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Colonization under threat of predation: avoidance of fish by an aquatic beetle, *Tropisternus lateralis* (Coleoptera: Hydrophilidae)

Abstract Documenting the role of past interactions in the assembly of present communities has proven problematic. Colonization is a key process in community assembly that is both potentially driven by past interactions and amenable to experimental approaches. Colonization and oviposition by an aquatic beetle (*Tropisternus lateralis*) was assayed in the presence and absence of both 'harmless' and tactilely/visually isolated predatory fish (*Lepomis gibbosus* and *L. macrochirus*). Beetles avoided each treatment with fish when compared to fish-free experimental pools. Activity levels after colonization also differed significantly between adults in fish and fish-free tanks. Predator effects on species composition are typically ascribed to contemporary predation events; the presence of a strong avoidance response demonstrates that past species interactions affect present distributions and may play an important role in the ongoing assembly of contemporary communities. Documentation of such avoidance behavior in a growing number of species fundamentally alters our view of the processes affecting species distributions and the process of community assembly.

Keywords Oviposition site choice · Habitat selection · Predation risk · Aquatic systems · Community assembly

Introduction

The study of community assembly is central to our understanding of community structure and species diversity in natural systems (Diamond 1975). Much of community theory pertains to the simple question of how patterns of

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species presence and absence observed in natural systems are generated. Consideration of the role of past interactions in present-day patterns of species distribution, resource use, and species co-occurrence, and what constitutes evidence for such effects, produced one of the most spirited ecological/evolutionary debates in recent times (e.g. Grant 1972; Diamond 1975; Connell 1978, 1980; Strong et al. 1979, 1984; Gilpin and Diamond 1982; Hastings 1987; see also Cody and Diamond 1975; Lewin 1983; May 1986). Equally central to understanding species distributions and species co-occurrences is the role of past interactions in the ongoing assembly of natural communities. How past interactions affect community assembly impacts strongly on our view of how communities arise and change, and brings evolution into community ecology in a very direct way.

Assuming that species interactions do effect the evolution of species within a community context, we would expect past interactions to leave a detectable signature, Connell's *Ghost of Competition Past* (1980). Unequivocally identifying that signature, as Connell pointed out, is a difficult proposition. Colonization is one critical process of community assembly that lends itself to experimental investigation and provides an opportunity to 'observe' the role of past interactions. Innate species avoidance (a form of habitat specialization) in the form of selective colonization can only arise if habitat overlap, species interactions, and thus selection are fairly intense at some point in the history of a species pair. Passive avoidance, i.e. simple non-overlap of habitats, precludes selection for active species avoidance, just as increasing specialization limits certain evolutionary directions (Holt 1985, 1987), because selection can only operate in occupied habitats.

Can species detect and respond to fine scale variation in their biotic environment? Aquatic ecologists have readily accepted the notion that habitat selection affects community assembly on a gross scale, i.e., in freshwater systems lotic species prefer lotic to lentic habitats, with the converse being true of lentic species. However, we have been reluctant to embrace the idea that this same

phenomenon can be applied to natural variation in environmental characteristics on a much finer scale, including factors such as the faunal composition of habitats. The extensive evidence from terrestrial phytophagous insects suggests a remarkable capacity to respond to fine-scale environmental variation (e.g. Rausher 1983, 1993; Singer 1984, 1986; Thompson and Pellmyr 1991; Renwick and Chew 1994; Camara 1997). However, examples from aquatic species are far less extensive and are limited largely to mosquitoes (e.g. Walton et al. 1990; Petranka and Fakhoury 1991; Blaustein and Kotler 1993; Sherratt and Church 1994; Stav et al. 1999) and amphibians (e.g. Resetarits and Wilbur 1989; Crump 1991; Petranka et al. 1994; Spieler and Linsenmaier 1997; Summers 1999; Kiesecker and Skelly 2000). How does such fine scale habitat selection affect the assembly of natural communities? Here the case is less clear for both terrestrial and aquatic systems, though certainly oviposition preferences of terrestrial insects affect patterns of distribution and abundance on host species. In order to examine these questions in more detail, I conducted a pair of experiments in aquatic mesocosms (e.g., Morin 1983; Resetarits and Wilbur 1989; Wilbur 1997) to test whether colonizing adults of the common, obligately aquatic hydrophilid beetle, *Tropisternus lateralis*, could preemptively detect and avoid colonizing (and ovipositing) in artificial mesocosms with predatory fish.

While many abiotic factors are presumed to influence colonization and oviposition in aquatic systems (e.g. differences between lentic and lotic habitats), the role of biotic factors has been largely ignored. The presence of predatory fish is perhaps the biotic factor most likely to influence the suitability of aquatic sites for colonization in many species with complex life cycles. Predation by fish dramatically affects species composition, species diversity, and community structure in aquatic systems (Hrbacek 1962; Brooks and Dodson 1965; Macan 1966; Morin 1984; Werner and McPeek 1994; Wellborn et al. 1996). Fish can prevent successful colonization and reproduction by many species of aquatic insects and amphibians. Their singular effectiveness as predators suggests that fish avoidance should be an important oviposition strategy for fish intolerant species and selection should be strong for the evolution of appropriate avoidance mechanisms.

The common hydrophilid beetle, *T. lateralis* fits the criteria for species likely to elicit selective colonization/oviposition in response to fish because adults, and especially larvae, are obligately aquatic and highly vulnerable to fish predation. Adult *T. lateralis* are widespread, locally abundant (Zalom et al. 1979a), aquatic grazers/scavengers/predators that disperse aerially to aquatic habitats after emergence from the obligately terrestrial pupal stage. Each adult, upon emergence or after leaving a previously occupied pond, must select a new habitat to occupy and in which to reproduce. Mating takes place in the pond and females lay conspicuous silken egg cases attached to stems or other structures (Zalom et al. 1979b), a feature which allows accurate

assay of oviposition responses. Larvae hatch in days to weeks and are highly voracious, generalist predators that can be locally abundant and play a potentially important role in aquatic systems (Zalom and Grigarick 1980; Walton et al. 1990; Batzer and Resh 1991; Magnusson and Hero 1991).

Materials and methods

Two experiments were conducted at the Experimental Pond Facility of the Illinois Natural History Survey, Champaign County, Illinois, USA. Experimental ecosystems for both were constituted in 1.8 m diameter round cattle tanks 0.6 m deep, holding 1,000 l, using standard protocols (Morin 1983; Resetarits and Wilbur 1989; Wilbur 1997). In experiment 1, all pools were filled, covered with lids of fiberglass screening, and allowed to age several weeks before receiving 1 kg each of dried grass litter taken from upland areas (to avoid introducing aquatic organisms). Six pairs of pools were placed 8 m apart at one end of a level 7×100 m gravel pad, with paired pools separated by 1 m. The pad had approximately 30% plant cover and was surrounded by old field vegetation. Two, 60–70 g, pumpkinseed sunfish (*Lepomis gibbosus*) were added to one randomly selected pool per pair. Fish were prevented from preying on colonists by having their mouths temporarily tied so that their gape was exceeded by even the smallest *T. lateralis*. Fish were added on 19 August and all pools were opened to colonization on 20 August; the experiment ran for 5 days. Observations on adult beetle activity were made twice daily (1 day, 1 night) from 21 to 23 August. Egg cases were counted and adult beetles removed on the evening/morning of 23–24 August. Lids were immediately replaced and tanks were again checked for adult beetles on 25 August when a few additional adults were collected.

The second experiment differed from the first in the following ways. Mesocosms received 0.5 kg of grass litter, were inoculated with a zooplankton/phytoplankton mixture, and were set up in two sets of three pairs each, with their schedules offset by 10 days. Fish enclosures were constructed from 115 l plastic trash cans from which two 25×50 cm sections were removed and replaced with an opaque covering consisting of one layer of 99% shade cloth and one of 'no-see-um' netting. One enclosure was placed into each tank and two, 50–60 g, bluegill sunfish (*L. macrochirus*) were randomly assigned to one of each pair of tanks and placed in the enclosures. An individual air line was placed into each enclosure (both fish and fish-free) and solid, tightly fitting lids were added, virtually eliminating any light penetration into the enclosures. Water from inside the enclosures was actively exchanged with water in the tanks once a day by slowly lifting the enclosures 90% out of the water, allowing the water inside to flow out through the mesh, and then slowly forcing the enclosure down in the tank as it refilled. This augmented passive exchange across the screening (which was enhanced by flow from the air lines) and assured adequate mixing and chemical communication between the enclosures and the tank proper; this procedure was done for both fish and fish-free tanks. Tanks were assayed for adult beetles only; the first set of six tanks was opened for colonization on 31 July and assayed on 5 August, and the second set opened on 9 August and assayed on 15 August. Tanks were tightly covered after being assayed, so that the two runs of the experiment could not share any individual beetles.

Both experiments used randomized block designs for analysis of variance, with pairs as blocks in experiment 1, and time as blocks, with pair nested within time, in experiment 2. Counts of beetles (experiments 1 and 2) and egg cases (experiment 1) were analyzed by ANOVA on square root transformed count data. Activity (experiment 1) was analyzed for differences between fish and fish free tanks using Fisher's Exact Test for 2×2 contingency tables. All tests used type III sums of squares and $\alpha=0.05$. Data were analyzed using SAS for Windows release 6.11 (SAS Institute 1995).
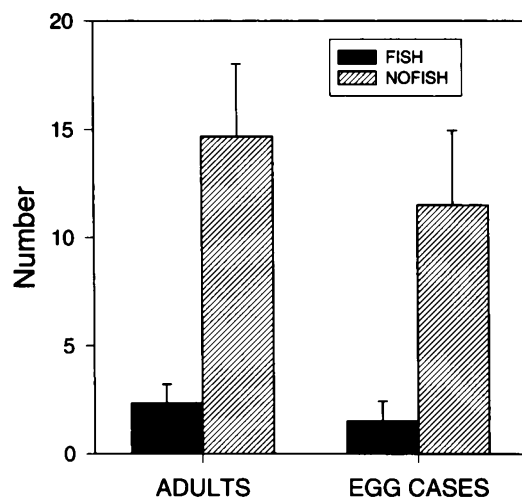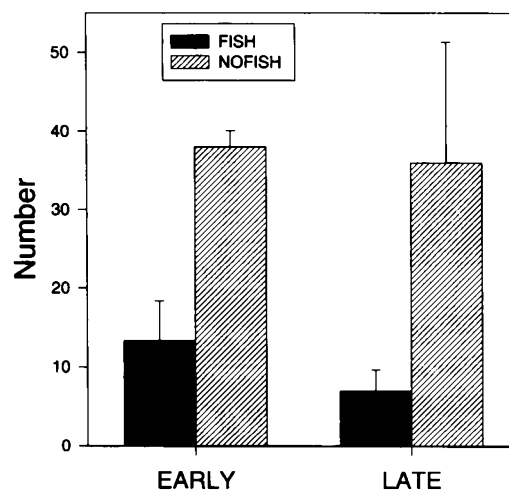
Fig. 1 Relative attractiveness of experimental pools to *Tropis-ternus lateralis* in experiment 1. Each *bar* represents the mean of six pools ±1 SE for the number of adult *T. lateralis* colonists (*left pair of bars*) and the number of egg cases produced (*right pair*) in pools containing 'sham' predatory fish (*dark bars*) and no fish (*light bars*). Differences for both adults and eggs are significant (see text)
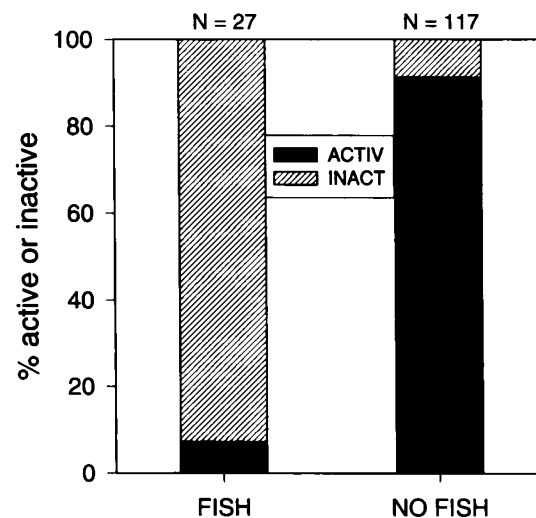
Fig. 2 Differences in activity of *T. lateralis* colonizing fish-free experimental pools (*right bar*) and pools with sham predatory fish (*left bar*). Bars divide the percent activity between beetles that were actively swimming (*dark segments*), which is typical behavior for *T. lateralis*, and those that were immobile (*light segments*). Numbers above each bar refer to the number of observations for each treatment. Difference is highly significant (see text)

Results

With the exception of tiny surface dwelling dipterans, *T. lateralis* comprised >90% of adult insect colonists over the first 6 days in both experiments. Adult beetles appeared in both fish and fish-free pools within 24 h of removing the screen lids and differences in the number of adult beetles were evident beginning with the first behavioral survey (24 h after lid removal in experiment 1). The distribution of *T. lateralis* among pools was dramatically affected by the presence of fish in both experiments although fish were incapable of consuming beetles. In experiment 1, adult *T. lateralis* clearly avoided pools with predatory fish resulting in significantly skewed distributions of adult beetles ($F_{1,5}$=17.87, P<0.01) (Fig. 1) and egg cases ($F_{1,5}$=9.88, P<0.02)(Fig. 1). Fish-free pools had, on average, 5.8 times more adults and 6.5 times more egg cases than pools with fish. The number of adult colonists explained 96% of the variance in the number of egg cases between treatments, suggesting that oviposition strategy did not differ between treatments and that number of adults is a reliable indicator of oviposition activity. The few beetles that did colonize pools with fish dramatically altered their activity levels and behavior compared to those in fish-free pools (Fig. 2). Adult beetles were significantly less active in the pools containing 'sham' fish (Fisher's exact test for a 2×2 contingency table, df=1, χ^2=86.05, P<0.00001), and were even found completely out of the water on the sides of the tanks. Most of the observations classified as inactive in the fish-free pools were amplectant pairs and females depositing egg cases. No individuals in fish-free pools were found immobile at the waters edge or out of the water, as was common in pools with fish.

Fig. 3 Relative attractiveness of experimental pools to *T. lateralis* in experiment 2. Each bar represents the mean of three pools ±1 SE for the number of adult *T. lateralis* in the early replicates (*left pair of bars*) and the late replicates (*right pair*) in pools containing caged, visually and tactilely isolated predatory fish (*dark bars*) and no fish (*light bars*). Difference between treatments is highly significant (see text)

The second experiment largely duplicated the first, but differed in isolating the fish from any interaction with the beetles, thus truly testing the dependence of colonization and species distribution on ongoing interactions. Again, significantly more beetles colonized fish-free pools ($F_{1,5}$=22.59, P<0.0051) (Fig. 3). Fish-free pools contained on average 37.00±6.92 (mean±1 SE) adult beetles, while pools with fish contained 10.17±2.91 adult beetles (a 3.6 fold difference). Time of the trials

did not significantly affect the number of beetles colonizing ($F_{1, 5}=0.50$, $P<0.2752$), nor did pair within time ($F_{4, 5}=2.65$, $P<0.1571$). Experiment 2 confirms that adult *T. lateralis* can detect cues produced by fish and use these cues to avoid colonizing ponds containing predatory fish. No physical interaction was necessary. The only cues available to the beetles were chemical and, perhaps auditory, with chemical being more likely based on work with other insects (Petranka and Fakhoury 1991; Scrimgeour et al. 1994; Åbjörnsson et al. 1997; Berendonk 1999; McIntosh et al. 1999). In this experiment only the threat of predation, not actual ongoing predation or attempted predation, was necessary to alter the distribution of *T. lateralis* among experimental pools.

Discussion

Habitat selection has tremendous potential to affect community structure, but has been largely ignored as regards assembly of aquatic communities. In particular the role of species responses to biotic features of the environment is poorly understood (but see Resetarits and Wilbur 1989; Blaustein and Kotler 1993; Petranka et al. 1994; Berendonk 1999). The potential variables to which terrestrial species may respond is illustrated by the plant-herbivore literature on oviposition site choice (Rausher 1983, 1993; Singer 1984, 1986; Thompson and Pellmyr 1991; Renwick and Chew 1994). Aquatic species should show similar types of habitat selection, though the specific variables may differ. My experiments dealt specifically with habitat selection and oviposition in response to the threat of predation by fish as a model of how such habitat selection may affect species distributions and, thereby, species composition and community structure. Thus, the results and ideas presented here have broad application to community assembly.

The importance of habitat selection is enhanced because the effects of selecting (or avoiding) a given habitat extends well beyond the specific site being considered. Models of population dynamics for fish-intolerant species in sets of fish-free ponds, where some number are subsequently invaded by fish, reveal striking differences when selective oviposition is incorporated into the models (Resetarits 1995). Colonization of unfavorable (fish) habitats results in local population decline or even local extinction, in spite of the persistence of favorable habitats, because 'fish' habitats function as population (propagule) sinks (Pulliam 1988). Similarly, avoidance of 'fish' habitats also affects local population dynamics by concentrating oviposition in a limited number of such favorable sites, thus affecting density-dependent processes in favored sites.

From an evolutionary perspective, natural selection, by favoring selective colonization/oviposition, may subsequently limit future opportunities for evolution (Holt 1985, 1987). Selective oviposition (or colonization) like any form of habitat specialization, initiates a feedback loop in which natural selection operates only within the selected habitat forcing greater specialization and further driving the evolution of specific habitat selection and specialization (Holt 1985; Resetarits 1996). This increasing specialization can be driven directly by oviposition preferences, even in the absence of fitness tradeoffs (Fry 1996; but also see Camara 1997 for an interesting counterexample).

Many aquatic systems are relatively isolated habitats linked by many species with complex life cycles. A large component of the fauna of most freshwater systems consists of the larval stages of organisms that are primarily terrestrial or semi-terrestrial as adults, or of the multiple life stages of species that must leave the water to complete their life cycle, disperse and subsequently (re)colonize new or previously occupied habitats (Merritt and Cummins 1984; Duellman and Trueb 1990; Hutchinson 1993; Schneider and Frost 1996). Persistence of many such species in aquatic systems is dependent upon seasonal invasion and/or oviposition by dispersing adults, thus providing a mechanism whereby colonization/oviposition behavior can play a major role in the assembly of aquatic communities. Similarly, variation in environmental conditions and concomitant variation in success rate provides the backdrop against which we would expect to see the evolution of selective colonization/oviposition in a variety of organisms. The presence of selective colonization/oviposition indicates that individuals allocate resources not only to production of offspring, but to sensory mechanisms and behaviors that facilitate placement of those offspring into favorable habitats (Rausher 1983, 1993; Singer 1984, 1986; Thompson and Pellmyr 1991; Renwick and Chew 1994; Resetarits 1996).

My data show that past interactions between predators and their prey do play a role in the assembly of present communities. Species presence/absence and relative abundance in natural ponds with and without fish should reflect differences attributable to both present (via ongoing lethal and non-lethal effects) and past (via habitat selection) effects of predators. The importance of this distinction is simply the difference between propagules (or adults) deposited, eaten, and converted to predator biomass, and propagules (or adults) that are deposited into another physical habitat and into another set of species interactions (Fig. 4). Ramifications are quite profound when integrated across the range of potential colonists, the range of axes across which species may be selective, and the mosaic nature of many habitats landscapes. We can add the fact that for many variables, even those as severe as predatory fish, species may react differently. Species may be attracted or repelled by a given stimulus and may segregate accordingly along a habitat gradient (Fig. 4). Even for closely related species, predatory fish may be catastrophic to some, but entirely necessary to others (McPeek 1990a, b; Werner and McPeek 1994; Wellborn et al. 1996). The results seen in *T. lateralis* should magnify as we consider multiple species responses to multiple environmental factors, and thus translate into significant community-level impacts (Resetarits and Wilbur 1989).
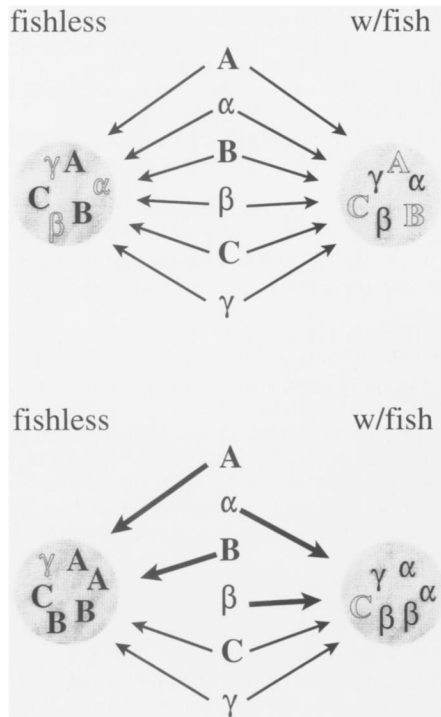
Fig. 4 Differences in mechanism and population/community consequences for cases with predation without habitat selection (*top*) and predation plus habitat selection (*bottom*). *Pairs of circles* within each panel represent pairs of adjacent ponds, one containing fish, the other fishless. *Letters* represent individual species; *Roman capital letters* represent fish intolerant species and *Greek lower case letters* fish tolerant (fish requiring) species (these can be thought of as species pairs of fish tolerant and fish intolerant species, e.g. A & α). *Solid letters* within each pond represent successful colonists, *open letters* unsuccessful colonists. In the *top panel* colonists are non-selective and essentially represent a 'propagule rain' into the two ponds. Fish intolerant species persist only in the fishless ponds, with propagules placed in fish ponds consumed and converted to predator biomass. The converse is true for fish tolerant species, though the mechanism of mortality may be competition or predation. In the *bottom panel* individuals of species pairs A and B exercise habitat selection, while species of pair C do not. The consequences for the respective populations and the community structure of each pond are readily seen. Incorporating habitat selection changes the dynamics of both ponds, even if habitat selection were unidirectional. Avoided ponds no longer receive colonists of pairs A and B, while the selected ponds each receive double the number of colonists of pairs A and B. Thus, the absolute and relative abundances of the three persisting species in each pond differ dramatically depending on whether or not species are selective. Habitat selection can generate essentially the same community pattern as simple predation, or can generate very different patterns, depending the availability of suitable habitats and on the nature of other biotic interactions (e.g. competition, density dependence, intraguild predation). However the mechanism involves redistribution rather than loss of adults/propagules. This figure also illustrates the evolutionary chronology of such a system, in which habitat selection (colonization) is random (*top*), but strong selection drives the evolution of avoidance behavior (*bottom*). Species in pairs A and B are able to respond to selection. Species in pair C may lack the necessary sensory mechanisms to discriminate among habitats, or may be otherwise constrained such that selection is ineffectual

Predators, competitors, pathogens, parasites, prey, etc. all play critical roles in the success of colonizing species. Species composition and, thus, potential biotic interactions, are a critical determinant of habitat favorability. The debate over whether contemporary communities reflect both ongoing interactions and the 'ghost of interactions past' has a long history (e.g. Hutchinson 1959; Grant 1972; Diamond 1975; Connell 1980; Resetarits and Wilbur 1989), but little direct experimental evidence has been brought to bear on the role of past interactions. My data support the idea that the distribution and abundance of species in contemporary communities is best viewed as a consequence of both ongoing species interactions and 'the ghost of interactions past.' In particular, assembly can be affected by behaviors driven not by contemporary species interactions, but by past interactions. Lethal effects on populations in the past give rise to non-lethal effects on distributions in the present via habitat selection, reinforced, if necessary by ongoing selection against 'errors'. If differential colonization and selective oviposition in response to other species prove to be widespread, we must fundamentally alter our view of the mechanisms by which species interact, and how those interactions, both past and present, drive community assembly.

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