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Is the Pirate Really a Ghost? Evidence for Generalized Chemical Camouflage in an Aquatic Predator, Pirate Perch *Aphredoderus sayanus*

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ABSTRACT: Camouflage occupies a central role in arsenals of both predators and prey and invokes visions of organisms possessing specific characteristics or altering their shape, color, or behavior to blend into the visual background or confound identification. However, many organisms use modalities other than vision. Chemical communication is particularly important in aquatic systems, and chemicals cues are used by a broad array of colonizing organisms to recognize and avoid risky habitats. Here we describe a habitat selection experiment with aquatic beetles and summarize results of 11 experiments involving colonizing beetles and ovipositing tree frogs that provide evidence that pirate perch *Aphredoderus sayanus* are chemically camouflaged with respect to a diverse array of prey organisms. We believe this to be the first example of a predator possessing a generalized chemical camouflage effective against a broad array of prey organisms, and we suggest that it may constitute a novel weapon in the predator-prey arms race.

Keywords: camouflage, cloaking, habitat selection, novel weapon, olfaction, predator-prey.

Introduction

Prey utilize a bewildering array of mechanisms to avoid detection by predators, and predators employ an equally bewildering array of mechanisms to avoid detection by prey (Edmunds 1974; Ruxton et al. 2004). Camouflage, in a variety of forms, is a central feature of such defensive and offensive arsenals (Edmunds 1974; Ruxton et al. 2004; Ruxton 2009). Camouflage typically invokes visions of organisms possessing specific characteristics or altering their shape, color, and/or behavior to blend into the visual background to avoid detection (crypsis) or confound identification (mimicry; Edmunds 1990; Stevens and Merilaita

2009). However, many organisms rely on modalities other than vision. Ruxton (2009) has suggested that camouflage can function within any sensory modality used in prey (or predator) detection. Many organisms use sound and smell to detect prey or predators—thus, classic images of deer or gazelle sampling the air or listening for the rustle of a predator in the grass. Ventriloquial qualities of many frog calls and bird songs may constitute aural crypsis, wherein specific song qualities alter the directional characteristics of the signal.

Chemical mimicry (in contrast to crypsis) is well documented in insects for highly coevolved interactions, such as brood parasites, specialist parasitoids, and other highly specialized interactions (Dettner and Liepert 1994). Certain plants, such as orchids that smell of rotting meat, mimic olfactory signals to gain an advantage, most commonly in the form of pollinator visitation (Wickler 1968). Organisms may also behaviorally acquire odors to avoid detection (Weldon 2004). In perhaps the best example of true chemical crypsis, the secretions of several species of African ants, specialist predators on termites, differ from related, nonspecialist ants and fail to elicit avoidance by termite prey (Longhurst et al. 1979). Ruxton (2009) provides other examples, such as caterpillars acquiring the chemical signature of host plants and thus avoiding detection by predatory ants (Akino et al. 2004; Portugal and Trigo 2005) or bark beetles *Ips pini* using a modified pheromone signature that reduces detection by three species of predatory beetles (Raffa et al. 2007). However, these again involve specific sets of predators and prey (Ruxton 2009). Thus, no known organism possesses chemical camouflage in any form that acts on a diverse array of taxa (review in Ruxton 2009). The scenario is as plausible as generalized visual camouflage; however, one inherent difficulty in implementing chemical camouflage is the nature of chemical cues, which often emanate from basic phys-

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iological processes, while our own chemosensory limitations constitute a serious difficulty in recognizing chemical camouflage.

Semiochemicals are especially important in aquatic systems, where vision and sound are less effective than in terrestrial environments and where taste and smell often interact. Interspecific communication, especially between predator and prey, often involve kairomones, which are semiochemicals that benefit receiver but not donor. Prey can be highly sensitive to chemicals emanating from predators or via the act of prey consumption, including both kairomones and alarm pheromones (Chivers and Smith 1998; Wisenden 2000; Fraker et al. 2009; Ferrari et al. 2010; Silberbush et al. 2010). Likewise, predators often locate and identify prey via olfaction. Thus, potential exists for both predators and prey to gain significant advantage in the arms race by confounding detection or identification via reduction or alteration of their chemical signal. Some of the most vivid biological images involve the myriad ways in which organisms achieve visual camouflage, from dramatic color matching in chameleons and flatfish to the morphology of phasmids. The idea that the olfactory landscape may contain equally dramatic examples of complex adaptations to avoid predators or fool prey is compelling.

Chemicals released from fish alter behavior (Petranka et al. 1987; Dodson 1988; Jones and Paszkowski 1997; Takahara et al. 2008; Dalesman and Rundle 2010; Hein and Crowl 2010), life history (Moore et al. 1996; Mirza et al. 2001; Jones et al. 2003; Orizaola and Brana 2003), population growth (Sarma et al. 2011), and morphology (Spaak and Boersma 1997; Tollrian and Dodson 1999) of both vertebrate and invertebrate prey. Behavioral responses to fish kairomones include colonization and oviposition site selection by a variety of organisms, including anurans (Resetarits and Wilbur 1989; Binckley and Resetarits 2003; Vonesh et al. 2009) and aquatic insects (Resetarits 2001; Åbjörnsson et al. 2002; Angelon and Petranka 2002; Brodin et al. 2006; Van Dam and Walton 2008; Resetarits and Binckley 2009; Kraus and Vonesh 2010).

Here we report on an experiment examining responses of colonizing aquatic beetles (Dytiscidae and Hydrophilidae) to two species of predatory fish and summarize our published and unpublished work in the context of chemical camouflage. Our results suggest that pirate perch *Aphredoderus sayanus*, which comprise the monotypic family Aphredoderidae, are chemically camouflaged to a broad array of colonizing prey organisms and may provide the first documented example of such generalized chemical camouflage.

Methods

Aphredoderus sayanus is a widespread, moderately sized (64–144 mm total length), nocturnal, predatory fish locally abundant in a variety of lentic and lotic habitats in the Mississippi River drainage and the Atlantic Coastal Plain of the southeastern United States (Gunning and Lewis 1955; Parker and Simco 1975; Shepherd and Huish 1978; Lee 1980; Monzyk et al. 1997). It comprises the monotypic family Aphredoderidae and belongs to a rather enigmatic order (Percosiformes) containing nine extant species in three families, all North American: *A. sayanus*, two species of Percopsidae (trout-perches), and six cavefish (Amblyopsidae). The monophyly of the Percosiformes and assignment of Aphredoderidae as sister taxa to Amblyopsidae, with divergence in early Eocene, is strongly supported (Dillman et al. 2011). *Aphredoderus* shares characters with Amblyopsid cavefish, including migration of the anus to the throat region in adults and a highly developed lateral line system (Moore and Burris 1956; Mansueti 1963; Poly 2004; Poly and Proudlove 2004; Dillman et al. 2011).

An important question is whether *A. sayanus* is somehow unique in its effects on prey and whether that unique effect, rather than camouflage, is responsible for lack of avoidance. Body size and gape are of primary importance in determining effects of fish predators on both larval amphibians and aquatic insects, and both are less limiting for *A. sayanus* than strongly avoided small fish, such as *Gambusia*, *Pimephales*, and even similarly sized fish, such as *Enneacanthus* and *Umbra* (see “Results”). Neither is *A. sayanus* a prey specialist. Though its common name derives from its observed voraciousness in consuming other fish in aquaria (Abbott 1872), *Aphredoderus* is primarily insectivorous (Forbes 1888; Forbes and Richardson 1908; Gunning and Lewis 1955; McLane 1955; Goldstein and Simon 1999), with diet consisting of as much as 80% (Flemer and Wolcott 1966) to 90% (Benke et al. 1985) aquatic insects (including midges, mayflies, stoneflies, caddisflies, beetles, hellgrammites, and dragonflies). This represents a greater proportion than in the diet of *Lepomis macrochirus* (bluegill) in the same studies (65%: Flemer and Wolcott 1966; 78%: Benke et al. 1985), and bluegill have strong effects on the distribution and abundance of aquatic insects (Smith et al. 1999). However, in contrast to *A. sayanus*, bluegill elicited the strongest avoidance response by beetles in our experiments. Other avoided species also have significantly lower proportions of aquatic insects in the diet, with crustaceans making up 55% of the diet of *Enneacanthus gloriosus* (Flemer and Wolcott 1966), while *Pimephales promelas* is largely planktivorous, consuming few aquatic insects except chironomids (<10%; Duffy 1998).

Larval amphibians are rarely reported in fish diets be-

cause palatable species (the vast majority in North America) rarely persist with fish and unpalatable species (e.g., bullfrogs) are rarely consumed (Duellman and Trueb 1986; Beebe 1996). However, most North American freshwater fish are generalist predators, including *A. sayanus*, and prey readily on eggs and larvae of palatable amphibians, limited only by co-occurrence and gape size. Thus, the importance of fish in limiting distribution of amphibians is well established (Duellman and Trueb 1986; Beebe 1996; Wellborn et al. 1996; Hecnar and McCloskey 1997; Knapp 2005). Bluegill and other centrarchids have repeatedly been shown to have strong effects on larval anurans (e.g., Smith et al. 1999; Boone et al. 2007; Resetarits and Chalcraft 2007), and bluegill and pirate perch have similar effects on larval Southern leopard frogs *Rana sphenoccephala* in predation trials (Albecker 2011). Thus, nothing in the feeding ecology of *A. sayanus* suggests anything unique or distinct from other generalist predatory fish.

Likewise, despite unique morphological characteristics and breeding mode, *A. sayanus* and Percopsiformes are not an obscure side lineage. Unique characteristics are derived within the Percopsiformes, which is embedded centrally in the phylogeny of Teleostei relative to the other orders represented in our studies—Esociformes, Salmoniformes, Siluriformes, Cypriniformes, and Perciformes—which together contain a large proportion of North American freshwater fish species (Broughton 2010; Wiley and Johnson 2010).

Beetle Experiment

Our experimental work typically tests responses of naturally colonizing populations to experimentally established habitat heterogeneity in realistic field settings (e.g., Resetarits and Wilbur 1989; Resetarits 2005). We established 12 experimental ponds (wading pools; 1.50 m × 0.29 m, 300 L) in four blocks (≈20 m apart) of three pools (≈1.3 m apart) in an old field surrounded by hardwood/pine forest on a remnant arm of the Great Dismal Swamp in Chesapeake, Virginia. On August 24, 2000, we covered ponds with tight-fitting fiberglass screens (1.3 × 1.13-mm mesh) to prevent premature colonization and filled pools with tap water. Two days later, we added randomized aliquots of 0.4 kg of dried leaf litter for nutrients and cover and 1.0 L inocula of zooplankton and phytoplankton from nearby ponds, and on August 28, we randomly assigned three treatments within blocks: two fish treatments, *Enneacanthus gloriosus* (blue-spotted sunfish, Centrarchidae; $n = 2$, mean total biomass/pool = 2.69 g) and *A. sayanus* (pirate perch; $n = 2$, mean total biomass/pool = 4.06 g), and fishless controls. Fish were placed under screens and screens pushed underwater, preventing physical interactions between fish and beetles but allowing chemical com-

munication. Beetles were collected weekly for 3 weeks and preserved in 95% ethanol. A single MANOVA was performed on mean beetle abundance/pool and mean species richness/pool (type III sums of squares, $\alpha = 0.05$), with univariate ANOVAs and nonorthogonal contrasts testing biologically relevant hypotheses. Block effects were all $P > .5$, so block effects were rolled into error. Analysis used SAS (ver. 9.2; SAS Institute, 2010).

Summary of Experiments

We compiled data from 11 habitat selection experiments assaying responses of colonizing/ovipositing organisms to fish. In all experiments, as described above, fish are prevented from interacting with colonizers, except via chemical cues. We employed methods in early experiments with both beetles (e.g., Resetarits 2001) and tree frogs (e.g., Binckley and Resetarits 2003) to ensure visual and tactile isolation, thus establishing the chemosensory basis of fish avoidance. Fish were placed inside 115-L opaque plastic trash cans with opaque lids, and each can had two 25 × 50-cm sections on opposite sides (and entirely below water level) removed and replaced with one layer of 99% shade cloth over one layer of No-See-Um netting (<1 × <1-mm mesh). When submerged in larger tanks, light penetration was essentially zero and motion cues eliminated, but water and chemical cues were exchanged (sound production is rare in fishes, and no species tested are known to produce sound). This barrier, with expected growth of algae and periphyton, also potentially blocked chemical cues, so water from inside the enclosures was actively exchanged once a day by slowly lifting enclosures 90% out of the water (allowing water inside to flow out) and then slowly forcing the enclosure down in the pool. This augmented passive exchange, assured adequate mixing, and was done for both fish and fish-free tanks. Once the chemical basis of avoidance was established, we modified procedures to use screen lids as the primary barrier between fish and eggs/colonists. This also aided in collecting eggs and colonists, thus greatly enhancing efficiency. Oviposition by frogs and the majority of beetle colonization occurs at night, so this simple barrier of 1.3 × 1.13-mm mesh provides a practical barrier to visual cues and, because of surface tension across the small mesh size, motion cues. Thus, variation in observed oviposition/colonization rates result from behavioral redistribution in response to fish presence determined by chemical cues.

Four experiments focused on colonization by multi-species assemblages of aquatic beetles (Dytiscidae and Hydrophilidae), and seven involved oviposition by one or two species of tree frogs. Most involved additional treatments (e.g., other species, nutrients) or multiple densities of fish, but all included fishless controls. For each exper-

iment, we express colonization/oviposition in fish treatments as a proportion of fishless control values. Multiple species of tree frogs within a single experiment were combined for simplicity; combining responses did not alter statistical results

Results

Our experiment examining beetle responses to two species of predatory fish, *Enneacanthus obesus* and *Aphredoderus sayanus*, was colonized by a total of 401 individuals representing 14 species. The MANOVA of abundance and species richness showed significant differences among treatments (Wilks's $\lambda = 0.174$, $F_{4,16} = 5.59$, $P = .0052$), as did univariate ANOVAs for abundance ($F_{2,9} = 9.71$, $P = .0057$) and species richness ($F_{2,9} = 19.41$, $P = .0005$; fig. 1a). MANOVA contrasts revealed that control and *Aphredoderus* treatments were not significantly different (Wilks's $\lambda = 0.778$, $F_{2,8} = 1.14$, $P = .3669$), but both were significantly different from the *Enneacanthus* treatment (control vs. *Enneacanthus*: Wilks's $\lambda = 0.186$, $F_{2,8} = 17.51$, $P = .0012$; *Enneacanthus* vs. *Aphredoderus*: Wilks's $\lambda = 0.291$, $F_{2,8} = 9.75$, $P = .0072$; fig. 1a). Univariate contrasts for abundance followed the same pattern, with control and *Aphredoderus* treatments not significantly different ($F_{1,9} = 0.93$, $P = .359$) but with both significantly different from *Enneacanthus* (control vs. *Enneacanthus*: $F_{1,9} = 17.7$, $P = .0023$; *Enneacanthus* vs. *Aphredoderus*: $F_{1,9} = 10.50$, $P = .0101$; fig. 1a). The same held true for species richness (control vs. *Aphredoderus*: $F_{1,9} = 2.45$, $P = .1516$; control vs. *Enneacanthus*: $F_{1,9} = 36.07$, $P = .0002$; *Enneacanthus* vs. *Aphredoderus*: $F_{1,9} = 19.70$, $P = .0016$; fig. 1a). Abundance in the *Enneacanthus* treatment was reduced to 23% of control values and species richness to 41% of controls (28% and 45% of *Aphredoderus* values). Data are uncorrected for average fish biomass, which was 51% higher in *Aphredoderus* pools. Figure 1b illustrates the consistency of beetle responses with respect to differences between fish species. Most species represented by more than a few individuals colonized *Aphredoderus* pools at equivalent or nearly equivalent rates to the controls, with the exception of *Copelatus glypticus*, which treated *Aphredoderus* as intermediate between control and *Enneacanthus*, and *Uvarus* sp., which colonized only fishless controls.

Figure 2 summarizes data from four experiments examining responses of aquatic beetles to six species of freshwater fish representing four families in four orders (including data from experiment 1 above). Experiments were colonized by between 14 and 34 species of Dytiscidae and Hydrophilidae. Density and biomass of fish varied, but all fish treatments, with the exception of *Aphredoderus*, elicited significant avoidance, and there were no other sig-

nificant differences among fish species in any experiments. Other fish treatments reached a maximum of 54% of the *Aphredoderus* value for abundance (*E. obesus* 2, 46% of control values) and a maximum of 63% of the *Aphredoderus* value for species richness (*E. obesus* 2, 57% of control). Notably, *Aphredoderus* biomass/L was 330% higher than for *E. obesus* in *E. obesus* 2.

Figure 3a summarizes data from experiments examining responses of ovipositing tree frogs—*Hyla chrysoscelis*, *Hyla femoralis*, and *Hyla squirella*—to nine species of freshwater fish representing six families in four orders. All fish species except *Aphredoderus* elicited significant avoidance, and there were no other significant differences among fish species in any experiment. Other fish species reached a maximum of 26% of the *Aphredoderus* values (12% of controls). Figure 3b shows the survival of tadpoles of three species (*Rana sphenoccephala*, *Bufo terrestris*, and *Pseudacris crucifer*), with three fish species also tested for avoidance (fig. 3a; data from Chalcraft and Resetarits 2003). All three species were strongly avoided, despite considerable variation in actual predation risk to larval anurans, suggesting a generalized response to fish.

Discussion

We have intensively examined responses of ovipositing tree frogs and multispecies assemblages of colonizing aquatic beetles to the nonlethal presence of fish—often in combination with other factors, such as canopy cover, productivity, and so on—in a total of 11 different field experiments (see figs. 2, 3). Taxa as disparate as tree frogs and aquatic beetles, using chemical cues only, distinguish between fish and fishless habitat patches and also between patches containing pirate perch and all other fish taxa tested. Reactions to fish by fish-intolerant species have been remarkably consistent (figs. 1–3). Tree frogs (*Hyla*) and beetles of two dominant aquatic families (Dytiscidae and Hydrophilidae) avoid habitats containing fish, and responses are very sensitive. Ovipositing tree frogs respond to chemical cues produced by 0.53 g of live fish/100 L of water (Rieger et al. 2004), and beetles avoid fish densities as low as 0.82 g/100 L (Binckley and Resetarits 2005; Resetarits and Binckley 2009). Species in both taxa show variation in sensitivity to fish density, but all those that respond (all three tree frogs and the majority of beetles) avoid fish (except *Aphredoderus*) at densities of <2 g of live biomass/100 L. Both groups also avoid fishless pools adjacent to fish pools (spatial contagion: Resetarits 2005; Resetarits and Binckley 2009), further attesting to the importance of fish in habitat selection.

Fish avoidance has been documented in response to six families of freshwater fish representing five major orders (figs. 2, 3a). Observed responses are similar for aquatic

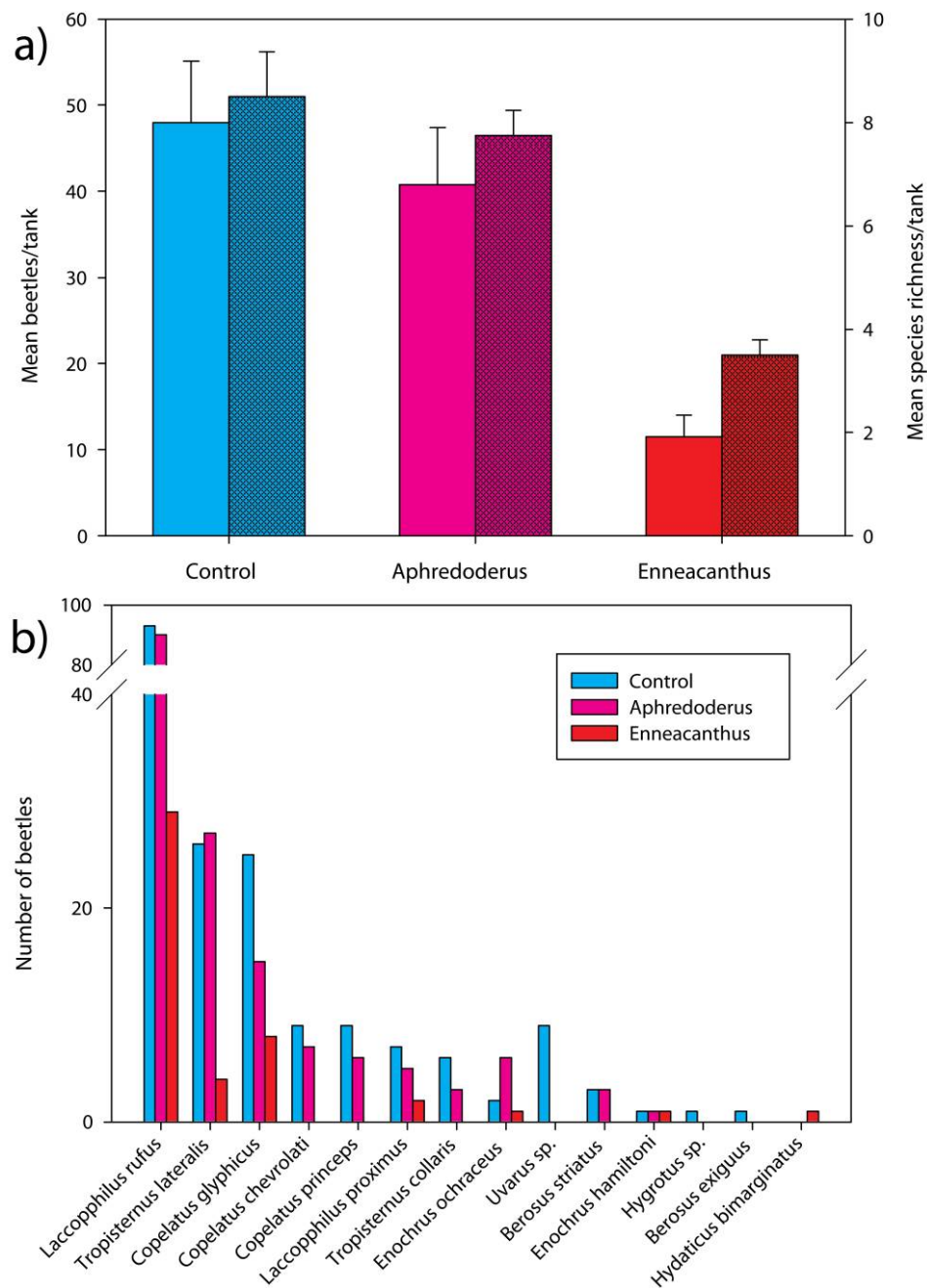


Figure 1: *a*, Beetle colonization in fishless controls and pools containing *Enneacanthus obesus* or *Aphredoderus sayanus*: mean number of beetles/tank (± 1 SE; solid bars) and mean beetle species richness/tank (± 1 SE; hatched bars). Data are not corrected for the 51% greater mean fish biomass/pool in the *Aphredoderus* treatment. Control and *Aphredoderus* treatments were not significantly different for either response variable, while both were significantly different from *Enneacanthus* for both variables. *b*, Responses of 14 species of colonizing beetles to treatments, as in *a*.

beetles and tree frogs, and despite tremendous variation in predatory potential among the fish themselves, planktivorous *Pimephales* are avoided as strongly by beetles as *Enneacanthus* (fig. 2), and insectivorous *Gambusia* and

planktivorous *Notemigonus* are avoided by tree frogs as strongly as *Enneacanthus* or *Umbra*, despite dramatic differences in predatory impacts. Thus, avoidance appears to be a generalized adaptive response by fish-intolerant spe-

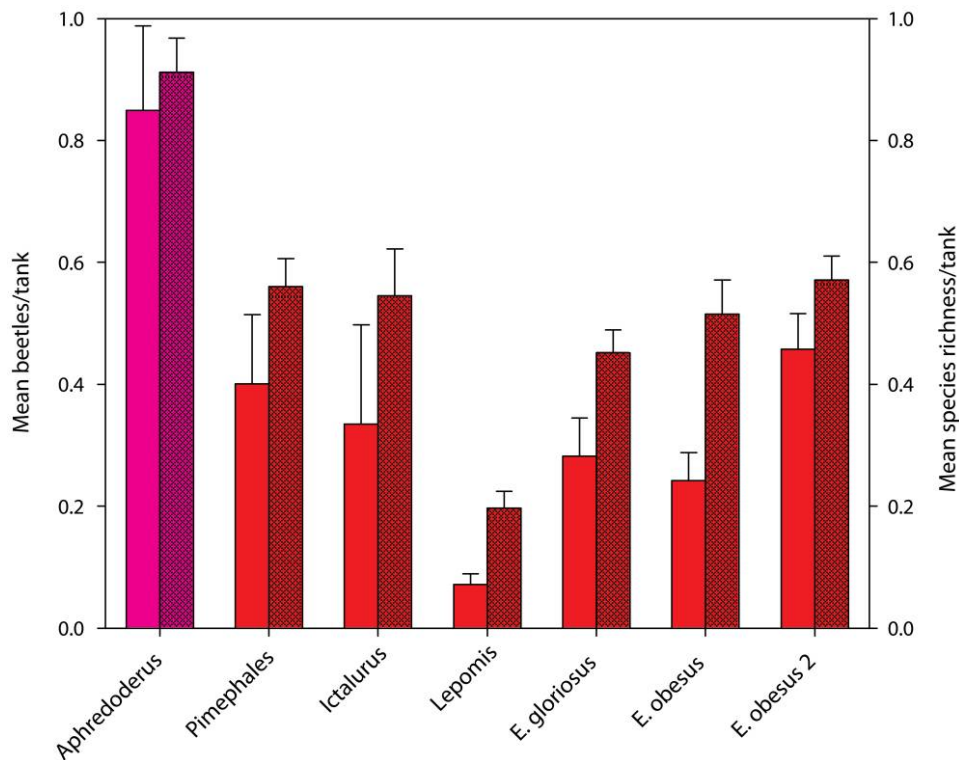


Figure 2: Summary of data from four experiments examining colonization responses of multispecies assemblages of dytiscid and hydrophilid beetles to fish. Mean number of beetles/tank (± 1 SE; solid bars) and mean beetle species richness/tank (± 1 SE; hatched bars). The six fish species represent three major North American freshwater families plus the Aphredoderidae. *Aphredoderus sayanus* did not elicit significant avoidance; all other fish treatments were significantly different from fishless controls in their respective experiments (Binckley and Resetarits 2005; Resetarits and Binckley 2009; this note; W. J. Resetarits and C. A. Binckley, unpublished data).

cies to fish presence, which is determined by chemical—rather than visual, mechanoreceptive, or auditory—cues. *Aphredoderus* provides a striking exception to this “fish is a fish is a fish” rule.

For many colonizing organisms, presence of fish indicates complete reproductive failure, even if adults persist (Wellborn et al. 1996). Thus, given the ubiquity and importance of chemical cues in aquatic systems (see Ferrari et al. 2010), it is not surprising that organisms colonizing freshwater habitats have evolved olfactory mechanisms to detect fish kairomones.

Is *Aphredoderus sayanus* chemically camouflaged? Perhaps tree frogs and beetles detect and recognize *Aphredoderus* but do not avoid them, either because pirate perch lack strong direct effects or because they consume something more dangerous, leading to positive indirect effects. Either scenario requires taxa as disparate as beetles and tree frogs to mount unique evolutionary responses to each fish taxa—or at least to *A. sayanus* versus all other fish tested—and differences between *A. sayanus* and other fish to be accessible to natural selection. Though reasonable,

there is no evidence even suggesting that pirate perch are unique in their effects on beetles, tree frogs, or any other taxa, except perhaps as a result of chemical camouflage. Predatory effects of pirate perch far exceed that of avoided species, and fish avoidance in general is not related to predatory potential (fig. 3). We also have evidence dating to Forbes (1888) that pirate perch are generalist predators, failing to demonstrate the prey specialization required under alternative scenarios. Thus, alternative hypotheses all suffer major difficulties versus the simple hypothesis that *A. sayanus* is chemically camouflaged, which requires only generalized detection/avoidance of fish via kairomones and possession of a different chemical signature by *Aphredoderus*, which is supported by preliminary data (A. Silberbush and W. J. Resetarits, unpublished data).

Is chemical camouflage another shared character within Percopsiformes? Subterranean aquatic habitats, as well as other low light habitats and nocturnal habits, are dominated by chemical and mechanoreceptive cues. Predators can minimize production of movement cues, but how does a predator deal with chemical cues? To be chemically cam-

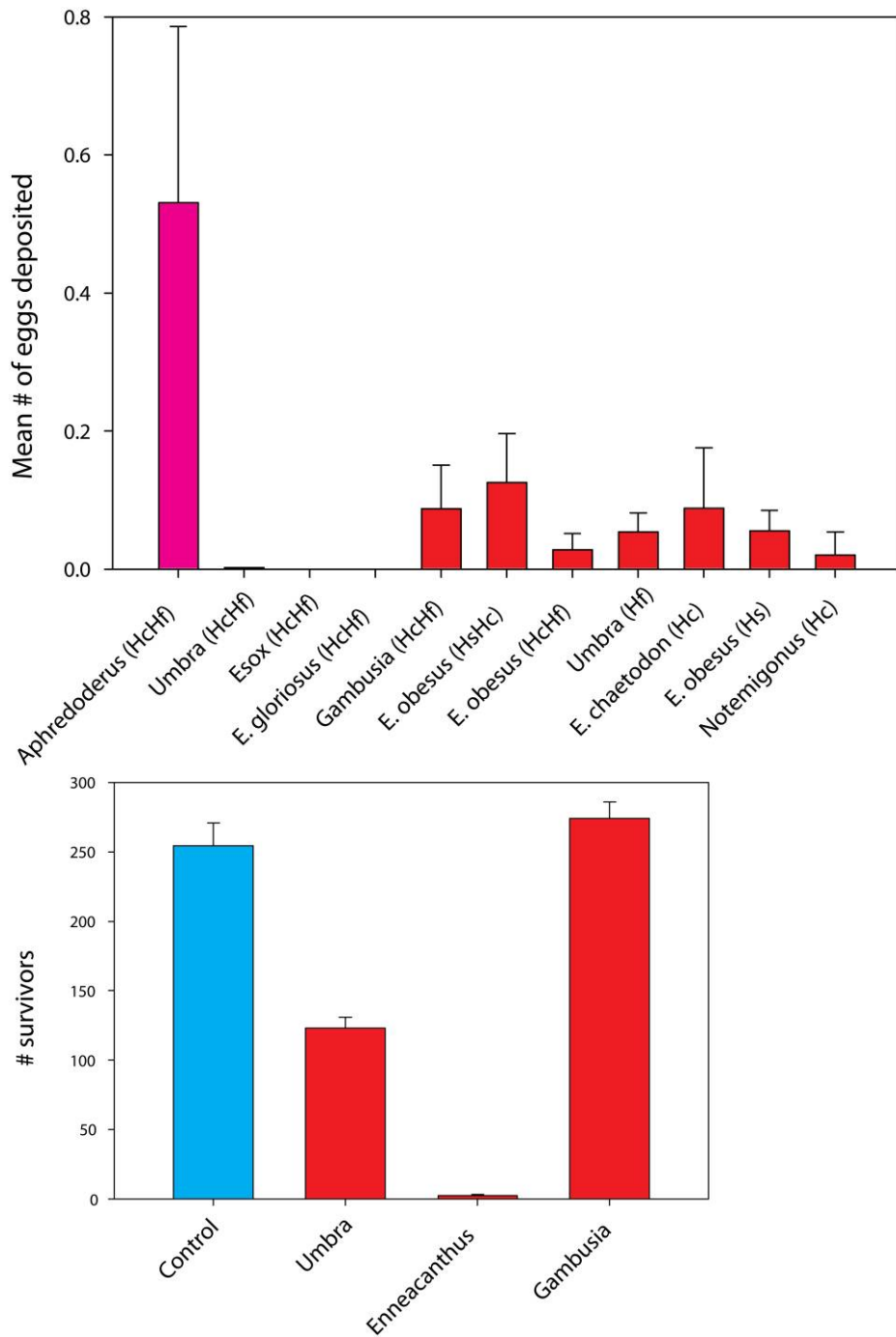


Figure 3: *Top*, summary of data from seven experiments examining the responses of ovipositing tree frogs—*Hyla chrysoscelis* (Hc), *Hyla femoralis* (Hf), and *Hyla squirella* (Hs)—to fish. Multiple species of tree frogs in the same experiment were combined for simplicity of presentation. Oviposition in treatments containing fish is expressed as a proportion of fishless control values for that experiment (± 1 SE). The eight species represent five major North American freshwater families plus Aphredoderidae. *Aphredoderus sayanus* did not elicit significant avoidance; all other fish treatments were significantly different from fishless controls in their respective experiments (Resetarits and Wilbur 1989; Binckley and Resetarits 2002, 2003, 2008; Rieger et al. 2004; Resetarits 2005; W. J. Resetarits and C. A. Binckley, unpublished data). *Bottom*, lethal effects of three fish species on larval anurans in a 60-day mesocosm experiment. Ensemble was comprised of 175 each of *Rana sphenoccephala*, *Bufo terrestris*, and *Pseudacris crucifer*, added at approximately Gosner stage 25. All three fish elicit strong avoidance (*top*) despite extreme variation in predation rates, suggesting a generalized fish response; data from unrelated work thus did not include *Aphredoderus*. Data from Chalcraft and Resetarits (2003).

ouflagged, a fish must not produce characteristic fish smell, produce so little that it blends into the olfactory background, smell like something else, or possess behaviors (or chemicals) that mask its odor. Thus, the actual mechanism of chemical deception employed by *A. sayanus* may be a form of camouflage (crypsis or mimicry) or a third alternative, cloaking, in which the organism simply does not produce or somehow masks signals that might register with potential receivers. It has been suggested that gulf toadfish *Opsanus beta* excrete urea to mask the signal of ammonia that may attract fish predators (Barimo and Walsh 2006). Unfortunately, this has been tested only once with a single predator species responding to synthetic chemicals, but it remains an intriguing possibility.

Camouflage was originally defined as a visual phenomenon, and visual deception in the natural world is limited to confounding identification or reducing detectability; an organism cannot achieve invisibility. The most carefully camouflaged individual is still “seen,” producing a detectable signal, but is simply not recognized. Even essentially transparent organisms, such as larvae of phantom midges *Chaoborus*, are not invisible. However, for modalities other than vision, organisms can potentially achieve invisibility by not emitting signals that register with potential receivers. Such organisms are cloaked (absence of signal) rather than camouflaged (confounding signals).

Whether *Aphredoderus* employs crypsis, mimicry, or cloaking as the mechanism of chemical deception is an open question that may be very difficult to tease apart; ruling out mimicry requires elimination of a potentially vast number of models. We are pursuing the identity of the kairomone(s) responsible for eliciting avoidance of fish and the mechanism by which *A. sayanus* achieves its chemical deception. We are also investigating whether chemical deception is adaptive with regard to prey acquisition, whether it functions against potential predators, and whether the trait is unique to *Aphredoderus*. The origin of the differences in the chemical signature of *Aphredoderus* may be unrelated to predator-prey interactions, but data suggest it may nonetheless confer a significant advantage in prey acquisition and perhaps predator avoidance.

We have clearly established, using behavioral bioassays, that pirate perch present a different chemical signature than any of the broad range of fish tested and that that chemical signature renders pirate perch more difficult to detect or identify by a diverse array of prey organisms. In contrast to examples of chemical camouflage confined to very specific species interactions, we believe we have the first evidence of a generalist predator possessing a form of chemical deception that functions to confound detection or identification by a broad range of prey species (Ruxton 2009). With further exploration, *A. sayanus* may provide a window into the evolution of a novel weapon

(sensu Callaway and Widenour 2004) in the context of animal predator-prey interactions. The data we have are compelling, but the next critical steps involve documenting the adaptive significance of this phenomenon, its mechanistic basis, phylogenetic distribution, and the resulting consequences for populations and communities. The idea that a generalist predator could use chemical deception against a suite of prey ranging from insects to amphibians—in a manner precisely analogous to visual camouflage—should change how we think about predator-prey interactions and the potential weapons brought to bear in the predator-prey arms race.

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