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Seed dispersal distributions resulting from landscape-dependent daily movement behaviour of a key vector species, *Anas platyrhynchos*

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Summary

1. Dispersal via animals (zoochory) is a primary mechanism for seed exchange between habitat patches. Recent studies have established that many plant species can survive waterbird gut passage. To quantify the patterns and consequences of waterbird-mediated dispersal, information on ingestion and gut passage must be combined with bird movement data. Such analysis has recently revealed seed dispersal kernels by migrating waterbirds. However, since many waterbird populations are largely resident, and migrating populations spend only a minor part of the main dispersal season (autumn–winter) on active migration, daily regional-scale movements probably cause more frequent dispersal.

2. We synthesized high-resolution empirical data on landscape-scale movements and seed gut passage times in a key disperser species, the mallard (*Anas platyrhynchos*), using a spatially explicit, mechanistic model to quantify dispersal distributions resulting from daily autumn–winter movements. We evaluated how landscape composition and seed traits affect these dispersal patterns.

3. The model indicates that mallards generate highly clumped seed deposition patterns, dispersing seeds primarily between core areas used for foraging and resting. Approximately 34% of all dispersed seeds are transported to communal roost areas, which may function as reservoirs for mallard-dispersed species, and 7% are transported between foraging areas. Landscape-dependent movement patterns strongly affect the dispersal distributions, resulting in multi-modal dispersal kernels, with dispersal distances increasing with fragmentation of freshwater foraging habitat. Seed size-related gut retention times determine the proportion of seeds being dispersed away from the ingestion area, with larger seeds (20 mm³) having a 8–10% higher potential for long-distance dispersal than smaller seeds (0·2 mm³), if surviving gut passage. However, twice as many small seeds will finally accomplish long-distance dispersal due to their higher gut passage survival.

4. *Synthesis.* Firstly, this study reveals how seed dispersal patterns resulting from daily waterfowl movements are shaped by landscape-dependent differences in movement patterns. Secondly, seed survival appears more important than retention time in determining the scale of long-distance dispersal by non-migrating mallards. We conclude that the frequent flights of staging waterbirds result in directed dispersal over distances inversely related to wetland availability, indicating that they maintain landscape connectivity across a range from wet to increasingly dry landscapes.

Key-words: *Anas platyrhynchos*, aquatic plants, dabbling ducks, dispersal, endozoochory, freshwater marshes, habitat fragmentation, landscape configuration, mallard, terrestrial plants

Introduction

The spatial pattern of seed deposition after dispersal forms a template for plant recruitment and subsequent ecological and evolutionary processes (Nathan & Muller-Landau 2000; Fraaije *et al.* 2015a,b) and is therefore of critical importance for plants. Seed transportation by animals (zoochory) that use the same habitat types as the adult plants may be expected to be an effective dispersal strategy, increasing the success rate of recruitment (Howe & Smallwood 1982; Schupp 1993;

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Wenny 2001). However, the extent to which this occurs in the field is difficult to assess, because dispersal by animals is notoriously difficult to quantify. Firstly, animal behaviour is often quite variable and involves long-distance movements (Swingland & Greenwood 1983; Patterson *et al.* 2008). Secondly, the transport of seeds depends strongly on seed traits and is therefore also highly variable (Howe & Smallwood 1982). If ingested, seeds have to pass the animal's digestive tract, which affects their survival and duration of transportation (retention time), depending on traits like seed volume and seed coat thickness (Janzen 1984; Soons *et al.* 2008; Reynolds & Cumming 2016). Therefore, mechanistic models are increasingly being used to predict seed dispersal distributions and to evaluate the consequences of zoochorous dispersal, despite the challenging implementation of the complex interplay between plant and animal traits that need to be obtained from field studies and lab experiments (Russo, Portnoy & Augspurger 2006; Will & Tackenberg 2008; Kleyheeg 2015).

Waterbirds have long been assumed to be important dispersal vectors for wetland plants (Darwin 1859; van Leeuwen *et al.* 2012), and recently also for more terrestrial plant species (Kleyheeg, Klaassen & Soons 2016; Soons *et al.* 2016a). Internal (endozoochorous) dispersal by waterbirds has been identified as an important mechanism for dispersal between isolated wetland areas (Amezaga, Santamaría & Green 2002; Green, Figuerola & Sánchez 2002). Particularly mallards (*Anas platyrhynchos*), the most abundant duck species worldwide with a large geographic distribution (del Hoyo, Elliot & Carbot 1992), are likely to significantly shape the dispersal distributions of plant species. Seeds are an important component of the mallard diet, including a wide range of species (Brochet *et al.* 2011; Kleyheeg, Klaassen & Soons 2016; Soons *et al.* 2016a), most of which have the potential to survive digestive tract passage (Charalambidou & Santamaría 2005; van Leeuwen *et al.* 2012). At the same time, mallards are highly mobile on the landscape scale (Sauter *et al.* 2012; Bengtsson *et al.* 2014; Kleyheeg *et al.* 2017) and capable of migrating over long distances (Krementz, Asante & Naylor 2012), providing ample opportunity for long-distance seed dispersal (Viana *et al.* 2013a). However, their opportunistic habitat use, nocturnal activity and rapid displacements have made it difficult to empirically quantify their contribution to seed dispersal in the field.

Mechanistic seed dispersal models have been applied to obtain a better understanding of the role of mallards in plant ecology. Current estimations of dispersal distances following transportation by mallards and other waterbirds are based on simple models, often identifying only maximum dispersal distances as estimated from gut retention time and flight speed during non-stop unidirectional flights directly after seed ingestion (e.g. Charalambidou, Santamaría & Langevoord 2003; Soons *et al.* 2008; Kleyheeg *et al.* 2015; but see Viana *et al.* 2013a). Indeed, long-distance dispersal (LDD) is of disproportional importance for spatial plant population dynamics (Cain, Milligan & Strand 2000; Nathan 2006), and migratory mallards and teal (*A. crecca*) were shown able to contribute

substantially to LDD by transporting seeds over distances up to 1582 km (Viana *et al.* 2013b). However, during the period that ripe plant seeds are available to waterbirds (autumn–winter) migratory flights are relatively rare events, typically undertaken on fewer than 10 days per autumn (Gaidet *et al.* 2010), and successful LDD events following migration are probably exceedingly rare (Clausen *et al.* 2002; Viana *et al.* 2016a). Daily, non-migratory waterbird movements in autumn and winter result in shorter, but much more frequent dispersal events, and may result in a higher probability of dispersal towards suitable sites with similar environmental (e.g. climatic) conditions.

Here, we quantify the dispersal patterns of seeds transported internally by mallards during their frequent daily movements in the autumn–winter period, taking advantage of the detailed information which has recently become available on all essential components of this dispersal mechanism: (i) the range of seed species ingested (Kleyheeg, Klaassen & Soons 2016; Soons *et al.* 2016a); (ii) empirically determined gut passage times and survival rates across a range of seed traits (Soons *et al.* 2008; van Leeuwen *et al.* 2012; Kleyheeg *et al.* 2015); and (iii) mallard movement data from high-resolution GPS tracks across a range of landscapes (Kleyheeg 2015). We combined these components in a single, mechanistic, spatially explicit model to analyse seed dispersal patterns. We specifically evaluated the relative contributions of landscape-dependent mallard movement behaviour and of seed volume, the latter being consistently reported as one of the most relevant seed traits determining gut passage time and survival (Figuerola & Green 2002; Soons *et al.* 2008; van Leeuwen *et al.* 2012; Kleyheeg *et al.* 2015), in establishing these patterns.

Materials and methods

We developed a spatially explicit, mechanistic model to identify seed deposition patterns following endozoochorous seed dispersal by mallards. This model combines information on all components of the endozoochorous dispersal process (ingestion, gut passage and movement) to simulate the spatial dispersal patterns. Using these model simulations, we explored the effects of variability in landscape configuration and seed volume on the resulting seed dispersal distributions. The model consists of two parts: (i) a seed part, simulating the ingestion, gut passage and excretion of plant seeds, and (ii) a bird part, describing mallard movements across landscapes. These two parts were integrated to obtain spatiotemporal patterns in seed dispersal distributions by coupling the time steps of the seed part of the model to the time and corresponding location of the GPS fixes of the mallard tracks.

STUDY SYSTEM

Mallards are the world's most abundant dabbling duck species, with an estimated 19 million individuals spread over most of the Northern Hemisphere (del Hoyo, Elliot & Carbot 1992; Wetlands International 2016). As opportunistic habitat generalists, they occupy a wide range of habitats from large natural wetlands to dry landscapes with few patches of open water, to cities and urban parks (del Hoyo, Elliot & Carbot 1992; Snow, Perrins & Gillmor 1998). They also feed highly opportunistically, seasonally shifting their diet from animal-based in

spring and summer to seed-based diet in autumn and winter, when ripe seeds are most abundantly available (Snow, Perrins & Gillmor 1998). Through GPS telemetry, we collected data on the daily movements of mallard at four localities in the Netherlands (Oud Alblas, Terra Nova, Juliusput and Enterveen; Kleyheeg *et al.* 2017). The landscapes surrounding these localities varied in their availability of freshwater habitat from very high to relatively low, representative for the range of conditions commonly found across the temperate zone. Oud Alblas is a wet peat area with a year-round high water-table and many interconnected ponds and ditches, representative for semi-natural and partly drained areas with high connectivity of aquatic habitat. Enterveen is the other extreme, a sandy area with few, isolated ponds and canals, representative for relatively dry, fragmented landscapes. Terra Nova and Juliusput are intermediate sites, with the former resembling Oud Alblas but including a large lake, and the latter having more scattered water bodies. The spatial scale of mallard movements (flight distances and home range size) was strongly inversely related to the availability of freshwater habitat in the landscape, with implications for their role in biotic connectivity of fragmented habitats (Kleyheeg *et al.* 2017). More details on the localities, their relation to other European wetlands, and the effects of their configuration on mallard movements can be found in Kleyheeg *et al.* (2017).

THE MODEL: SEED PART (INGESTION AND GUT PASSAGE)

Mallards have a clear circadian activity pattern, consisting of mainly resting during the day at a roost site and foraging primarily during the night at one or several foraging areas (Bengtsson *et al.* 2014; Kleyheeg *et al.* 2017). In the model, we assumed that seed intake occurred only during the night and only when mallards were away from the day roost and not in flight (i.e. only when present at foraging areas). During these periods, we assumed that the mallards were continuously foraging. Although some information is available on seed intake rates under lab conditions (Klaassen, Nolet & De Fouw 2006; van Dijk *et al.* 2012), it is difficult to estimate the number of seeds actually consumed by mallards in the field (and thus how many seeds are potentially dispersed). We therefore designed the model to estimate the spatial probability distribution of seed deposition rather than the absolute numbers, and assumed a constant intake rate of 1000 seeds h^{-1} during foraging periods to facilitate interpretation of the results. The number of ingested seeds was multiplied by an empirically identified size-dependent seed survival probability (eqn 2) to take into account relative differences in the proportion of dispersed seeds between differently sized seed species, following:

$$I = c \cdot s(V) \cdot dt \qquad \text{eqn 1}$$

where I is the number of ingested seeds per time step that will eventually survive digestion and be excreted, c is the constant intake rate (seeds h^{-1}), $s(V)$ is a seed volume-dependent survival probability, and dt is the time step (0·25 h, which equals the GPS interval, see below). The relation between survival (the proportion of seeds passing through the digestive tract intact) and seed volume was based on a logarithmic function fitted on seed retrieval data from a feeding experiment with 20 differently sized seed species fed to mallards (Soons *et al.* 2008; see Fig. S1, Supporting Information):

$$s(V) = 0·2121 - 0·039 \cdot \log V \qquad \text{eqn 2}$$

where V is the volume of an individual seed in mm³. This results in survival probabilities between approximately 30% for small seeds and 3% for very large seeds within the range of seed volumes that have

been found in the mallard diet (Soons *et al.* 2016a). Seed excretion (E) per time step was calculated based on the 48-h history of seed intake and an excretion probability as a function of time after intake:

$$E = \int_{-48}^{0} (I(t) \cdot \Gamma(|t|; k, \theta(V))) dt \qquad \text{eqn 3}$$

where $I(t)$ is the rate of intake of seeds (that will eventually pass the digestive tract intact) during time step t, and $\Gamma(|t|; k, \theta(V))$ is the gut passage time drawn from a gamma distribution. The gamma distribution sums to one and we assumed that all surviving seeds passed the digestive tract within 48 h, so that in our model the surviving seeds were excreted in the subsequent time steps after intake (up to 48 h) in proportions determined by the gamma distribution. The 48-h integral was approximated using discrete time steps equal to the time interval between the GPS positions. The temporal pattern of gut passage is variable between seed species, between and within individual waterbirds, and between studies (van Leeuwen *et al.* 2012), but generally, the first seeds are excreted shortly after ingestion, with peak excretion within a few hours and a fat tail. We used a gamma distribution because it is one of the most frequently used probability distributions to characterize retention times and fits at least as accurately as log-normal and Weibull distributions (Viana, Santamaría & Figuerola 2016b). The two parameters of the gamma distribution (shape k and rate θ) were estimated from cumulative empirical distributions of differently sized seeds of 18 plant species passing mallard guts (extracted from Soons *et al.* 2008; Fig. S2). Since seeds in Soons *et al.* were retrieved at discrete time intervals, we fitted the distributions while explicitly accounting for the interval-censored nature of the data using the R-package *fitdistrplus* (Delignette-Muller & Dutang 2015). Gut passage time showed a positive correlation with seed volume, which was best estimated by a constant shape parameter ($k = 2·7$, computed by minimizing the mean D-statistic of Kolmogorov–Smirnov tests for the 18 species, see Fig. S2) and a varying rate parameter following a logarithmic function of seed volume (linear regression: $P = 0·022$, $R^2 = 0·29$):

$$\theta(V) = 0·5646 - 0·042 \cdot \log V \qquad \text{eqn 4}$$

Increasing the rate parameter relative to the shape parameter results in a more peaked curve at a shorter retention time. This translates to peak excretion of very small seeds at around 2 h after ingestion and around 7 h after ingestion for the largest seeds in the mallard diet.

THE MODEL: BIRD PART (MALLARD MOVEMENTS)

To best approach a realistic spatial pattern of seed deposition, we used high-resolution movement trajectories of mallards from a GPS tracking study at the localities described above during autumn–winter 2012–2013 (Kleyheeg *et al.* 2017). We used GPS tracks of five individual mallards in each of the four landscapes. We restricted the 20 individual trajectories to 9 days, corresponding to the length of the shortest track. GPS positions had been recorded at a 15-min interval ($\pm$ GPS logger inaccuracy). We assumed there were no seeds inside the mallard's digestive tract at the start of the simulation, as we did not have GPS positions of the 48 h history from all mallards prior to the 9-day simulation period. This means that excretion started one time step after the first arrival of an individual at a foraging site. Similarly, seeds that were still inside the mallard at the end of the simulation were not taken into account in the calculation of the dispersal distances. To create spatial maps of seed deposition patterns, the probability of mallard presence between GPS fixes was estimated using Brownian bridges, an interpolation technique for estimating the movement path of an

animal based on the properties of a conditional random walk between successive locations (Horne *et al.* 2007). Establishing a Brownian bridge between two locations requires a mean GPS error and a Brownian motion variance. The GPS error was estimated at 10 m (based on 24·081 positions of three loggers fixed to a pole). The Brownian motion variance was estimated dynamically for different behaviours (Kranstauber *et al.* 2012; Kranstauber, Safi & Bartumeus 2014). We separated the data into flight (distance between GPS fixes >100 m) and non-flight (<100 m) behaviour and assigned a constant Brownian motion variance to each. For non-flight data, the Brownian motion variance was estimated using the classical leave-one-out approach assuming a purely Brownian random walk and homogeneous movement between two locations, as described in Horne *et al.* (2007). This way, the motion variance was found by using a window of three consecutive GPS fixes and estimating the second GPS fix based on the first and last GPS fix and a Brownian random walk between these points with a motion variance that is to be optimized. This optimization was done for all possible windows of three consecutive GPS fixes and maximizing the likelihood of predicting the left out GPS fixes correctly. This Brownian motion variance yielded 55 m^2 at Oud Alblas, 56 m^2 at Terra Nova and Juliusput, and 52 m^2 at Enterveen. For flight data, we selected all flights where one location was sampled during the flight from one core area to another. In this way sequences of three GPS points were created (i.e. core area A, flight and core area B) from which a single Brownian motion variance was estimated using the leave-one-out approach (Horne *et al.* 2007). The Brownian motion variance during flight was 200 m^2 at Oud Alblas, 260 m^2 at Terra Nova, 280 m^2 at Juliusput and 330 m^2 at Enterveen. We also calculated seed dispersal kernels using the measured GPS tracks. As opposed to the seed deposition probability maps, we based the dispersal kernels on actual dispersal distances (without Brownian Bridges). This was done to keep it mathematically feasible to track the ingestion and excretion locations of all individual seeds.

SIMULATIONS: LANDSCAPE AND SEED VOLUME EFFECTS

To assess the effect of landscape configuration on seed deposition patterns, we ran dispersal simulations for all four study landscapes. We linked the spatial behaviour of mallards (bird part) to seed deposition (seed part) by calculating the number of excreted seeds for each recorded GPS position of a mallard based on its history of seed ingestion in the previous 48 h (eqn 3). For all seeds excreted at any time step, we calculated the distance to the site of their ingestion to establish seed dispersal distributions.

To assess the effect of seed volume on seed deposition patterns, we performed model runs for three seed volumes: $V = 0·2$ mm^3, $V = 2$ mm^3 and $V = 20$ mm^3, corresponding to the lower, median and higher ranges of the volume distribution of seeds in the mallard diet (Soons *et al.* 2016a). We described differences in seed dispersal distributions (deposition patterns and dispersal distances) and specifically analysed the proportion of seeds dispersed away from the site of ingestion using chi-square tests.

All model simulations were run in Matlab version R2014b.

## Results

SEED DISPERSAL PATTERNS

The mallards foraged in distinct patches in all landscapes, resulting in highly spatially concentrated seed intake, centred around shorelines of waterbodies and some agricultural fields (Fig. 1 and Fig. S3). Seed survival, retention times and movement activity of mallards together determined the subsequent seed deposition patterns. Most seed excretion occurred within foraging and roosting areas across the entire home range of the mallards, and several orders of magnitude less between core areas (Fig. 1 and Fig. S3). Due to the rapid gut passage and relatively long time spent in each foraging area, seeds excreted in the foraging areas had usually been ingested in the same area several hours earlier (Fig. 2). On average, c. 40% of the ingested seeds were excreted in another core area than where they were ingested, depending on seed volume. Model simulations for seed volumes ranging from 0·2 to 20 mm^3 showed that this 'LDD' (dispersal between core areas) occurred on average in 35·6% (range 33·0–40·9%) of the smallest surviving seeds, compared to 44·9% (range 41·8–51·2%) of the largest surviving seeds. However, due to the lower gut passage survival of large seeds, a much lower proportion of large seeds initially ingested (including those that do not pass the digestive tract intact) is dispersed away from the area of ingestion than small seeds. The absolute number decreased exponentially with volume, ultimately resulting in 2·3 times less LDD for seeds of 20 mm^3 than for seeds of 0·2 mm^3, with little variation between landscapes (range 2·2–2·4). Most of the seeds dispersed away from the site of ingestion were dispersed to the roost: 22·4–35·0% (small seeds) and 28·4–44·3% (large seeds) were excreted at the main roost (Fig. 2). The seed size most ingested by mallards is around 2 mm^3, and for surviving seeds of this size class, LDD occurred in 39·8% on average. Between 25·1% and 39·2% were excreted at the main roost. The highest percentage of excreted seeds of 2 mm^3 that were transported to another foraging area was found at Juliusput (12·3%), while this percentage was the lowest at Oud Alblas (3·1%, Fig. 2). However, the proportion of seeds dispersed within or outside the areas of ingestion did not differ significantly between seed volumes ($P > 0·71$ for each locality) or between localities ($P > 0·52$ for each of the three tested seed volumes).

DISPERSAL DISTANCE DISTRIBUTIONS

Since most seeds were deposited at the foraging and roost core areas (Fig. 2), and rarely *en route* (Fig. 1), the distances between these areas strongly affected the dispersal kernels (Fig. 3). Accordingly, dispersal distances were longest in the driest landscape where wetland areas were most scattered (up to c. 8000 m at Enterveen) and lowest in the wettest landscape where wetland habitat was most abundant (up to c. 1600 m at Oud Alblas; Fig. 3). The dispersal distances were clearly related to the home range sizes of the mallards across the varying landscapes (Fig. 4). The higher probability of larger seeds to be dispersed away from their original patch resulted in marginally longer mean dispersal distances of large seeds (Table 1, Fig. S4).

To evaluate how gut passage time affects dispersal distances at the landscape-scale, we analysed the net
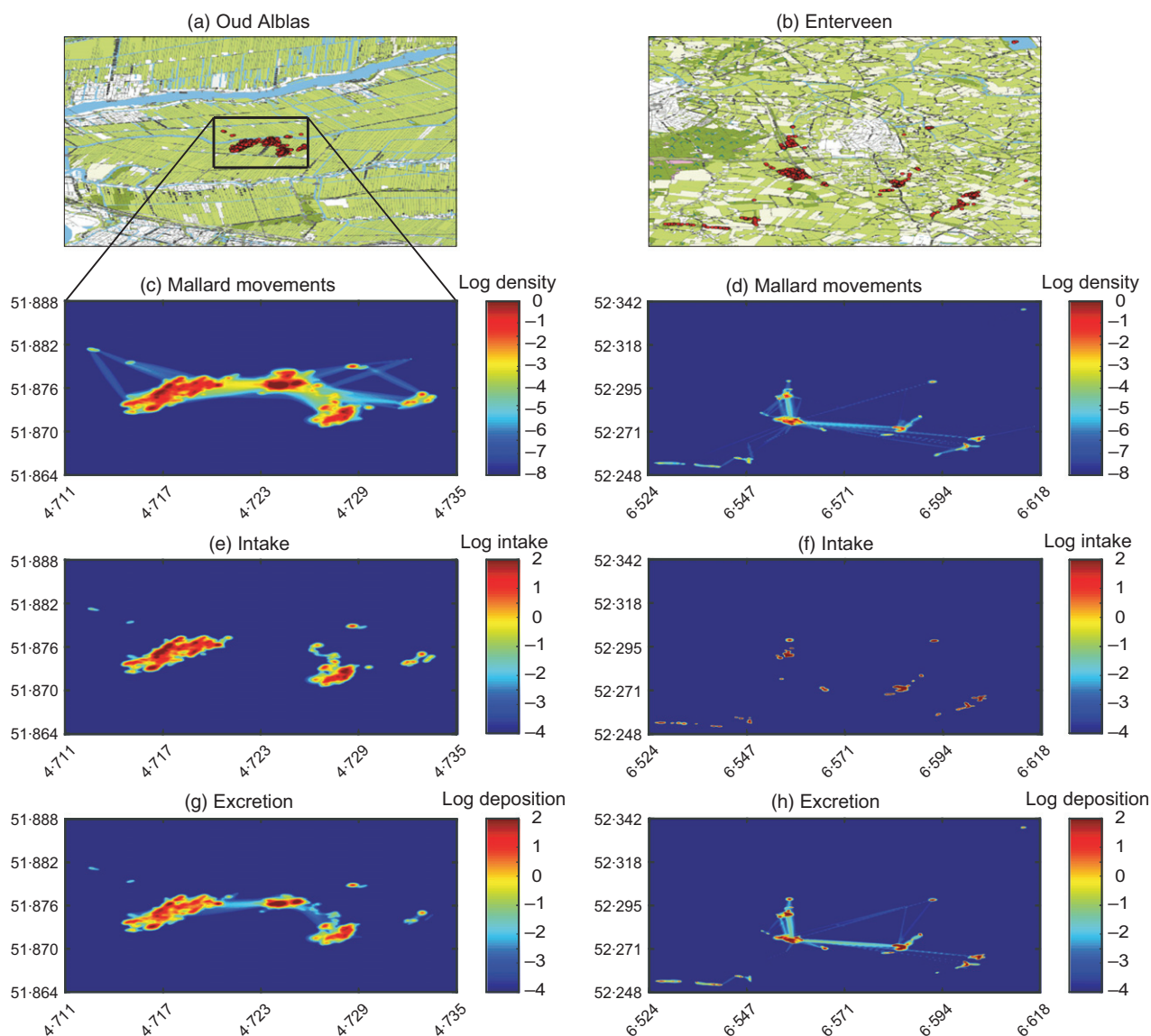
Fig. 1. Landscape use by mallards (based on the density of GPS positions with Brownian bridges) and corresponding spatial patterns of seed ingestion and excretion at Oud Alblas (left; homogeneous, wet landscape) and Enterveen (right; fragmented, dry landscape). Graphs are based on 9-day tracks of five mallards in each area, feeding on seeds at the foraging sites at night and spending the day at a communal roost. Upper panels (maps) are of the same scale. Plots for the intermediate landscapes of Terra Nova and Juliusput are in Fig. S3. [Colour figure can be viewed at wileyonlinelibrary.com]

displacement of mallards over time and compared this with realized dispersal distances over gut passage time (Fig. 3). The spatial behaviour of mallards showed a clear diel pattern with repeated visits to the same core areas for foraging and roosting. Therefore, at any time of the day, mallards were likely to be at the same area as where they were 24 h earlier (either at the foraging or roosting site). Conversely, at 12-h intervals, mallards had most likely switched between areas, from foraging to roosting or vice versa. Therefore, potential dispersal distances increased only for gut passage times up to 12 h. The median dispersal distance of seeds retained in the guts for 12 h was between 600 m (Oud Alblas) and 3000 m (Enterveen). Gut passage times from 12 to 24 h led to decreasing dispersal distances and an increasing probability

for seeds to be dispersed back to the area where they had been ingested. From 24 to 48 h after ingestion this pattern repeated itself (Fig. 3).

Discussion

Our results show that the daily movement behaviour of mallards during the seed dispersal period, which is governed by landscape configuration, and the generally regular circadian pattern of core area use by mallards, strongly determine the spatial deposition patterns of the seeds they disperse. While seed volume is a main determinant of gut passage survival and hence of the numbers of viable seeds dispersed, it has little effect on the shape of the seed dispersal kernels. Through
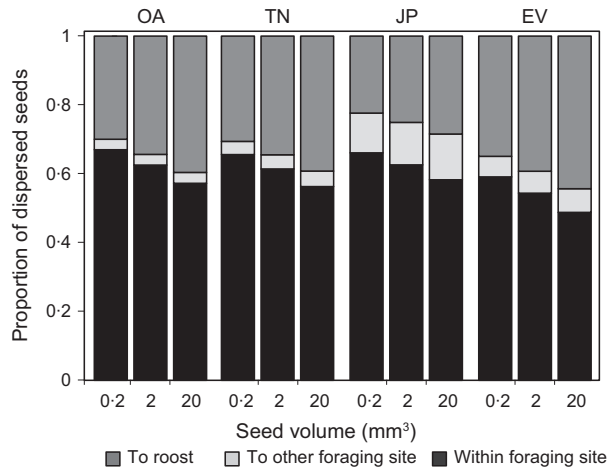
Fig. 2. The proportion of seeds dispersed by five mallards per landscape over 9 days, towards either the roost area (grey), another foraging area (light grey) or to the same foraging area as where the seeds were ingested (dark grey). The proportions are based on model runs for differently sized seeds (0·2, 2 and 20 mm^3) at Oud Alblas (OA), Terra Nova (TN), Juliusput (JP) and Enterveen (EV), ordered from homogeneous (wet) to fragmented landscapes. The proportion of seeds excreted during flight is very low (Fig. 1) and not shown here.

its effect on gut retention time, and considering only seeds that survived gut passage, larger seeds have a slightly higher probability to be dispersed away from the area of ingestion.

DISPERSAL PATTERNS AND DISTRIBUTIONS

The dispersal kernels resulting from mallard-mediated dispersal do not have the typical shapes known from hydrochory or anemochory, or from estimations of LDD by migratory waterbirds, which are characterized by a monotonically decreasing dispersal probability over distance. Instead, the kernels are multi-modal, connecting a number of frequently visited core areas and the in-between matrix within the extent of the mallard's home range. During autumn–winter, the home range size of mallards varies greatly between individuals, from less than 0·1 km^2 to more than 30 km^2 (Legagneux *et al.* 2009; Sauter *et al.* 2012; Kleyheeg *et al.* 2017), suggesting that mallards maintain the connectivity between core areas over potentially large distances, depending on the landscape.

The consistency in the use of these relatively well-defined core areas results in highly clumped seed deposition in and around wetland habitat. Earlier studies on mallard habitat use show that mallards have a preference for shoreline habitat, both aquatic and terrestrial (Sauter *et al.* 2012; Bengtsson *et al.* 2014; Kleyheeg *et al.* 2017). This indicates a high potential for directed dispersal for a wide range of plant species typical for aquatic, open water as well as shoreline and more terrestrial habitats (such as riparian zones, terrestrializing fens, banks, etc.). Indeed, this habitat range is also reflected by the species composition of plant seeds found in the mallard diet (Soons *et al.* 2016a). Mallards may thus play an equally important role in connecting plant populations of aquatic and wetland habitats, as of more terrestrial systems,

such as the dispersal-limited successional stages following colonization of open water (e.g. species-rich floating fens; Sarneel *et al.* 2011).

Mallards and many other waterbird species use communal roost sites (e.g. Tamisier 1978). Assuming that mallards ingest seeds only (or mainly) at the foraging sites, combined with few switches between foraging sites during the night, our model predicts that mallards disperse seeds disproportionally towards the daytime roost. This particularly applies to large seeds. The resulting asymmetric gene flow may result in spatial population dynamics of the dispersed species which resemble a 'mainland-island' system more closely than a network of equal patches (such as the traditional metapopulation; Hanski 1999). This suggests that waterbird roosts may function as a dead end for the dispersed species if habitat conditions at the roost are unfavourable for establishment. In contrast, if species dispersed to the roost encounter suitable conditions, roosts may serve as a 'reservoir' for the population dynamics and biodiversity in the surrounding landscape. From there, mallards sharing foraging areas but using a different roost (and *vice versa*) create a network of dispersal pathways across the landscape. Importantly, such networks may connect foraging and roost sites in different catchments (without hydrological connection), so that in many cases the seeds are dispersed to habitat patches that would be unreachable by hydrochory, and unlikely reached by anemochory. In this way, mallard-mediated dispersal complements other (directed) dispersal modes (Soons *et al.* 2016b). Secondary dispersal by other mechanisms after seed excretion, for example, by water, may lead to even further extension of the final seed shadow.

INTERACTIONS BETWEEN DISPERSAL AND GUT PASSAGE TIME

If seeds are dispersed outside of the area of ingestion, dispersal distances are often relatively high: at Oud Alblas and Enterveen 50% of these seeds were dispersed over more than 600 m and 3000 m respectively. Since plant seeds normally end up close to the mother plant, landscape-scale dispersal by mallards should be considered LDD (i.e. exceeding the threshold of 100 m as suggested by Cain, Milligan & Strand 2000; or 250 m as suggested by Traveset, Heleno & Nogales 2013). Due to the typical fat-tailed dispersal kernels traditionally associated with zoochory (Nathan *et al.* 2008), longer retention times of seeds within animals are often associated with longer dispersal distances. This may be the case for instance for grazing mammals, moving continuously through the landscape (Will & Tackenberg 2008), or for other animals heading in a dominant direction. Similarly, waterbird-mediated dispersal distances during migration, estimated based on an assumed unidirectional flight, range up to few thousands of kilometres for seeds retained in the digestive tract for >24 h (e.g. Soons *et al.* 2008; Viana *et al.* 2013a). In contrast, the cyclic daily movement patterns of non-migratory mallards (Sauter *et al.* 2012; Bengtsson *et al.* 2014; Kleyheeg *et al.* 2017) result in dispersal kernels with the highest median dispersal distances after gut retention of 12 h
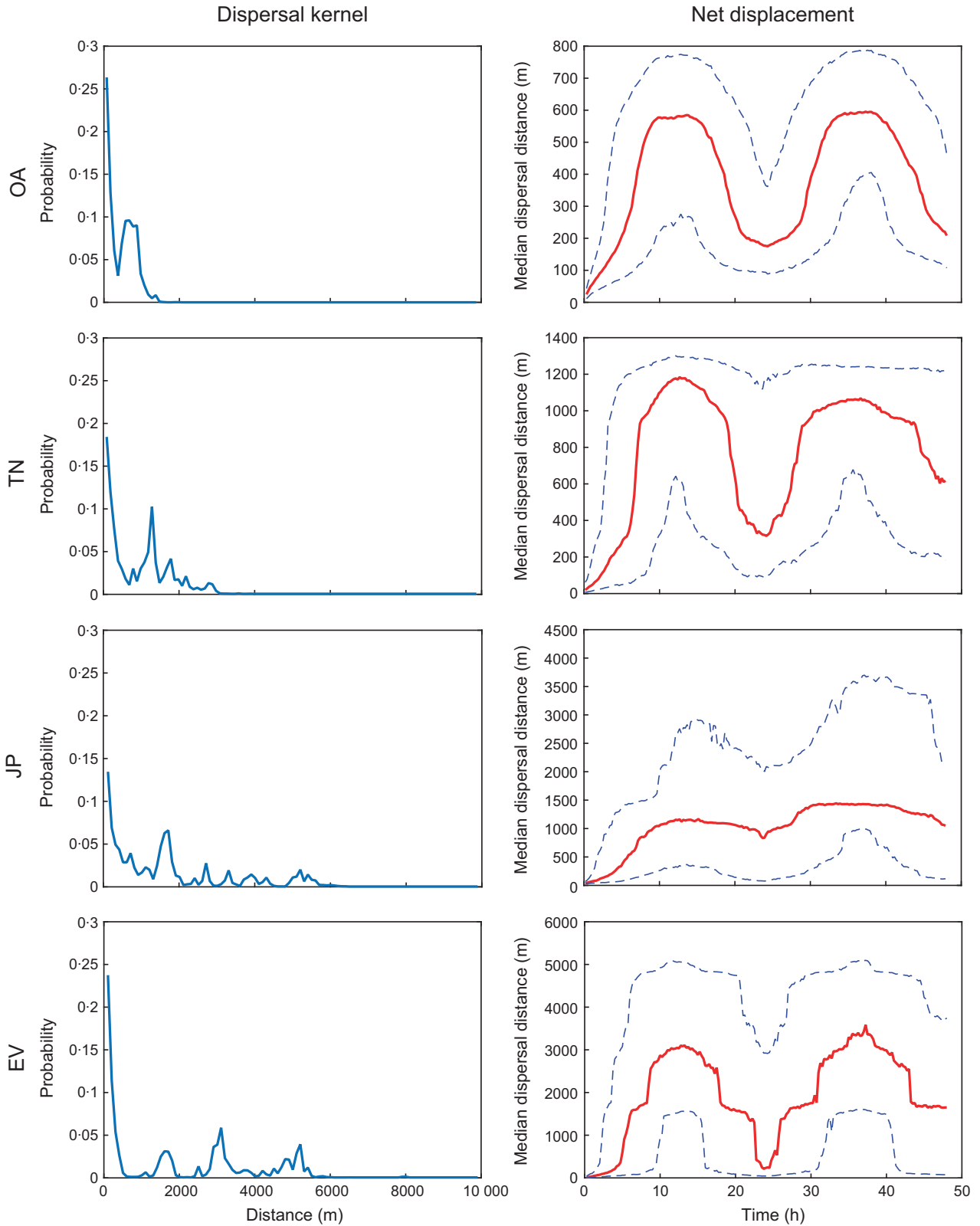
Fig. 3. The left panels show seed dispersal kernels (deposition probability over realized dispersal distance) for seeds of 2 mm^3 (kernels for 0·2 and 20 mm^3 in Fig. S4) in all four study landscapes: Oud Alblas (OA), Terra Nova (TN), Juliusput (JP) and Enterveen (EV), based on five mallards tracked for 9 days in each landscape. Dispersal distances increase and kernels show more peaks towards the drier landscapes where wetland areas are scarcer. The right panels present net dispersal distance over retention time up to 48 h (median ± 5th and 95th percentiles). [Colour figure can be viewed at wileyonlinelibrary.com]
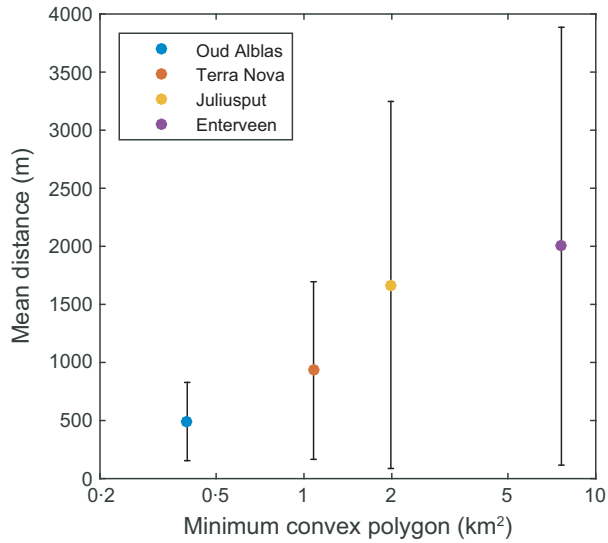
Fig. 4. Relation between mean dispersal distance ($\pm$ SD) of 2·0 mm^3 seeds and the mean home range size of individual mallards expressed as the area of the minimum convex polygon (MCP) around 100% of the GPS positions of individual mallards. MCPs were calculated using the adehabitatHR package (Calenge 2006) in R (R Core Team 2014) and shown earlier to depend on landscape configuration (Kleyheeg *et al.* 2017). [Colour figure can be viewed at wileyonlinelibrary.com]

and decreasing distances for seeds retained longer. Since retention times in mallard guts rarely exceed 12 h (van Leeuwen *et al.* 2012), the positive relation between time and dispersal distance remains for most seeds. However, very long retention times, which are often emphasized as particularly important for extremely LDD during migration (Cain, Milligan & Strand 2000; Nathan 2006; Nathan *et al.* 2008), may actually result in relatively short dispersal distances in the majority of dispersal events, when mallards are not migrating.

The peaks of retention curves for large seeds approach 12 h, which appears the optimal retention time for dispersal away from the original site of ingestion (Fig. 3). However, such long retention comes with the cost that survival is generally very low (<5% according to van Leeuwen *et al.* 2012). To optimize dispersal by waterbirds, plants need to adopt a strategy within the trade-off between retention time and survival by producing seeds that are small enough and
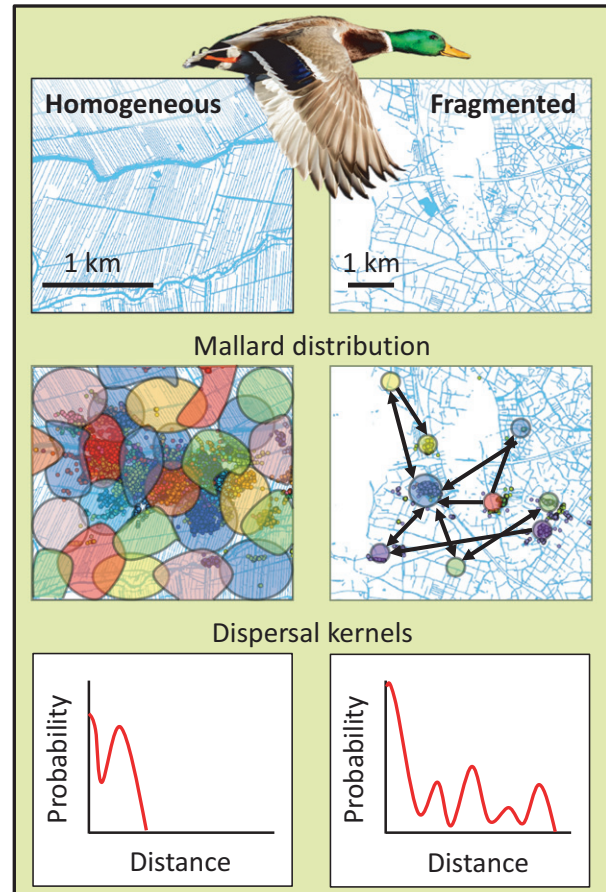
Fig. 5. Conceptual diagram of how mallard movement behaviour and landscape configuration translate into connectivity and seed dispersal distributions across landscapes. In homogeneous landscapes with high wetland availability, mallard abundances are high but home ranges of individual mallards are small, resulting in a 'patchwork' of interconnected areas covering the entire landscape. In fragmented landscapes where wetlands are widely scattered, mallard abundances are lower but home ranges larger, resulting in a 'network' of few but tightly connected areas and strongly multi-modal dispersal distributions. [Colour figure can be viewed at wileyonlinelibrary.com]

with a tough enough seed coat to survive (Kleyheeg 2015; Reynolds & Cumming 2016), but large enough to optimize their retention time. *Sparganium erectum* might represent an example of such an adaptation, as it produces seeds with a

Table 1. Modelled mean dispersal distance (D_{mean}) and the proportion of seeds dispersed away from the site of ingestion (P_{ldd}) for five plant species commonly found in mallard diets. The frequency of occurrence is calculated as the proportion of mallards carrying seeds of the species based on a review of diet studies in Europe (Soons *et al.* 2016a). Model output for mallard-mediated dispersal is provided for the landscape types of Oud Alblas (relatively wet) and Enterveen (relatively dry). Note the contrasting effects of seed volume and location on the dispersal parameters

Plant species	Freq. occur.	Vol. (mm^3)	Oud Alblas		Enterveen	
			D_{mean}	P_{ldd}	D_{mean}	P_{ldd}
Carex aquatilis	0·438	1·77	479 $\pm$ 339	0·372	1973 $\pm$ 1873	0·454
Eleocharis palustris	0·212	2·20	481 $\pm$ 339	0·377	1976 $\pm$ 1874	0·459
Scirpus lacustris	0·222	5·34	487 $\pm$ 338	0·396	1990 $\pm$ 1880	0·479
Carex rostrata	0·290	6·69	489 $\pm$ 337	0·402	1994 $\pm$ 1882	0·485
Empetrum nigrum	0·477	9·94	491 $\pm$ 337	0·412	2001 $\pm$ 1885	0·495

seed coat so thick that it even requires damaging (for instance by digestive forces) to germinate (Soons *et al.* 2008), while the thick seed coat also makes the seeds large enough for relatively long retention (Kleyheeg 2015). It should be noted, however, that the 8–10% lower probability of small seeds (0.2 mm^3) to be dispersed away from the site of ingestion compared to large seeds (20 mm^3) is more than compensated by their 2.9 times higher gut passage survival probability (eqn 2).

FUTURE DIRECTIONS

We here aimed to identify the dispersal distributions of seeds dispersed by mallards in realistic landscapes, using dispersal probability distributions. The next step will be to translate these to actual numbers of seeds dispersed and to estimate the quantitative role of mallards in seed dispersal. This especially requires additional information on seed intake, particularly intake rates and foraging times under natural foraging conditions. Seed intake rates by mallards have been quantified under artificial, controlled conditions (e.g. van Dijk *et al.* 2012) and shown to be seed size-dependent (Fritz, Durant & Guillemain 2001). However, for realistic quantification of seed intake in the field, this should be studied using natural seed densities provided to the animals in a way they also encounter seeds in the field. Therefore, natural seed densities, seed size distributions and mallard microhabitat use should be assessed in the field (Arzel & Elmberg 2004). In our model, we assumed that mallards were continuously foraging when present at foraging sites at night, which is a very generalized and simplified representation of reality (Jorde, Krapu & Crawford 1983; Guillemain, Fritz & Duncan 2002). The use of accelerometry in combination with GPS tracking would be a suitable method for estimation of when and where mallards forage, as accelerometry provides detailed long-term data series of activity patterns (Wilson *et al.* 2006) and can be used to distinguish different types of behaviour, including foraging (e.g. Shamoun-Baranes *et al.* 2012; Kölzsch *et al.* 2016).

CONCLUSIONS AND IMPLICATIONS

This study provides the first spatially explicit identification of seed dispersal patterns generated by waterbird-mediated dispersal, and reveals important characteristics of waterbird daily movement behaviour and landscape configuration. During the autumn and winter season, when most plant seeds are available in the environment, mallard movements result in frequent long-distance seed dispersal with highly clumped deposition patterns at relatively well-defined, discrete areas within individual's home ranges used for foraging and/or roosting. Resulting seed dispersal kernels are clearly multi-modal, as typical for directed dispersal, and reveal dispersal distances at the scale of kilometres. In landscapes with decreasing availability of typical wetland foraging and roosting areas, dispersal distances between core areas increase and mallards maintain the connectivity between these areas for their associated species (Fig. 5). Seed volume largely determines the

probability of viable seed dispersal (as it determines viable gut passage), but in contrast to their important role in wind dispersal and water dispersal, seed traits play a very limited role in determining dispersal distributions following mallard dispersal. However, by modulating retention time, seed volume does co-determine the proportion of seeds that are dispersed away from the area of ingestion. Most seeds are dispersed towards the communal roost site of the mallards, suggesting such areas play a key role in regional plant population dynamics and biodiversity. Yet, a significant proportion of dispersed seeds also ends up in other foraging areas which are likely to consist of similar suitable habitat for establishment for a wide range of plant species. The long-distance, directional dispersal between wetland areas emphasizes the important role of mallards – and potentially other waterbirds – in maintaining regional plant species persistence and biodiversity in a world facing ongoing habitat fragmentation.

Authors' contributions

E.K. and M.B.S. conceived the ideas and led the writing of the manuscript; E.K., J.T., B.A.N. and M.B.S. designed the methodology; E.K. and J.T. collected the data; E.K., J.T. and M.J. analysed the data. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

The movement data used in this study are available on Movebank.org, study name: "Mallard movements in the Netherlands (data from Kleyheeg *et al.* 2017)" and are published in the Movebank Data Repository with DOI: 10.5441/001/1.p9c4nc97 (Kleyheeg *et al.* 2017). Matlab scripts are available in the online Supporting Information.

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Relation between intact gut passage and seed volume.

Fig. S2. Parameter estimation for gamma distribution of seed retention curves.

Fig. S3. Seed deposition patterns for all four localities.

Fig. S4. Dispersal kernels for differently sized seeds in all four localities.

Matlab script 1. Code to calculate Euclidean distance between locations.

Matlab script 2. Code for simulation of seed dispersal kernels.