in the design of individual reserve size and shape (Basse and McLennan, 2003; Westbrooke, 2007).

The empirical models presented here may improve basic and applied population and metapopulation biology studies by extending the applicability and the accuracy of dispersal distance estimation to a large number of mammals.

References

Bakker V.J., Van Vuren D., 2004. Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. Cons. Biol. 18: 689–697.

Basse B., McLennan J., 2003. Protected areas for kiwi in mainland forests of New Zealand: how large should they be? N. Z. J. Ecol. 27: 95–105.

Blaum N., Mosner E., Schwager M., Jeltsch F., 2011. How functional is functional? Ecological groupings in terrestrial animal ecology: towards an animal functional type approach. Biodivers. Conserv. 20: 2333–2345.

Bowman J., Jaeger J.A.G., Fahrig L., 2002. Dispersal distance of mammals is proportional to home range size. Ecology 83: 2049–2055.

Bradbury I.R., Laurel B., Snelgrove P.V.R., Bentzen P., Campana S.E., 2008. Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. Proc. R. Soc. Lond. B Biol. Sci. 275: 1803–1809.

Bunn A., Urban D.L., Keitt T., 2000. Landscape connectivity: a conservation application of graph theory. J. Environ. Manag. 59: 265–278.

Cabeza M., Moilanen A., 2003. Site-Selection Algorithms and Habitat Loss. Conserv. Biol. 17: 1402–1413.

Clarke A., Rothery P., Isaac N.J.B., 2010. Scaling of basal metabolic rate with body mass and temperature in mammals. J. Anim. Ecol. 79: 610–619.

Cook R.D., 1977. Detection of influential observation in linear regression. Technometrics 19: 15–18.

D'Eon R.G., Glenn S.M., Parfitt I., Fortin M.J., 2002. Landscape connectivity as a function of scale and organism vagility in a real forested landscape. Conserv. Ecol. 6: 10.

Damuth J., 1987. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. Biol. J. Linn. Soc. 31: 193–246.

Doebeli M., Ruxton G.D., 1998. Stabilization through spatial pattern formation in metapopulations with long–range dispersal. Proc. R. Soc. Lond. B Biol. Sci. 265: 1325–1332.

Fagan W., Calabrese J., 2006. Quantifying connectivity: balancing metric performance with data requirements. In: Crooks K.R., Sanjayan M. (Eds.) Connectivity conservation. Cambridge University Press, New York, pp. 297–317.

Fahrig L., 2007. Non optimal animal movement in human altered landscapes. Funct. Ecol. 21: 1003–1015.

Greenwood P.J., 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28: 1140–1162.

Harestad A.S., Bunnel F., 1979. Home range and body weight–a reevaluation. Ecology, 60: 389–402.

Hastings A., Gavrilets S., 1999. Global dispersal reduces local diversity. Proc. R. Soc. Lond. B Biol. Sci. 266: 2067–2070.

Hayman R., 1959. American bats reported in Iceland. J. Mammal. 40: 245–246.

Ibrahim K.M., Nichols R.A., Hewitt G.M., 1996. Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. Heredity 77: 282–291.

Iriarte-Dìaz J., 2002. Differential scaling of locomotor performance in small and large terrestrial mammals. J. Exp. Bio. 205: 2897–2908.

Jenkins D.G., Brescacin C.R., Duxbury C.V., Elliott J.A., Evans J.A., Grablow K.R., Hillegass M., Lyon B.N., Metzger G.A., Olandese M.L., 2007. Does size matter for dispersal distance? Glob. Ecol. Biogeogr. 16: 415–425.

Jetz W., Carbone C., Fulford J., Brown J.H., 2004. The scaling of animal space use. Science 306: 266–268.

Johnson M.L., Gaines M.S., 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annu. Rev. Ecol. Syst. 21: 449–480.

Jones K.E., Bielby J., Cardillo M., Fritz S.A., O'Dell J., Orme C.D.L., Safi K., Sechrest W., Boakes E.H., Carbone C., 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90: 2648–2648.

Keitt T.H., Urban D.L., Milne B.T., 1997. Detecting Critical Scales in Fragmented Landscapes. Conserv. Ecol. 1: 4.

Kelt D.A., Van Vuren D., 2001. Energetic constraints and the relationship between body size and home range area in mammals. Ecology 80: 337–340.

Koenig W.D., Van Vuren D., Hooge P.N., 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends. Ecol. Evol. 11: 514–517.

Macdonald D., Bacon P., 1982. Fox society, contact rate and rabies epizootiology. Comparative Immunology, Microbiology and Infectious Diseases 5: 247–256.

Macdonald D.W., Johnson D.D.P., 2001. Dispersal in theory and practice: consequences for conservation biology. In: Clobert J., Danchin E., Dhondt A.A., Nichols J. D. (Eds.) Dispersal. Oxford University Press, Oxford, pp. 358–372.

Matthysen E., 2005. Density-dependent dispersal in birds and mammals. Ecography 28: 403–416.

McDowall R., 2004. What biogeography is: a place for process. J. Biogeogr., 31: 345–351.

McNab B.K., 1963. Bioenergetics and the determination of home range size. Am. Nat. 97: 133–140.

Moilanen A., Franco A.M.A., Early R.I., Fox R., Wintle B., Thomas C.D., 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proc. R. Soc. Lond. B Biol. Sci. 272: 1885–1891.

Morris D., 1982. Age-specific dispersal strategies in iteroparous species: Who leaves when? Evolutionary Theory 6: 53–65.

Nathan R., Perry G., Cronin J.T., Strand A.E., Cain M.L., 2003. Methods for estimating long-distance dispersal. Oikos 103: 261–273.

Paradis E., Baillie S.R., Sutherland W.J., Gregory R.D., 1998. Patterns of natal and breeding dispersal in birds. J. Anim. Ecol. 67: 518–536.

R Development Core Team, 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Available from http://www.R-project.org.

Rondinini C., Di Marco M., Chiozza F., Santulli G., Baisero D., Visconti P., Hoffmann M., Schipper J., Stuart S.N., Tognelli M.F., Amori G., Falcucci A., Maiorano L., Boitani L., 2011. Global habitat suitability models of terrestrial mammals. Philos. Trans. R. Soc. Lond. B Biol. Sci., 366: 2633–2641.

Ruxton G.D., Beauchamp G., 2008. Time for some a priori thinking about post hoc testing. Behav. Ecol. 19: 690–693.

Silva M., Downing J.A., 1995. The allometric scaling of density and body mass: a nonlinear relationship for terrestrial mammals. Am. Nat. 145: 704–727.

Soulé M.E., 1985. What is Conservation Biology? Bioscience 35: 727–734.

Sprugel D., 1983. Correcting for bias in log-transformed allometric equations. Ecology 64: 209–210.

Stenseth N.C., Lidicker W.Z., 1992. Animal dispersal: small mammals as a model. Springer.

Stevens V.M., Trochet A., Van Dyck H., Clobert J., Baguette M., 2012. How is dispersal integrated in life histories: a quantitative analysis using butterflies. Ecol. Lett. 15: 74–86.

Sutherland G.D., Harestad A.S., Price K., Lertzman K.P., 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. Conserv. Ecol. 4: 16.

Swihart R.K., Atwood T.C., Goheen J.R., Scheiman D.M., Munroe K.E., Gehring T.M., 2003. Patch occupancy of North American mammals: is patchiness in the eye of the beholder? J. Biogeogr. 30: 1259–1279.

The PostgreSQL Global Development Group, 2012. PostgreSQL. Available from http://www.postgresql.org.

Tischendorf L., Bender D.J., Fahrig L., 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. Landscape Ecology 18: 41–50.

Trewhella W., Harris S., McAllister F., 1988. Dispersal distance, home-range size and population density in the red fox (*Vulpes vulpes*): a quantitative analysis. J. Appl. Ecol. 25: 423–434.

Urban D., Keitt T.H., 2001. Landscape connectivity: a graph-theoretic perspective. Ecology 82: 1205–1218.

van Langevelde F., 2000. Scale of habitat connectivity and colonization in fragmented nuthatch populations. Ecography 23: 614–622.

van Teeffelen A.J.A., Cabeza M., Moilanen A., 2006. Connectivity, probabilities and persistence: comparing reserve selection strategies. Biodivers. Conserv. 15: 899–919.

Van Vuren D., 1998. Mammalian dispersal and reserve design. In: Caro T. (Ed.) Behavioral ecology and conservation biology. Oxford University Press, New York, USA, pp. 369–393.

Westbrooke I., 2007. How large a managed area is needed to protect a threatened animal species? Combining simple dispersal and population models. New Zeal. J. Ecol. 31: 154–159.

Wood A., 1986. A potential bias in log-transformed allometric equations. Wader Study Group Bullettin 47: 137–138.

Associate Editor: L.A. Wauters

Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1. List of studies collected reporting species' mean, median, and maximum dispersal distance, sample, and study type.

Table S2. Results of the ANCOVA measuring the effect of taxonomic order on the regression parameters of dispersal models.

Table S3. Mean residuals and sample size divided by categories.

Table S4. Average absolute difference of intercept and slope coefficients' of each subsampling decrement from the coefficients of the original model.

Table S5. Frequency of the subsample coefficients that falls within 95% confidence interval of the models' coefficients.

Table S6. Confidence interval width (2.5-97.5%) for intercept and slope coefficients from 1000 regressions for each subsampling decrement of the original dataset.

Table S7. Coefficients of the quantile regressions performed on the relationships in Table 2.

Figure S1. Kernel density of body size from PanTHERIA database plus other available source and the datasets used to derive the models in this study.

Figure S2. Kernel density of home range from PanTHERIA database plus other available source and the datasets used to derive the models in this study.

Appendix S1. How to account for residuals in the estimation.

Appendix S2. Scientific literature consulted to collect home range and body size.