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Functional equivalence of non-lethal effects: generalized fish avoidance determines distribution of gray treefrog, *Hyla chrysoscelis*, larvae

Christopher A. Binckley and William J. Resetarits Jr.

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How patterns of prey abundance are generated determines how predation influences population and community level dynamics. We investigated how a natural population of ovipositing treefrogs, *Hyla chrysoscelis*, partitioned their eggs amongst experimental ponds differing in the non-lethal presence of five fish predators, each representing a distinct family. Four fish predators were functionally equivalent in terms of the behavioral response they induced in *H. chrysoscelis* females and hence the distribution of larval *H. chrysoscelis*. Mean number of *H. chrysoscelis* eggs deposited was significantly decreased by the mere presence of these predators relative to controls, with three species eliciting a complete avoidance (e.g. no eggs deposited). One fish predator, *Aphredoderus sayanus*, was statistically indistinguishable from the control treatment. These data mimic patterns of species distribution observed in nature in response to the presence of fish, but suggest an alternative mechanism for generating patterns of prey abundance amongst habitats differing in their predator composition. Furthermore, our results expand the importance of predator induced non-lethal effects as a process that could dramatically affect population and community level dynamics.

C. A. Binckley and W. J. Resetarits Jr., Dept of Biological Sciences, Old Dominion Univ., Norfolk, Virginia 23529, USA (cbinc001@odu.edu).

The extent to which patterns of prey abundance are produced by behavioral responses to predators verses direct consumption determines how predation influences population and community level dynamics (Hassell and May 1985, Sutherland 1996, Fryxell and Lundberg 1998). Predation is a critical process influencing the distribution and abundance of many organisms (Brooks and Dodson 1965, Paine 1966, Jeffries and Lawton 1984, Sih et al. 1985), particularly in aquatic ecosystems (Zaret 1980, Morin 1983, Kerfoot and Sih 1987, Resetarits 1991). While direct consumption of prey has been the most well studied aspect of predation, ecologists have recently begun quantifying the non-lethal effects induced by the presence or activities of a predator (Lima and Dill 1990, Kats and Dill 1998, Lima 1998a, b). Non-lethal effects are often manifested as changes in prey microhabitat use (Werner et al. 1983), activity (Sih 1982, Skelly and Werner 1990), and morphology (Van Buskirk et al. 1997), and such responses incur "costs" which can alter life history attributes of prey (Skelly 1992, Ball and Baker 1996, Resetarits 1996, Belk 1998), and modify the outcome of species interactions (Werner 1991, Werner and Anholt 1996). While these studies suggest that non-lethal effects might be an important factor structuring populations and communities, its unclear whether the magnitude of non-lethal effects are strong enough to produce presence/absence patterns of prey abundance.

Most aquatic taxa sort amongst habitats with regard to the presence of their predators (reviewed by Wellborn et al. 1996). Changes in amphibian assemblages correlated with the presence and abundance of preda-

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tory fish is a particularly well-documented field pattern; certain species do not occur or occur at reduced densities where fish are present (Hecnar 1997, Babbitt and Tanner 2000, Snodgrass et al. 2000). The exact mechanism by which sorting occurs, however, remains debatable. Since fish readily consume eggs and larvae of many amphibian species (Heyer et al. 1975, Kats et al. 1988, Kurzava and Morin 1998), the mechanism most often cited to explain observed field patterns has been consumption (Brönmark and Edenhamn 1994, Fisher and Shaffer 1996, Azevedo-Ramos et al. 1999, Knapp et al. 2001). Thus, after an assumed random colonization/oviposition phase, fish presumably function as a non-random "sieve" or "filter" by eliminating eggs and larvae of species which lack defenses against these predators. Predatory fish, however, can interact with multiple life history stages of amphibians in very different ways.

A growing body of evidence suggests that adult female anurans can assess the faunal composition of potential breeding sites and actively avoid ovipositing in aquatic habitats containing egg and larval predators, including fish (Resetarits and Wilbur 1989, Hopey and Petranka 1994, Binckley and Resetarits 2002). Mortality of eggs and larvae need not occur (e.g. fish consume conspecifics) in order for these effects to be produced, as predators interact directly, but non-lethally, with reproductive adult females. Oviposition site choice constitutes an alternative larval "filter" or "sieve" that could explain species-specific presence/absence and abundance patterns of amphibians across a landscape of breeding sites, especially if multiple predatory fish species elicit similar behavior (strong avoidance) in ovipositing amphibians.

The importance of oviposition site selection as a mechanism structuring natural communities will depend upon the distribution of any "avoidance signal" amongst predators. Since fish constitute an important class of predators in terms of amphibian distribution and abundance, it is especially crucial to determine the distribution of induced behavioural avoidance. Previous oviposition site selection studies have primarily utilized predatory fish representing a single family, Centrarchidae (Kats and Sih 1992, Hopey and Petranka 1994, Holomuzki 1995, Binckley and Resetarits 2002, but see Laurila and Aho 1997). Thus we asked; What patterns of amphibian distribution and abundance are produced by oviposition site selection in response to the presence of a variety of different fish predators that characterize natural landscapes?

We experimentally examined the reproductive behavior of a natural population of ovipositing gray treefrogs, *Hyla chrysoscelis*, when encountering the non-lethal presence of five species of fish predators representing five different families that differ vastly in their phylogenetic history, ecology, behavior and morphology (Page and Burr 1991). Specifically, we tested whether ovipositing *H. chrysoscelis* females could detect the presence of these predators commonly encountered in their natural habitat by quantifying the number of eggs deposited in experimental ponds with and without these different predators.

Material and methods

Hyla chrysoscelis typically breeds during and after heavy rainfall events in late spring and summer, and larvae are typically encountered in small fishless pools and ponds. It is one of the most abundant anurans on the Coastal Plain of Virginia and at Naval Security Group Activity northwest (NSGA) in Chesapeake, Virginia where the experiment was conducted. Females deposit eggs in clusters that float on the pond surface before hatching, and a single clutch (approximately 1000 eggs, Chalcraft, unpubl.) can be partitioned amongst multiple breeding ponds.

We established 40 experimental ponds using wading pools approximately 1.50 m in diameter and 0.29 m in depth (Resetarits and Wilbur 1989), arranged in five rectangular blocks of eight pools each. Experimental ponds mimic natural breeding sites to the extent that they are readily colonized by natural populations of a variety of species, including *Hyla chrysoscelis*, whose larvae can complete their life stage in these enclosures. All pools were approximately 1.3 m from each other, and blocks were located on average 20 m apart in a field surrounded by hardwood and pine forest. All procedures were carried out within a single block before moving on to the next block. We filled all pools (approximately 400 l total volume) with tap water 11–13 May 2000, and allowed them to sit for several days before 0.4 kg of dried leaf litter was randomly added to each pool. We inoculated pools on 16 and 25 May 2000 with 1.0 l random aliquots of zooplankton collected from fishless temporary ponds located at NSGA as a food source for the predators. Pools were kept covered with tight fitting fiberglass mesh lids to prevent colonization by aquatic insects (Morin 1983). Fish enclosures were constructed using smaller wading pools, 0.90 m in diameter and 0.14 m in depth, covered with tight fitting fiberglass mesh lids. One enclosure was sunk into each of the 40 larger experimental pools.

The experiment employed a randomized complete block design for analysis of variance with replication of controls within each block. Five experimental treatments and three controls were assigned at random to the eight pools in each of the five blocks. Treatments consisted of the addition of known numbers of potential fish predators of *Hyla* eggs and/or larvae to the pools. Fish predators were collected from a small blackwater creek and borrow pits at NSGA using dip nets and plastic minnow traps and species were kept in separate 1000 l cattle watering tanks which had been inoculated with zooplankton, until the experiment began. The five treatments were four adult *Aphredoderus sayanus* (Aphredoderidae), four adult *Umbra pygmaea* (Umbridae), one to two adult *Esox americanus* (Esocidae), four adult *Enneacanthus gloriosus* (Centrarchidae), and 25 to 30 adult *Gambusia affinis* (Poeciliidae), plus control pools receiving no addition of predators. Differences in predator numbers reflect differences in predator biomass and availability (*E. americanus* were larger and less abundant). Predators were stratified by body size among blocks, and average treatment biomass was 18.8 g for *A. sayanus*, 15.8 g for *U. pygmaea*, 20.2 g for *E. americanus*, 14.9 g for *E. gloriosus*, and 16.2 g for *G. affinis*. These are five of the most abundant fish predators found at our study site, and densities/biomasses used in the experiment represent the lower range of natural densities where these species occur. Furthermore, all of these predators have been found to invade ephemeral wetlands used by *H. chrysoscelis* for reproduction after flood events (unpubl.).

Predators and controls were assigned to randomly selected pools in each block on 25 May 2000, and the experiment ran until August 1, 2000. The use of enclosures eliminated all physical interactions between predators and *H. chrysoscelis*, but allowed for non-lethal communication. While the exact cue or cues used by ovipositing females to detect the presence of predatory fish is unknown, aquatic habitats favor the detection of chemical cues (reviewed by Wisenden 2000) making them a leading candidate (Kats and Dill 1998, Resetarits 2001). Immediately after adding fish, and once a week thereafter, we slowly raised all enclosures (fish and fishless) out of the pools and then forced them back into the water to enhance water flow and chemical communication between the enclosures and the pools. Fish most likely fed on zooplankton, and any fish that died during the experiment were replaced to keep initial densities constant.

On nights with heavy rain, we removed lids from all pools to permit access by the natural breeding population of *H. chrysoscelis* located at NSGA. Pools were re-covered with the fiberglass mesh lids at sunrise after reproductive activity had ceased. We removed eggs the same morning and placed them in separate containers (one for each pool) before counting them.

We examined the effect of treatment and block on a single response variable, the mean number of eggs deposited in each treatment. Because we are interested in the ecological consequences of oviposition site choice, rather than the actual behavioral dynamics, we analyzed the overall distribution of eggs among treatments using analysis of variance. This is equivalent to an analysis using the estimated mean number of females based on mean clutch size (no. of eggs/clutch size), but is ecologically more intuitive. Data were analyzed using SAS for Windows version 6.11 (SAS Institute 1994), and were square root transformed (square root $Y + 0.5$) before ANOVA using type III sums of squares and $\alpha = 0.05$. Hypothesis testing used Dunnett's procedure (Dunnett 1955), a test designed specifically for analysis of experiments in which each of a number of treatment means is compared with a control mean. This test controls the experimentwise Type 1 error rate, and necessitates hyper-replication of the control treatment (Dunnett 1955, 1964, Kuehl 2000). The a priori null hypothesis was that each treatment mean would be equal to the control mean for all comparisons.

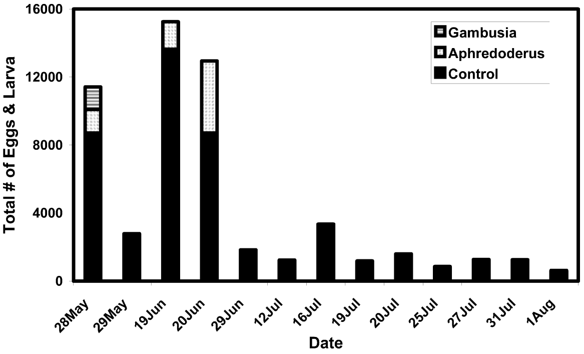

Fig. 1. Total number of *Hyla chrysoscelis* eggs and tadpoles recovered for each of the 13 nights on which reproduction took place during the summer of 2000. The eight experimental ponds in each block contained five with different fish predators (see Methods) and three controls. The majority of eggs were deposited in the control treatments. Eggs were laid in the *Aphredoderus sayanus* and *Gambusia affinis* treatments only on nights with the most oviposition activity.

Results

Hyla chrysoscelis bred on 13 nights during the experiment, resulting in a total of 55 625 eggs (Fig. 1). Eggs laid with fish only occurred on nights with the most oviposition activity (Fig. 1), and represent a single experimental pond for *Gambusia affinis* but multiple ponds for *Aphredoderus sayanus*. One block did not receive any eggs, perhaps due to heavy shading, and was removed from the analysis. Treatment had a significant effect ($P = 0.0079$) on mean number of eggs

Table 1. Summary of ANOVA for number of *Hyla chrysoscelis* eggs deposited (data square-root transformed).

Source	df	SS	MS	F	P
Block	3	1679.69	559.89	0.95	0.4598
Treatment	5	21062.04	4212.40	7.17	0.0079
Blk × trt	15	4850.58	323.37	0.55	0.8480
Error	8	4698.05	587.25		
Total	31	32290.36			

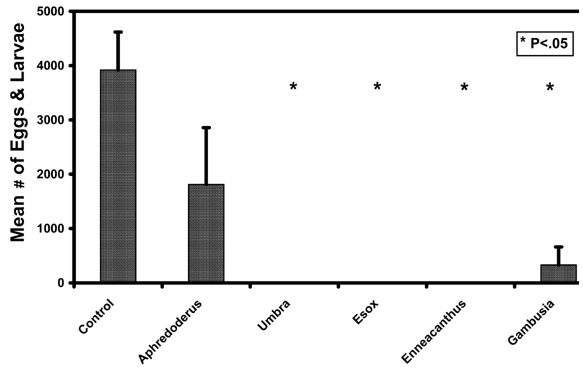

Fig. 2. Mean number (+ 1 S.E.) of *Hyla chrysoscelis* eggs and tadpoles recovered from pools containing five fish predators and from fishless controls. Fish could not prey upon either eggs or tadpoles (see Methods).

deposited (Fig. 1, Table 1), indicating that females responded to the non-lethal presence of fish and deposited their eggs non-randomly. There was no significant block effect ($P = 0.4589$) or block × treatment interaction ($P = 0.8480$) indicating that, besides the one removed from the analysis, all blocks received similar number of eggs and females responded similarly to treatments within blocks.

Pairwise comparisons of treatment means with the control means using Dunnett's procedure revealed significant differences between the *Umbra pygmaea*, *Esox americanus*, *Enneacanthus gloriosus* and *Gambusia affinis* treatments and the control, with the *Umbra*, *Esox* and *Enneacanthus* treatments producing complete avoidance (Fig. 2, Table 2). The *Aphredoderus sayanus* treatment, however, was statistically indistinguishable from control ponds (Fig. 2, Table 2).

Table 2. Summary of hypothesis tests using Dunnett's procedure to compare all treatments to a control for the response variable mean number of eggs oviposited (data square-root transformed). *

Treatment	Mean	$\bar{Y}_i - \bar{Y}_c$	D(0.05,5) †	Prob. (> t)
Control	57.97			
Aphredoderus	30.45	−27.51	39.47	NS
Umbra	0.70	−57.26	39.47	$P < 0.05$
Esox	0.70	−57.26	39.47	$P < 0.05$
Enneacanthus	0.70	−57.26	39.47	$P < 0.05$
Gambusia	9.61	−48.35	39.47	$P < 0.05$

* Dunnett's procedure with adjustments for unequal variances of means and allocation of more observations to the control (Dunnett 1955). Dunnett's procedure controls the experimentwise error rate.

† If the absolute value of $\bar{Y}_i - \bar{Y}_c$ exceeds the critical value of Dunnett's t, D(0.05,5) then the treatment mean is significantly different from the control.

Discussion

Oviposition site selection is a critical form of habitat selection in which females choose the habitat for their offspring. The most common and phylogenetically widespread reproductive strategy in amphibians (including *Hyla chrysoscelis*) is the deposition of eggs in lentic habitats with little or no post-oviposition parental care (Duellman and Trueb 1986). This strategy results in a larval stage with limited dispersal capabilities relative to adults of the same species, paralleling that of many other aquatic and terrestrial oviparous organisms (Rausher 1981, Thompson 1988, Bentley and Day 1989, Mayhew 1997). While amphibian breeding sites have been described as unpredictable due to large spatial and temporal variation in both abiotic and biotic characteristics (Petranka and Kennedy 1999), the presence of predatory fish represents a predictable and reliable indication of reproductive failure for ovipositing *Hyla chrysoscelis* females.

The suite of predators encountered at any given locale will vary greatly in species composition. This is certainly true for freshwater fish in the southeastern United States (Meffe and Sheldon 1990, Snodgrass and Meffe 1998). Free ranging *Hyla chrysoscelis* females demonstrated the capacity to detect and avoid a diverse phylogenetic sample of potential fish predators and obviously did not disperse their eggs amongst experimental ponds randomly (Fig. 1 and 2). Fish species were largely functionally equivalent with regard to their effects on oviposition site selection in *H. chrysoscelis* by producing a complete or nearly complete avoidance (Fig. 2). These data confirm and expand the presence of a primary larval "filter"(Hopey and Petranka 1994, Resetarits 2001, Binckley and Resetarits 2002), that can produce presence/absence and abundance patterns in experimental settings that have typically been ascribed to egg and larval mortality in observational field studies.

Aphredoderus sayanus did not elicit a statistically significant oviposition response in *H. chrysoscelis* (Fig. 2). *A. sayanus* readily consume *H. chrysoscelis* tadpoles (pers. obs.) and tadpoles would likely never reach a size refuge from predation (Zaret 1980) due to the large gape of this species (Page and Burr 1991). The dramatically different result for *A. sayanus* could be viewed as a type II error resulting from low statistical power, but colonizing/ovipositing aquatic beetles also do not avoid *A. sayanus* (unpubl.), suggesting a general lack of response to this species for a variety of aquatic organisms. Since *A. sayanus* often co-occurs with other fish that do elicit strong behavioral repulsion, its ecological effect on *H. chrysoscelis* and other ovipositing species might be minimal. However, what produces this deviation from the general pattern and its implications for aquatic communities are currently under investigation.

Our data combined with past research unequivocally demonstrate that when natural populations of certain aquatic organisms encounter experimental ponds with and without fish, avoidance of these predators is striking (Resetarits and Wilbur 1989, Resetarits 2001, Binckley and Resetarits 2002, Rieger 2002). We hypothesize that oviposition behavior of *H. chrysoscelis* females, and species with similar responses (Resetarits 2001, Rieger 2002), at natural breeding sites will depend on the combined distribution and abundance of all fish species that are behaviorally avoided, simplifying aquatic landscapes into fish and fishless habitat given the functional equivalence of multiple fish predators. The extent to which this behavior ultimately determines the field distribution of prey is an important question, but beyond the scope of this study. Based on the existing evidence, habitat selection is at least as plausible a mechanism as random oviposition and subsequent predation for producing observed patterns of distribution in *H. chrysoscelis* and similar species (Bradford 1989, Brönmark and Edenhamn 1994, Fisher and Shaffer 1996, Hecnar 1997, Azevedo-Ramos et al. 1999, Babbitt and Tanner 2000, Snodgrass et al. 2000). The extent to which prey distributions are produced by behavioral avoidance versus differential mortality clearly affects population and community level dynamics in different ways.

How individual decisions affect population and community structure has received relatively little attention (Real and Levin 1991, Sutherland 1996). The persistence of certain amphibian populations is thought to reflect a balance between local extinction and recolonization events at breeding ponds (Semlitsch and Bodie 1998, Skelly et al. 1999). The stability of such dynamics might depend on the degree to which these events are produced by the behavior of ovipositing individuals. The presence of predatory fish may produce extinction events, albeit non-lethal, representing a cryptic form of habitat loss, at least until a disturbance (pond drying) removes these predators. Incorporating oviposition site selection (habitat selection) into population models affects population size (Holt 1985, Smith et al. 2000, Spencer et al. 2002), growth rate, and persistence (Pulliam and Danielson 1991) as individuals actively avoid population "sinks" while seeking out and selecting "source" habitats. In spatially and temporally dynamic landscapes, where the distribution of "sink" habitat (e.g. those with fish for many amphibians) changes, habitat selection provides a mechanism for coping with the changing fitness landscape (Pulliam and Danielson 1991, Resetarits 2001), as individuals are not lost from the population by mortality or reproductive failure, but are simply redistributed spatially and concentrated into remaining "source" habitat (Resetarits and Wilbur 1989, Abrams 1993, Blaustein 1999, Resetarits 2001).

Community ecology emphasizes the role of species interactions in producing patterns of species distribution and abundance (Morin 1999). Our data demonstrate that spatial co-occurrence is not a prerequisite for strong species interactions, and for some species the nature and extent of species interactions may be determined at the habitat selection stage. However, the consequences of such redistribution and concentration in limited favorable habitats are not trivial, and constitute another line of research into the consequences of habitat selection. Subsequent experiments have documented that *Hyla femoralis*, *Hyla squirella*, *Gastrophryne carolinenis*, and numerous species of aquatic beetles avoid ovipositing and/or colonizing experimental ponds containing fish predators (Resetarits 2001, Binckley and Resetarits 2002, Rieger 2002). Hence, the probability of such fish intolerant species co-occurring in the same pond increases as they respond similarly to the presence of predatory fish.

Habitat selection models based on ideal free or ideal despotic distribution (Fretwell and Lucas 1970, Fretwell 1972, Rosenzweig 1987) emphasize that habitats differ in their suitability (e.g. fitness), and that these differences in quality are detectable to individuals who then match their choice of habitats with these expectations. Habitat suitability declines as densities of conspecifics, competitors and predators increase such that the use of alternative habitats (e.g. breeding ponds) will occur. Ovipositing *H. chrysoscelis* avoid high densities of conspecific larva just as strongly as they do certain fish predators (Resetarits and Wilbur 1989), and oviposition might conceivably switch back to areas containing fish when conspecific densities are high. For example, the eggs laid with fish in this experiment only occurred on nights with the most oviposition activity (Fig. 1), which might have been a response to increased egg density in control pools. Thus, habitat selection, and hence oviposition site choice, is a context dependent process, where the suitability of any given habitat is relative to the suitability of all other potential habitats. Field distribution patterns of species such as *H. chrysoscelis*, where females pick and choose amongst ponds, should depend not only on the relative quality of potential breeding sites, but perhaps more importantly, on their frequency distribution in complex landscapes.

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