Why do no specialized necrophagous species exist among aquatic insects?

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Abstract: Among terrestrial insects, there is a rich guild of specialized necrophagous taxa, i.e., that feed directly on carrion. These organisms constitute a significant functional component of terrestrial ecosystems, and have recently been extensively studied because of their importance in forensic entomology. Nothing similar exists in lotic environments, although paradoxically, insects are the most important group of invertebrates in streams and rivers, where they constitute up to 70 to 90% of benthic communities. We present some hypotheses as to why specialized necrophagous taxa have evolved among terrestrial, but not among aquatic insects. We suppose that the lack of specialized necrophagous aquatic insects was the result of many synergic evolutionary pressures, partly related to the distinctive physical features of lotic environments and partly to processes of competitive exclusion with other closely related arthropods.
Keywords: necrophagous taxa, aquatic insects, carrion

A rich and diverse fauna of specialized necrophagous or scavenger (i.e., feeding on carcasses) insects lives in terrestrial environments. These organisms mostly belong to the orders Diptera and Coleoptera. They constitute an important functional component of terrestrial ecosystems and have been studied extensively because of their importance in forensic entomology (Castner and Byrd 2009). Members of the families Calliphoridae, Sarcophagidae (Diptera), and Silphidae (Coleoptera), among others, are the result of a long evolutionary process that selected specialists in the detection and consumption of nonliving animal organic matter. Only a few examples exist (e.g., caddis larvae feeding on salmon carcasses) in lotic environments, although insects are the most important group of benthic invertebrates in streams and rivers (Merritt et al. 2008). Thirteen orders, almost ½ of those in the class Insecta, include species with aquatic or semiaquatic habits. In 5 of these orders, all taxa are aquatic (Merritt and Wallace 2009) with only terrestrial adults. In fact, aquatic insects exhibit high diversity and abundance, a broad distribution, and play a key role in the functional structure of running water ecosystems, where they occupy almost all trophic niches (Giller and Malmqvist 1988) except one: no truly necrophagous aquatic insects have evolved functionally to feed entirely on carrion (Castner and Byrd 2009).

Compared to the large number of studies published in aquatic entomology in recent decades, the number of studies dedicated to freshwater insects associated with animal carcasses is small (Merritt and Wallace 2010). Some investigators have focused on the decomposition of salmonid carcasses primarily from Nearctic rivers with spawning migrations of anadromous salmonids (Elliott 1997, Monaghan and Milner 2008a, b, c, Hocking et al. 2013). These carcasses are a significant source of organic material and inorganic nutrients in such streams (Wipfli et al. 1998, Chaloner and Wipfli 2002, Wipfli et al. 2003). Studies of the decomposition process of trout carcasses in northern Italy were done by analyzing mass loss, colonizing assemblages, and the importance of macro- and mi-

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DOI: 10.1086/677038. Received 20 October 2013; Accepted 10 January 2014; Published online 29 May 2014.

croconsumers (Fenoglio et al. 2005, 2010a). Other investigators have focused on the forensic aspects of aquatic insect–carrion associations (Merritt and Wallace 2010). For example, aquatic insects have been used as indicators of postmortem submersion intervals (Haskell et al. 1989, Keiper et al. 1997, Wallace et al. 2008). Numerous aquatic insects are usually found in association with carrion, and a summary of taxa was reported by Keiper and Casamatta (2001). Studies have been done on types of carrion, such as fish (Chaloner and Wipfli 2002, Fenoglio et al. 2005, 2010a), pigs (Vance et al. 1995), rats (Keiper et al. 1997, Tomberlin and Adler 1998), and humans (Merritt and Wallace 2010), but specialized necrophagous aquatic insect taxa have never been found. Here we present 6 hypotheses regarding why specialized necrophagous taxa have evolved among terrestrial but not among aquatic insects. For each hypothesis, we present and compare evolutionary and ecological drivers that could explain the absence of specialized necrophagous insects in aquatic habitats.

HYPOTHESES

Specialized necrophagous taxa constitute a relatively small proportion of all terrestrial insects, so the probability of finding necrophagy among aquatic lineages may be low

This hypothesis may be phylogenetic and related to the presence of evolutionary constraints that prevented the colonization of freshwater environments by some lineages of Insecta. Both fossil records and morphological evidence (such as the presence of tracheal systems in nearly all aquatic insects) support the hypothesis that insects are a terrestrial group secondarily adapted to living in freshwater (Pritchard et al. 1993, Chapman 2013). Several groups of insects independently invaded aquatic habitats during various geological eras (Wichard et al. 2002). Both Coleoptera and Diptera colonized freshwaters, but the main necrophagous phylogenetic lineages among these groups have no aquatic representatives, except for some cases, such as Syrphidae (Diptera; Wagner et al. 2008). This notion of phylogenetic constraint is supported by the following ecological arguments.

Aquatic insects have significant trophic plasticity, including consumption of carrion, without functioning as specialists

Most of the energetic support for lotic food webs in small (low-order) streams originates from riparian terrestrial-plant organic matter, such as dead leaves introduced during autumn abscission (e.g., Petersen and Cummins 1974, Vannote et al. 1980, Merritt et. al. 2008). This dead organic matter, in combination with stream microbes, constitutes the primary food resource for detritivores (shredders and collectors; Merritt et al. 2008). Thus, in small streams, detritus rather than living plant material is the base of most invertebrate food chains (e.g., Allan and Castillo 2007).

In general, aquatic insects have considerable plasticity in the foods they ingest (e.g., Cummins and Klug 1979, Clifford and Hamilton 1987). As pointed out by Merritt et al. (2008), based on food ingested, all aquatic insects are omnivores, at least in their early instars. For this reason, lotic insects have been grouped into functional feeding groups (FFG) according to morphological and behavioral mechanisms associated with food acquisition: shredders, scrapers, collectors, and predators (Cummins 1974, Cummins and Klug 1979, Merritt et al. 2008). Ingestion varies substantially within FFG categories, and large trophic differences can exist among these categories, depending on possible variations in food availability or ontogenetic shifts in diet (Malmqvist et al. 1991, Fenoglio et al. 2010b). For example, in a laboratory experiment, a terminal-instar limnephilid (Trichoptera) shredder shifted to a carnivorous diet (Anderson 1976). In other studies, some functional predators were able to ingest differing amounts of live plant material (Lucy et al. 1990, López-Rodríguez et al. 2009). Some limnephilid shredders can burrow into and ingest dead salmonid flesh (Minshall et al. 1991, Wallace et al. 2008). Fenoglio et al. (2010a) found shredders, mainly limnephilids and nemourids (Plecoptera), burrowing, residing in, and ingesting tissue of trout carcasses. Apart from the direct ingestion of fish tissue, these aquatic insects indirectly increase carrion breakdown rates by fragmentation and increased action of flows, and can produce large quantities of fine organic particles. Fine particulate organic matter (FPOM) attracts many gathering collectors, in particular Chironomidae (Diptera), Baetidae, Caenidae, and Ephemerellidae (Ephemeroptera) (Wipfli et al. 1998, Chaloner and Wipfli 2002, Fenoglio et al. 2005, Merritt and Wallace 2010). Filtering collectors, such as Simuliidae (Diptera), Hydropsychidae, and Philopotamidae (Trichoptera), can use carrion as shelter and as a food source, collecting FPOM derived from the carcasses (Minakawa et al. 2002). Some predators, such as Chloroperlidae (Plecoptera), scavenge on dead fish (Nicola 1968, Ellis 1970), whereas others, such as Gomphidae, Calopterygidae (Odonata), Perlidae, and Perlodidae (Plecoptera), probably are attracted by the high concentration of prey associated with carrion (Fenoglio et al. 2005, Merritt and Wallace 2010). Chaloner and Wipfli (2002) suggested that the use of nonliving animal material by aquatic insects can vary by species, with a main role played by collector–gatherers and shredders.

Carrion is more difficult to locate in lotic than in terrestrial environments

Evolutionary pressures to select specialized necrophagous taxa may have been stronger in terrestrial than in fluvial environments because of the different physical characteristics of these habitats. Carrion begins to decompose immediately after the death of the animal, and undergoes a complex transformation that includes emission of gases and volatile organic compounds (Paczkowski and Schütz 2011). In terrestrial systems, these chemicals spread in all directions by diffusion and long-distance transport by the wind. Chemoreception, and in particular olfaction (sensu Chapman 2013), enables terrestrial necrophagous insects to detect these chemical stimuli even at great distances and to locate the carrion rapidly by flying along a plume of odor. Chemoreception and olfaction (i.e., the ability to detect compounds in the gaseous state), in particular, has been widely studied in terrestrial insects, but this topic has been investigated to a much lesser extent in aquatic insects (Motyka et al. 1985, Crespo 2011). Aquatic insects are secondarily adapted to living in water (Pritchard et al. 1993), and their chemoreception is likely to depend mostly on contact chemoreception (i.e., the ability to detect compound in solutions) (Motyka et al. 1985, Chapman 2013). The diffusion of chemicals can be much more rapid, widespread, and multidirectional in terrestrial than in lotic environments because the diffusion coefficients of chemicals in water are much lower than in air (Denny 1993). Moreover, in streams and rivers, the unidirectional flow of water strongly influences the diffusion of chemicals, creating chemical plumes that originate from the carrion and disperse in only one direction. Unidirectional flow implies that only downstream insects can intercept this cue and locate its source, thereby severely limiting the access to and the importance of carrion as a food source. Moreover, the differences in carrion detection between terrestrial and lotic environments influence the relative importance of this resource for adult and larval consumption by aquatic insects. In addition to direct consumption by adults, a significant part of carrion consumption in terrestrial environments is through the activity of larval stages (especially among Diptera: Castner and Byrd 2009). Maggots hatch from eggs that are directly laid on carrion by females, which identify and reach the resource by flying, This requires a precision that is not often possible in lotic environments for the above-mentioned reasons.

Greater diversity in the availability of animal wastes exists in terrestrial vs lotic systems

Dung (i.e., animal excrement) and carrion share some important characteristics: both are discrete, patchily distributed, ephemeral trophic resources, and serve as temporary microhabitats for many insect species (Hanski 1987). Terrestrial insects find both food sources by moving along a chemical plume of odor, and both are rapidly colonized and used. Both are affected by direct consumption by adult insects, egg-laying, and consumption by preimaginal stages. These similarities suggest that similar evolutionary pressures selected specialists in the consumption of carrion and fecal material. In terrestrial systems, dung and carrion are the main trophic resources for some families in the same 2 orders: Diptera and Coleoptera (Putman 1983). For example, among Sarcophagidae, some species consume dung, whereas others prefer nonliving animal matter, and some Calliphoridae and Silphidae larvae feed indiscriminately on dung or carrion. The evolution of necrophagous specialists may have occurred or otherwise been enhanced within lineages that included dung consumption. Thus, evolutionary pressures for the trophic use of animal wastes (dung or carrion) have been very different in terrestrial and in lotic systems. Terrestrial ecosystems usually have large numbers of herbivorous mammals and their predators that produce large amounts of feces, a rich and widespread trophic resource. Terrestrial herbivores also are generally larger and produce larger localized fecal masses than aquatic ones, such as fish. A different situation occurs in rivers and streams, where large primary consumers are usually lacking. For this reason, evolutionary pressures for the selection of taxa specialized in the consumption of animal wastes (including both carcasses and dung) were certainly stronger in terrestrial than in lotic systems.

The permanence and availability of carrion is shorter in lotic than in terrestrial environments

Another secondary aspect is that carrion in lotic environments is subject to physical fragmentation and chemical degradation to a much greater extent than in terrestrial systems. Organic detritus in streams is subject to important physical forces, such as fragmentation and abrasion by current (Paul et al. 2006). This process reduces the temporal persistence of the resource and its importance for potential specialized consumers.

Exclusive competition with Crustacea may have occurred in aquatic environments

In aquatic environments, scavenger insects would have to compete with other arthropods for carrion. Very few crustaceans live in terrestrial environments, so that insects evolving on land were able to occupy almost all the available ecological niches, including those based on carrion consumption. In contrast, Crustacea are diverse and competitive in aquatic environments, where they have evolved as nonspecialized scavengers (Dauby et al. 2001, de Broyer et al. 2004). With their prior invasion of freshwaters, crustaceans were easily able to occupy the scavenger ecological niche, thereby limiting or excluding insects. In fact, where they are present, freshwater crustaceans (e.g., crayfish) are an important nonspecialized group of necrophagous invertebrates (Davis and Huber 2007, Gherardi 2007, Vanin and Zancaner 2011)

CONCLUSION

We hypothesize that the lack of specialized necrophagous aquatic insects was the result of many synergic evolutionary and ecological pressures, partly related to the unique physical and functional features of lotic systems and partly to processes of competitive exclusion with noninsect arthropods.

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