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Passive internal dispersal of insect larvae by migratory birds

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It has long been assumed that the resistant eggs of many zooplankton are able to survive passage through the gut of migratory waterbirds, thus facilitating their dispersal between isolated aquatic habitats. We present the first evidence that such passive internal transport within birds may be relevant for insect populations. In three out of six faecal samples from black-tailed Godwits on autumn migration in southwest Spain, we found larvae of the chironomid *Chironomus salinarius* which had survived gut passage. Although adult chironomids can fly, they are likely to disperse greater distances when transported as larvae via birds. In insects with discrete generations, such passive transport also enables colonization of new habitats at times when flight by adults is not an option.

Keywords: chironomidae; endozoochory; internal transport; passive dispersal; waders

1. INTRODUCTION

Darwin (1859) suggested that the wide distribution of many aquatic invertebrates could be explained by the passive dispersal of their eggs by migratory waterbirds. Although he was particularly concerned with molluscs, it was later shown that the resistant propagules of Cladocera and other zooplankton, as well as of bryozoans, can attach themselves to birds or survive passage through their gut (see Figuerola & Green 2002; Green & Figuerola 2005). There is increasing evidence that such dispersal by ducks (Anatidae), waders (Charadriiformes) and coots (Rallidae) is indeed commonplace in the field (Figuerola *et al.* 2003; Green *et al.* 2005).

To the best of our knowledge, no one has previously suggested or demonstrated that aquatic insects can also be dispersed by migratory birds. While studying the diet of shorebirds in the Odiel marshes (Sánchez *et al.* 2005), it came to our attention that apparently intact chironomid larvae were sometimes visible in fresh faeces. Here, we present a preliminary study of the viability of larvae recorded in the faeces of the black-tailed Godwit *Limosa limosa*.

2. MATERIAL AND METHODS

Six faecal samples were collected from the saltworks of the Odiel marshes in Huelva province in southwest Spain (37°17' N, 06°55' W) on 21 August 2002 during autumn (southwards) migration. These saltworks are a site of international importance for waders migrating through the East Atlantic flyway (Sánchez *et al.* in press *a*). The black-tailed Godwit is the second most abundant wader at this site, with up to 7000 at any one time (Sánchez *et al.* in press *a*). An

estimated 15.5 million waders (including 200 000 black-tailed Godwits) migrate along the East Atlantic Flyway (Stroud *et al.* 2004).

We collected fresh faeces from a roost site on a dyke used by a monospecific flock of godwit. Each sample was found approximately 5 m from the water's edge and was carefully separated from the soil (discarding that part in contact with soil) and placed in a tube. Within 2 h, each sample was resuspended in a Petri dish in the laboratory containing filtered water from the saltworks, and the number of live larvae was counted. Individuals exhibiting normal undulation behaviour, responding to physical stimuli and displaying normal shape and colour were scored as 'living'. Using a binocular microscope, the number of intact (but dead) chironomid larvae and digested larvae (represented by countable sclerotized heads) were counted. The total proportion of the faecal sample made up by chironomid larvae was estimated visually.

3. RESULTS AND DISCUSSION

Three out of six faecal samples contained at least one live fourth instar chironomid larva (table 1). In total, 12 out of 95 intact larvae recorded were still alive. They were observed for 4 h, with no sign of harmful effects of gut passage. Although the great majority of larvae were digested (table 1), at the time of defecation the number of larvae that remained alive may have been higher, due to the delay between sample collection and analysis.

All larvae were of *Chironomus salinarius* Kieffer. This taxon has a cosmopolitan distribution in brackish and saline wetlands (Armitage *et al.* 1995) which is compatible with a capacity to disperse long distances via migratory birds, although it may be a species complex and requires further study via molecular techniques.

Godwits and other waders move regularly over distances of up to 20 km between feeding and roosting sites while at stopover sites (Farmer & Parent 1997, P. M. Potts, personal communication 2004), thus facilitating passive dispersal between different water-bodies within a wetland complex. Godwits fly at speeds of 60 km h⁻¹ (Welham 1994), and could potentially disperse chironomid larvae for great distances during their migrations between breeding areas in northern Europe and wintering areas in Africa (Wetlands International 2002). The minimum retention time recorded for brine shrimp *Artemia* eggs consumed by a different wader in captivity (the Killdeer *Charadrius vociferus*) was 5–15 min, although the mode was 90 min and the maximum 26 h (Proctor *et al.* 1967). Although our faecal samples were collected on dry land, most Godwits rest and defecate over water, thus facilitating the survival and effective dispersal of any larvae within.

Chironomid larvae are extremely abundant in aquatic ecosystems (Armitage *et al.* 1995) and benthic larvae are a major component of the diet of migratory waders (Rehfish 1994) and ducks (Krapu & Reinicke 1992), such that internal dispersal events may be commonplace. *C. salinarius* has a high resistance to desiccation (Suemoto *et al.* 2004) and tolerates extreme salinity fluctuations (Armitage *et al.* 1995), adaptations that are likely to help it survive gut passage.

It is well known that, as the ingestion rate of animals increases, their digestive efficiency and transit time through the gut decreases. As waders consume more brine shrimp eggs, the proportion that is

Table 1. Numbers of chironomid larvae recorded in each sample of godwit faeces, and proportions of sample volume constituted by chironomid larvae. All larvae recorded intact or alive were fourth instars.

	1	2	3	4	5	6
percentage of larvae	>90	>90	<10	>90	>90	>90
total larvae	530	176	3	88	373	432
larvae intact	18	76	0	0	0	1
larvae alive	5	6	0	0	0	1

destroyed decreases (Sánchez *et al.* submitted). As ducks consume more seeds, the proportion that is destroyed decreases (Figuerola *et al.* 2002). If common toads *Bufo bufo* are given earthworms *ad libitum*, they gorge themselves to such an extent that the worms can survive passage through the gut (Frazer 1983). Likewise, chironomid larvae are more likely to survive gut passage when waders are feeding intensely on large concentrations of larvae, such as those found in the sediments of saltpans (Velasquez 1992; Sánchez *et al.* in press *b*).

Is passive dispersal of insect larvae via birds important, given the capacity of adult insects to disperse via active flight? Adult chironomids generally disperse over short distances of less than 1 km (Delettre & Morvan 2000), although passive dispersal via wind sometimes takes adults much further (Armitage *et al.* 1995). Dispersal of adults by wind is restricted in its orientation and unlikely to be directed towards suitable habitats. Waterbirds may disperse larvae upwind as well as downwind, and will direct them to other aquatic habitats. Genetic studies to date often suggest surprisingly low rates of interchange between aquatic insect populations on neighbouring streams (see Bohonak & Jenkins 2003 for review). Thus, even rare dispersal events mediated by birds may be of importance in the metapopulation ecology of aquatic insects. Furthermore, for taxa with discrete generations, passive dispersal at the larval stage can enable colonization of newly available habitat (e.g. temporary wetlands fed by unpredictable rainfall) when active dispersal by adult insects is not an option. In chironomids (Armitage *et al.* 1995) and many other insects, the larval stage is much longer than the adult stage, providing a much wider window of opportunity for dispersal. It is also conceivable that insect eggs or larvae could be transported externally on feet or feathers (Green & Figuerola 2005), although we are unaware of any evidence for this.

At present, there is no information about which other chironomid taxa or other insect groups can be readily dispersed via waterbirds. Corixid eggs are often observed in waterbird faeces (Figuerola *et al.* 2003; Fuentes *et al.* 2004), although to date, there is no evidence that they are viable. Passive dispersal via birds may play a hitherto overlooked role in the population ecology and evolution of aquatic insects. The extent and importance of insect dispersal via birds requires further study.

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