Research

Migratory strategies of waterbirds shape the continental-scale dispersal of aquatic organisms

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Long distance dispersal (LDD) of propagules is an important determinant of population dynamics, community structuring and biodiversity distribution at landscape, and sometimes continental, scale. Although migratory animals are potential LDD vectors, migratory movement data have never been integrated in estimates of propagule dispersal distances and LDD probability. Here we integrated migratory movement data of two waterbird species (mallard and teal) over two continents (Europe and North America) and gut retention time of different propagules to build a simple mechanistic model of passive dispersal of aquatic plants and zooplankton. Distance and frequency of migratory movements differed both between waterbird species and continents, which in turn resulted in changes in the shapes of propagule dispersal curves. Dispersal distances and the frequency of LDD events (generated by migratory movements) were mainly determined by the disperser species and, to a lesser extent, by the continent. The gut retention time of propagules also exerted a significant effect, which was mediated by the propagule characteristics (e.g. seeds were dispersed farther than *Artemia* cysts). All estimated dispersal curves were skewed towards local-scale dispersal and, although dispersal distances were lower than previous estimates based only on the vector flight speed, had fat tails produced by LDD events that ranged from 230 to 1209 km. Our results suggest that propagule dispersal curves are determined by the migratory strategy of the disperser species, the region (or flyway) through which the disperser population moves, and the propagule characteristics. Waterbirds in particular may frequently link wetlands separated by hundreds of kilometres, contributing to the maintenance of biodiversity and, given the large geographic scale of the dispersal events, to the readjustment of species distributions in the face of climate change.

Dispersal is recognised to be a fundamental process in ecology. Defined as the movement of individuals away from their source location (across population boundaries), it directly affects the survival, growth and reproduction of individual organisms and, in turn, has ecological consequences across the various levels of biological organization. Dispersal promotes gene flow among populations; affects population and community composition, structure and dynamics (Clobert et al. 2001); and controls the dynamics of population and community foundation, persistence and extinction, i.e. the dynamics of metapopulations and metacommunities (Hansky 1991, Leibold et al. 2004). Dispersal capacity is also a key determinant of both the response of organisms to climate change (in addition to local adaptation and persistence; Alsos et al. 2007), and the invasive potential of alien species (Wilson et al. 2009).

Amongst all dispersal events, those involving long distances can have disproportionately strong effects in relation to their characteristic low frequency (long distance dispersal, LDD; Nathan et al. 2008). LDD may have important effects on population structure and species distribution, and may also result in self-accelerating processes of range expansion following major changes in environmental conditions (Clark et al. 1998, Higgins et al. 2003). In spite of their potential importance, little is known about the factors modulating fat-tailed dispersal kernels (highly leptokurtic dispersal curves, i.e. those with relatively high frequencies of LDD; Nathan et al. 2008) produced by animal vectors, largely owing to the methodological challenges involved in their study (Trakhtenbrot et al. 2005, Nathan et al. 2008).

The spatio-temporal patterns of animal movement (disperser movement) represent an important component of passive dispersal and are, therefore, a key determinant of seed shadows (the spatial distribution of dispersed seeds and other propagules; Russo et al. 2006). For example, propagule dispersal curves are affected by the movement behaviour of different disperser species (Holbrook and Smith 2000, Westcott et al. 2005), as well as by spatial variation, such as the configuration of landscapes and the patchiness of resources (Morales and Ellner 2002, Carlo and Morales 2008). Despite its importance, the mechanism and

effectiveness of LDD events mediated by migratory animals, especially birds, remain almost unexplored.

In aquatic ecosystems, waterbirds are important dispersal vectors for aquatic plants and invertebrates, both by external (ectozoochory) and internal (endozoochory) transport of their propagules (Charalambidou and Santamaría 2002, Figuerola and Green 2002, Santamaría and Klaassen 2002, Brochet et al. 2009a). Other animals, such as amphibians (Bohanak and Whiteman 1999), fish (Pollux 2011) and mammals (Vanschoenwinkel et al. 2008, Waterkeyn et al. 2010), as well as wind (Brendonck and Riddoch 1999) and water, may contribute to the passive dispersal of aquatic organisms among nearby wetlands or within hydrologically-connected catchments. Local movements of waterbirds might also contribute to propagule short-scale dispersal, but LDD might depend almost exclusively on migratory movements (at least at the scale of hundreds of kilometres), since during migratory seasons waterbirds often ingest propagules of aquatic organisms, travel regularly over long distances, and land in suitable habitat (water) where propagules can be deposited and germinate or hatch (Brochet et al. 2009b). While local movements may ensure connectivity among local-populations, migratory movements are probably responsible for most directional, long-distance dispersal events.

Several studies have already addressed the dispersal potential of aquatic organisms by combining the gut retention time of propagules with the flight speed of waterbirds (Charalambidou et al. 2003a, Soons et al. 2008). However, they provide estimates of dispersal distances that are based on a particularly weak assumption: that the movement performed by the vector was linear, took place at constant speed, and ended at the exact point of propagule defecation (otherwise the propagule would be defecated on flight, when the chances of landing on adequate habitat are virtually nil, as pointed out by Clausen et al. 2002). As a result,

the dispersal distances they reported are likely to be severely overestimated (albeit still useful as a first approximation; equivalent to the maximum dispersal distance depicted in Fig. 1). Others simulated the effect of the bird migratory strategy on the potential gene spread of aquatic organisms, though the lack of data on propagule gut retention time limited the estimation of propagule dispersal distances and consequent gene flow derived from this model (Lurz et al. 2002).

In this paper, we exemplify how existing information collected to characterise waterbird migration may improve our knowledge of propagule LDD mediated by migratory birds (process 2 in Fig. 1). Although novel technologies such as satellite and GPS tracking devices are now being used to record bird movement, only a handful of individuals of a few waterbird species have been tracked to date with these devices (Gaidet et al. 2010). In contrast, ringing-recovery activity has been applied to virtually all waterbird species occurring in Europe and North America for the last one hundred years, generating several millions of movement-tracking records (Clark et al. 2009). These data can be used to extract species- and population-specific movement patterns. We used ring recoveries from Europe and North America to describe and compare the migratory strategies of two waterbird species known to ingest and transport propagules of aquatic organisms, and investigate their effect on the dispersal curves of four species of aquatic plants and one species of zooplankton. First, we characterized the migration strategies of both waterbird species, as well as its variation between continents (Europe and North America), by analysing their movement distances during migration. Then, we combined these data with information on propagule gut retention time of the five aquatic organisms to model their dispersal distances and investigate the effects of waterbird movement patterns and propagule gut retention time on the characteristics of the estimated dispersal curves.
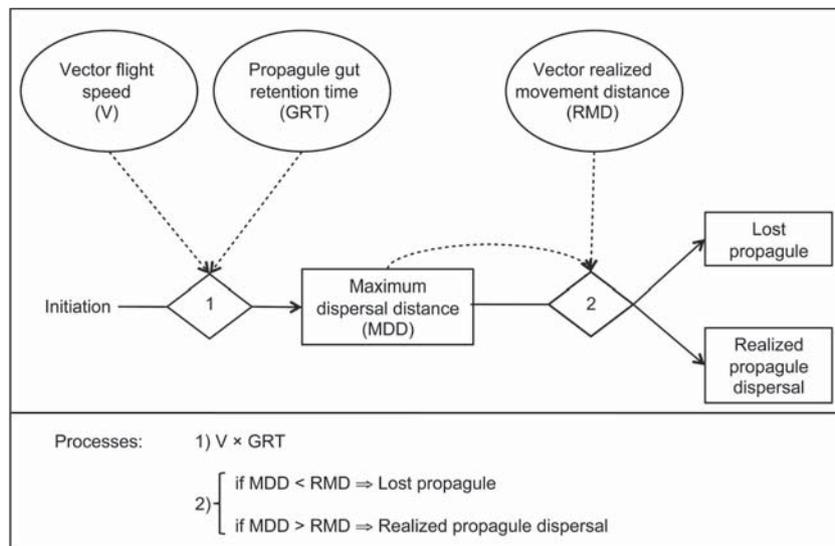

Figure 1. Conceptual model of internal propagule dispersal by migratory birds. It illustrates the method used to incorporate vector movement data into estimates of propagule dispersal distance. Rectangular boxes represent state variables, solid arrows with diamonds represent fluxes (processes are shown in the lower panel) and dashed lines represent relations. Note that, although realized dispersal distances can often be achieved in a flight time well below GRT, the time elapsed between propagule ingestion and initiation of flight may lead to a systematic overestimation of the frequency of realized dispersal.

Methods

Waterbird movement data

We used ringing databases acquired from EURING (European Union for Bird Ringing) and freely provided by the Bird Banding Lab (BBL) of the United States Geological Survey (USGS) to explore the movement patterns of two migratory waterbird species, mallard *Anas platyrhynchos* and teal *Anas crecca*, in Europe and North America. Databases included 91 565 and 878 698 recoveries of mallard; and 35 930 and 28 573 recoveries of teal, in Europe and North America respectively. All ringing and recovery records for which the accuracy exceeded one day (in the case of dates) and/or 10 km (in the case of geographical position) were excluded from the analyses. Proportions of birds recovered dead and alive were not homogeneous across Europe and North America; hence, we decided to use exclusively dead-bird recoveries – since the distribution of recoveries of dead wildfowl (mainly shot by hunters) has been shown to be more widespread and representative than those recaptured alive by ringers (Wernham et al. 2002). Only records from the fall migration season (which include moult migration and juvenile dispersal) were included due to the limited number of recoveries during the spring migration. Finally, to ensure that the vast majority of migratory movements (those > 100 km; see below) consisted of a single displacement bout (and not of indirect movements), we only included in the analyses recoveries in which the time elapsed from ringing to recovery was equal or less than the species' minimum stopover time during the migration season (Supplementary material Appendix 1). According to the available literature (referenced in Supplementary material Appendix 1), a minimum stopover time of 6 d represents a reasonable choice. The ringing data confirmed that choice, since migratory distance and time were not correlated within the 6-d time window, as would be expected if movement bouts accumulated over time (Supplementary material Appendix 1, Table A1). This condition is necessary because the time needed for a bird to make more than one migratory movement (i.e. more than 6 d) far exceeds the maximum gut retention time recorded for propagules (50 h).

The combination of all these restrictions reduced our dataset to 900 and 1741 recoveries of mallard; and 607 and 101 recoveries of teal, in Europe and North America respectively.

Analyses of migratory movements

During migration, waterbirds adopt different migratory strategies, depending on the species and regions where they live, which are expected to influence propagule dispersal curves. In order to characterize the migratory strategies of the two waterbird species and their variation between Europe and North America (the geographical distributions of ring recoveries are shown in Supplementary material Appendix 2), we assessed the effect of species and continent on the frequency and distance of migratory movements (> 100 km) by means of generalized linear models (GLMs).

Distances moved by waterbirds were calculated assuming movement at constant compass direction (along loxodromic paths) between ringing and recovery places, as suggested by Imboden and Imboden (1972).

The frequency of migratory movements relative to the total of movements (local plus migratory) was analyzed by fitting a GLM with a binomial error distribution and a logit link function. The proportion of migratory movements was used as the response variable and the total of movements (sample size) were included as regression weights; species and continent (fixed factors), as well as their interaction, were included as the independent terms. Migratory distances were also fitted by a GLM, but using a negative binomial error distribution with a log link function. In the latter model, the response variable was the migratory distance (in km) and the independent terms were the same as above (species, continent and their interaction). In both models, the significance of effects was assessed by means of likelihood ratio tests (LRT) between the full model and the nested model lacking the tested independent term.

Estimation of dispersal curves

Dispersal curves were estimated by combining data on gut retention time (GRT) of the different propagules with waterbird movement data (the ringing data used in the 'Analysis of migratory movements' section). We used GRT data from two previous studies in which the survival, retention time and viability of propagules of different aquatic organisms was investigated – seeds of three species of *Scirpus* experimentally fed to mallard *Anas platyrhynchos* and/or teal *Anas crecca* (Figuerola et al. 2010), as well as seeds of *Potamogeton pectinatus* and cysts of the crustacean zooplankton *Artemia franciscana* experimentally fed to mallard (Charalambidou et al. 2005). In the latter study, the effect of two types of diet (animal- and seed-based diets) on the gut retention time of seeds and cysts was tested, but no differences were found; therefore all duck individuals were used in this study, independently of the diet to which they were submitted. Briefly, in these experiments ducks accustomed to captivity were force-fed a known number of propagules, and the droppings were then collected at regular 4-h intervals (starting at 1 or 2 h, depending on the experiment) up to 72 h. Retrieved propagules were then hatched or germinated under controlled conditions. Only the GRTs of hatched/germinated propagules were used to estimate dispersal curves, as unviable propagules do not lead to successful dispersal (the GRT distributions of each of the five species are shown in Supplementary material Appendix 3).

To estimate dispersal curves, the GRTs of the different propagules were combined with the movement distances of the vector waterbirds (Fig. 1). For each individual duck used in the GRT experiments, the model ran as follows. 1) One value of propagule GRT was randomly sampled from the frequency distribution of GRTs derived from the empirical data (see above) and multiplied by the average flight speed of the respective vector waterbird species (74.16 km h^{-1} for teal and 73.80 km h^{-1} for mallard; Welham 1994, Bruderer and Boldt 2001, Alerstam et al. 2007), so that a maximum propagule-dispersal distance

(MDD) was calculated. 2) The MDD value was then associated to a realized vector-movement distance (RMD), randomly sampled from the frequency distribution of movement distances of the respective waterbird vector (shown in Fig. 2), derived from the ringing-recovery datasets; if MDD < RMD, the propagule was assumed to be defecated during the flight in inhospitable habitat ('lost propagule'), and no dispersal event occurred; otherwise, the propagule was assumed to be defecated in a waterbody (after its vector concluded the movement bout and landed on it), hence being successfully dispersed (realized propagule dispersal). In this case, the realized dispersal distance corresponded to the RMD. This procedure was repeated 999 times for each individual duck used in the GRT experiments, producing one dispersal curve per individual duck. The realized dispersal curve was obtained by averaging (across the N individuals of the same species used in the GRT experiments; Supplementary material Appendix 4) the number of propagules dispersed to each 10-km distance class. For a comparative purpose, we also estimated the 'maximum dispersal curve' based on the frequency distribution of MDDs (process 1 in Fig. 1), following a procedure analogous to Soons et al. (2008). Maximum dispersal curves assume that waterbirds initiated their movement immediately after ingestion of the propagule. This assumption is however relaxed for realized dispersal curves, because realized waterbird movements could often be covered (assuming an average flight speed) in times well below the GRT. Even so, the time elapsed between propagule ingestion and initiation of flight would tend to result in overestimates of the frequency of realized dispersal.

To compare realized dispersal curves, obtained for each combination of vector species (teal and mallard), continent (Europe and North America), and propagule species (four seed species and one cyst species), we performed pairwise

comparisons of four different components of the dispersal curves (the mean, median and maximum dispersal distances, as well as the frequency of LDD events). Again, the sample for each component corresponded to that of the GRT experiments (each individual duck was a replicate; see Supplementary material Appendix 4 for sample sizes). Significance of the comparisons was assessed by calculating p-values for two-sample t-tests using permutation tests. Comparisons were conducted only between different levels of each single factor (i.e. between duck species for the same propagule and continent; among propagule types for the same waterbird species and continent; and between continents for the same waterbird species and propagule species), and the p-values of the respective permutation tests were corrected with a progressive Bonferroni procedure. All analyses were performed using R (R Development Core Team).

Results

Waterbird migration patterns

During the fall migration season, the frequency of migratory movements varied significantly between the two waterbird species and the two continents (29.3 and 46.2% for teal, 12.0 and 22.4% for mallard, in Europe and North America respectively; n = 607, 101, 900 and 1741 respectively). Teals made more frequent migratory movements than mallards ($\chi^2 = 51.29$, 2 DF, p < 0.001) and these were more frequent in North America than in Europe for both species ($\chi^2 = 27.53$, 2 DF, p < 0.001; no interaction detected: $\chi^2 = 0.003$, 1 DF, p = 0.954).

The distance distributions of waterbird movements during the fall migration had the peak at distances corresponding
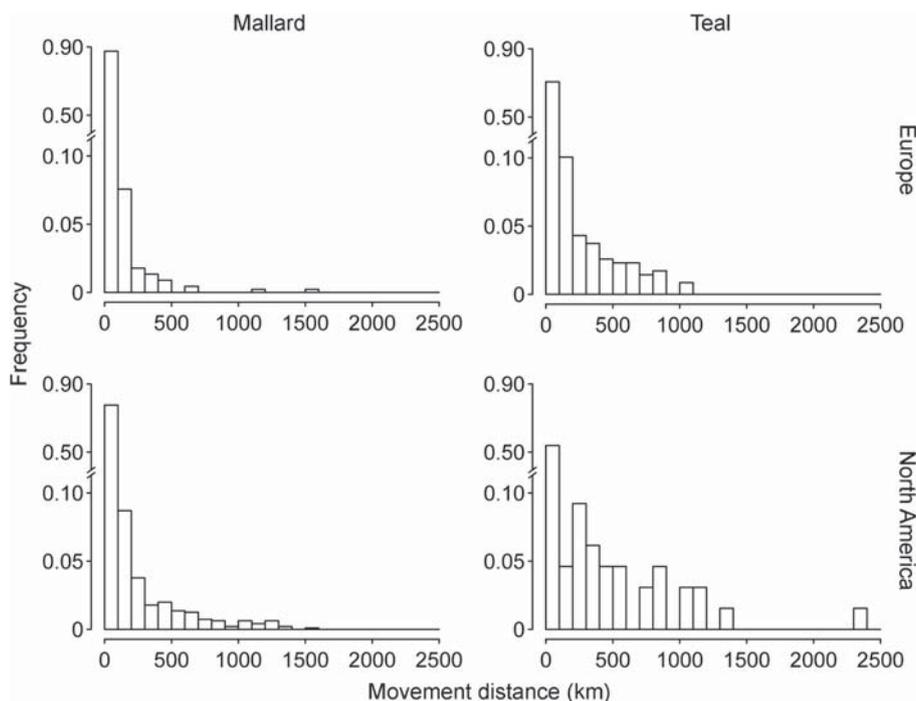

Figure 2. Frequency distributions of the movement distances (100-km distance classes) of teal and mallard in Europe and North America.

to local movements (always < 100 km) and a long tail that included all migratory movements (> 100 km; Fig. 2). The distance of migratory movements varied significantly between both species ($\chi^2 = 20.48$, 2 DF, p < 0.001) and continents ($\chi^2 = 24.37$, 2 DF, p < 0.001), but the interaction between these two factors was not significant ($\chi^2 = 0.11$, 1 DF, p = 0.74). The detected outliers neither influenced model estimates nor changed the significance of effects. Jacknife residuals showed that the most influent observation caused a maximum change of 7%, which corresponded to an insignificant difference of 0.03, in a slope estimate. As also illustrated by the thicker tails of the distance distributions (Fig. 2), the model confirmed that teals rather than mallards, as well as waterbirds in North America rather than in Europe, covered longer migratory distances. Nonetheless, maximum migratory distances seemed to be independent of species or continent, as for example mallards could reach longer distances than teals in Europe but not in North America.

Overall, both the relative frequency of local vs migratory movements and migratory distance varied considerably between species and continents, which suggest differences in migratory movement patterns.

Dispersal curves of aquatic organisms

Realized dispersal distances based on actual waterbird movements were considerably shorter than maximum dispersal distances (MDD), which are based only on the vector average flight speed (Fig. 3; e.g. median range = 21–63 vs 148–840 km, LDD frequency range = 6–36 vs 98–100%,

respectively). However the frequency of realized dispersal events, i.e. the frequency of propagules landing in suitable habitat, was still high (84–97%) and varied among the dispersal curves generated by the different combinations of vector species, continent and propagule species (especially between the two continents: 94–97% in Europe and 84–90% in North America; Supplementary material Appendix 4).

The vector species predominantly determined the shape of the dispersal curves. The different migratory patterns shown by the two duck species generated different propagule dispersal curves, as illustrated by the differences in the rates of cumulative (realized) dispersal distances (Fig. 3). Propagules dispersed by teals reached two- to four-fold longer mean, median and maximum distances than those dispersed by mallard; and LDD was three to four times more frequent for the former (quantification of the different components of the dispersal curves and statistical significance are shown in Supplementary material Appendix 4 and 5). Differences between continents were also found, as in North America propagules tended to be dispersed over longer distances (up to two-fold mean and median distances).

Differences in the gut retention time of propagules ingested by mallard also resulted in differences in their dispersal curves (Fig. 4 upper panel) – but not in the case of the teal. For example, the maximum dispersal distance and the frequency of LDD (except in Europe) differed significantly among some of the propagule species – in most cases between the cysts of *Artemia franciscana* and all seed species, and sometimes also between seed species (Fig. 4 lower panels; see Supplementary material Appendix 4 and
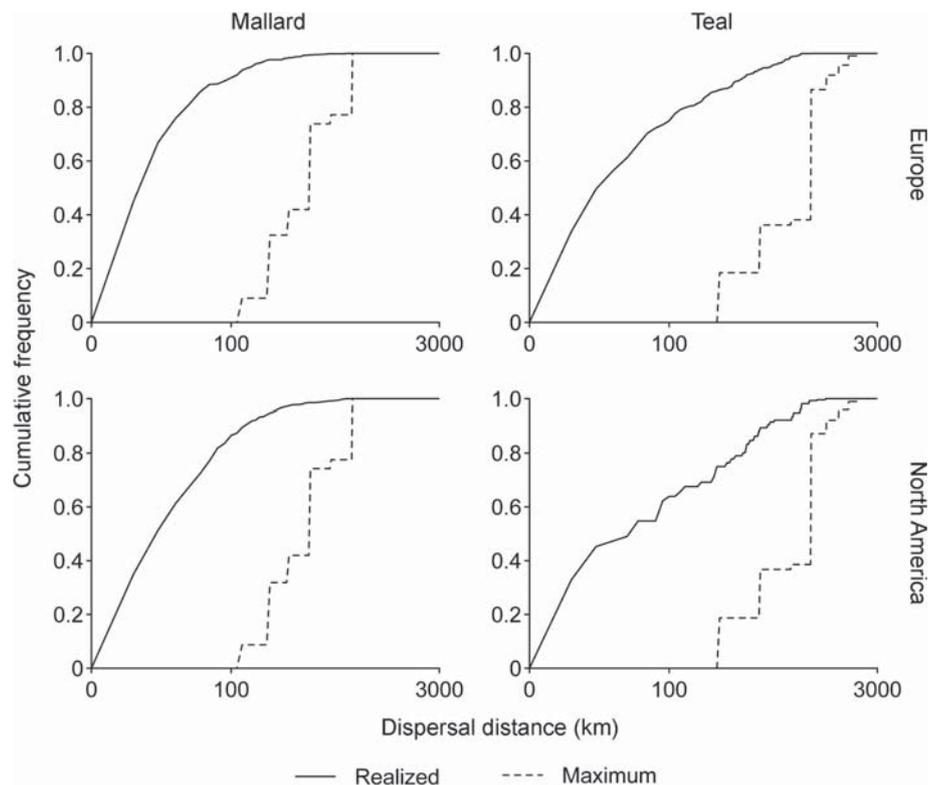

Figure 3. Cumulative frequency of *Scirpus maritimus* dispersal distances produced by two vector waterbird species (teal and mallard) in Europe and North America. Realized and maximum dispersal curves are represented.
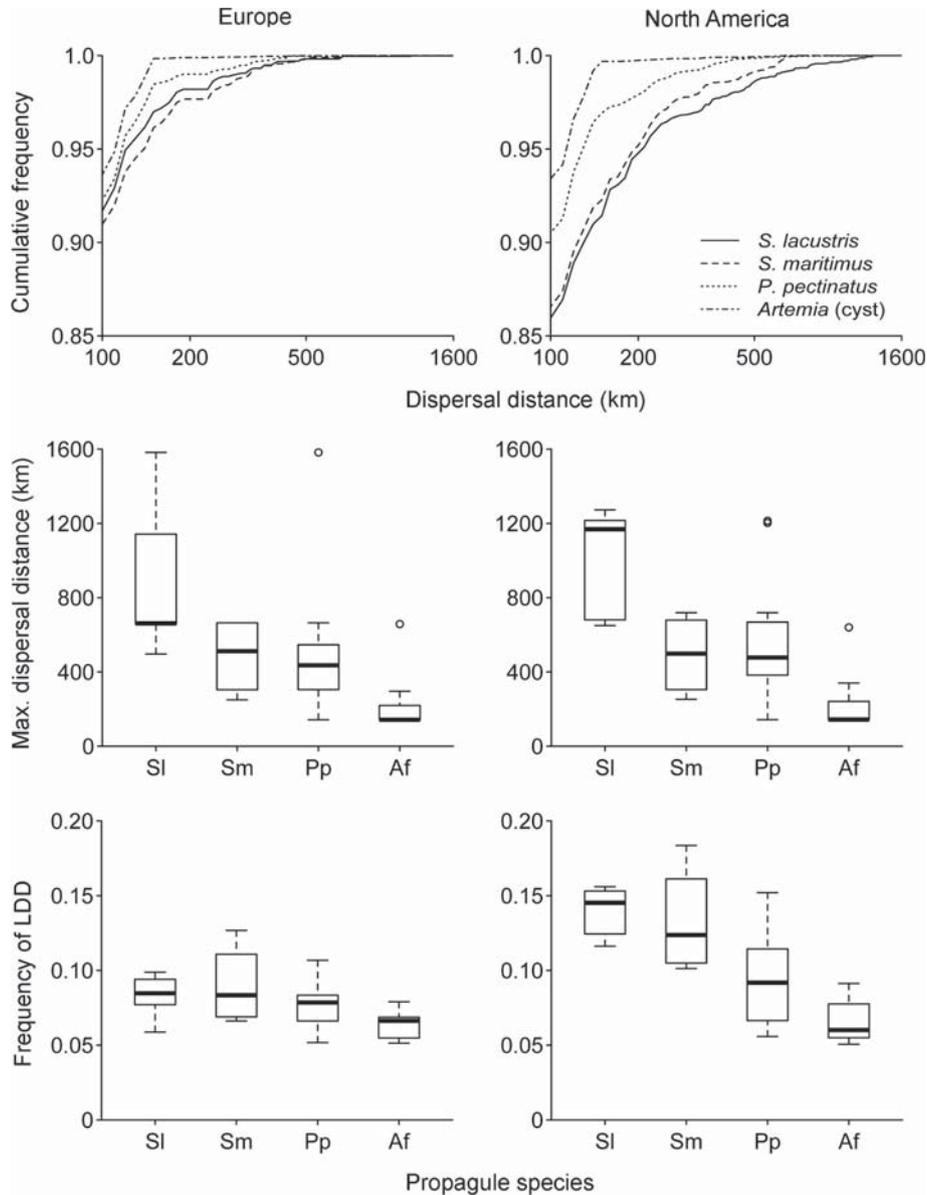
Figure 4. Comparison among the dispersal curves of the different propagules dispersed by mallard. Cumulative frequency of LDD events (upper panel), maximum dispersal distances (middle panel) and the frequency of LDD events (lower panel) are shown. Sl, *S. lacustris* (seed); Sm, *S. maritimus* (seed); Pp, *Potamogeton pectinatus* (seed); Af, *Artemia franciscana* (cyst).

5 for statistical significance and quantification of the other components).

All estimated dispersal curves were highly skewed towards local-scale dispersal distances (median dispersal distances ranged from 21 to 64 km) and leptokurtic, in that long and heavy tails produced by LDD events were observed (Supplementary material Appendix 6). The frequency of LDD events ranged from 6 to 36% and maximum dispersal distances ranged from 230 to 1209 km (averaged distance), reaching, however, 1582 km (absolute maximum dispersal distance; Supplementary material Appendix 4).

Discussion

Many migratory animals are thought to have the potential to be effective LDD vectors for various plant species (Nathan et al. 2008). Our work illustrates a simple and straightforward way of integrating vector migratory movement data to estimate more realistic propagule dispersal curves and further supports the idea that vector migratory movements can lead to propagule long distance dispersal. Birds, in particular, may promote frequent and ubiquitous LDD, as both frugivorous landbirds and waterbirds that feed on seeds or invertebrate propagules (or ingest them involuntarily) are numerous, widespread and, in, many cases, migratory. The application of our method to other migratory bird species might contribute to assess the dispersal capacity of many terrestrial and aquatic passively-dispersed organisms.

The movement patterns of different waterbird dispersers (belonging to different species and continents) strongly shaped the estimated dispersal curves of ingested propagules of four aquatic plant species and one invertebrate species,

in that the migratory strategy of the disperser influenced the frequency of realized dispersal, the distances at which propagules were dispersed and the likelihood of long distance dispersal. Differences in the gut retention time of the various propagules had also a considerable influence on the dispersal curves, particularly on those of different propagule types (angiosperm seeds vs crustacean cysts).

Previous work on waterbird-mediated dispersal completely disregarded the dispersers' movement patterns, and focused primarily on the variation introduced by interspecific differences in propagule characteristics or the average flight speed of waterbirds. Soons et al. (2008) estimated dispersal curves of aquatic plant seeds by mallards, by multiplying seed gut retention times by the disperser (average) flight speed, and reported maximum dispersal distances of 780 and 3000 km for larger and smaller seeds, respectively. These distances overestimate potential dispersal, because defecated seeds were sampled at long intervals (5, 10 and 48 h after ingestion) and assigned to the time of sampling (i.e. a seed defecated after 11 h was assigned a defecation time of 48 h). On the other hand, Charalambidou et al. (2003a) estimated the median and maximum dispersal distances of *Ruppia maritima* seeds dispersed by five waterbird species (range = 80–320 and 400–1000 km, respectively) by multiplying their gut retention time by a range of potential flight speeds (from 10 to 70 km h^{-1}). Here, the inclusion of actual movement patterns of vector waterbirds altered the shape of the dispersal curves by considerably reducing peak (median) and maximum dispersal distances, as well as the frequency of LDD. Still, migratory waterfowl were able to disperse invertebrate and plant propagules regularly over tens of kilometres (e.g. median dispersal distances ranging from 21 to 64 km, for *A. franciscana*/*S. lacustris* dispersed by mallards and *S. litoralis* dispersed by teals respectively; Supplementary material Appendix 4) and, occasionally, over much longer distances that span from hundreds to more than a thousand kilometres (maximum dispersal distances ranging from 230 to 1209 km, for *A. franciscana* cysts and *S. litoralis* seeds, respectively; Supplementary material Appendix 4). Because other aquatic angiosperm and zooplankton propagules show gut retention times comparable to those used in this study (Charalambidou et al. 2003b, c, Wongsriphuek et al. 2008), and many waterfowl species show fairly small differences in gut retention time (Charalambidou et al. 2003a), our results are probably a good representation of what can be expected for other aquatic angiosperm and zooplankton species. Therefore, differences in dispersal patterns between vector species are more likely to arise from behaviour (movement patterns) and, perhaps, diet (probability of ingestion) than from physiology (gut passage rate).

However, the use of captive birds to obtain data on propagule gut retention time (as in all previous seed dispersal studies using mechanistic models) might bias the estimates of dispersal distance, as bird activity affects propagule gut retention time (van Leeuwen et al. in press). Incorporating the effect of the vector activity in the model should thus be a next step for future research on endozoochorous dispersal by migratory birds. It has also been suggested that wild birds empty and/or reduce (undergo atrophy) their guts before taking-off to a migratory flight, which could reduce or even prevent propagule internal dispersal. This may be the case in waders departing for extreme long-distance migratory flights (transoceanic; Piersma and Gill 1998). However, migratory waterfowl have been observed to resume migration immediately after feeding (e.g. Bewick's swans and blue teals; Owen 1968, Nolet and Drent 1998). For species migrating in a stepping-stone fashion, such as waterfowl (at least those migrating through overland flyways), the advantages of adopting such drastic morphological changes are probably larger than the associated costs (Piersma 1998).

Varying movement patterns observed for different vector species and in different continents affected propagule dispersal patterns. Species-specific movement patterns might be explained by different migratory strategies determined by how birds manage their energy expenditure and total migration time, i.e. by how they adjust flight and stopover times (Hedenström 2008). On the other hand, the differences between continents (Europe and North America) might be due to external factors, such as the spatial configuration of the landscape (i.e. the location of habitat patches and of geographical and environmental barriers). For example, migratory movement was shown to differ depending on the chosen flyway (Miller et al. 2005). In addition, different sampling efforts, i.e. different hunting efforts in this study, might also underlie the differences between continents. However our results show that, despite the longer distances observed in North America (which might reflect the landscape configuration), the differences observed in migratory distance between teal and mallard were not dependent on the continent (the interaction between species and continent was not significant). Overall, both intrinsic (e.g. species-specific) and extrinsic (regional) factors might create different migratory movement patterns (e.g. different frequencies and distances of migratory movements), and thus different vector species and populations may contribute in a different manner to the total dispersal curve (sensu Nathan 2007) of a given, passively-dispersed organism.

Estimated dispersal curves reached relatively high levels of LDD (ranging from 6 to 36% of the realized dispersal events). The significance of these estimations, i.e. how they translate into absolute frequencies of LDD, depends on a number of additional factors, including the actual number of migrating waterbirds, the consumption of propagules immediately before each migratory flight, the viability of these propagules after gut passage, and the probability of successful colonization at the 'landing site'. An overview of these factors reveals however that LDD might be effective. Firstly, millions of waterbirds migrate seasonally (e.g. 1 250 000–1 875 000 teals and 7 500 000 mallards in Europe, and 2 160 000 teals and 9 330 000 mallards in North America; Delany and Scott 2006) and show high feeding rates in their stopover sites (Kvist et al. 2001), which probably results in considerable amounts of ingested propagules. Secondly, field evidence shows that 8–80% of waterbird droppings contain intact propagules (Figuerola and Green 2002, Figuerola et al. 2003, Charalambidou and Santamaría 2005, Green et al. 2008), of which 8 to 50% are viable (Figuerola and Green 2002,

Green et al. 2008, Brochet et al. 2009a). Thirdly, many aquatic propagules regularly consumed by ducks occur throughout their migratory ranges, such as those of most plant species (Brochet et al. 2009b) and of many invertebrates (Brochet et al. 2010). Indeed, both the wide distribution of aquatic plant species (Santamaría 2002) and the results of zooplankton colonization experiments (Louette and De Meester 2005) suggest high dispersal and colonization capacities for these two groups of organisms. However, it should be noted that the successful establishment of dispersed organisms depends on the environmental and biotic conditions of the host community. In fact, the high dispersal capacity of aquatic organisms contrasts with the high level of genetic differentiation among many of their populations, suggesting that local effects can be strong enough to prevent successful establishments. Such paradox might be the consequence of community monopolization by early colonizers (through priority effects), i.e. invaders might be excluded by competition with locally-adapted conspecifics or other species (Urban and De Meester 2009).

Notwithstanding the observed strong local effects, many aquatic organisms have high levels of population connectivity (Freeland 2000). For example, Figuerola et al. (2005) showed that the genetic structure of three cladoceran species across North America was explained, to a considerable extent, by the influence of waterfowl flyways. The existence of a strong genetic structure that is accounted for by waterbird movements was consistent with a scenario of accumulated, occasional events of long-distance dispersal, not frequent enough to swamp genetic structure but recurrent enough to be reflected in it. Although invertebrate eggs are thought to have shorter gut retention times than angiosperm seeds, as observed for other zooplankton propagules (Charalambidou et al. 2003b, c), and, consequently, much shorter dispersal distances (Supplementary material Appendix 4), long dispersal distances can still be achieved through repeated events of stepping-stone dispersal.

Many migratory birds are also disease vectors, in particular waterfowl. Therefore, the type of models developed here might have important applications to understand the epidemiology of vector-borne emerging diseases (Kilpatrick et al. 2006). However, direct extrapolation from models based on aquatic organisms is not possible, because pathogens may limit the capacity of infected individuals to migrate over long distances (van Gils et al. 2007).

This study is the first example showing that bird migratory movements can be used to estimate propagule dispersal and that ingested propagules have the potential to actually be dispersed over extremely long distances (hundreds of kilometres). The results of our modelling exercise suggest that different species are likely to provide largely different dispersal services, and that these services may differ greatly between geographic regions. Although they await empirical confirmation (e.g. by a comparison of gene flow estimates obtained form molecular markers), they suggest that fundamental differences may exist in both the risk of spread of biological invasions and the readjustment of species distributions in the face of climate change, and therefore in the management and policy responses to the challenges posed by these threats.

References

Alerstam, T. et al. 2007. Flight speeds among bird species: allometric and phylogenetic effects. – PLoS Biol. 5: e197.

Alsos, I. G. et al. 2007. Frequent long-distance plant colonization in the changing Arctic. – Science 316: 1606–1609.

Bohanak, A. J. and Whiteman, H. H. 1999. Dispersal of the fairy shrimp *Branchinecta coloradensis* (Anostraca): effects of hydroperiod and salamanders. – Limnol. Oceanogr. 44: 487–493.

Brendonck, L. U. C. and Riddoch, B. J. 1999. Wind-borne short-range egg dispersal in anostracans (Crustacea: Branchiopoda). – Biol. J. Linn. Soc. 67: 87–95.

Brochet, A.-L. et al. 2009a. Plant dispersal by teal *Anas crecca* in the Camargue: duck guts are more important than their feet. – Freshw. Biol. 55: 1262–1273.

Brochet, A.-L. et al. 2009b. The role of migratory ducks in the long-distance dispersal of native plants and the spread of exotic plants in Europe. – Ecography 32: 919–928.

Brochet, A.-L. et al. 2010. Field evidence of dispersal of branchiopods, ostracods and bryozoans by teal (*Anas crecca*) in the Camargue (southern France). – Hydrobiologia 637: 255–261.

Bruderer, B. and Boldt, A. 2001. Flight characteristics of birds: I. Radar measurements of speeds. – Ibis 143: 178–204.

Carlo, T. A. and Morales, J. M. 2008. Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density and landscape aggregation. – J. Ecol. 96: 609–618.

Charalambidou, I. and Santamaría, L. 2002. Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. – Acta Oecol. 23: 165–176.

Charalambidou, I. and Santamaría, L. 2005. Field evidence for the potential of waterbirds as dispersers of aquatic organisms. – Wetlands 25: 252–258.

Charalambidou, I. et al. 2003a. Effect of ingestion by five avian dispersers on the retention time, retrieval and germination of *Ruppia maritima* seeds. – Funct. Ecol. 17: 747–753.

Charalambidou, I. et al. 2003b. How far can the freshwater bryozoan *Cristatella mucedo* disperse in duck guts? – Arch. Hydrobiol. 157: 547–554.

Charalambidou, I. et al. 2003c. Endozoochory by ducks: influence of developmental stage of *Bythotrephes* diapause eggs on dispersal probability. – Divers. Distrib. 9: 367–374.

Charalambidou, I. et al. 2005. Digestive plasticity in mallard ducks modulates dispersal probabilities of aquatic plants and crustaceans. – Funct. Ecol. 19: 513–519.

Clark, J. S. et al. 1998. Reid's paradox of rapid plant migration. – Bioscience 48: 13–24.

Clark, J. A. et al. 2009. Quantifying the movement patterns of birds from ring recoveries. – Ringing Migr. 24: 180.

Clausen, P. et al. 2002. Long-distance endozoochorous dispersal of submerged macrophyte seeds by migratory waterbirds in northern Europe – a critical review of possibilities and limitations. – Acta Oecol. 23: 191–203.

Clobert, J. et al. 2001. Dispersal. – Oxford Univ. Press.

Delany, S. and Scott, D. 2006. Waterbird population estimates. – Wetlands International.

Figuerola, J. and Green, A. J. 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. – Freshw. Biol. 47: 483–494.

Figuerola, J. et al. 2003. Passive internal transport of aquatic organisms by waterfowl in Doñana, south-west Spain. – Global Ecol. Biogeogr. 12: 427–436.

Figuerola, J. et al. 2005. Invertebrate eggs can fly: evidence of waterfowl-mediated gene flow in aquatic invertebrates. – Am. Nat. 165: 274–280.

Figuerola, J. et al. 2010. Internal dispersal of seeds by waterfowl: effect of seed size on gut passage time and germination patterns. – Naturwissenschaften 97: 555–565.

Freeland, N. O. 2000. Genetic consequences of the metapopulation biology of a facultatively sexual freshwater invertebrate. – J. Evol. Biol. 13: 383–395.

Gaidet, N. et al. 2010. Potential spread of highly pathogenic avian influenza H5N1 by wildfowl: dispersal ranges and rates determined from large-scale satellite telemetry. – J. Appl. Ecol. 47: 1147–1157.

Green, A. J. et al. 2008. The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. – Freshw. Biol. 53: 380–392.

Hansky, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. – Biol. J. Linn. Soc. 42: 17–38.

Hedenström, A. 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. – Phil. Trans. R. Soc. B 363: 287–299.

Higgins, S. I. et al. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? – Ecology 84: 1945–1956.

Holbrook, K. M. and Smith, T. B. 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. – Oecologia 125: 249–257.

Imboden, C. and Imboden, D. 1972. Orthodromic and loxodromic formula for the calculation of distance and direction between ringing and finding place. – Vogelwarte 26: 336–346.

Kilpatrick, A. M. et al. 2006. Predicting the global spread of H5N1 avian influenza. – Proc. Natl Acad. Sci. USA 103: 19368–19373.

Kvist, A. et al. 2001. Carrying large fuel loads during sustained bird flight is cheaper than expected. – Nature 413: 730–732.

Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – Ecol. Lett. 7: 601–613.

Louette, G. and De Meester, L. 2005. High dispersal capacity of cladoceran zooplankton in newly founded communities. – Ecology 86: 353–359.

Lurz, P. W. W. et al. 2002. Modelling the consequences of duck migration patterns on the genetic diversity of aquatic organisms: a first step towards a predictive tool for wetland management. – Acta Oecol. 23: 205–212.

Miller, M. R. et al. 2005. Spring migration of northern pintails from California's Central Valley wintering area tracked with satellite telemetry: routes, timing, and destinations. – Can. J. Zool. 83: 1314–1332.

Morales, J. M. and Ellner, S. P. 2002. Scaling up animal movements in heterogeneous landscapes: the importance of behavior. – Ecology 83: 2240–2247.

Nathan, R. 2007. Total dispersal kernels and the evaluation of diversity and similarity in complex dispersal systems.

– In: Dennis, A. J. et al. (eds), Seed dispersal: theory and its application in a changing world. CAB International, pp. 252–276.

Nathan, R. et al. 2008. Mechanisms of long-distance seed dispersal. – Trends Ecol. Evol. 23: 638–647.

Nolet, B. A. and Drent, R. H. 1998. Bewick's swans refuelling on pondweed tubers in the Dvina Bay (White Sea) during their spring migration: first come, first served. – J. Avian Biol. 29: 574–581.

Owen, R. B. 1968. Premigratory behavior and orientation in blue-winged teal (*Anas discors*). – Auk 85: 617–632.

Piersma, T. 1998. Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of fueling and flight. – J. Avian Biol. 29: 511–520.

Piersma, T. and Gill, R. E. Jr 1998. Guts don't fly: small digestive organs in obese bar-tailed godwits. – Auk 115: 196–203.

Pollux, B. J. A. 2011. The experimental study of seed dispersal by fish (ichthyochory). – Freshw. Biol. 56: 197–212.

Russo, S. E. et al. 2006. Incorporating animal behaviour into seed dispersal models: implications for seed shadows. – Ecology 87: 3160–3174.

Santamaría, L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. – Acta Oecol. 23: 137–154.

Santamaría, L. and Klaassen, M. 2002. Waterbird-mediated dispersal of aquatic organisms: an introduction. – Acta Oecol. 23: 115–119.

Soons, M. B. et al. 2008. Small seed size increases the potential for dispersal of wetland plants by ducks. – J. Ecol. 96: 619–627.

Trakhtenbrot, A. et al. 2005. The importance of long-distance dispersal in biodiversity conservation. – Divers. Distrib. 11: 173–181.

Urban, M. C. and De Meester, L. 2009. Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. – Proc. R. Soc. B 276: 4129–4138.

van Gils, J. A. et al. 2007. Hampered foraging and migratory performance in swans infected with low-pathogenic avian influenza A virus. – PLoS One 2: e184.

van Leeuwen, C. et al. in press. Vector activity and propagule size affect dispersal potential by vertebrates. – Oecologia.

Vanschoenwinkel, B. et al. 2008. Dispersal of freshwater invertebrates by large terrestrial mammals: a case study with wild boar (*Sus scrofa*) in Mediterranean wetlands. – Freshw. Biol. 53: 2264–2273.

Waterkeyn, A. et al. 2010. Invertebrate dispersal by aquatic mammals: a case study with nutria *Myocastor coypus* (Rodentia, Mammalia) in southern France. – Hydrobiologia 654: 267–271.

Welham, C. V. J. 1994. Flight speeds of migrating birds: a test of maximum range speed predictions from three aerodynamic equations. – Behav. Ecol. 5: 1–8.

Wernham, C. V. et al. 2002. The migration atlas: movements of the birds of Britain and Ireland. – T. and A. D. Poyser.

Westcott, D. A. et al. 2005. Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. – Oecologia 146: 57–67.

Wilson, J. R. U. et al. 2009. Something in the way you move: dispersal pathways affect invasion success. – Trends Ecol. Evol. 24: 136–144.

Wongsriphuek, C. et al. 2008. Dispersal of wetland plant seeds by mallards: influence of gut passage on recovery, retention, and germination. – Wetlands 28: 290–299.