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Differential Vulnerability of Hyla chrysoscelis Eggs and Hatchlings to Larval Insect Predators
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Source: *Journal of Herpetology*, Vol. 32, No. 3 (Sep., 1998), pp. 440-443
Published by: Society for the Study of Amphibians and Reptiles
Stable URL: http://www.jstor.org/stable/1565462
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LITERATURE CITED

AXTELL, R. W., AND N. HASKELL. 1977. An interhiatal population of *Pseudacris streckeri* from Illinois, with an assessment of its postglacial history. Chicago Acad. Sci. Nat. Hist. Misc. No. 202.

BLANCHARD, F. N. 1933. Late autumn collections and hibernating situations of the salamander *Hemidactylium scutatum* (Schlegel) in southern Michigan. Copeia 1933:216.

BODMAN, G. B., AND P. R. DAY. 1943. Freezing points of a group of California soils and their extracted clays. Soil Sci. 55:225–246.

BRECKENRIDGE, W. J., AND J. R. TESTER. 1961. Growth, local movements and hibernation of the Manitoba toad, *Bufo hemiophrys*. Ecology 42:637–646.

BROWN, L. E., AND G. B. ROSE. 1988. Distribution, habitat, and calling season of the Illinois chorus frog (*Pseudacris streckeri illinoensis*) along the lower Illinois River. Illinois Nat. Hist. Surv. Biol. Notes 132:1–13.

BROWN, L. E., H. O. JACKSON, AND J. R. BROWN. 1972. Burrowing behavior of the chorus frog, *Pseudacris streckeri*. Herpetologica 28:325–328.

CARPENTER, C. C. 1953. A study of hibernacula and hibernating associations of snakes and amphibians in Michigan. Ecology 34:74–80.

COCROFT, R. B. 1994. A cladistic analysis of chorus frog phylogeny (Hylidae: *Pseudacris*). Herpetologica 50:420–437.

CONANT, R., AND J. T. COLLINS. 1991. A Field Guide to Reptiles and Amphibians [of] Eastern and Central North America, 3rd ed. Houghton Mifflin Co., Boston, Massachusetts.

LAYNE, J. R., JR. 1991. External ice triggers freezing in freeze-tolerant frogs at temperatures above their supercooling point. J. Herpetol. 24:129–130.

———, AND J. KEFAUVER. 1997. Freeze tolerance and postfreeze recovery in the frog *Pseudacris crucifer*. Copeia 1997:260–264.

———, R. E. LEE, JR., AND J. L. HUANG. 1990. Inoculation triggers freezing at high subzero temperatures in a freeze-tolerant frog (*Rana sylvatica*) and insect (*Eurosta solidaginis*). Can. J. Zool. 68:506–510.

MACARTHUR, D. L., AND J. W. T. DANDY. 1982. Physiological aspects of overwintering in the boreal chorus frog (*Pseudacris triseriata maculata*). Comp. Physiol. Biochem. A 72:137–141.

PINDER, A. W., K. B. STOREY, AND G. R. ULTSCH. 1992. Estivation and hibernation. *In* M. E. Feder and W. W. Burggren (eds.), Environmental Physiology of the Amphibians, pp. 250–274. Univ. Chicago Press, Chicago.

RUIBAL, R., L. TEVIS, JR., AND V. ROIG. 1969. The terrestrial ecology of the spadefoot toad *Scaphiopus hammondii*. Copeia 1969:571–584.

SAS INSTITUTE. 1990. SAS/STAT User's Guide. SAS Institute, Cary, North Carolina.

SCHMID, W. D. 1982. Survival of frogs in low temperature. Science 215:697–698.

SMITH, P. W. 1961. The amphibians and reptiles of Illinois. Illinois Nat. Hist. Surv. Bull. 28:1–298.

STOREY, K. B., AND J. M. STOREY. 1986. Freeze tolerance and intolerance as strategies of winter survival in terrestrially hibernating amphibians. Comp. Biochem. Physiol. A 83:613–617.

SWANSON, D. L., B. M. GRAVES, AND K. L. KOSTER. 1996. Freezing tolerance/intolerance and cryoprotectant synthesis in terrestrially overwintering anurans in the Great Plains, USA. J. Comp. Physiol. B 166:110–119.

SWEENEY, T. E., AND C. A. BEUCHAT. 1993. Limitations of methods of osmometry: measuring the osmolality of biological fluids. Am. J. Physiol. 264:R469–R480.

TUCKER, J. K., J. B. CAMERER, AND J. B. HATCHER. 1995. *Pseudacris streckeri illinoensis* (Illinois Chorus Frog). Burrows. Herpetol. Rev. 26:32–33.

Accepted: 10 April 1998.

Journal of Herpetology, Vol. 32, No. 3, pp. 440–443, 1998
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Differential Vulnerability of *Hyla chrysoscelis* Eggs and Hatchlings to Larval Insect Predators

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Predation is an important component of temporary pond ecosystems and plays a critical role in the structure of larval anuran assemblages in temporary habitats (Morin, 1983; Fauth and Resetarits, 1991; Werner and McPeek, 1994). Because of the absence of predatory fish and the often reduced density of other vertebrate predators, especially in temporary ponds which dry frequently, invertebrate predators may play an especially important role (Wellborn et al., 1996). Among the most abundant and widespread predatory larval insects in temporary ponds are dragonflies (Odonata) of the families Libellulidae and Aeschnidae, and beetles (Coleoptera) of the families Dytiscidae and Hydrophilidae. Dragonfly naiads are known to be important predators of larval anurans (e.g., Brockelman, 1969; Caldwell et al., 1980), especially in temporary habitats (e.g., Heyer et al., 1975; Smith, 1983; Van Buskirk, 1988). Van Buskirk (1988) showed that predation by larval dragonflies not only reduced the overall abundance of larval anurans, but reduced the diversity of larval anuran assemblages. Larval dytiscids have been implicated as potentially important predators on larval anurans (Young, 1967; Formanowicz and Brodie, 1982; Brodie and Formanowicz, 1983), but less is known about their potential effects on larval anuran assemblages.

The two types of predators have distinctly different predatory habits and life histories. Dragonfly naiads are visual predators that attack actively moving animals (Pritchard, 1965; Oakley and Palka, 1967) and hunt using active or sit-and-wait modes (Van Buskirk, 1988). Dragonfly eggs are deposited from spring throughout the summer and development may take several months to more than a year (Paulson and Jenner, 1971). Ponds may contain many different species during the summer and each species may be represented by several size classes (instars) (Paulson and Jenner, 1971). Many larval dytiscid (and hydrophilid) beetles are extremely active cursorial predators that are in seemingly constant motion at times, capturing and consuming anything they encounter, including conspecifics, but they may also utilize a sit and wait mode (Formanowicz 1982; pers. obs.). Larval dytiscids may use visual, tactile, or chemical cues to detect prey (Formanowicz, 1987). Dytiscid eggs may appear at any time during the active season. The larvae grow rapidly and even relatively large species may leave the ponds in a matter of weeks (pers. obs.). Larval dytiscids and hydrophilids tend to appear in the ponds in pulses, perhaps representing single clutches or adult emergence classes (pers. obs.), and many species may co-occur at individual sites (Juliano and Lawton, 1990).

Both types of predators are abundant in temporary aquatic habitats utilized by Cope's gray treefrog, *Hyla chrysoscelis*, in the North Carolina piedmont. *Pachidiplax longipinnis* (Odonata: Libellulidae) and *Ilybius* sp. (Coleoptera: Dytsicidae) are especially common predators in small temporary ponds used by *H. chrysoscelis. Pachidiplax longipinnis* uses primarily a sit-and-wait hunting mode, while *Ilybius* sp. is an extremely active hunter. Observations of natural predation by both species suggested that the two predators also differed in their responses to early life stages of *H. chrysoscelis*, perhaps using different feeding cues. A simple feeding experiment was performed to examine the relative predation rate of late instar larvae of *P. longipinnis* and *Ilybius* on the eggs and newly hatched larvae of *H. chrysoscelis*. Differences between these predators in their ability to exploit vulnerable early life stages of larval anurans would be expected to generate very different effects on larval anuran populations.

The experiment was conducted at the Duke Zoology Field Station (DZFS), Durham County, North Carolina. Thirty-six 300 ml paper cups were used as experimental containers and were filled with 150 ml aged tap water and arranged on a table under a canopy. Fifty eggs of *H. chrysoscelis* approximately 24 h post oviposition (approx. Gosner stage 17, Gosner, 1960) or 20 newly hatched tadpoles approximately one week post oviposition (approx. Gosner stage 24–25), both collected from wading pools at DZFS and each represented by several clutches, were randomly assigned, each to half (18) of the containers. These two life stages provided a very clear contrast between the essentially inanimate and vulnerable eggs, and the mildly animate but equally vulnerable hatchlings, with other characteristics, such as mass and nutrient content, essentially equal. Three treatments were assigned randomly to the two sets (one with eggs, one with larvae) of 18 containers, (1) eggs (or larvae) alone, (2) eggs (or larvae) plus one individual of *Ilybius* sp., and (3) eggs (or larvae) plus one individual of *P. longipinnis*. Individual predators were assigned randomly to containers within the treatments. There were six treatments each replicated six times for a total of 36 experimental units. Positions of all containers and treatments were completely randomized on the table top and screen was placed over the containers to prevent escape or invasion by other species. Predators were late instar larvae (all approximately 10 mm total length) also collected from wading pools at DZFS. Random samples of eggs and larvae of *H. chrysoscelis* (identity based on call and distribution; *H. versicolor* is not known from this area) and random samples of larvae of both *P. longipinnis* (Huggins and Brigham, 1982) and *Ilybius* sp. (Brigham, 1982) were preserved as vouchers (currently held by author). The experiment was begun at 2400 h on 15 July and ended with removal of the predators at 2000 h the following day. The surviving eggs and hatchlings were then counted.

Data were analyzed using separate analyses of variance on the completely randomized designs for each life stage. Survival proportions were arcsine square-root transformed to meet the assumptions of the analysis of variance. Tukey's procedure for multiple comparisons was used to compare consumption of eggs and tadpoles by larvae of the two families (SAS Institute, 1988).

Analysis of variance revealed a highly significant effect of treatments on the survival of *Hyla* tadpoles ($F_{2,15} = 63.11$, $R^2 = 0.894$, $P = 0.0001$). Mean tadpole survival was 97.5% (mean ± 1 SE: 19.5 ± 0.34 tadpoles) in the predator-free controls, but was reduced to 62.5% (12.5 ± 2.08) with dragonfly naiads and to 0.84% (0.17 ± 0.17) with dytiscid larvae (Fig. 1b). Tukey's procedure showed that both the dragonfly and dytiscid treatments were significantly different from the controls, and that the dytiscid treatment was significantly different from the dragonfly treatment. Dragonfly naiads and dytiscid larvae were both significant predators of newly hatched *Hyla* tadpoles in the experiment, but the predation rate by dytiscid larvae was much greater than that of dragonfly naiads.

There was also a highly significant effect of treatments on the survival of *Hyla* eggs ($F_{2,15} = 62.20$, $R^2 = 0.892$, $P = 0.0001$). Mean egg survival was 97% (48.7 ± 0.49 eggs) in the controls and 89% (44.3 ± 1.96) in the dragonfly treatment, but was reduced to only 16% (7.83 ± 2.6) in the presence of dytiscid larvae (Fig. 1a). In contrast to the results for tadpoles, the control and dragonfly treatments were not significantly different from each other, but the dytiscid treatment was significantly different from both the dragonfly treatment and the control. Therefore, only dystiscid larvae were important predators on the eggs of *H. chrysoscelis*.

Several factors contribute to the overall effect of a predator on populations of a prey species. Size, density, feeding mode, and other characteristics of the predator are most frequently discussed in this regard, along with specific characteristics of the prey (Morin, 1983; Formanowicz, 1986; Van Buskirk, 1988). One important factor is the relative vulnerability of different life stages of a species to different predators. The effects of a particular predator must be integrated over the life cycle of the prey to assess the net effect on prey populations and prey life histories. Predators that prey on several life stages of a prey species may have a greater impact on prey populations than those that are limited to a particular life stage or size range.

Though the vulnerability of prey species is often dependent on the relative sizes of the predator and the prey (Wilbur, 1988), it may also depend upon the hunting mode used by the predator. For instance, many sit-and-wait visual predators often require the stimulus of moving prey, while actively hunting predators may utilize other modes for prey location and

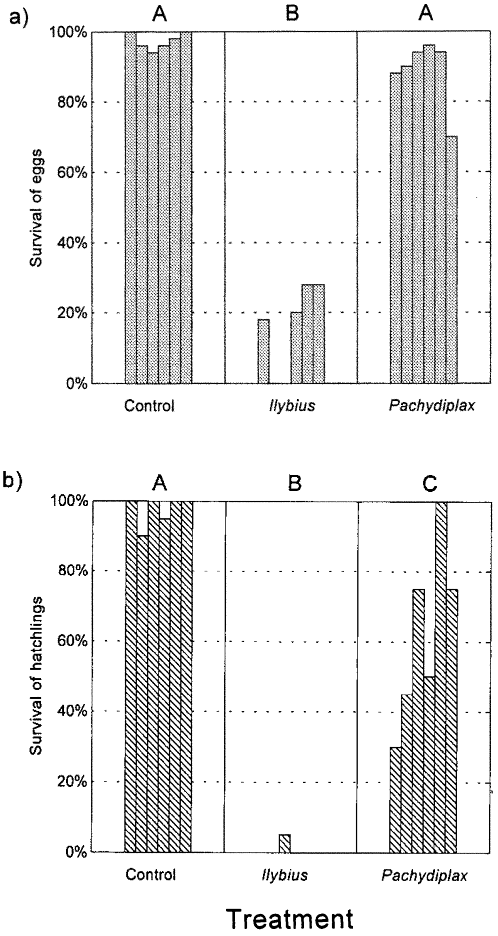

Fig. 1. Survival of eggs (a) and hatchlings (b) of *H. chrysoscelis* under predation by larval dragonflies, *P. longipinnis*, and larval dystiscid beetles, *Ilybius* sp. The individual bars represent the six replicates of each treatment. Letters at the top of each graph indicate which treatments were significantly different (indicated by different letters) using Tukey's procedure.

identification (Pritchard, 1965; Formanowicz, 1987). This difference is important for anuran amphibians, which lay large numbers of highly vulnerable, immobile eggs that hatch into highly vulnerable, but mobile, hatchling tadpoles.

The two species of predators used in this study have markedly different predatory habits, though they are generally thought of as generalist predators on much the same range of prey. The results indicate that while larval *P. longipinnis* and *Ilybius* sp. both take significant numbers of hatchling *H. chrysoscelis*, only larval *Ilybius* sp. can be considered an important predator of *H. chrysoscelis* eggs (Fig. 1). This difference is important because the eggs are both a vulnerable and concentrated prey resource. Larval *Pachidiplax* took significantly fewer hatchlings than *Ilybius* and destroyed eggs only incidentally by walking over them in the confines of the containers. In extra wading pools set out at DZFS to observe colonization and collect animals for experiments, larval dytiscids were often seen in large numbers on newly laid clutches of *H. chrysoscelis*, consuming the majority of eggs (extracting them from the jelly) in individual clusters of 30–100 eggs (pers. obs.). Because the upper limits of tadpole size taken by the late instar larvae of small dytiscids and small odonates are similar (pers. obs.), the local effects of dytiscids may be more dramatic than those of odonates in the same ponds. In addition, the presence of larval dytiscids may decrease the survival of individual clutches and the fitness of individual females because significant predation may occur before any mixing of larval cohorts can occur. Thus, although larval odonates are more common and generally more abundant predators than larval dytiscids, the latter may have dramatic effects on populations of larval anurans when periods of high larval dytiscid abundance coincide with egg laying by anurans. The rapid development of larval dytiscids, coupled with high activity levels and high consumption rate of eggs, hatchlings, and larger tadpoles of *H. chrysoscelis*, implicate larval dytiscids as potentially important predators on larval anurans early in the development of temporary pond communities. They may be particularly important in small ephemeral pools where a few clutches of dytiscids, or perhaps even a single clutch, could significantly affect larval anuran populations and alter the structure of the larval anuran assemblage.

Acknowledgments.—Cheryl Resetarits helped conduct this experiment. The research was supported by the Department of Zoology, Duke University.

LITERATURE CITED

BRIGHAM, W. U. 1982. Dytiscidae. *In* A. R. Brigham, W. U. Birgham, and A. Gnilka (eds.), Aquatic Insects and Oligochaetes of North and South Carolina, pp. 10.47–10.71. Midwest Aquatic Enterprises, Mahomet, Illinois.

BROCKELMAN, W. Y. 1969. An analysis of density effects and predation in *Bufo americanus* tadpoles. Ecology 50:632–644.

BRODIE, E. D., JR., AND D. R. FORMANOWICZ, JR. 1983. Prey size preference of predators: differential vulnerability of larval anurans. Herpetologica 39:67–75.

CALDWELL, J. P., J. H. THORP, AND T. O. JERVEY. 1980. Predator-prey relationships among larval dragonflies, salamanders, and frogs. Oecologia 46:285–289.

FAUTH, J. E., AND W. J. RESETARITS, JR. 1991. Interactions between the salamander *Siren intermedia* and the keystone predator *Notophthalmus viridescens*. Ecology 72:827–838.

FORMANOWICZ, D. R., JR. 1982. Foraging tactics of larvae of *Dytiscus verticalis* (Coleoptera: Dytiscidae): the assessment of prey density. J. Anim. Ecol. 51: 757–767.

———. 1986. Anuran tadpole/aquatic insect predator–prey interactions: tadpole size and predator capture success. Herpetologica 42:367–373.

———. 1987. Foraging tactics of *Dytiscus verticalis* larvae (Coleoptera: Dytiscidae): prey detection, reactive distance and predator size. J. Kans. Entomol. Soc. 60:92–99.

———, AND E. D. BRODIE, JR. 1982. Relative palatabilities of members of a larval amphibian community. Copeia 1982:91–97.

GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16:183–190.

HEYER, W. R., R. W. MCDIARMID, AND D. L. WEIGMANN. 1975. Tadpoles, predation, and pond habitats in the tropics. Biotropica 7:100–111.

HUGGINS, D. G., AND W. U. BRIGHAM. 1982. Odonata. *In* A. R. Brigham, W. U. Brigham, and A. Gnilka (eds.), Aquatic Insects and Oligochaetes of North and South Carolina, pp. 4.11–4.100. Midwest Aquatic Enterprises, Mahomet, Illinois.

JULIANO, S. A., AND J. H. LAWTON. 1990. The relationship between competition and morphology. I. Morphological patterns among co-occurring dytiscid beetles. J. Anim. Ecol. 59:403–419.

MORIN, P. J. 1983. Predation, competition and the composition of larval anuran guilds. Ecol. Monogr. 53:119–138.

OAKLEY, B., AND J. M. PALKA. 1967. Prey capture by dragonfly larvae. Amer. Zool. 7:727–728.

PAULSON, D. R., AND C. E. JENNER. 1971. Population structure in overwintering larval Odonata in North Carolina in relation to adult flight season. Ecology 52:96–103.

PRITCHARD, G. 1965. Prey capture by dragonfly larvae (Odonata: Anisoptera). Can. J. Zool. 43:271–289.

SAS INSTITUTE. 1988. SAS/STAT User's Guide, Release 6.03 Edition. SAS Institute Inc., Cary, North Carolina.

SMITH, D. C. 1983. Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. Ecology 68:344–350.

VAN BUSKIRK, J. 1988. Interactive effects of dragonfly predation in experimental pond communities. Ecology 69:857–867.

WILBUR, H. M. 1988. Interactions between growing predators and growing prey. *In* B. Ebenman, and L. Persson (eds.), Size-structured Populations, pp. 157–172. Springer-Verlag, Berlin.

WELLBORN, G. A., D. K. SKELLY, AND E. E. WERNER. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Ann. Rev. Ecol. Syst. 27:337–363.

WERNER, E. E., AND M. A. MCPEEK. 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. Ecology 75:197–213.

YOUNG, A. M. 1967. Predation in the larvae of *Dytiscus marginalis* Linnaeus (Coleoptera: Dytiscidae). Pan-Pacific Entomologist 43:113–117.

Accepted: 12 April 1998.

Journal of Herpetology, Vol. 32, No. 3, pp. 443–446, 1998
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Predation by Tadpoles on Toxic Toad Eggs: the Effect of Tadpole Size on Predation Success and Tadpole Survival

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The majority of anuran larvae are opportunistic omnivores, supplementing their primarily herbivorous diet with alternate food items when available (Wassersug, 1974, 1975; Wilbur, 1980; Alford, *in press*). The eggs of con- and heterospecific anurans are one such alternate source of nutrition (for recent reviews see Crump, 1983; Polis and Myers, 1985; Alford, *in press*). In most instances such predation is opportunistic, although at least one anuran species is known to feed unfertilised eggs to its tadpoles (Weygoldt, 1980; Brust, 1993).

Although the eggs of many anuran species may provide an energetically rich food source for tadpoles, the eggs of some species (e.g., *Bufo* spp.) possess toxins (Licht, 1967, 1968, 1969; Akizawa et al., 1994) which may have adverse effects on tadpoles that consume them. Several studies have documented predation on *Bufo* eggs by anuran larvae. *Bufo calamita* eggs are preyed upon by tadpoles of *Rana temporaria* (Heusser, 1970; Banks and Beebee, 1987), *Bufo bufo* (Beebee, 1977; Banks and Beebee, 1987), *Pelobates cultripes* (Tejedo, 1991), and *Pelodytes punctatus* (Tejedo, 1991). Heusser (1970) reported predation on *Bufo bufo* eggs by *Rana temporaria* tadpoles. Wells (1979) observed *Leptodactylus pentadactylus* tadpoles preying upon eggs of *Bufo typhonius*. Hearnden (1991) found *Bufo marinus* tadpoles to be important predators of conspecific eggs, while Petranka et al. (1994) demonstrated that *Rana sylvatica* tadpoles are voracious predators of *Bufo americanus* eggs. None of these studies report post-ingestive ill effects to tadpoles following the consumption of *Bufo* eggs. However, recent studies have demonstrated that all egg stages (from fertilization through to hatching) of the introduced toad *Bufo marinus* are highly toxic to oophagous native Australian tadpoles (Crossland, 1997; Crossland and Alford, 1998.

Many native Australian tadpoles appear unable to detect the highly toxic nature of *B. marinus* eggs (Crossland and Alford, 1998) and often consume them despite the presence of alternate non-toxic food (Crossland, 1997). Therefore, any factor that prevents native tadpoles from consuming *B. marinus* eggs should enhance tadpole survival in the presence of *B. marinus* eggs. One such factor may be tadpole size. Previous studies have noted that small tadpoles are often less effective predators of anuran eggs than large tadpoles (Crump, 1983; Tejedo, 1991; Petranka and Thomas, 1995). If certain size classes of native Australian tadpoles are unable to consume *B. marinus* eggs, these individuals are likely to experience higher survival rates in the presence of *B. marinus* eggs than larger tadpoles that are capable of consuming *B. mar-*