Seed dispersal by animals:
A theoretical model

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1. Introduction

Seed dispersal is a key element of plant regeneration (Traveset et al. 2014). The movement of individuals determines the potential location for recruitment and thereby the future distribution of the species (Bullock et al. 2006). Dispersal is defined as 'the departure of a diaspore (e.g. seed or fruit) from the parent plant' (Howe & Smallwood 1982). There are multiple theories for the advantage of dispersal, dependent on the species and area, ranging from escaping sibling competition to colonization of new areas and conservation of diversity (Howe & Smallwood 1982; Wang & Smith 2002; Traveset et al. 2014). Seed dispersal research is challenging due to the many processes involved in dispersal and the difficulty to track individual seeds (Wang & Smith 2002). Especially in the case of secondary dispersal, important dispersal vectors are easily missed (Bullock et al. 2006).

Seeds can be dispersed by different means. The morphology of the seed and fruit of a plant often displays the primary mechanism of dispersal. Different modes of seed and fruit include adaptations to float or be tossed, to stick or to be eaten. More than 60% of tree species in temperate regions are dispersed by vertebrates (zoochory; Howe & Smallwood 1982). Zoochorous dispersal is influenced by many animal and plant characteristics (Will & Tackenberg 2008). Qualitative and quantitative data on the many factors involved in zoochorous dispersal was lacking, but has accumulated in the last years (Myers et al. 2004; Westcott et al. 2005; Russo et al. 2006; Santamaria et al. 2007; Campos-Arceiz et al. 2008; Will & Tackenberg 2008). Of animal dispersers, birds are of special interest due to their ability to link apparently isolated landscape patches (Garcia et al. 2010). The fruit production of most bird-dispersed plant species seems to be timed to the presence of migratory birds, bearing nuts or fruits that ripen in the late summer and early fall (Howe & Smallwood 1982). The movements of these birds consequently determine the spatial scale of dispersal (Westcott & Graham 2000). An example of small-scale isolated landscape patches are inland wetlands. These are often isolated islands with aquatic organisms that are unable to move to another wetland on their own accord, although many of these species are widely distributed (Figuerola & Green 2002). The distribution of these organisms is aided by migratory waterbirds. More information is required on this means of dispersal, to investigate the importance of bird-mediated dispersal on the distribution and abundance of plant populations, relative to other local factors (Figuerola & Green 2002).

Difficulties in tracking seeds from source plant to final location make it difficult to quantify seed dispersal directly (Russo et al. 2006). To this end, models are often used as an alternative for quantitative data to illustrate seed dispersal. In seed dispersal studies, models are employed to represent or predict patterns; investigate processes; elucidate consequences or explain dispersal evolution (Levin et al. 2003). Models are defined here as the formal expression of the relationship between defined entities in physical or mathematical terms (Jeffers 1982). Word models can provide agreement on definitions and relations between factors, but incorrect interpretation of word models due to language differences is possible. Mathematical models provide the abstraction we need to reduce ambiguity in complex problems, by replacing words and concepts by symbols (Jeffers 1982). Which model is used for a research question can radically change the outcome. In seed dispersal, models can be used to integrate theoretical and empirical knowledge to improve understanding of key processes (Nathan & Casagrandi 2004). Zoochorous dispersal is influenced by many animal and plant characteristics, making the development of models for zoochorous dispersal challenging (Will & Tackenberg 2008).

In this thesis, I will provide an overview of models used in zoochorous dispersal studies and recommend a modelling approach to describe seed dispersal between wetlands by mallards in a spatial context. For this, a case study on seed dispersal by mallards is used, based on a study by Erik Kleyheeg. The aim of Kleyheeg's project is to identify key factors and their relations in seed dispersal by mallards (Kleyheeg, personal communication).

First, I will evaluate the models that are used in zoochorous dispersal studies(chapter 2). Then, I will introduce a conceptual model to illustrate the key factors of seed dispersal between wetlands by mallards, based on Kleyheeg's study (chapter 3). Lastly, I will recommend a realistic model based on the factors in the conceptual model (chapter 4).

2. Models for zoochorous seed dispersal

2.1 Methods of seed dispersal experiments

There are many different ways to measure seed dispersal. Zoochorous dispersal is influenced by many animal and plant characteristics, making it challenging to capture all the processes of dispersal in one method. Modelling approaches can help in understanding zoochorous dispersal by estimation or prediction of the observed patterns (see Ch. 2.2). These observed patterns are based on data obtained from real dispersal events which can be gathered with the use of different methods. Here, these different methods to gather basic data on dispersal are described.

Traditionally, research on animal-mediated seed dispersal was 'seed-centred', with the focus on seed characteristics determining by which mechanisms and over what distances they are dispersed. In recent years there has been a shift to more 'vector-centred' research, with the focus on the dispersal vector and how many seeds it disperses over what distances (Tsoar et al. 2011). Furthermore, there is increasing interest in the relative occurrence of long-distance dispersal and the mechanisms that promote it (Higgins et al. 2003; Nathan et al. 2003, 2008; Levey et al. 2008), encouraging the use of techniques that have the ability to capture these events. With the introduction of these new techniques it is becoming easier to follow seeds during dispersal or relocate them afterwards.

Animal-mediated dispersal can be measured in either a direct or indirect approach. In the direct approach, seeds or dispersers are tracked (Lagrangian methods) (Bullock et al. 2006). The more indirect approach to investigate dispersal is by measurement of the amount and type of seeds that are dispersed to a specific location (Eulerian methods). This is done mostly with seed traps, quadrats or transects. Here, techniques will be discussed that belong to the direct approach of tracking seeds or dispersers (Lagrangian methods). Some passive tags on seeds to relocate them are discussed: stable isotope analysis, molecular genetic techniques, radioactive labeling and fluorescent microspheres. Furthermore, active tags on animals such radio transmitters or other telemetric devices to track them are addressed.

Passive tracking of seeds and animals

The seeds themselves can be relocated by marking them with a passive tag. One of the methods to track seeds passively is by looking at stable isotopes. Stable isotopes can be used to track seeds back to their parent populations (Wang & Smith 2002). Tissues of organisms have specific isotopic values, as a consequence of their location based on different factors on multiple scales (Hobson 1999). Analyses of the natural stable isotopes can aid in the identification of long-distance dispersal events by animals, by analyzing the spatial origin of defecated seeds. In addition to the naturally present isotopes, plant tissues can be enriched with isotopes to trace the specific offspring through the landscape (Carlo et al. 2009). Individual animal dispersers can also be injected with isotopes that it will shed with its faeces (Kenward et al. 2002). Another way to mark seeds is by irradiation with high-energy γ radiation (Wang & Smith 2002). The radiation does not harm the animal disperser that eats or handles the irradiated seeds. This method is a semi-visible marker, not visible by the eye, but detectable without analysis of seeds, with a Geiger counter (van der Wall 2003). Thirdly, fluorescent microspheres (15 µm in diameter) can be administered to fruits that are ingested by animals. The microspheres can be found back on fruits and seeds within

the fruits after defecation. The chances of false positive outcomes are small and the adhesion of microspheres does not affect animal fruit choice (Levey & Sargent 2000). Although the passive tracking of seeds by relocating them afterwards with these techniques can be useful, it is difficult to track dispersal over long distances with these techniques because the chance of finding marked seeds diminishes further from the source.

Another method to track seeds passively is with molecular genetic techniques. Genotypes can be compared with maximum likelihood estimations to match seeds or adults to parent individuals or populations. Because of the 'direct' measurement of the genome of offspring and parent, individual dispersal can be measured besides gene flow (Ouborg et al. 1999; Dow & Ashley 1996; Wang & Smith 2002). Genetic structures among populations can also be used 'indirectly' as a proxy for gene flow (Wang & Smith 2002). The more variation in genetic structure, the more gene flow and hence long-distance dispersal is more likely to have happened. This approach permits indirect estimation of seed dispersal events by measuring its consequences, but lacks quantitative details (Ouborg et al. 1999; Wang & Smith 2002). It cannot replace ecological methods but may serve as a complementary source of information (Ouborg et al. 1999). Moreover, molecular genetic techniques are expense and time-consuming and especially the indirect method is based on many assumptions that restrict the application of the method (Bullock et al. 2006).

Active tracking of animals

When seeds in animal defecation cannot be observed directly, other methods must be used to gain knowledge on dispersal distances. To this end, Animals may be tracked with active tags such as radio transmitters or other telemetric devices to gather data on animal movement (speed, distance and direction) (Bullock et al. 2006). This approach is particularly applicable when one is interested in the individual movements or home range of animal dispersers. It may be necessary when the animal under investigation is not easily spotted by the eye or travels great distances. It is not a method that allows for many individuals to be marked due to the cost of the tracking devices but on the other hand it does not need many observers (Kenward et al. 2002).

Satellite tracking provides much data on movements of waterbirds (Fiquerola & green). Especially light transmitters (<30 g) are useful when tracking smaller animals, as they do not affect bird movement (Holbrook & Smith 2000; Westcott & Graham 2000; Bartuszevige & Gorchov 2006). Campos-Arceiz et al. (2009) used radio collars with GPS-satellite transmitters to follow the movements of three wild elephants for three consecutive weeks, showing the use of GPS for the detection of long-distance dispersal. On shorter distances, radio transmitters with unique frequency may be more suitable to relocate birds by searching for the transmitted frequency with a receiver (Bartuszevige & Gorchov 2006).

In addition to telemetry devices, birds are often banded with a unique color code and combination (Holbrook & Smith 2000; Bartuszevige & Gorchov 2006). Although this method is not expensive, passive tags have low recovery rates (1-5% or less) and are only appropriate when many individuals can be banded. Therefore this method is best used on animals that are easily spotted by the eye and many competent observers take part in the investigation (Kenward et al. 2002).

There are two principal approaches to investigate and understand seed dispersal (Wang & Smith 2002). The approach to work forwards entails the following of the natural order of events, from fruit removal to seed dispersal by different vectors. Researchers studying these processes on animal-mediated dispersal typically use (active or passive) markers to track seeds or animals. The other approach is to work backwards, studying the consequences of dispersal by looking at seed and plant distributions and try to derive the processes that resulted in these distributions. Molecular markers are often employed to this backwards approach to measure dispersal after the event (Kenward et al. 2002). For an event that is rare or difficult to track, this approach seems suitable, but it leaves many question on the when, where and how of the dispersal processes that provide the understanding of dispersal and enable the modelling of processes (Kenward et al. 2002).

In conclusion, there are many methods to investigate seed dispersal. Bullock et al. (2006) suggests doing a pilot study to collect basic data and use that data to simulate seed distribution, after which sampling methods can be simulated and tested with goodness of fit to select the method that best describes the distribution kernel. (Bullock et al. (2006) also emphasize the importance of replications. To account for seasonal variation, they advise to do many small studies throughout the season. Doing replications is not a custom in seed dispersal studies, with many researchers opting to maximize the number of traps in their study, instead of repeating the entire design at another location, though it gives information on the variation in dispersal and helps in tracking long-distance dispersal.

2.2 What types of models are used?

In seed dispersal studies, we distinguish between phenomenological and mechanistic models. Phenomenological models are employed for the characterization of observed patterns, whereas mechanistic models are used for the explanation of observed patterns to accommodate understanding of seed dispersal (Levin et al. 2003).

Seed dispersal is mainly represented in a distance distribution or dispersal kernel, standing for the 'frequency distribution of dispersal distances' and the 'two-dimensional distance function of postdispersal seed densities', respectively (Nathan & Muller-Landau 2000). The distance distribution and dispersal kernel are both dispersal curves (Box 1). Phenomenological models represent the observed data with the best fitted function to estimate dispersal curves, taking no note of quantity or identity of dispersal vectors (Tsoar et al. 2011). Functional forms used to fit distance distributions are generally Gaussian, negative exponential or inverse power law.

For the estimation of dispersal kernels, two-dimensional probability functions are mostly used. In two-dimensional functions, Cartesian coordinates are used to show the probability that a seed originating from point (0, 0) lands at point (x, y) (Causton 1983; Levin et al. 2003). It is also possible to use polar coordinates, though more rare in biomathematics, marking how far away a point is (r) and by what angle (θ) (Causton 1983). Polar and Cartesian coordinates are easily convertible by the use of trigonometry. The choice between the two depends on the aim of the study, using polar coordinates for direction and Cartesian coordinates for location.

Phenomenological models

Phenomenological models can be used to assess the potential of the study species to spread, by analyzing the tail of the dispersal curve. In many cases of such long-distance dispersal (LDD), the Gaussian, exponential or inverse power law functions are not suitable to fit the observed data. Only the inverse power law has a fat enough tail, but it does not go to zero (Levin et al. 2003). LDD is often observed to be the result of multiple vectors (Cain et al. 2000; Nathan et al. 2008b). Many studies on LDD therefore combine two or more functions to create a mixture function that can model distributions resulting from multiple processes, fitting both the observed short- and long-distance dispersal (Russo et al. 2006). The disadvantage of these mixed dispersal models is that they assume that seed dispersal by animals can be seen as a decreasing function of distance (Will & Tackenberg 2008). Phenomenological models are very sensitive to variation in data and therefore fitted functions can differ accordingly to other populations or collection procedures (Tsoar et al. 2011).

Mechanistic models

Mechanistic models use data on factors that influence dispersal to predict dispersal curves and identify key factors in the dispersal processes (Levin et al. 2003; Tsoar et al. 2011). Where phenomenological models merely fit functions to the observed data, for the construction of mechanistic models the separate processes of dispersal need to be identified (Nathan & Muller-Landau 2000; Levey et al. 2008; Tsoar et al. 2011). In mechanistic modelling, the quantity and identity of dispersal vectors is important. Mechanistic models are complex to construct, because it requires parameterization of separate factors of dispersal. The use of these models is essential for better understanding of seed dispersal processes, because it can predict dispersal. Parameters are

based on true characteristics of the study system and give insight in the system, making it possible to generalize beyond the study system (Nathan & Muller-Landau 2000; Levin et al. 2003).

Extensive mechanistic models have been developed for seed dispersal by wind. Zoochorous dispersal is more complex, including behavioural patterns that need to be quantified to allow for parameterization (Nathan & Muller-Landau 2000). An often used approach to the development of mechanistic models for zoochorous dispersal is the extension of a wind dispersal model with inclusion of behavioral patterns. More studies now include an animal component (e.g. Campos-Arceiz et al. 2008; Holbrook & Smith 2000; Santamaría et al. 2007). Nathan & Casagrandi (2004) employ a simple mechanistic model generating different recruitment patterns dependent on distance, seed predator activity and seed escape from predation. Based on conceptual models of recruitment patterns, they aimed to characterize all spatial patterns of predators leading to consumption. They chose a less complex approach, not including individual animal movements and considering seed dispersal from a point source with animal movement in a one-directional plane. For this purpose, they used polar coordinates and one-dimensional equations. Nathan & Casagrandi (2004) argue that although modeling seed dispersal provides the option to include many factors that influence the dispersal, such as population dynamics of the plants and their animal dispersers, spatial arrangement and landscape variation, a more simplistic approach with fewer factors may be more effective in analyzing the essence of the original problem. A minimal model provides the opportunity to detect significant factors in the processes and how these influence observed patterns (Nathan & Casagrandi 2004).

Phenomenological models are often chosen because of the complexity of the seed dispersal processes (Nathan & Muller Landau 2000). Mechanistic models however, also provide the opportunity to simplify complex mechanisms (Nathan & Casagrandi 2004). Mechanistic models can aid in the identification of the relative contributions of the many factors of seed dispersal processes (Nathan & Muller Landau 2000). The employment of mechanistic approaches for zoochorous dispersal is lagging on the models for wind dispersal, but with new and improving techniques for animal tracking, field data necessary for (often phenomenological) parameterization is mounting on zoochorous dispersal.

Box 1. Terminology

Seed dispersal: the departure of a diaspore (e.g. seed or fruit) from the parent plant. Seed
Dispersal curve: summarizes the distribution of distances traveled by seeds.
Distance distribution: Frequency distribution of seed dispersal distances.
Dispersal kernel: two-dimensional distance function of postdispersal seed densities.
Seed shadow: spatial distribution of seeds deposited from a single plant.
Seed dispersion pattern: the spatial pattern of dispersed seeds; the sum of seed shadows from all sources in a population.

Sources: Howe & Smallwood 1982; Nathan & Muller-Landau 2000; Levin et al. 2003; Russo et al. 2006.

2.3 Incorporation of animal behavior and movement patterns - Spatially explicit models

Seed dispersal is the movement away from the place of birth (Levin et al. 2003). Hence, dispersal intrinsically requires the ability to move. Animals differ considerably from plants in their ability to move (Tsoar et al. 2011). A plant's reproductive structures are generally the only mobile parts (Damschen et al. 2008), whereas animals can often move at any time during their life cycle. In seed dispersal, non-animal-mediated dispersal can be characterized by the plant traits and its ability to move with the aid of wind, water or ballistics. Zoochorous dispersal includes a component of animal movement (Levin et al. 2003). Therefore, including animal movement in animal-mediated seed dispersal modelling is important, because net displacement of the seed is a consequence of displacement of the animal that carries it (Holbrook & Smith 2000; Westcott et al. 2005). Nathan et al. (2008a) have proposed a movement ecology framework that structures organismic movements into four components: 'the internal state (why move), motion capacity (how to move), navigation capacity (when and where to move) and external factors' affecting these. Organisms of all kinds use these components when moving, be it on a small (bacteria) or large scale (mammals). The movement of organisms belongs to the Lagrangian approach, quantifying movement of individuals. Nathan et al. (2008a) suggest the use of this framework in a mechanistic manner to improve the understanding of dispersal mechanisms, though it is difficult to quantify the internal and external components of the model. According to Tsoar et al. (2011) application of the movement ecology framework to zoochorous dispersal demands a twofold nested design. In the inner loop a seed-centred approach with the animal vector as an external factor and in the outer loop a vector-centred approach, the combination of the two determining the eventual displacement of the seed.
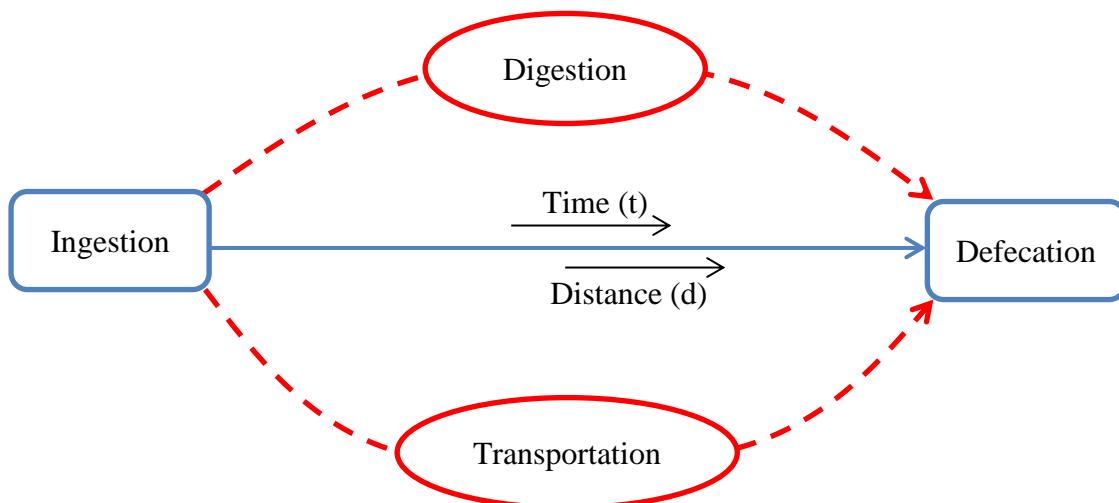

Figure 1. Basic conceptual model of zoochorous dispersal.

Similarities in zoochorous dispersal models

Most studies on zoochorous dispersal distinguish between three phases in dispersal: ingestion, digestion and transportation (fig. 1; Nathan et al. 2008b; Mueller & van der Valk 2002). The dispersal event is typically said to start with the ingestion of seeds by the disperser. This is the initiation of the seed dispersal event and represents the moment in time and space when seeds are ingested. Ingestion can be characterized by the number of seeds/time unit (Tsoar et al. 2011) or per visit (Schupp 1993). After ingestion, digestion takes place in the animal gut. Seeds may also

be regurgitated without digestion (Holbrook & Smith 2000), but here we only consider endozoochorous dispersal through digestion in the gut. The result of digestion for dispersal is often characterized as seed retention time, which is dependent on seasonal and individual differences. Digestion can also influence the viability of the seed, so seed germination probability of intact seeds is often tested after passage through the intestines (Mueller & van der Valk 2002; Santamaría et al. 2007; Bartuszevige & Gorchov 2006), to complete the seed dispersal cycle to probability of recruitment (Wang & Smith 2000; Myers et al. 2004). Studies on digestion as part of the dispersal cycle are thus often parameterized by retention time, intact gut passage and viability. Most studies concerning zoochorous dispersal depict the transportation of the seed by incorporating a component of animal movement in their models (e.g. Russo et al. 2006; Campos-Arceiz et al. 2008; Holbrook & Smith 2000; Mueller & van der Valk 2002; Westcott et al. 2005; Westcott & Graham 2000). Often, researchers use tracking devices such as radio or GPS transmitters to follow the movements of the animal disperser (see Ch. 2.1). Such devices can measure location of the animal in time, which can be translated to speed, direction, distance and frequency of displacement, giving information on the motion and navigation capacity of the disperser (how, when and where to move) (Nathan et al. 2008a). The displacement of the animal is not equal to seed displacement from the parent plant (Tsoar et al. 2011). It is often difficult to actively follow the disperser around and wait for it to defecate, although some studies succeeded (e.g. Wenny et al. 2000; Bartuszevige & Gorchov 2006). Most researchers refrain from this method and track animals more passively with GPS devices or radio transmitters. With this approach, source and end points of dispersed seeds are not known, posing the use of other methods to measure net seed displacement (Nathan & Muller-Landau 2000). Most zoochorous dispersal studies combine the vector seed load (ingestion), retention time (digestion) and net seed displacement (transportation) to calculate dispersal curves (Holbrook & Smith 2000; Westcott &Graham 2000; Santamaría et al. 2007; Campos-Arceiz et al. 2008; Tsoar et al. 2011). Distance distributions (one-dimensional; Box 1) can be calculated by substituting the time axis of retention time distributions by the mean net displacement corresponding to those times, resulting in a graphical representation of probability of seed deposition against net displacement from the moment in space and time of ingestion (Westcott et al. 2005). In a similar way seed shadows or dispersal kernels (two-dimensional; Box 1) can be constructed from the combination of retention times and two-dimensional movement data. Although this method does not measure actual dispersal distributions, but derives it from other parameters, it provides an estimation for the entire seed shadow (Westcott &Graham 2000). Combined with number of seeds ingested and percentage of viable defecated seeds, this method provides a quantification of seed dispersal.

Random vs non-random movements

The use of net seed displacement provides the possibility to calculate dispersal curves, but does not describe the animal behavior and in response to what (why) it moves. Observation studies may elucidate the why of the movement, giving insight in the motivations of the animal to move and facilitating the subsequent simulation of the movement. The movement ecology framework (Nathan et al. 2008a) typically describes movements that are non-random, since it incorporates a motivation by an internal goal (why move) and a direction towards a target (where and when move). Random movements can occur when the vector is assumed to have no information or no specific target to navigate to. Then, the internal motive to find food can result in a random foraging 'walk'. Though the movement ecology framework assumes non-random movements, many models of zoochorous dispersal do assume animals to move randomly in space, depositing seeds at a constant rate during movement (Levin et al. 2003). This creates a simplicity

in modelling that may be desirable to generalize to other systems, but might also miss important animal characteristics (Russo et al. 2006). Will & Tackenberg (2008) simulated animal movement as a correlated random walk, using speed and angle as parameters, but emphasized that to increase reality of the model, gathering specific data on animal movements is advised. Non-randomness can occur both in space (resting sites, foraging sites, avoid specific sites) and in time (diurnal activities) and the choice for inclusion of non-random behavior can strongly affect the resulting dispersal curve (Westcott et al. 2005). Russo et al. (2006) investigated the spatial variance in seed density due to spider monkey behavior. They found spider monkeys have a diurnal lifestyle, aggregating seeds in sleeping sites and scattering seeds during foraging. This resulted in a multimodal seed dispersal curve and a heterogeneous seed shadow. They emphasize that this result was only detected through study of animal behavior, improving spatial dispersal prediction that would not have been possible with seed traps alone. They state that mechanistic dispersal models based on seed passage time and displacement rate alone is not sufficient in the case of non-random seed distribution; displacement must be spatially explicit in order to not underestimate the aggregation of seeds. Westcott et al. (2005) also found non-randomness in time, with cassowaries being more active in the morning. Consequently, the timing of ingestion may influence the dispersal distance.

Incorporation of landscape variation

Non-random animal movements can be the result of a heterogeneous habitat. In the movement ecology framework, the landscape in which the animal moves is classified within the fourth component, as one of the external factors that affect the movement of the disperser (Nathan et al. 2008a). The animal disperser can react to the heterogeneous landscape, generating non-random movement and consequently non-random, aggregated seed distributions (Russo et al. 2006). Habitat structure, parent plant distribution and the subsequent disperser space utilization are key determinants for the dispersal curves (Santamaría et al. 2007; Tsoar et al. 2011), suggesting that spatial and temporal variation need to be included in zoochorous dispersal studies (Bullock et al. 2003). For seed dispersal by birds, landscape corridors have an effect on the animal movements, as many bird species typically follow edges (Levey et al. 2005; Bartuszevige & Gorchov 2006; Levey et al. 2008). Because of the difficulty to gather data on a landscape-scale, Levey et al. (2005) gathered data on small-scale local movements from which they deduced parameters of animal movements in reaction to habitat. With these parameters, animal movements were simulated at the landscape-scale and afterwards validated with landscape-scale experimental data. Levey et al. (2008) employed the same simulation model to test the effect of patch shape on dispersal by birds. Their model showed that heterogeneity of the landscape affects the dispersal kernel, generating smooth kernels with long tails in homogenous landscapes and more irregular kernels with shorter tails in patchy landscapes. The individual-based spatially explicit model they used was based on the idea that when an animal encounters a specific habitat feature, it reacts with a certain behavior, which may be a change of direction and/or speed of movement. Such 'decision rules' can be used to predict the disperser's movements in any given landscape. Bartuszevige & Gorchov (2006) made a similar model on the effect of landscape structure on animal movements with parameters based on observations. The collected data was converted to a probability matrix, combining time spent in various habitats with retention times to predict the seed shadows per habitat-type (Bartuszevige & Gorchov 2006). Whereas the models by Levey et al. (2005; 2008) and Bartuszevige & Gorchov (2006) are based on observations of small-scale bird movements, Will & Tackenberg (2008) based their simulated animal movements on estimations. They employed an individual-based spatially explicit model to predict zoochorous

dispersal in various landscapes. Their model contains two alternative landscape modes which differ in landscape characteristics based on real maps, fragmented or continuous landscape, respectively. The simulated landscapes are characterized by percentage of plant cover, size, and number, size and position of attractive sites. Animal movements are simulated depending on the landscape-characteristics they encounter (Will & Tackenberg 2008).

Conclusion

Difficulties in tracking seeds from source plant to final location make it challenging to quantify seed dispersal directly (Russo et al. 2006). In zoochorous dispersal, additional processes of animal movements and digestion add to this challenge. In studies on zoochorous dispersal, most researchers distinguish between three phases in dispersal: ingestion, digestion and transportation (Nathan et al. 2008b; Mueller & van der Valk 2002). By parameterization of these phases, models can be constructed that illustrate zoochorous dispersal. Ingestion is often parameterized as the number of seeds per visit or time, also called the vector seed load. Digestion is mostly parameterized by retention time, intact gut passage and percentage of viability. Transportation stands for the movement of the seeds in space and can be characterized as speed, direction, frequency and distance of movement. From these parameters of transportation that typically characterize the disperser's movements, the net displacement of the seed can be calculated, that, combined with the retention time, is transformable into a distance distribution. Two-dimensional dispersal kernels can also be calculated from these basic data. The elaboration with which the transportation of the seed is studied, varies between studies. Some assume random movements of the disperser, while others observe the animal's behavior to capture its responses to heterogeneous habitats and its subsequent non-random movements in space and time. Such non-randomness can then be estimated and simulated in mechanistic models that incorporate the landscape as an input variable that affects behavior and hence movements of the disperser, generating heterogeneous seed dispersion patterns.

2.4 Evaluation of models

The danger of mechanistic models is that their reliability may be unclear or overestimated (Bart 1995). Therefore, many researchers advocate a thorough evaluation of the constructed models (Bart 1995; Levin et al. 2003; Canham & Uriarte 2006). A proper assessment of a model consists of an evaluation of assumptions, parameter estimations and predictions, keeping in mind the relevance of the finished model for the original research question (Jeffers 1982; Bart 1995; Levin et al. 2003; Bullock et al. 2006; Canham & Uriarte 2006). To this end, the objectives and description of the model must be clearly stated to provide a solid base for the evaluation (Jeffers 1982; Bart 1995). Evaluation should provide a measure for the reliability of the model. In both phenomenological and mechanistic models, parameter estimations are crucial to the functioning of the model (Levin et al. 2003). Parameters should always be validated with independent real data that was not used to derive the parameters (Jeffers 1982; Levin et al. 2003; Bullock et al. 2006). In mechanistic models, parameters estimations from simulations should also be validated to 'true' values (Schurr et al. 2008). Besides the parameters, the model's primary and secondary predictions should also be tested for their reliability by comparison with real data (Bart 1995; Levin et al. 2003). Analyses of parameters and predictions can be done by the testing of a traditional null hypothesis with the output of a P value and confidence intervals (Bullock et al. 2006) or with likelihood analysis (Canham & Uriarte 2006). Likelihood analysis can compare

alternative predictions or parameter values and calculate a measure for the reliability (Canham & Uriarte 2006). After validation of the model and its parameters and predictions, these results can be integrated in a synthesis that describes the reliability of the entire model, for example by providing a 'minimum' and 'maximum' case scenario (Bart 1995).

3. Seed dispersal between wetlands by mallards

3.1 Which factors and processes play a role and how do these interact?

Erik Kleyheeg studies seed dispersal between wetlands by mallards in the Netherlands. Mallards are the most abundant duck species in the northern hemisphere, partly migratory with both resident and migratory populations in the non-breeding season in the Netherlands. Mallards are identified as an important vector for seed dispersal, making frequent local movements between wetlands (between roosting and foraging sites). The goal of Kleyheeg's study is to identify key factors and their relations in seed dispersal by mallards. Kleyheeg's study is both vector- and seed-centred, with the focus on the dispersal vector and how many seeds it disperses over what distances, but including also seed characteristics (Tsoar et al. 2011). Seed dispersal is considered out of the mallard's perspective and dispersal by vectors other than mallards is not considered (for this model). The study on seed dispersal by mallards has the same basic design as other studies on zoochorous dispersal (see Ch. 2, fig. 1), including the factors ingestion, digestion and transportation (fig. 2).

Ingestion

Here, ingestion stands for the diet. The diet (what do they eat) is determined by a combination of seed availability, accessibility and selection by mallards. The diet of mallards is known so did not need to be investigated for this study. Seed availability and accessibility is dependent on seasonal differences. The combination of seeds that are eaten by mallards are considered the diet and can be used to quantify seed dispersal.

Digestion

Digestion was studied through controlled feeding trials. Mallards were fed a known number of seeds at time 0, after which they were put on a grid in a crate to collect defecations at time intervals. The influence of seed and animal characteristics on digestion was also studied. Seed characteristics of interest include: seed size, seed coat thickness and permeability, shape etc.. These characteristics are more or less fixed per plant species. Animal characteristics include gizzard size and intestine length. The availability of seeds is dependent on seasonal differences, and diet influences the gizzard size and intestine length. Furthermore, physical activities can influence the digestion.

Transportation

Mallards were actively tracked in a forward approach (see Ch. 2.1) with GPS devices. Animal movements were measured in a direct approach (Lagrangian method), by tracking dispersers in various landscapes (Bullock et al. 2006). With the GPS devices, locations of tracked mallards were determined every 15 minutes, generating maps of point locations in time intervals. From these data, the distance, speed, direction and frequency of movements can be calculated. The mallard's movements can be influenced by landscape configuration, weather conditions (cold) and time of day (diurnal behaviour).

Chronologically, the process of seed dispersal can be divided into three steps. Firstly, the mallard eats a number of seeds at time and location A (ingestion). Secondly, while digesting the seeds (digestion), it may move through the landscape (transportation). Thirdly, when the seeds reach the end of the digestive track, a number of intact seeds are defecated by the mallard at time (retention time) and location B (fig. 2).
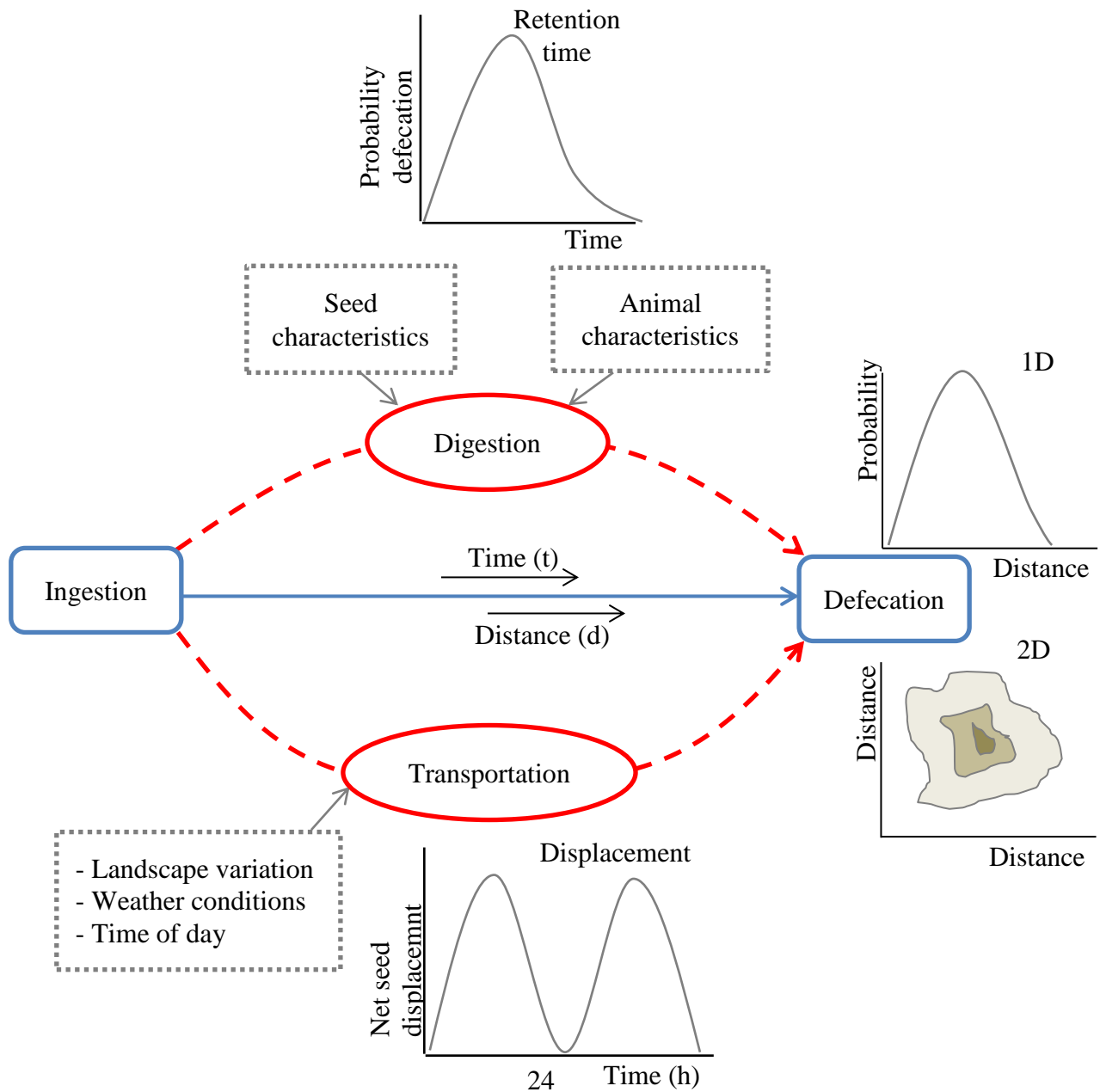

Figure 2. Conceptual model of seed dispersal by mallards.

4. Which (combination of) model(s) is best suited for seed dispersal by mallards?

Mallards are migratory birds. The combination of long retention times and long-distance flights during migration suggests an important role of mallards for long-distance dispersal (Mueller & van der Valk 2002). However, there are also reports that birds empty their digestive tract previous to migration, decreasing the amount of seeds dispersed by long-distances (Figuerola & Green 2002). Therefore mallards probably have a larger share in short-distance dispersal (Traveset et al. 2014). For this case study, long-distance dispersal by migration is left out of account and only local movements of mallards are considered.

The goal was to design a realistic model that predicts how many seeds are dispersed how far and to which locations by mallards (Kleyheeg, personal communication). By applying a theoretical model to an empirical study, key factors and their relative importance can be identified.

The data from Kleyheeg's study do not contain the source and end points per dispersed seed. From the feeding trials, digestion can be parameterized as retention time, percentage of intact gut passage and viability. Retention time is the time between ingestion and defecation, and thus gives a timeframe for the dispersal event from the source to end point. From the GPS tracking data, the distance, speed, direction and frequency of mallard movements can be derived. From these, net seed displacement (net distance from source against time) can be calculated. To predict how far seeds are dispersed, net seed displacement can be combined with retention times to calculate a distance distribution. To include a quantification of the number of viable seeds that is dispersed, percentage of intact gut passage and viability can be added to generate a phenomenological dispersal curve that gives more information on possible future recruitment rates.

In order to identify key factors and their interactions and to be able to generalize to other systems, the amount of and complexity in variables should be minimalized (Nathan & Casagrandi 2004). The raw data of the mallard tracking experiment suggest clear diurnal behavior with mallards going to a resting site during the day and to a nearby ditch or pool to forage during the night (Kleyheeg, personal communication). This non-randomness in space and time can strongly affect the predicted dispersal curve (Westcott et al. 2005). A mechanistic dispersal model based on retention time and seed displacement alone is not sufficient in the case of such non-random seed distribution. Displacement must be spatially explicit in order to not underestimate the aggregation of seeds (Russo et al. 2006). If we are to understand the processes of zoochorous dispersal, we must study why the animal moves instead of simply where it goes. Kleyheeg tracked mallards in different habitats to study the effect of landscape variation on seed dispersal. These effects can be predicted with a spatially explicit mechanistic model, incorporating landscape structure and animal movement parameters based on observations. To build such an individual-based spatially explicit simulation model requires several steps.

Firstly, I suggest showing the distance distribution and dispersal kernel with phenomenological models. Secondly, the various studied landscapes can be analyzed to incorporate landscape parameters (Will & Tackenberg et al. 2008) such as type of vegetation, wetland patchiness, percentage of plant cover, and number, size and position of attractive resting

and foraging sites. Various landscape structures can then be simulated in a matrix model based on these parameters (Jeffers 1982). Thirdly, mallard movement can be simulated in response to landscape structure. Mallard movement parameters can be based on the collected data to represent its response to landscape and time of day (Bartuszevige & Gorchov (2006). One could model the individual's reaction to specific landscape features to derive 'decision rules' from observations to predict the disperser's movements in any given landscape (Levey et al. 2005; 2008). To illustrate the seed dispersion pattern (Box 1) of intact seeds from these simulated mallard movements, retention time and percentage of intact gut passage should be added to the model. To finish the modelling approach, the mechanistic model must be evaluated. The parameter estimations and predicted seed dispersion patterns in simulated landscapes need to be validated with 'real' data from which the parameters where not initially derived. A likelihood analysis can compare alternative predictions or parameter values and calculate a measure for the reliability of the model and its separate processes (Canham & Uriarte 2006).

This individual based, spatially explicit simulation model provides the opportunity to predict seed dispersal by mallards in various landscape structures. The possibility to extrapolate to other landscapes exists because the simulated animal movements in the model are constructed of parameters that describe the reaction to habitat features instead of an entire landscape (Levey et al. 2005). Theoretically, such a model could be extrapolated to landscapes on larger scales than the ones that data was collected from (Levey et al. 2005), though Westcott & Graham (2000) state that the movement complexity (D) of the disperser should be tested to be scale independent in order to allow scaling up of animal movement. Here, in seed dispersal by mallards, simulating dispersal on a larger scale would mean that different mechanisms of movement such as migration would play a role. Migration works with different 'decision rules' than local movements and should therefore need other data to allow for parameterization.

The model described here is a mechanistic model, but with parameters based on phenomenological models of collected data. This points out that models are not necessarily one or the other, but that each case to be modelled is unique and should be regarded as such. A modelling approach should always be fitted to the goal of the study for which it is needed. A model can therefore never address the question at hand properly when the objectives are not clearly stated. Where the words to describe a problem end, mathematical models continue.

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