Epizoochory by large herbivores: merging data with models

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Summary

The dispersal of plant seeds in the fur of large herbivores (epizoochory) is an important but complex long-distance dispersal mechanism. We developed a spatially explicit simulation model of epizoochorous seed dispersal, which was parameterized based on empirical studies of the movement and behaviour of donkeys, and the distribution, seed production, seed accessibility, seed adhesion, and seed retention on donkey fur of selected plant species in a coastal dune nature reserve in Flanders, Belgium. We compared predicted and observed seed numbers of the 14 plant species on donkey fur.

Modelled seed shadows indicate that for most species about half of all seeds dispersed by donkeys should travel a net distance of $> 100\,\text{m}$, and about 1% should travel $> 500\,\text{m}$ within this more or less isodiametric 100 ha nature reserve. Seeds with longer retention times are expected to travel further than those with short retention times. Enlarging the reserve area had little impact on the forecasted dispersal distances.

Variation among plant species in the observed seed numbers found on donkey fur were well predicted by the model ($R^2 = 0.56$, $P = 0.002$), though the predictions relied on relatively crude estimates of seed production and accessibility to donkeys, indicating that more accurate estimates of these parameters are needed.

Our model confirms the important role of epizoochory in affecting long-distance seed dispersal, and provides a modelling framework for integrating the multiple components of the dispersal process.
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Zusammenfassung

Die Verbreitung von Pflanzensamen im Fell von großen Herbivoren (Epizoochorie) ist ein wichtiger aber komplexer Verbreitungsmechanismus über große Distanzen. Wir entwickelten ein explizites räumliches Simulationsmodell der epizoochorischen Samenverbreitung. Die Parametrisierung erfolgte aufgrund empirischer Untersuchungen der Bewegung und des Verhaltens von Eseln sowie der Verteilung, der Samenproduktion, der Samenzugänglichkeit, der Samenanheftung und der Samenanhaftung am Eselsfell von bestimmten Pflanzenarten in einem Küstendünen-Naturschutzgebiet in Flandern, Belgien. Wir verglichen die vorhergesagte mit der beobachteten Samenanzahl der 14 Pflanzenarten im Eselsfell.

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Die modellierten Samenverbreitungen ließen erkennen, dass bei den meisten Arten ungefähr die Hälfte aller durch Esel verbreiteten Samen in diesem mehr oder weniger isodiametrischen Naturschutzgebiet von 100 ha eine Distanz von >100 m zurücklegte, und ungefähr 1% >500 m zurücklegten. Bei Samen mit größeren Anhaftungszeiten wird erwartet, dass sie weitere Strecken zurücklegen als diejenigen, die kürzere Anhaftungszeiten haben. Eine Vergrößerung der Schutzgebietsfläche hatte nur einen geringen Einfluss auf die vorhergesagten Verbreitungsdistanzen.

Die Variation der Pflanzenarten, die in den Samenmengen auf Eselsfell gefunden wurde, wurde durch das Modell gut vorhergesagt ($R^2 = 0.56$, $P = 0.002$), obwohl die Vorhersagen auf relativ groben Einschätzungen der Samenproduktion und Zugänglichkeit für Esel beruhten, und zeigt an, dass genauere Einschätzungen dieser Parameter notwendig sind.

Unser Modell bestätigt die wichtige Rolle der Epizoochorie bei der Verbreitung von Samen über große Distanzen und liefert einen Modellierrahmen, um vielfältige Komponenten beim Verbreitungsprozess zu integrieren.

Introduction

Seed dispersal is a key factor in plant spatial dynamics, influencing the distribution of populations and communities, both at local and regional scales (e.g. Bullock et al., 2002; Cain, Milligan, & Strand, 2000; Levin, Muller-Landau, Nathan, & Chave, 2003). Range shifts of plants are determined largely by long-distance seed dispersal (i.e. seed dispersal >100 m; Cain et al., 2000), as demonstrated in the context of Holocene plant migrations (Cain, Damman, & Muir, 1998), and in the context of actual and future plant migrations in response to land use changes (e.g. Poschlod & Bonn, 1998; Verheyen, Honnay, Motzkin, Hermy, & Foster, 2003) and climate change (Watkinson & Gill, 2002). Considering the present degree of habitat deterioration and fragmentation throughout the world, the long-term survival of many plant species and communities hence depends on successful long-distance dispersal. This prospect highlights the need for predictive models of plant dispersal, which generate realistic behaviour, and which are validated with field observations (Levin et al., 2003).

Among the major long-distance dispersal mechanisms, the transport of seeds in animal fur (epizoochory) receives increasing attention (Couvreur, Christiaen, Verheyen, & Hermy, 2004; Couvreur, Cosyns, Hermy, & Hoffmann, 2005; Couvreur, Vandenberghe, Verheyen, & Hermy, 2004; Couvreur, Verheyen, & Hermy, 2005; Fischer, Poschlod, & Beinlich, 1996; Heinken & Raudnitschka, 2002; Kiviniemi, 1996; Römermann, Tackenberg, & Poschlod, 2005). However, compared to, e.g., wind dispersal (Bullock & Clarke, 2000; Tackenberg, Poschlod, & Bonn, 2003), attempts to model zoochorous dispersal are relatively scarce, likely because of the inherent difficulty of tracing zoochorous long-distance dispersal, and the associated problem of incorporating this component, which is influenced by complex animal behaviour, into a model. Vellend,

Myers, Gardescu, and Marks (2003) and Higgins, Lavorel, and Revilla (2003) have recently used data on animal movement patterns and seed retention to model endozoochory by white-tailed deer in eastern North America, and epizoochory by lynx in southwestern Spain, respectively. Mouissie, Lengkeek, and Van Diggelen (2005) modelled epizoochorous dispersal distances by sheep and cattle using literature data and field observations. However, these models did not take account of the influence of habitat preferences on animal movement patterns, nor did they allow for predictions of variation among plant species in the number of seeds dispersed. Considerable challenges in constructing and parameterizing models of zoochorous seed dispersal therefore remain.

Here, we present a spatially explicit simulation model of epizoochorous seed dispersal, parameterized with empirical data concerning most key features of the dispersal process. The model simulates the movement of donkeys, and the simultaneous uptake and epizoochorous dispersal of seeds of 14 local plant species in a fenced coastal dune nature reserve (or any arbitrarily large area with a specified distribution of habitat types). Our two principal objectives were (1) to estimate seed shadows for plant species with different seed retention characteristics on animal fur, and (2) to attempt to predict the number of seeds of each species found on donkey fur in the field.

Material and methods

Study site and vegetation

The study site was the 100 ha coastal dune nature reserve 'Houtsaegerduinen', in western Flanders, Belgium (51°05′N, 2°35′E). The maximum distance between any two points in this more or less isodiametric nature

reserve is only 1.4 km. For nature management purposes, six donkeys were released in the reserve in 1997. The herd comprised 15 animals in 2000, the period of data collection. The variation in abiotic conditions and the historical land use in this coastal dune ecosystem have led to relatively high plant species richness and a range of different plant communities. Flowering and fruiting of the plant species in the study site is concentrated from April to October. Vegetation surveys were used to divide the study area into four main vegetation types: shrub, forest, grassland including moss dunes, tall herbage. These surveys used Tansley scaled ordinal abundance estimates in combination with percentage cover estimates in 1, 4 or 9 m^2 (grassland) or 100 m^2 (forest and shrub) quadrats, collected on several occasions between 1990 and 2000). Plant species abundance estimates included reproductive as well as vegetative individuals. The most abundant vegetation type was shrub, dominated by *Hippophae rhamnoides* and *Ligustrum vulgare*, and to a lesser extent *Prunus spinosa* and *Crataegus monogyna*. Forest was the second most abundant vegetation type, dominated by planted *Alnus glutinosa* and *Populus × canadensis* trees. The third most abundant was the 'open' vegetation type, consisting of grassland and moss dunes. The grassland generally occurs as scattered patches and represents species poor remnants of dune grassland, characterized by low-growing *Rosa pimpinellifolia* and several grasses (*Avenula pubescens*, *Arrhenatherum elatius*, *Poa pratensis*). Typical but rare species in dune grasslands are *Thymus pulegioides*, *Helianthemum nummularium* and *Silene nutans*. The moss dunes were characterized by mosses and lichens (*Tortula ruralis* ssp. *ruraliformis*, *Hypnum cupressiforme* var. *lacunosum*, *Cladonia* spp.), in combination with *Carex arenaria* and *Koeleria albescens*. Finally, the least abundant vegetation type was 'tall herbage', typically established after scrub degradation, and existing of rather species poor *Calamagrostis epigejos*-*Arrhenatherum elatius* dominated patches with local stands of *Eupatorium cannabinum* and *Epilobium angustifolium*.

Model

Estimating epizoochorous seed shadows requires information on animal movement patterns and seed retention times. The movement pattern (i.e., the probability that an animal will be at different distances from the point of seed adhesion at different times following adhesion) depends, in turn, on the rate of animal movement and its behaviour with respect to different habitat types it may travel through. Predicting the average number of seeds adhering to an animal over time requires additional knowledge of the spatial distribution, seed production, seed accessibility, and seed adhesion to animal fur of the different plant species. In our model, we incorporated data on these components derived from our own empirical studies, from the literature, and from inferences based on plant morphology. The model was implemented in Matlab 6.5 (MatLaboratory, 2002), and the first step was to convert a vegetation map of the study area into a grid of 10 × 10 m cells, with each cell assigned to one of the four main vegetation types (shrub, forest, grassland/moss dune, tall herbage).

Animal movement

Movement rate and habitat preference of donkeys in the study site were derived from observational data, recorded during 32 observation sessions, conducted between 3 May 2000 and 25 June 2001, spread over the four seasons and more or less evenly distributed between morning (6–12 h), afternoon (12–18 h) and evening (18–24 h) (see Lamoot, Callebaut, Demeulenaere, Vandenberghe, & Hoffmann, 2005). Each session consisted of a 5 h 45 min visual observation period on one randomly chosen focal animal of the herd, whose exact position was located on a map every 15 min (total locations = 768). The Euclidean distance between each consecutive donkey location was calculated, resulting in a vector of 'distances covered in 15 min'. To obtain a donkey habitat preference factor for each of the four main vegetation types in the study site, the proportion of observed donkey locations in each vegetation type was divided by the proportional area of that vegetation type. The habitat preference factors were then rescaled to numbers between 0 and 1, by dividing them by the highest obtained habitat preference factor. These rescaled values were named 'permeability coefficients' (reflecting the relative permeability of the four vegetation types for the donkeys, see Table 1) and assigned to all 10 m × 10 m cells according to their vegetation type.

The movement of donkeys in the reserve was simulated by a restricted random walk, in which the distance covered in one 15 min step was randomly selected from the observed vector of 'distances covered in 15 min'. The direction of each step was chosen randomly, but a step was only accepted with probability equal to the vegetation-specific permeability coefficient (cells outside the fence were accepted with probability zero). A new random direction was drawn until the step was accepted. Initial results of the movement model (1000 simulations of 5 h 45 min) were checked for consistency with empirical data in two ways. First, we compared the predicted and observed proportions of time spent in each habitat type. Second, we compared predicted and observed probabilities of finding a donkey at different distances from its starting point during 15 min time intervals. Both comparisons revealed a close

Table 1. The four main vegetation types in the study site, their proportional area (total area = 100 ha) and the observed and simulated proportional visits of the donkeys (total visits = 768). The ratio of these figures gives the habitat preference factor of the donkeys, or after rescaling to a maximum of 1, the permeability coefficient of each vegetation type.

Vegetation type	Proportion of area	Proportion of visits: observed (simulated)	Habitat preference factor	Permeability coefficient
Shrub	0.58	0.38 (0.40)	0.66	0.262
Forest	0.25	0.25 (0.25)	0.99	0.394
Grassland + moss dunes	0.13	0.33 (0.31)	2.51	1.000
Tall herbage	0.04	0.03 (0.04)	0.97	0.385

correspondence between model predictions and empirical observations (see Table 1 and Fig. 1 in Supplementary Appendix A). Therefore, we used the above-described restricted random walk to model donkey movement for longer time periods. For use in estimating seed shadows, 1000 movement simulations of 40 h each were conducted to build the **MOV** matrix, in which each element represents the probability that a donkey has travelled a given net distance (in 100 m intervals) at different times since the beginning of the simulation (in 15 min intervals; see also Vellend et al., 2003). Of those seeds with the longest retention times (based on data for *Geum urbanum*) fewer than 1% are expected to be still attached after about 10 h. We used 40 h simulations to allow for inclusion of the rare longer retention times required for long-distance dispersal. To test whether the constrained reserve area influenced the predicted seed shadows, the largest possible rectangular block within the reserve (50 ha) was replicated 25 times to create a reserve of 1250 ha, which is larger than the home range of free-ranging equids (King 2002). Again, 1000 simulations of 40 h each were run to build a second **MOV** matrix. The proportional area of the vegetation types and the habitat preference factor in this landscape were nearly identical to those observed in Table 1.

Plant species, distribution and seed production

Among the 335 plant species present in the study site, the 14 most abundant species germinating from epizoochorous seed loads of the donkeys (see Couvreur, Cosyns et al., 2005) were selected for our simulations. Several seed types were represented by the 14 species: hooked, awned, with a pappus and unspecialized; see Table 3 in Supplementary Appendix A). The distribution and abundance of each species in each of the four main vegetation types in the study area was recorded in the field (cf. above) and included in the model as the proportion of 10 m × 10 m cells occupied, and the number of plants per occupied cell (Table 1 Supplementary Appendix A). Approximate seed numbers per plant were derived from the literature (Table 2 in Supplementary Appendix A).

Seed adhesion and release

Since the degree of 'accessibility' of a plant's seeds for epizoochory depends on the degree of seed exposure and the height of the plant (cf. Fischer et al., 1996), the number of accessible seeds per plant was calculated by multiplying seed number per plant by a seed 'accessibility factor'. This factor was arbitrarily set to 1.0 for plants with exposed seeds on a stem > 30 cm; the factor was set to 0.01 for plants with enclosed on a short stems (<30 cm) and to 0.1 for all others (Table 2 in Supplementary Appendix A). It is important to emphasize that the accessibility factors were determined a priori based on knowledge of plant traits. The resulting 'accessible seed number' represented the fraction of the total seed number potentially available for epizoochorous dispersal.

Seed uptake and seed loss were modelled using plant-specific parameters obtained from experimental data on seed adhesion (Couvreur, Vandenberghe et al., 2004) and retention on horse fur (Couvreur, Verheyen et al., 2005). This appears justified, since the behaviour of donkeys and horses is quite similar (Cosyns, Degezelle, Demeulenaere, & Hoffmann, 2001) and since donkey fur is at least as suited for seed dispersal as horse fur (see also Couvreur, Vandenberghe et al., 2004). If no experimental data were available, the selected parameters were taken from species with morphologically or functionally similar seeds (Table 3 in Supplementary Appendix A). Support for such procedure is provided by Römermann et al. (2005) and Tackenberg, Römermann, Thompson, and Poschlod (2006): they found seed size, shape and the presence of adhesive appendages to be key-traits and hence, these traits were used to select analogues for the study species. This procedure allowed us to include considerably more species in the analysis. Seed uptake was modelled using a seed adhesivity score (Table 3 in Supplementary Appendix A), which reflects the attachment capacity of seeds to fur as experimentally quantified by Couvreur, Vandenberghe et al. (2004). Nine different adhesivity scores were used to characterise the 14 focal plant species in this study (Table 3 in Supplementary Appendix A). From the model species represented by species with morphologically or functionally similar seeds, the most adhesive ones (with hooks) were represented by *Erodium cicutarium*; the medium sized

grass seeds without seed appendage by *Festuca pratensis*, and the tiny seeds of *Cerastium semidecandrum* by *Myosoton aquaticum*. The subsequent loss of attached seeds from the fur was modelled using experimental data on the retention time of seeds on a moving horse in field conditions over 20 h periods (see Couvreur, Verheyen et al., 2005). To characterise the 14 focal plant species in this study, retention parameters from five different plant species were used (Table 3 in Supplementary Appendix A). The most adhesive species (with hooks) were represented by the hooked-seeded *G. urbanum* (as was *Senecio jacobaea*, since pappus hairs are generally quite adhesive, see Couvreur, Christiaen et al., 2004; Couvreur, Vandenberghe et al., 2004); the medium-sized grass seeds without seed appendage by *Centaurea jacea* (and with seed appendage by *Anemone nemorosa*); the small and irregularly shaped ones by *Oenothera biennis*; and the tiny ones by *Prunella vulgaris*. The species-specific seed retention parameters were used for all four vegetation types, since in a previous study it was demonstrated that seed retention times did not vary considerably with vegetation type (Couvreur,Vandenberghe et al., 2004, also see Bullock & Primack, 1977). The proportion of seeds remaining attached after adhesion (which occurs at time $t = 0$) was modelled as $\exp(b \times t)$, with R^2 ranging from 0.75 to 0.78 ($P < 0.001$) across species.

Seed shadows and seed numbers

The seed retention curves for each species were used to generate a retention-time vector $\mathbf{RT_S}$ (**s** refers to the species), in which each cell represents the proportion of seeds dropped in 15 min time intervals from 0 to 40 h. The species-specific seed shadows were then calculated as $\mathbf{MOV} \times \mathbf{T_S}$ (see also Vellend et al., 2003).

Finally, independent data on observed seed numbers per plant species on donkeys were compared with model predictions. The empirical seed numbers (see Table 2 in Supplementary Appendix A) were obtained by Couvreur, Cosyns et al. (2005) after inspection of the seeds brushed from the fur of individual donkeys in the study site at several occasions during the growing season of 2000. Mean observed seed numbers were calculated including only sampling dates when the species was present in the fur samples. Predicted seed numbers from the model were calculated as the mean across time during five simulations with 1000 15 min time steps (i.e. 10.4 days). Linear regression on log-transformed values was used to compare predicted and observed seed numbers (SPSS, 2001).

Results

Since seed retention data of five different plant species (see Couvreur, Verheyen et al., 2005) were used to represent the range of seed characteristics among the 14 species used in this study, five different seed shadow profiles were obtained (Fig. 1). All showed approximately exponential decreases in the proportion of seeds dispersed with distance, with mean net seed dispersal distances ranging from 135 to 166 m. Despite the relatively narrow range of mean dispersal distances, seeds with longer retention times (e.g., Fig. 1) should be dispersed further than seeds with shorter retention times (e.g., Fig. 1). For most species about half of all seeds dispersed by the donkeys will travel a net distance of >100 m, and about 1% will travel >500 m within this nature reserve, where the maximum distance between any two points is only 1.4 km. Interestingly, very similar results were obtained in the hypothetic 1250 ha extended reserve, with mean dispersal distances ranging from 141 to 177 m and 99% percentile distances $\leqslant 700$ m.

The number of seeds of each of the 14 plant species in donkey fur was systematically (with approximately one order of magnitude) overestimated by the model (Fig. 2). However, given the relatively crude estimates of seed availability, the predicted seed number was a strong and significant predictor of variation in the observed data ($F = 15.2$, $R^2 = 0.56$, $P = 0.002$; Fig. 2). The ability of the model to predict variation among species in observed seed number depended on inclusion of the accessibility factor, as revealed by a lack of significant relationship between observed and predicted values when the accessibility factor was excluded (i.e., $= 1$ for all species, $F = 1.1$, $R^2 = 0.08$, $P = 0.315$; Fig. 2).

Discussion

The simulation model applied in this study allows prediction of the number of plant seeds in animal fur, as well as animal-generated seed shadows for plant species with different seed characteristics. The fact that the model is parameterized with extensive empirical data on most key aspects of the dispersal process, and compared with independent field observations, distinguishes it from other recent models presented in the context of long-distance seed dispersal by animals (e.g. Higgins et al., 2003; Mouissie, Lengkeek et al., 2005; Mouissie, Vos, Verhagen, & Bakker, 2005; Vellend et al., 2003). Here, the model was applied to donkeys, which are expected to be reasonably representative for other large herbivores (see Couvreur, Christiaen et al., 2004).

Animal movement and epizoochorous seed shadows

Modelling animal movement has been the subject of considerable research. Animal species may perceive the same landscape differently, and are likely to be influenced by different plant characteristics, such as
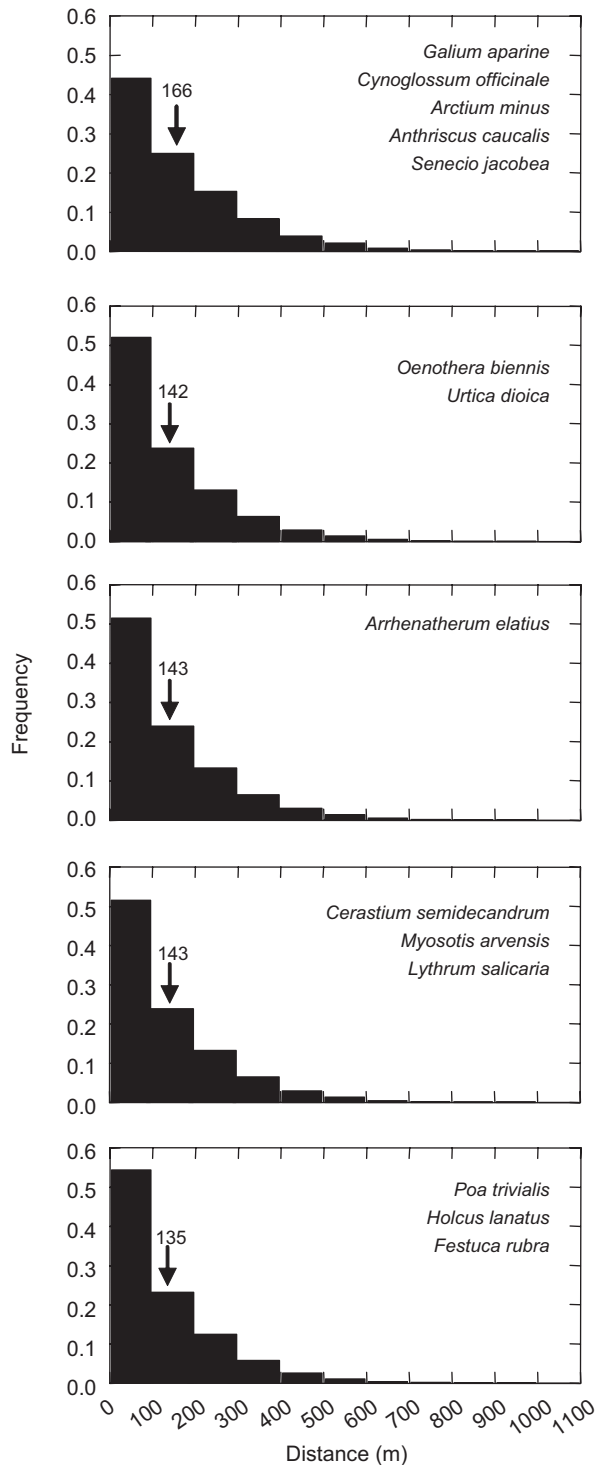
Fig. 1. Modelled seed shadows generated by epizoochory: distribution of net realized dispersal distances of the seeds in donkey fur in the 100 ha study site. Five different seed shadow profiles are modelled because seed retention characteristics for five different species (cf. Couvreur et al., 2005; see Appendix A: Table 3) were used to represent the 14 species used in this study. Arrows indicate the mean net dispersal distance.

plant species, shape and distribution (Etzenhouser, Owens, Spalinger, & Murden, 1998). For simplicity, animal movement is often described by a correlated random walk, depending on three variables: number of steps, step size, and distribution of random turning angles (Byers, 2001). The simplest form is an uncorrelated random walk, with a uniform random distribution of turns with a maximum angle of 180° right or left. In this paper, realistic animal behaviour was achieved by combining the mathematically convenient uncorrelated random walk with a donkey movement rate distribution and a simple movement rule based on observational data on habitat preference of donkeys (Fig. 1 in Supplementary Appendix A). The fact that the nature reserve was fenced simplified movement rules, but this did not have an important effect on the obtained seed shadows. This is probably due to the combination of short-distance movements by the donkeys (see Fig. 1 in Supplementary Appendix A) and the generally short retention times of the seeds (50% of the studied seeds 1–1.5 h after attachment as reported in Couvreur, Verheyen et al., 2005). For animals with longer fur than donkeys and horses (e.g., sheep), much longer dispersal distances may be predicted with less constrained movement.

Our results demonstrate that seeds are likely to be dispersed via epizoochory by donkeys throughout the entire study site, with half of all donkey-dispersed seeds moving further than 100 m from their point of attachment (Fig. 1). Likewise, Mouissie, Lengkeek et al. (2005), Mouissie, Vos et al. (2005) reported mean dispersal distances of 65, 125 and 380 m for Fallow Deer, cattle and sheep, respectively and Higgins et al. (2003) obtained mean simulated epizoochorous dispersal distances of 572 m for burrs of *Xanthium strumarium* by free-ranging Iberian lynx in a Spanish national park.

At least 29 species in our study site are prone to epizoochorous dispersal (Couvreur, Cosyns et al., 2005), with well over 100 seeds expected to be on a donkey at any one time. The panels in Fig. 1 represent a realistic range of seed shadows that may be generated by the donkeys in the study site, with highly adhesive seeds (e.g., *Galium, Arctium*, Fig. 1) showing longer dispersal distances than less adhesive seeds (e.g., *Poa, Holcus*, Fig. 1). In combination with higher dispersed numbers of the more adhesive seeds (Fig. 2), this may well represent a significant ecological difference. Again, animals with longer fur may generate larger differences among plant species. Particularly for species with hooked seeds such as *G. urbanum*.

Seed numbers in animal fur

Seed numbers observed on animals are of interest both for determining the importance of epizoochory for
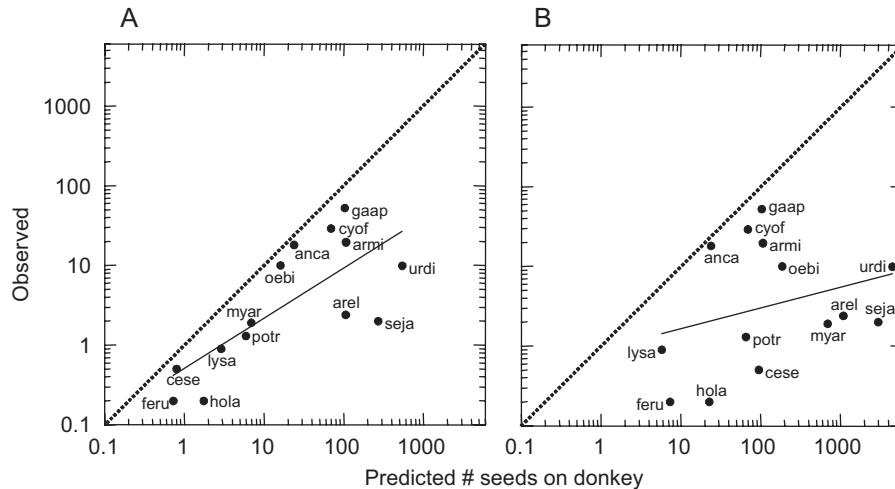
Fig. 2. Observed vs. predicted seed numbers in donkey fur of 14 plant species (represented by their abbreviations, see Appendix A: Table 1 for full names) (A) using the seed accessibility factor ($F = 15.2$, $R^2 = 0.56$, $P = 0.002$), (B) without the seed accessibility factor ($F = 1.1$, $R^2 = 0.08$, $P = 0.315$).

different plant species and for providing an independent source of data for testing of the model. Seed numbers in donkey fur were overestimated by the model, typically by one order of magnitude (Fig. 2). The overprediction was almost certainly a consequence of our relatively crude determinations of seed numbers per plant and seed accessibility. Reliable data on seed production per plant are available for only very few plant species, and seed production can vary enormously between contrasting habitats and even between years. There has been relatively little study of relative accessibility of seeds to seed-dispersing animals. The accessibility factor used here was mainly based on expert knowledge and only three values were possible, differing by one order of magnitude. Nevertheless, the resulting attachment probabilities (i.e. accessibilitiy factor × adhesivity score) more or less spanned the same range as the values reported in Mouissie, Lengkeek et al. (2005) and Mouissie, Vos et al. (2005). Through empirical research these authors found values ranging from 0.00034 to 0.128 and from 0.00009 to 0.013 for sheep and cattle, respectively, while we used values between 0.0016 and 0.464. This may partly explain why our model was able to predict variation among species in seed number on donkeys. The importance of seed accessibility was clearly indicated by the relatively poor correspondence between model predictions and data in its absence (compare Figs. 2A and B), pointing to an important focus of future studies. Indeed, our conclusion that the model can predict seed numbers in animal fur must be tentative, until more refined estimates of seed accessibility are made. Assessing accessible seed numbers should take into account animal behaviour with respect to particular plant species (e.g., avoidance of *Urtica dioica* because of low forage value, Klotz, Kühn, and Durka, (2002) and of *S. jacobaea* because of toxicity)

and seed numbers should be determined in the field rather than derived from the literature. For instance, reproduction in *Holcus lanatus* and *A. elatius* may largely be vegetative rather than sexually due to over-grazing at our study site (personal observation).

Multiple modes of dispersal

The present study focused on the simulation of epizoochorous seed dispersal by donkeys, although seeds of most plants are dispersed by multiple vectors (e.g. Higgins et al., 2003). Rabbits, the most prevalent wild mammals in the study site, probably contribute to epizoochory on a smaller scale, since they have small home ranges (approximately 4 ha, Bond, Leopold, Burger, & Godwin, 2001). On the other hand, as the rabbits can reach all microsites in the thorny shrub patches and are not constrained by the fences, they may be important seed-dispersal links with the landscape surrounding the nature reserve. Herbivores such as donkeys and rabbits disperse seeds not only by epizoochory, but also by endozoochory (Pakeman, Atwood, & Engelen, 1998; Couvreur, Cosyns et al., 2005). The quantitative contribution of endozoochory to seed dispersal is expected to be higher (Janzen, 1984), yet both epi- and endozoochory are important, since they operate on a complementary set of species (Couvreur, Cosyns et al., 2005). In contrast to epizoochory, endozoochory is characterized by an extended lag prior to defecation (approximately 60 h in donkeys, Cosyns, Delporte, Lens, & Hoffmann, 2005), a high loss of seeds through chewing or digestive processes (Cosyns et al., 2005), and retention times which are restricted by gut passage time. Another important dispersal vector in dune ecosystems is probably wind.

Anemochory is promoted by thermal updrafts, and is more effective for species with a low falling velocity and a high seed release height (Tackenberg et al., 2003). However, seed dispersal distances generated by anemochory are for most plant species restricted to a few metres from the parent plant (Jongejans & Telenius, 2001). Although wind is generally more omnipresent than animal vectors, it may be more important in the open habitats of the coastal dunes (grasslands and moss dunes) than in the closed ones (shrub and forest).

Conclusions

Our modelling approach should be generally applicable to systems in which epizoochorous seed dispersal is important, with appropriate adjustments based on local details of animal and plant characteristics. This kind of model can provide a critical building block for modelling plant migration in the face of future environmental and landscape changes. For ecosystem conservation and restoration purposes, such a model can be an instrument to evaluate current dispersal potential of plants, and to help guide decisions, for instance concerning the introduction of large herbivores. Dispersal vectors provide a critical ecosystem function in a conservation context by linking fragmented patches of natural habitat (see Lundberg & Moberg, 2003; Wenny, 2001). In our study site, a 100 ha coastal dune landscape, the donkeys clearly dispersed seeds among all habitat types throughout the reserve (see also Couvreur, Christiaen et al., 2004).

Acknowledgements

Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2006.12.002

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