BIODIVERSITY RESEARCH

Recent advances in the study of long-distance dispersal of aquatic invertebrates via birds

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ABSTRACT

Although Darwin pioneered the study of long-distance dispersal (LDD) of aquatic invertebrates via waterbirds, it remains in its infancy as a modern discipline. A handful of recent studies have quantified internal or external transport in the field, confirming that a variety of long-distance migrants carry invertebrates both internally and externally. These studies show that variation in the morphology of vectors influences the frequency and size of propagules transported, and suggest that more invertebrate groups disperse via birds than was previously thought. Dispersal limitation has mainly been investigated for zooplankton in small experimental systems from which waterbirds were effectively excluded, and the extent of such limitation for invertebrate populations in wetlands interconnected by waterbird movements remains unclear. We expect that the spatial and temporal scales at which dispersal limitation constrains geographical ranges, species richness and genetic structure of invertebrates depends partly on the density of migratory birds using the area. Birds may have a major role in the expansion of exotic species. We propose several avenues for future research. There is a particular need for more quantitative studies of LDD by birds that will enable modellers to assess its role in maintaining invertebrate biodiversity among increasingly fragmented wetlands and in the face of climate change, as well as in the spread of invasive species.

Keywords

Aquatic invertebrate, biological invasions, exotic species, external transport, internal transport, long-distance dispersal, migratory waterbirds, scale effects, vector morphology.

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INTRODUCTION

Darwin (1859) referred repeatedly to the capacity of migratory waterbirds for dispersing aquatic invertebrates and plants between locations separated by hundreds of miles. Major advances in our understanding of this passive dispersal have been made since then. However, whereas dispersal of aquatic plants by birds has been researched actively for a long time (Ripley, 1930), the importance of birds as vectors for aquatic invertebrates has received less attention. Various field studies suggest that protozoa undergo long-distance dispersal (LDD) readily via birds (Maguire, 1959; Schlichting, 1960; Sides, 1973; Jenkins & Underwood, 1998). However, we are not aware of studies relating their distribution or genetic differentiation to waterbird movements, and recent reviews of dispersal of freshwater invertebrates concentrate on metazoans (Bilton *et al.*, 2001; Bohonak & Jenkins, 2003).

Darwin (1859, 1878) recognized that a variety of metazoan groups can disperse via migratory birds, but paid specific attention

to molluscs and how they can be transported externally on feet or plumage attached directly, or indirectly via plant material. Another pioneer in this field recorded resting eggs (ephippia) of Cladocera and statoblasts of Bryozoa attached to feathers and feet of ducks and grebes (de Guerne, 1887, 1888). By culturing material after washing feet and bills, he also recorded nematodes and rotifers (de Guerne, 1888). Darwin failed to recognize the potential for internal transport when invertebrate propagules survive passage through the digestive tract of birds. As far as we know, this was not demonstrated until Brown (1933) showed that statoblasts fed to mallards *Anas platyrhynchos* could be defecated in a viable condition after being retained for up to 26 h. Since 1964, a series of studies have demonstrated that a variety of crustaceans, rotifers and gastropods can survive digestion by waterbirds (Charalambidou & Santamaría, 2002; Figuerola & Green, 2002a).

In this article, we review the evidence for and significance of LDD of metazoan invertebrates by birds, focusing on advances in the past five years to avoid duplication of previous reviews.

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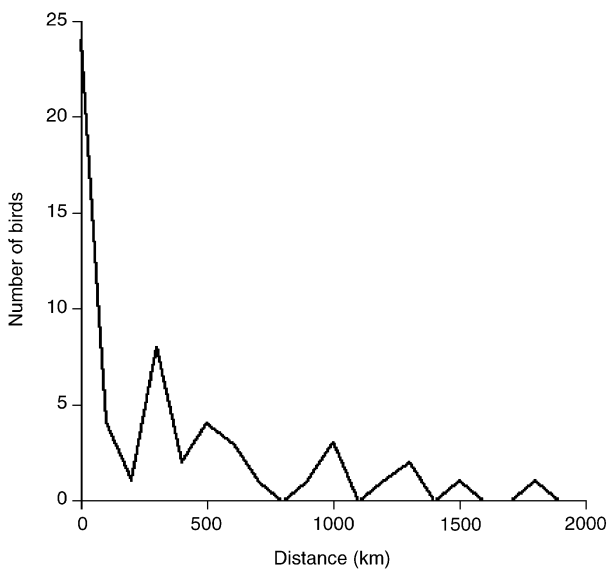
Figure 1 Distances (0–100, 100–200 km, etc.) travelled by ducks and coot ringed and/or recovered in Spain and recovered within a week of ringing. *N* = 56 including 15 recoveries at the ringing location. Mean distance travelled = 384 km, range 59–1801 km. Birds were likely to be ringed some time before moving and recovered some time after, and to have made these movements in much less than a week. Maximum retention times by ducks recorded for intact invertebrate propagules vary from 22 to 44 h (Charalambidou & Santamaría, 2002; Charalambidou *et al.*, 2003b). Ducks fly at 60–78 km/h (Welham, 1994).

Defining LDD of invertebrates

Many definitions of LDD exist and, for the purpose of this paper, we define LDD of aquatic invertebrates as their overland dispersal between wetlands separated by at least 10 km and not connected hydrologically. Such dispersal is not possible via currents, fish or other vectors operating within the water and is unlikely via other animal vectors. However, small propagules can undergo LDD via wind or rain. Combining flight speeds (Welham, 1994) and behaviour (Iverson *et al.*, 1996; Driscoll & Ueta, 2002) of waterbirds with data on retention times of invertebrate eggs (Charalambidou & Santamaría, 2002) indicates that maximum dispersal distances of propagules via endozoochory may easily exceed 1000 km (see also Fig. 1). There are few data on how long invertebrates remain attached to birds, and the nature of dispersal kernels for ectozoochory is open to speculation. However, survival in response to desiccation during attachment has been quantified to estimate limits for external transport (Schlichting, 1960; Malone, 1965; Boag, 1986).

Long-distance dispersal is not restricted to major bird movements during spring and autumn migrations and can occur at any time of the annual cycle (Green *et al.*, 2002b). Important movements likely to facilitate LDD regularly occur during winter (Warnock *et al.*, 1995; Lovvorn & Baldwin, 1996) and while at migration stopover sites (Farmer & Parent, 1997). Ducks fly up to 50 km daily between feeding and roosting sites in winter (Cox

& Afton, 1996). Waterbirds are least mobile during the breeding period, but female ducks leave their broods temporarily to feed in other wetlands (Ringelman & Longcore, 1982).

A series of elegant studies have led to major advances in the understanding of LDD of seeds in terrestrial ecosystems (Nathan & Muller-Landau, 2000). In comparison, studies of LDD in aquatic systems remain in their infancy. In any ecosystem, the rarity of LDD events poses a major challenge when studying dispersal patterns. Long-distance flights made by concentrations of waterbirds make it impractical to track individuals between propagule ingestion and defecation. Satellite and radio-transmitters could be used to estimate dispersal distances of invertebrates along a flyway if the rate of passage through the gut is known. Nevertheless, waterbirds change their gut functioning on commencing and during long-distance migratory flights (Figuerola & Green, 2002a). It is difficult to know whether data on passage time collected in captivity (Charalambidou & Santamaría, 2002; Charalambidou *et al.*, 2003a, 2003b) is representative for migrations. It seems more likely to reflect retention times during shorter flights made throughout the year. Some species fast before initiating a migratory flight (Fransson, 1998), and this may actually increase the maximum retention time and dispersal distance for propagules (Figuerola & Green, in press).

Recent progress in the study of LDD

Some authors (Dzialowski *et al.*, 2000; Bailey *et al.*, 2003) have questioned the importance of LDD by birds compared to other vectors (e.g. man or wind). Few field studies demonstrate that birds carry propagules internally or externally, this being an interdisciplinary field that has attracted little attention. Ornithologists tend not to be interested in the implications of their work for invertebrate dispersal. This is a pity, as studies of diet or migratory behaviour could provide vital information about LDD with little extra effort. On the other hand, aquatic ecologists and limnologists tend to have little interest in waterbirds. Leading aquatic journals publish much research on fish while ignoring birds that feed in water. In 2003, 17 papers in *Freshwater Biology* referred to fish in the title or abstract and none to birds. From 2002 to 2003, 12 papers in *Limnology & Oceanography* referred to fish, and none to birds. One reason is that limnologists have sought to study closed systems. The inclusion of birds requires a system to be treated as open and connected with others. Limnologists have also often focused on deep lakes and reservoirs, relatively unattractive habitats for waterbirds.

Despite the lack of field studies, experiments, which show propagules survive gut passage (Figuerola & Green, 2002a), combined with data showing that invertebrates are consumed by waterbirds (Green *et al.*, 2002b), suggest that many invertebrates (notably crustaceans and bryozoans) readily undergo internal LDD. Although some snails and their eggs can survive passage through ducks, external transport of molluscs seems to occur more often and allows dispersal over longer distances (Wesselingh *et al.*, 1999). Work on horseshoe crabs (Merostomata) suggests that internal LDD by waders is important in marine systems (Castro *et al.*, 1989; Castro & Myers, 1993).

Several experiments have addressed limitations to dispersal in zooplankton under experimental conditions using mesocosms (Cáceres & Soluk, 2002; Cohen & Shurin, 2003). These studies have revealed major variation between taxa in their potential to disperse to and colonize new habitats at local scales (< 1 km), as well as evidence that zooplankton communities rapidly saturate and resist invasion by further species (Bohonak & Jenkins, 2003; Havel & Shurin, 2004). Nevertheless, apart from identifying invertebrates (especially rotifers) that disperse effectively at local scales in the absence of birds, they do not help us in assessing the role of waterbirds in zooplankton dispersal. Although different mesh sizes on the top of mesocosms have partly been designed to exclude birds, the experimental blocks are too small and isolated to attract waterbirds.

Recent field studies support a major role for birds in LDD. In coastal marshes in Spain used by hundreds of thousands of waterbirds during migration, transport of ephippia, statoblasts and other propagules by ducks and coots, whether internally or externally, were frequent (Figuerola & Green, 2002b; Figuerola *et al.*, 2003; Figuerola *et al.*, 2004). Furthermore, large numbers of corixid eggs of unknown viability were transported internally (Figuerola *et al.*, 2003), suggesting a previously unknown role for birds in dispersing aquatic insects. Ringing recoveries show that the waterbirds studied move to and from a vast area in Europe and Africa and undergo regular long distance movements (Fig. 1). Furthermore, they were undergoing continuous movements between wetlands within the study area.

For a given propagule type, there were multiple vectors and the rate of internal transport varied between waterfowl species and seasons, although seasonal trends were not consistent between vectors (Figuerola *et al.*, 2003). Thus, much variation in LDD is expected in space, time and between vectors. The importance of different vectors was related to ecomorphology. Bill structure influenced internal transport, with those duck species having a higher density of filtering lamellae (e.g. the Northern Shoveller *Anas clypeata*) evacuating a greater number of propagules (Figuerola *et al.*, 2003). Ecomorphology also influences the size distribution of propagules transported, as species with higher lamellar densities transported relatively more small propagules (Fig. 2). Gut morphology is also important. For a given bird species, statoblasts are more likely to be evacuated intact when they pass through a smaller gizzard, and more likely to have long retention times when they pass through birds with longer caecae (Figuerola *et al.*, 2004).

Recent experiments to calculate retention times suggest that maximum LDD distances for internal transport exceed 1500 km although, even during migrations, more than 90% of propagules will be dispersed to less than 500 km (Charalambidou *et al.*, 2003a, 2003b). Little difference was observed between bird species in retention times and propagule survival, perhaps owing to the elimination of interspecific diet variation in captive conditions. More *Artemia* cysts survived gut passage by mallards fed on a plant diet than by those fed on animal material (Charalambidou *et al.* in press).

The most detailed study of external transport shows that, whilst seeds are mainly transported in plumage, invertebrate eggs are mainly attached to feet (Figuerola & Green, 2002b). Darwin
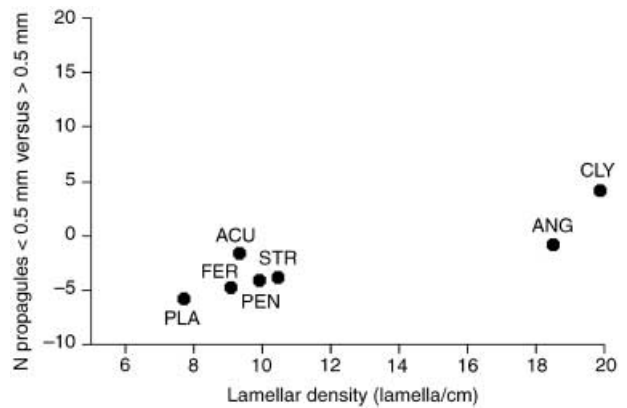
Figure 2 Relationship between bill lamellar density and propagule size (invertebrate and plant combined) found in the faeces of ducks in early winter in Doñana, southwest Spain. Data reanalysed from Figuerola *et al.* (2003). The *y* axis represents residuals from an OLS regression of the number of small propagules (mainly invertebrates) passing through a 0.5 mm sieve but retained on a 0.04 mm sieve against the number of large propagules (mainly seeds) retained on a 0.5 mm sieve. For a given number of large propagules, duck species with a higher lamellar density transported more small propagules ($R_{spearman} = 0.89$, $P = 0.007$). PLA = *Anas platyrhynchos*, ACU = *Anas acuta*, STR = *Anas strepera*, PEN = *Anas penelope*, CLY = *Anas clypeata*, FER = *Aytha ferina*, ANG = *Marmaronetta angustirostris*.

Figure 3 Common cockle *Cerastoderma edule* attached to a Dunlin *Calidris alpina* mist-netted in the Odiel Marshes, Spain. Photo by José Manuel Sayago.

(1878) showed that bivalves can be transported externally by attaching themselves to feet (see also Wesselingh *et al.*, 1999). Here we present unique data on the frequency of these events. During the handling of 17,000 waders during autumn migration through the Odiel Marshes in southwest Spain, four individuals (two sanderling *Calidris alba*, one dunlin *Calidris alpina* (Fig. 3),

one curlew sandpiper *Calidris ferruginea*) were found to have a live cockle *Cerastoderma edule* attached to one of their digits. Furthermore, around 3% of waders had amputated digits that were probably caused by such bivalve dispersal events (J.M. Sayago, pers. comm.). An estimated 15.5 million waders migrate through this east Atlantic flyway each autumn (Stroud *et al.*, 2004).

Darwin (1859) was concerned with the role of LDD via waterbirds in colonization events, especially postglacial expansions and island colonization, as well as allopatric speciation. All aquatic ecosystems are subject to ecological change from human activities and climate change. Man's activities result in a net loss of wetlands (Green *et al.*, 2002a), yet new wetlands are being created whereas others are being restored. Thus, transport by birds probably plays a major role in contemporary changes in distribution of indigenous invertebrates (see also Watkinson & Gill, 2002). We are also concerned with its role in gene flow within and between established populations and in metapopulation ecology. The role of LDD via birds in gene flow has been questioned. Whilst accepting that such LDD may be frequent, de Meester *et al.* (2002) argue that it is unlikely to influence patterns of genetic variation among established populations of most sexual or cyclically parthenogenetic zooplankton, owing to their abundant propagule banks and the monopolization of available habitat by locally adapted genotypes. Propagules arriving via LDD are not likely to compete successfully and become detectable amongst locally adapted genotypes (de Meester *et al.*, 2002). Thus, transport of propagules by birds into established populations should not translate into significant recruitment or gene flow.

This monopolization hypothesis has yet to be supported for invertebrate populations known to be connected via bird dispersal. Microsatellite data for the bryozoan *Cristatella mucedo* support ongoing gene flow via waterfowl in Europe (Okamura & Freeland, 2002). The distribution of major genetic groups in the *Daphnia laevis* complex roughly coincides with waterfowl flyways (Taylor *et al.*, 1998). Recognizing that discrete flyways do not exist for most waterbird species and relating matrices of bird movement probabilities to matrices of genetic distances between invertebrate populations, Figuerola *et al.*, 2005) found that bird movements explain significant variation in the relationships between North American *Daphnia ambigua*, *Daphnia laevis* and *C. mucedo* populations for mitochondrial DNA, even when controlling for Euclidean distances. Although mtDNA may reflect historical colonization events in which LDD via birds played a crucial role, similar results were recorded for more rapidly evolving nuclear markers, suggesting that transport via birds influences ongoing gene flow.

LDD of exotic species

Invasion by alien species is second only to habitat loss as a threat to global biodiversity, and has its greatest impact in aquatic ecosystems (Mooney & Cleland, 2001). Alien aquatic invertebrates are typically moved between continents by man in the ballast of ships or intentionally for aquaculture or fisheries purposes (Leppäkoski *et al.*, 2002). Once established, they are generally assumed to disperse using their own active mechanisms, via

ocean or river currents, or via intraregional boat traffic (Wasson *et al.*, 2001). The role of birds in spreading alien invertebrates has received no attention (but see Green *et al.*, 2005).

Future studies may confirm that dispersal by birds is a major mechanism for the spread of aquatic aliens, and that the capacity to exploit dispersal by birds helps to explain which invertebrate species become invasive. There are increasing numbers of exotic cladocerans, copepods and bryozoans observed in aquatic systems (Leppäkoski *et al.*, 2002), these being groups well able to disperse as resistant eggs via birds (see above). Reid and Reed (1994) suggested that Neotropical copepods have been transported to North America via waterbirds. Anecdotal evidence suggest that adult or larval exotic amphipods, molluscs or other invertebrates can hitch-hike between wetlands on waterbirds (Wesselingh *et al.*, 1999; Figuerola & Green, 2002a). Darwin (1859) attributed the spread of some exotic freshwater snails to birds.

The expansion of exotic *Daphnia lumholtzi* in North America may provide an opportunity to assess the role of LDD by birds. It has been suggested that boat traffic is the primary vector for *D. lumholtzi* (Dzialowski *et al.*, 2000; Havel & Stelzleni-Schwent, 2000). The ephippia of this species (Havel & Hebert, 1993) appear well adapted for bird dispersal as shown by other *Daphnia* species (Mellors, 1975; Figuerola & Green, 2002b). Havel and Stelzleni-Schwent (2000) suggested that *D. lumholtzi* is poorly matched with the seasonality of waterfowl as it is most abundant in late summer, yet waterfowl make regular movements between wetlands during the breeding season and ephippia are transported by birds long after their production (Green *et al.*, 2002b; Figuerola *et al.*, 2003). The observed dispersal kernel for *D. lumholtzi* in reservoirs is consistent with transport by birds (as well as other vectors), because invasion is more likely within 20–30 km of source populations (Havel *et al.*, 2002), and the majority of bird movements occur below this threshold.

Neither does the failure of *D. lumholtzi* to colonize small ponds inaccessible to boats indicate that birds are not important vectors (Dzialowski *et al.*, 2000). Small ponds are not attractive to waterbirds compared to larger wetlands (Brown & Dinsmore, 1986; Elmberg *et al.*, 1994). Invasion probability increases with wetland size as expected under LDD via birds (Dzialowski *et al.*, 2000; Havel *et al.*, 2002). Although flowing water is probably one means of *D. lumholtzi* dispersal, it also disperses overland (Shurin & Havel, 2002). We suspect that birds are an important vector for this species. However, human-mediated dispersal is undoubtedly also important and is likely to explain the east to west 1200 km jump from Texas to Arizona (J.E. Havel, pers. comm.).

Rapid expansion of *D. lumholtzi* contrasts with slower expansions of other exotic crustaceans in North America: the Eurasian *Bythotrephes longimanus* and *Bythotrephes cederstroemi* (Jarnagin *et al.*, 2000; Yan *et al.*, 2002). *Bythotrephes* eggs (Jarnagin *et al.*, 2000) are morphologically less suited to external transport and less able to survive gut passage by waterfowl than *Daphnia* ephippia (Charalambidou *et al.*, 2003a). Whereas ephippia float making them accessible to waterbirds, *Bythotrephes* eggs sink (Ketelaars & Gille, 1994). Thus, *D. lumholtzi* may partly be expanding faster owing to a greater capacity for LDD via birds. The conservation

of migratory waterbirds is essential to maintain connectivity and indigenous invertebrate biodiversity in the world's wetlands (Amezaga *et al.*, 2002). Nevertheless, their capacity to disperse invasive species makes the need to control the importation and release of exotic species all the more urgent (see also Trakhtenbrot *et al.*, 2005).

Effects of scale and bird density on dispersal

We expect great variation in the importance of propagule dispersal by birds in different aquatic systems and at different times, as observed in terrestrial systems (Nathan & Muller-Landau, 2000). We expect that the frequency and ecological importance of LDD by migratory waterbirds will be positively related to their density. Migratory waterbirds are not distributed evenly across the earth's land masses or between aquatic ecosystems. They are highly concentrated in certain areas during migration and wintering periods (Scott & Rose, 1996), leading to the identification of flyways (Boyd & Pirot, 1989). Saunders *et al.* (1993) considered the distribution of the anostracan *Branchinecta paludosa* to be dependent on a North American flyway.

At least for waterfowl (ducks, geese and swans), the density of birds is higher in the Northern than the Southern Hemisphere (Gaston & Blackburn, 1996). Furthermore, long-distance migrants are concentrated at higher latitudes during the breeding season whereas species breeding at lower latitudes tend to be non-migrants (Gaston & Blackburn, 1996). Most long-distant migrants stop far from the equator (Wetlands International, 2002). Similar patterns are likely for waders except that many species breed in the extreme north and cross the equator in winter. In general we expect bird-mediated LDD to be more important at northern and intermediate latitudes, and less important around the equator, with the exception of coastal sites used by migrating waders. In the wetlands of some regions (e.g. coastal areas of Europe and North America), the density of long distance migrants is much higher than in other regions (e.g. the Amazon). These differences may have fundamental consequences for the dispersal of invertebrates.

Havel and Shurin (2004) suggest that dispersal of zooplankton among wetlands separated over short spatial scales (< 10 km) is sufficiently rapid that local interactions (e.g. competition or predation) should limit species diversity and composition more than the supply of colonists via dispersal. They argue that, at broader spatial scales, dispersal limitation may constrain geographical ranges and influence community structure. Such scale effects on dispersal undoubtedly exist but we expect that, for many invertebrates, they are dependent on the movements of waterbirds and whether or not the wetlands lie on flyways. We expect waterbirds to increase the effectiveness of dispersal of many, but not all, species of zooplankton and other invertebrates over medium (1–10 km) and long (> 10 km) distances.

Proposals for future research

At a given latitude, it is possible to find wetlands used by different densities of migratory waterbirds, allowing for comparative studies of their influence on invertebrate biodiversity. In the East and West Indies, there are great differences between islands in the numbers of migratory birds (Ricklefs, 1980). In the Mediterranean region, the density of migrants in wetlands with a similar hydrology and morphology can vary by several orders of magnitude depending on whether or not they are on flyways (Martí & del Moral, 2002). If LDD via birds is important compared to other modes of dispersal, we would predict greater invertebrate species richness but reduced genetic differentiation between populations for wetlands with more waterbirds. To test this hypothesis, similar wetlands should be compared on and off flyways, and within flyways those wetlands used by birds (e.g. larger, shallower wetlands) should be compared with those avoided by them (e.g. very small or deep wetlands).

We would expect invertebrates specialized in the use of habitats used little by waterbirds to be less widely distributed (i.e. have a reduced extent of occurrence and area of occupancy *sensu* IUCN/SSC, 1994) and to show greater genetic differentiation on a continental scale than related species using habitats favoured by birds. Likewise, those invertebrate species that can be shown experimentally to have a greater propensity to attach themselves to birds or to survive passage through their gut should be more widely distributed with less genetic differentiation. These ideas should be tested, taking care to tease apart the influence of humans and other vectors. It should be borne in mind that wetlands avoided by waterbirds may be visited by other migratory birds for drinking and bathing, and that they can disperse rotifers and other invertebrates (Maguire, 1963). In order to test the monopolization hypothesis (De Meester *et al.*, 2002), the population genetics of closely related species with a similar capacity for LDD but different life history strategies and capacities for local adaptation (e.g. sexual and obligately parthenogenetic species of *Artemia*) should also be compared.

Another exciting area for future research is LDD of those invertebrates (e.g. many cestodes or acanthocephalans) that parasitize migrating waterbirds and have aquatic intermediate hosts (typically crustaceans, insects or molluscs). These organisms undergo LDD between wetlands inside their avian hosts, and the relationship between the distributions and population genetics of these parasites and their intermediate and final hosts should be studied. For example, do the distributions of major genetic groups in a given cestode (e.g. one parasitizing waders along several flyways and using various invertebrate species as intermediate hosts) coincide with those of its invertebrate hosts or with different waterbird populations? The importance of LDD of aquatic insects by birds should also be further investigated. Darwin (1859) was fascinated by the potential of fish-eating birds for indirect dispersal of propagules consumed by fish and later expelled elsewhere by birds. Indirect dispersal is important in terrestrial systems (Nogales *et al.*, 1998), and should be investigated in aquatic ecosystems.

There is a particular need for more quantitative studies of LDD of invertebrates by birds, including better estimates of dispersal kernels. One approach to quantify transport of propagules separated by land is to search for propagules carried by birds at one wetland that can only have come from a different wetland,

e.g. screening birds at saline wetlands for freshwater invertebrates. As yet, the manner in which size, shape and other aspects of propagule morphology affect the chances of internal or external dispersal via birds has hardly been addressed. Comparative experimental studies of survivorship and retention times should be integrated with field studies of propagule transport frequencies and bird movements and of genetic structure in the same organisms. Such multidisciplinary studies will enable us to establish how important birds are compared to other means of invertebrate dispersal. They will also enable modellers to assess the potential role of waterbirds in maintaining viable metapopulations and metacommunities among increasingly fragmented wetlands and in the face of climate change, which affects both bird migration routes and the distribution of habitat suitable to invertebrates. Studies of this type would also allow us to predict the spread of aliens able to disperse via birds. We encourage aquatic ecologists and ornithologists to seek common areas of interest and collaborate to fill gaps in knowledge.

CONCLUSIONS

Increasing evidence suggest that bird-mediated transport is an important mechanism of LDD for many invertebrates. However, there is a need for much more focused research to assess the relative contribution of birds and other vectors in explaining the distribution and overland dispersal of aquatic invertebrates. In general, propagules below 1 mm in diameter have great potential for internal and external transport by birds and the smaller the propagules, the more readily they are likely to be dispersed. Smaller seeds (and perhaps smaller eggs) have a double advantage for internal dispersal because they are better at surviving digestion and have longer retention times (authors and coworkers submitted manuscript).

The largest propagules or other individuals transported internally by birds are likely to be in the order of 2 mm in diameter, whereas larger organisms may be transported externally when they have special means of attachment (e.g. molluscs, leeches, propagules with hooks). It is possible that the smallest propagules, especially those of protozoans and rotifers, are dispersed in such abundance in air currents and by rain that other vectors are irrelevant. While there is good evidence for this over short distances (< 1 km), the importance of dispersal via birds will generally increase as either distance or propagule size increases. Unlike wind or rain, waterbirds tend to direct dispersal to other aquatic habitats, this being a major advantage as such a high proportion of the earth's surface is sea or dry land. However, Nathan *et al.* (2005) show that wind can also direct propagules to wetlands in forested landscapes. Over medium scales (1–10 km), mammals, insects and other animal vectors may be as or more important than birds, depending on the system in question. Some wetlands avoided by waterbirds are used by other vectors (Maguire, 1963). Movements of such vectors over longer distances of > 10 km will be much rarer than for birds. How important man has now become as a vector compared to birds is likely to vary between regions and be correlated with human density, such that, e.g. humans are relatively more important vectors in

the Mediterranean region than in Siberia. There is also likely to be a correlation with wealth and economic activity, which affects the frequency of long distance movements by boats or water sports enthusiasts.

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