

Research Article

High dispersal capacity of a broad spectrum of aquatic invertebrates via waterbirds

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Received: 4 August 2006; revised manuscript accepted: 1 January 2007

Abstract. Speculation about the role of waterbirds in the dispersal of aquatic invertebrates pre-dates Darwin. However, there is a critical shortage of field studies quantifying such dispersal. We quantified the viability of aquatic invertebrates in the faeces of different waterfowl species collected in the field at different times during winter. Faeces were collected from four duck species (Northern Pintail *Anas acuta*, Mallard *A. platyrhynchos*, Shoveler *A. clypeata*, Eurasian Teal *A. crecca*) and Eurasian Coot *Fulica atra* in November 2004 and January 2005. We also collected soil samples from resting sites as an indicator of what may be transported on birds' feet and plumage. Faecal and soil samples were incubated using two treatments (0.4 and 4.0 mS cm⁻¹) to quantify the potential for dispersal between aquatic habitats of

different salinities. We found that viable Nematoda, Rotifera, Copepoda, Ostracoda, Insecta (Tipulidae), and *Daphnia* and *Moina* cladocerans were transported internally by birds in the wild. We also found evidence that nematodes, rotifers, ostracods, copepods, tipulids, chironomids and hemipterans can be dispersed on birds' feet and feathers. The overall incidence of hatching from all samples was higher in January (59.4 %) than in November (11.5 %). With the exception of bdelloid rotifers, we found no evidence that the potential for dispersal between two habitats would be impeded by salinity in the range tested. Our data suggest that the taxonomic range of dispersed invertebrates and the frequency of their dispersal via waterfowl has previously been underestimated.

Key words. Internal transport; zooplankton; *Daphnia*; *Moina*.

Introduction

The role of dispersal in the assemblage of communities is a central issue in aquatic ecology. In the case of aquatic ecosystems, Darwin (1859) suggested that migratory waterbirds play a major role in dispersing invertebrates. While major advances have been made in the understanding of avian dispersal in terrestrial plant communities, (see e.g. Nathan and Muller-Landau, 2000), relatively few field studies have been

carried out to evaluate the role of such passive dispersal via birds in explaining the structure of aquatic communities. In their authoritative review on invertebrate dispersal, Bilton et al. (2001) relied mainly on experiments in captivity and the overlap between avian flyways and the distribution of bryozoan and *Daphnia* genotypes as evidence for the role of birds in dispersing invertebrates (see also Havel and Shurin, 2004).

Potential dispersal vectors for zooplankton and other invertebrates include wind and rain (Cáceres and Soluk, 2002; Cohen and Shurin, 2003; Havel and Shurin, 2004), surface waters between connected

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Published Online First: September 24, 2007

waterbodies (Michels et al., 2001; Frisch et al., 2005), ballast water (Bailey et al., 2003), and other shipping activities (Havel and Shurin, 2004). Darwin (1859) highlighted the potential role for migratory waterbirds, and a range of anecdotal observations and laboratory studies have since shown the potential of birds for transporting propagules both externally (stuck to feet, bills or plumage) and internally (via gut passage, see Figuerola and Green, 2002a; Green and Figuerola, 2005 for reviews). However, the importance of waterbirds as dispersers of invertebrates has recently been questioned (Jenkins and Underwood, 1998; Bohonak and Jenkins, 2003), largely owing to the lack of field studies demonstrating such dispersal.

Proctor (1964) recorded viable ostracods and cladocerans in faeces collected from the digestive tract of three ducks shot in the wild. Figuerola et al. (2003) quantified the internal transport of invertebrate propagules by a community of wintering waterfowl (Anatidae and Coot) species, but did not test viability of propagules. Here, we present a field study to quantify the viability of aquatic invertebrates in the faeces of different wintering waterfowl species, and address the potential for effective dispersal between aquatic environments varying in salinity. Salinity is a major determinant of the structure of invertebrate communities in aquatic systems (Wollheim and Lovvorn, 1995; Hobæk et al., 2002), and major differences in salinity between neighbouring wetlands are common in coastal areas and regions with high evaporation rates. We identified invertebrate taxa emerging from fresh faeces collected in the Doñana marshes. This wetland complex totals 120,000 ha and is one of Europe's most important wetland complexes for migratory waterfowl, with up to 500,000 individuals recorded in winter (Martí and del Moral, 2002). We quantified viability of propagules using two salinity treatments to test the potential for dispersal between different habitats. We compared faeces collected in early and mid-winter, periods that differed in the abundance of waterfowl species and the nature of their movements. We also conducted similar experiments on samples of soil likely to become stuck to waterfowl feet and plumage (Figuerola and Green, 2002a).

In this paper we test the following hypotheses: 1) that waterfowl transport a diverse spectrum of freshwater invertebrates, 2) that some invertebrates are better able to disperse internally and others externally, 3) that dispersal potential is limited by differences in salinity between sites where invertebrates are picked up and deposited.

Materials and methods

Samples were collected in Veta la Palma (6° 14'W, 36° 57'N), an area of former marshland of 3125 ha in Doñana, south-west Spain that was transformed into extensively farmed fishponds between 1990 and 1993. The ponds are adjacent to natural, temporary marshes. More detailed information on the area can be found in Figuerola et al. (2003), and Frisch et al. (2006a). The ponds contain over 20,000 ducks and Coot in winter (Rodríguez-Pérez and Green, 2006).

Monospecific flocks of birds were identified with binoculars when roosting on the shore, then samples of fresh faeces (each sample containing one dropping) were obtained by approaching the birds, scaring them away and collecting only the freshest samples. Different samples collected were separated by at least 1 m and usually much more. Care was taken to collect only samples without attached soil to prevent contamination of faeces, and the surface in contact with the soil was removed with a knife before storing each sample separately in an airtight plastic vial. On 20 November 2004, faeces were collected from Northern Pintail *Anas acuta* ($N=20$ samples), Mallard *Anas platyrhynchos* ($N=20$), and Eurasian Coot *Fulica atra* ($N=20$). On 18 January 2005, faeces were collected from Coot ($N=10$), Shoveler *Anas clypeata* ($N=9$) and Eurasian Teal *Anas crecca* ($N=10$). Dry masses of additional faecal samples taken from Mallard and comparison with faecal production in captivity for this species (Gere and Andrikovics, 1994) suggests that each of our samples contained approximately 10% of daily faecal production of a given individual (authors, unpublished data). Coot was the only species sampled on both dates because seasonal movements of ducks to and from inaccessible parts of the Doñana wetland complex made it impossible for us to sample the same duck species twice. Given the number of birds present and the collection of only fresh faeces, we are confident that each sample came from a separate bird. From each dryland site where birds were roosting and faeces were collected, we also collected samples of dry surface soil (for sample sizes and treatments see below). This soil was a fine clay that stuck readily to damp objects such as a biologist's boot or a duck's foot (Figuerola and Green, 2002b). Samples were stored overnight in a refrigerator, until the start of the hatching experiment the following day.

The viability of invertebrate propagules in faeces or soil was assessed in the laboratory. For the purpose of this study, we defined a propagule as any developmental stage of an invertebrate with the potential to disperse between two waterbodies, e.g. individual resistant eggs, ephippia, juvenile stages or adults of invertebrates observed in this study. The experimental

setup contained two salinity treatments (equivalent to conductivities of 0.4 and 4.0 mS cm⁻²). Mineral water was used for the 0.4 mS cm⁻² treatment, and sea salt (commercially available in supermarkets) was added to make the 4 mS cm⁻² treatment. These treatments were chosen to simulate the range of salinities found in the majority of aquatic habitats within the Doñana wetland complex (Frisch et al., 2006b), to quantify to what extent the successful dispersal of invertebrates between different parts of the complex might be limited by salinity differences.

Faecal samples were not mixed before being used. Approximately 0.5 cm³ of each fresh faecal sample was placed into a separate 100 ml plastic beaker filled with 30 ml of water of the respective treatments. This represented approximately 30% of each faecal sample for Teal, and 15% for other bird species. The sample was carefully mixed with water, using the rounded end of a plastic Pasteur pipette. To prevent contamination of samples, we used new equipment for each faecal sample. Soil samples were treated in the same way, using approximately 0.5 cm³ of soil. We also installed controls that only contained water. The samples were kept for 3 weeks (November samples) and 6 weeks (January samples) in a light and temperature controlled chamber at conditions that resemble photoperiod and temperatures in the field during early spring (15°C, 12:12 h LD). In the first week, samples were monitored for emerging or hatching invertebrates every 1 to 3 days using a binocular microscope. After that they were monitored on a weekly basis. Water lost by evaporation was replaced with distilled water to avoid an increase in salinity. For the hatching experiment with November samples, we used 10 different individual faecal samples from each waterbird species, nine different soil samples and nine water controls for each salinity treatment. For the hatching experiment with January samples, approximately 0.5 cm³ of the same faecal sample was used in each of the two salinity treatments. Soil samples ($n=8$) were divided between treatments in a similar way, and there were six water controls for each treatment. The time required to monitor each sample carefully limited the number of samples we could use in each experiment. We changed the design for January samples with the aim of providing a stronger (paired) test for salinity effects, given major individual variation in the content of faecal samples.

All statistical analyses were carried out using Statistica 6.0, StatSoft Inc. Differences in taxon richness between November and January samples were tested with the Mann-Whitney-U test, adjusted for small samples. The same method was used for November samples to test for differences in taxon richness between the two salinity treatments or

between sample types (species-specific faecal samples or sediment). For January samples, the effect of salinity on taxon richness was analysed with Wilcoxon-matched-pairs tests. The proportion of samples in which hatching occurred was compared between months, salinities or sample types using two-tailed Fisher Exact tests.

Results

No invertebrates were recorded in any of the water controls. A variety of taxa were found to emerge from the faeces and soil samples (Tables 1, 2), including nematodes, rotifers, cladocerans, copepods, ostracods, dipterans and hemipterans. In three samples of Shoveler faeces, live adult ostracods (Cypridae) were observed on the second and third day, indicating their survival of passage through the bird gut as adults. In all other samples, only juvenile ostracods were observed (from day 13 onwards). Nematodes appeared after 3 to 16 days of incubation. The cladocerans *Daphnia magna* Strauss 1820 and *Moina brachiata* Jurine, 1820 hatched from ephippia in Teal and Shoveler faeces in the second and third week of the experiment and were kept alive in the beakers until they reached the adult stage and reproduced. *Brachionus plicatilis* Müller 1786 and bdelloid rotifers generally did not hatch until day 7 of the experiment. In all samples with *Brachionus plicatilis*, it was observed to reproduce in the beakers within a few days of hatching. Individuals of the harpacticoid copepod *Cletocampus retrogressus* Shmankevich 1875 appeared in the adult stage in January samples of both sediment (after 2 and 6 days) and Coot faeces (after 13 days). Cladoceran ephippia were the only propagules that could be clearly identified within the beakers, and were only observed in Teal and Shoveler samples.

The overall incidence of hatching in the January faecal and soil samples was significantly higher than in the November samples (59.4% vs. 11.5% hatching respectively, Fisher Exact test $p<0.0001$). The November samples were relatively low in taxon richness, with three different taxa recorded overall (two in faecal and two in soil samples, Table 1). In contrast, 10 taxa were recorded in January samples (seven in faecal and eight in soil samples, Table 2). For soil samples, the difference between months in median taxon richness was significant for both high and low salinities (Mann-Whitney-U test, $U=14$, $p=0.020$ and $U=18$, $p=0.019$, respectively). In contrast, for Coot samples the difference between months in median taxon richness was not significant for either high or low salinities (Mann-Whitney-U test, $p>0.05$).

Table 1. Presence of viable invertebrate taxa in faeces from Coot, Pintail and Mallard and soil collected in November, listing the number of samples in which live individuals were recorded in two conductivity treatments, and within-sample richness. Different soil and faecal samples were used for each treatment.

N= number of faecal samples. – = no living individuals observed.

Conductivity (mS cm ⁻²)	Soil		Eurasian Coot		Pintail		Mallard	
	0.4	4.0	0.4	4.0	0.4	4.0	0.4	4.0
N	9	9	10	10	10	10	10	10
N with hatching	0	1	0	7	0	0	0	1
Nematoda	-	-	-	1	-	-	-	-
Rotifera (Bdelloida)	-	1	-	7	-	-	-	1
Crustacea								
Ostracoda								
Cyprididae ¹	-	1	-	-	-	-	-	-
Within-sample richness								
Median	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0
Range	0	0–1	0	0–2	0	0	0	0–1

¹ *Cyprideis torosa* is the only species recorded in Veta la Palma, but we could not confirm the identity of this individual.**Table 2.** Presence of viable invertebrate taxa in faeces from Coot, Teal and Shoveler and soil collected in January, listing the number of samples in which live individuals were recorded, and within-sample richness. Each soil or faecal sample was divided and used in both conductivity treatments.

N=number of faecal samples. – = no living individuals observed.

Conductivity (mS cm ⁻²)	Soil		Eurasian Coot		Eurasian Teal		Shoveler	
	0.4	4.0	0.4	4.0	0.4	4.0	0.4	4.0
N		8		10		10		9
N with hatching (total sample)		6		6		6		4
N with hatching (divided samples)	5	6	2	5	4	2	0	4
Nematoda	5	5	-	1	-	-	-	1
Rotifera (Monogononta)								
<i>Brachionus plicatilis</i>	-	1	2	3	1	2	-	1
unidentified species	1	1	-	-	-	-	-	-
Crustacea								
Cladocera								
<i>Daphnia magna</i>	-	-	-	-	2	-	-	-
<i>Moina brachiata</i>	-	-	-	-	1	1	-	2
Copepoda								
<i>Cletocamptus</i> cf. <i>retrogressus</i>	1	1	-	1	-	-	-	-
Ostracoda								
Cyprididae ¹	2	-	1	2	1	-	-	3
Insecta								
Chironomid larvae	1	3	-	-	-	-	-	-
Tipulid larvae	2	3	-	1	-	-	-	-
Hemipteran nymph ²	1	-	-	-	-	-	-	-
Within-sample richness								
Median	1.0	1.0	0.0	0.5	0.5	0.0	0.0	0.0
Range	0–5	0–5	0–2	0–2	0–1	0–1	0	0–3

¹ *Cyprideis torosa* is the only species recorded in Veta la Palma, but we could not confirm the identity of these individuals.² Ochteridae or Gelastocoridae.

In November, invertebrates were recorded in a relatively small proportion of soil or faecal samples, and only in the higher salinity treatment (Table 1). Overall, in November samples, hatching from faecal and soil samples was recorded significantly more often in the higher than in the lower salinity treatment (Fisher Exact test, $p=0.001$). However, at the taxon level there was only a significant difference for bdelloid rotifers (Fisher Exact test, $p=0.002$). Within

bird species, richness of hatching taxa differed significantly between salinity treatments for Coot faeces (Mann-Whitney-U test, $U=15.0$, $p=0.008$), but not for the two duck species or for soil samples. Taxon richness did not differ between soil and faecal samples (Mann-Whitney U test, $p>0.05$).

In January (Table 2) the hatching frequency of chironomids, nematodes and tipulids was higher in soil than in faeces (Fisher Exact test, $p=0.007$, $p=0.002$

and $p=0.026$, respectively). In contrast, the cladocerans *Daphnia magna* and *Moina brachiata* were only observed to hatch from duck faeces, although this difference with soil was not statistically significant. Hatching frequency tended to be lower in the lower salinity treatment (Table 2), but differences were not significant (Fisher Exact test, $p>0.05$). There were also no significant differences in taxon richness between salinities for soil or faecal samples (Wilcoxon matched-pairs tests, $p > 0.05$). Individuals of an unidentified monogonont rotifer species, chironomids and a hemipteran hatched from soil but not from faeces (Table 2).

Discussion

We found a wide range of invertebrate taxa to be transported internally by birds in the wild. These taxa included nematodes, rotifers (bdelloids and monogononts), *Daphnia*, *Moina*, copepods (harpacticoids), ostracods (Cyprididae) and crane-flies (Tipulidae). The incidence of hatching was low in November but much higher in January, possibly reflecting a seasonal change in the availability of propagules. However, this may also be because Teal and Shoveler were only studied in January, since these species feed largely on invertebrates and have a high density of lamellae in their bills, making them likely to be particularly good dispersers (Green and Figuerola, 2005). Ostracods and chydorid and macrothricid cladocerans (*Alona guttata*, *Macrothrix laticornis*) were previously reported to hatch from faeces of three ducks shot in the field (Proctor, 1964). Adult ostracods have previously been shown to survive gut passage through bird guts in a captive experiment (Proctor et al., 1967). Eggs of brine shrimps (anostracans) and chironomid larvae have recently been shown to be transported internally by shorebirds (Green et al., 2005b; Green and Sánchez, 2006). Viable nematodes and bdelloid rotifers were recovered previously from external surfaces of birds (de Guerne, 1888; Thienemann, 1950; Schlichting, 1960; Örstan, 1998), but not from faeces. Contrary to Green and Figuerola (2005, p. 149), we are unaware of previous studies showing that rotifers can survive digestion by waterbirds. Experiments in captivity have shown various invertebrate taxa to have the capacity to survive digestion (see Green and Figuerola, 2005 for review) but, as pointed out by Bohonak and Jenkins (2003), studies such as ours are required to demonstrate that internal transport is realised in the field. The results presented here provide further demonstration that waterfowl are important vectors for aquatic organisms. Future research should focus on differences between habitats

and taxa in the rates with which birds move invertebrates. Information on excretion rates, retention times within the bird gut and bird movements should eventually be combined to quantify dispersal patterns.

Our results suggest that adult harpacticoid copepods are able to survive digestion by birds. Encystment as adults has been observed in harpacticoids (Bruno et al., 2001), a mechanism that might facilitate both survival of dry periods and of digestion. Further evidence for the internal transport of harpacticoids, and for their ability to survive digestion in an advanced developmental stage, comes from an observation of three live *Cletocamptus retrogressus* adults within a fresh Mallard dropping collected from the Sanlúcar salt pans within the Doñana complex on 19 April 2005 (M. I. Sánchez and A. J. Green, unpublished data).

By filtering faecal samples taken previously at the same study site, Figuerola et al. (2003) showed that all the waterfowl species included in the present study transport cladoceran ephippia, although they did not test viability of ephippia or other propagules recorded. By using more labour intensive methods on a smaller number of samples in the present study, we have confirmed transport of viable cladoceran ephippia and recorded many taxa not previously reported by Figuerola et al. (2003), although they did record many invertebrate eggs that could not be identified owing to the absence of suitable keys. Despite the reasonably large sample size used in the present study (a total of 115 faecal or soil samples placed into 152 beakers), we are likely to have underestimated the number of viable taxa transported by wintering waterfowl in Doñana for several reasons. We sampled a very small proportion of the birds present in the area, and are not likely to have provided the right hatching cues for all taxa. Furthermore, we sampled only two of the five months (October to February) when wintering waterfowl are abundant, and only three of 10 abundant Anatidae species. Due to the difficulties inherent in identifying and counting propagules in our samples, and because many taxa reproduced within the beakers, we were not able to establish how many individuals of each taxon were present in the original samples. However, inspection of the faeces remaining after taking subsamples for the hatching experiment showed that the remaining Shoveler faeces contained up to 16 ephippia per sample and Teal faeces up to 35 ephippia (see also Figuerola et al., 2003 for data on numbers of ephippia per dropping in the same study area).

The broad spectrum of taxa recorded and the relatively high proportion of faecal samples containing viable invertebrates in the present study suggests that internal dispersal via waterfowl is a common

process of major importance. Average counts of wintering waterfowl in the Doñana marshes exceed 200,000 birds, and we used less than 5 % of mean daily faecal output in each of our samples (see methods). Thus, our results suggest that millions of droppings containing viable invertebrate propagules are excreted each day in Doñana. The rapid colonisation of newly created aquatic habitats (Louette and De Meester, 2005) and the close link between waterfowl movements and the genetic structure of cladoceran populations (Figuerola et al., 2005) has led to recent suggestions that waterfowl are major vectors for cladoceran dispersal. Our results complement these studies by providing direct field evidence of transport of two cladoceran genera (*Daphnia* and *Moina*) which has been lacking until now. Waterfowl-mediated dispersal is likely to have a particularly important influence on invertebrate communities in dynamic, temporary aquatic systems such as those found in Doñana. Data on numbers of birds, their movements and gut retention times suggest that most invertebrates dispersing via waterfowl passing through Doñana will be transported over shorter distances (< 20 km), but that long distance dispersal events over hundreds of km will still occur on a regular basis (Green and Figuerola, 2005). However, viable propagules dispersed to new habitats will not necessarily become established there (De Meester et al., 2002; Green et al., 2005a).

Observations of feeding behaviour suggest that the Coots sampled had been feeding within Veta la Palma ponds, where conductivity usually exceeds 4 mS cm⁻² (Frisch et al., 2006b). The ducks were feeding at night, and it is likely that the Mallard, Pintail and possibly other ducks had been feeding outside Veta la Palma in wetlands of lower salinity. This would explain the hatching of cladocerans from duck faeces and their absence from soil samples or Coot faeces. Cladocerans are rare in fish ponds where the faeces were collected (Frisch et al., 2006b), suggesting that the ephippia were consumed in other areas of the Guadalquivir marshes and transported to the ponds.

As the soil studied consists of very fine clay and sticks easily to any damp surface, it is a likely source of propagules transported externally on birds that move between aquatic habitats. Because the soil was dry upon collection, it is likely that the propagules that hatched in our samples are resistant to desiccation and could therefore survive during flight, at least for short periods. As ducks fly at speeds of around 1 km/min (Welham, 1994), these propagules are likely to be readily transported between different waterbodies. Waterbirds have long been known to move soil on their feet (de Guerne, 1888; Green and Figuerola, 2005). Our results suggest that insects and nematodes

are more likely transported by birds externally than internally, although more data are required to confirm this. The amount of propagules transported would depend partly on the relative mass of soil and faeces transported between habitats, which is unknown. Coot and Mallard have previously been shown to transport cladoceran ephippia on feet and in plumage at our study site (Figuerola and Green, 2002b).

With the exception of bdelloid rotifers, we found no evidence that salinity generally impedes hatching over the range of 0.4–4 mS cm⁻². Although hatching of propagules after dispersal between waterbodies within and beyond the Doñana complex may thus be successful in habitats with different salinities, subsequent colonization is also dependent on various other factors (De Meester et al., 2002). Species richness of invertebrates is generally lower in highly saline wetlands (Green et al., 2005a), and our results may have been different if we had used a broader salinity range. Furthermore, if we had used a larger sample size or quantified reproductive rates within our cultures, we might have detected significant treatment effects with the salinities used.

Our study suggests that dispersal via waterfowl is a more frequent and important process for more invertebrate groups than has previously been proposed. For example, the concept that insects may disperse passively via birds is practically absent from the literature (but see Green and Sánchez, 2006). Many authors have assumed implicitly that only invertebrates with resistant eggs or ephippia are able to disperse passively via animals (see e.g. Bilton et al., 2001). Our results suggest that this assumption is incorrect, since various organisms that emerged from faeces as adults or larvae (e.g. *Cletocamptus*, ostracods and tipulids) appeared to have survived digestion in a more advanced developmental stage (see also Bartholmé et al., 2005; Green and Sánchez, 2006). This has major implications for our understanding of dispersal processes in aquatic systems, as it suggests that the spectrum of invertebrates which are able to disperse via birds is not necessarily limited to those producing dormant eggs. More quantitative studies are needed to compare the importance of bird-mediated dispersal for different invertebrate taxa with that of dispersal by wind, rain and other vectors.

Acknowledgments

We are grateful to E. García Macarro for help in monitoring the samples and to C.-P. Stelzer for his help with the identification of *Brachionus plicatilis*. DF was supported by a postdoctoral fellowship from the Spanish Ministry of Education and Science (MEC)

and JF by a Ramon y Cajal contract from MEC. Our research was funded by the Spanish Ministry of Environment's Doñana 2005 restoration project. J. E. Havel, D. G. Jenkins and anonymous referees provided helpful comments on earlier versions of the manuscript.

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