

## Activity level and the susceptibility of anuran larvae to predation

DAVID K. SKELLY\*

*Department of Biology, University of Michigan, Ann Arbor, MI 48109, U.S.A.*

*(Received 8 February 1993; initial acceptance 16 April 1993;  
final acceptance 24 June 1993; MS. number: sc-848)*

Animal behaviour is often influenced by conflicting demands (e.g. Belovsky 1981; Travers & Sih 1991). Among many potential trade-offs influencing foraging behaviour, the conflict between the needs to acquire food and avoid predation has received perhaps the most attention (reviewed by Lima & Dill 1990). There are good reasons to expect that such a trade-off will be widespread among organisms and systems. Spatial refuges from predation can become depleted of food resources (e.g. Werner et al. 1983) and behaviour associated with encounter, detection and consumption of food resources can also be associated with higher rates of encounter, detection and consumption by predators (e.g. McPeck 1990a). Models of behaviour incorporating trade-offs between resource gain and predation risk have assumed that behaviour that fosters increased rates of food intake also increases the likelihood of being consumed by predators (e.g. Gilliam & Fraser 1987). Larval amphibians and their predators have proved a model system for demonstrating that individuals can perceive and respond to changes in predation risk (Petranka et al. 1987; Kats et al. 1988; Lawler 1989), and that these responses can have costs in terms of reduced rates of growth and development (Skelly & Werner 1990; Skelly 1992). There have also been suggestions, based on interspecific comparisons, that behaviour promoting resource gain, such as an increased proportion of time spent active, also increases predation risk (Woodward 1983; Lawler 1989; Azevedo-Ramos et al. 1992; Chovanec 1992). While supportive, these correlations are potentially confounded by other differences between species (e.g. coloration, palatability, swimming speed) that could influence susceptibility to predators. The purpose of this study is to examine the role of activity in determining predation risk within a single species, the larva of the wood frog (*Rana sylvatica*; Anura: Ranidae), by experi-

mentally manipulating behaviour of larvae and examining the consequences to rates of predation by larvae of the dragonfly, *Anax junius* (Odonata: Aeschnidae). These species commonly co-occur in semi-permanent ponds in southeastern Michigan, U.S.A. (unpublished data).

I conducted two experiments simultaneously to evaluate the relationship between activity and susceptibility to predation. Both experiments used the same stocks of tadpoles and predators and shared the same treatments. Tadpoles were raised in the laboratory from several clutches of eggs collected from natural populations on the E. S. George Reserve (Livingston County, Michigan). Tadpoles weighed  $84.8 \pm 5.9$  mg ( $\bar{X} \pm 1$  SE;  $N=6$ ) and were approximately 7 mm long (snout-vent length) at the time of the experiments. While in laboratory culture tadpoles were fed, ad libitum, a 3:1 mixture of Purina Rabbit Chow and Tetra Min Fish Flakes finely ground with a mortar and pestle. Late instar *Anax* larvae (50–60 mm total length) were also collected from local populations on the E. S. George Reserve and were fed a single wood frog tadpole immediately prior to the experiment to standardize hunger levels among predators. Tadpoles to be used in the experiments were soaked for 3 h, immediately prior to introduction into experimental containers, in a 1:4000 solution of tricaine methanesulphate (hereafter tricaine), or a control solution (aged well water). Tricaine is widely used as a general anaesthetic for vertebrates (e.g. Wayson et al. 1976). At the end of 3 h, 12 tadpoles were placed into each experimental container and allowed to acclimatize for 30 min prior to the introduction of predators (see below). The experiments lasted 2.5 h after the introduction of predators. Both experiments were conducted in plastic containers holding 8.0 litres of aged well water and a 3.8 m length of coiled 'camouflage colour' polypropylene rope to provide structural complexity. Containers were placed on shelves in the laboratory and lit by fluorescent fixtures. Water temperature during the experiments was 21.5°C.

\*Present address: Department of Biological Sciences, University of Wollongong, Wollongong, NSW 2522, Australia.

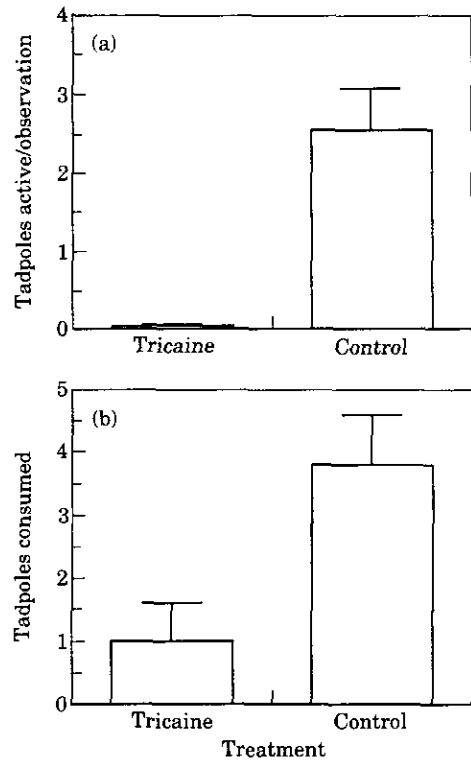
The first experiment examined treatment effects (prior exposure to either tricaine or the control solution) on tadpole activity. Each treatment was replicated four times for a total of eight containers. Each container in this experiment held a cylindrical cage measuring  $7.5 \times 2.8$  cm, made of aluminium wire, plastic mesh, and fibreglass window screening. Immediately prior to the experiment a single fed *Anax* was placed in each cage. For each container I measured activity by counting the number of tadpoles moving out of 12. When scoring activity, I stood approximately 0.5 m away from the containers and the tadpoles were not noticeably disturbed by my presence. This methodology has yielded results consistent with observations made using video cameras (personal observations). Ten observations, each separated by 15 min, were taken over the course of the experiment. The first observation was not taken until 15 min after the predators had been introduced into the cages. The average number of tadpoles active per observation was calculated for each container.

The second experiment examined the effect of prior exposure to the two solutions on susceptibility to predation. Each treatment was replicated six times for a total of 12 containers. *Anax* in this experiment were placed directly into the containers allowing them to attack the tadpoles. After 2.5 h, the *Anax* were removed and the number of tadpoles remaining within each container counted. There was no evidence that any *Anax* had captured but not consumed tadpoles.

The activity experiment demonstrated that prior exposure to tricaine rendered tadpoles almost completely inactive; only one tricaine-exposed tadpole was seen moving on one occasion while an average of over two tadpoles were moving within each control container at each observation ( $t$ -test:  $t = 4.75$ ,  $df = 6$ ,  $P < 0.001$ ; Fig. 1a).

Exposure to tricaine also influenced predation rates by *Anax*. Within the predation rate experiment, control tadpoles were almost four times as likely to be consumed as those exposed to tricaine ( $t$ -test:  $t = 2.83$ ,  $df = 10$ ,  $P < 0.02$ ; Fig. 1b). However, an average of one tadpole was consumed in each container where tadpoles had been exposed to tricaine.

The immobilizing effect of tricaine on wood frog tadpoles was related to a strong drop in risk of predation. This finding corroborates previous comparisons across taxa where more active tadpole species have been shown to be more susceptible to



**Figure 1.** Activity responses of wood frog larvae (a), and predation rates of *Anax* dragonfly larvae on wood frog larvae (b). Wood frog larvae were previously exposed to a solution of tricaine methanesulphonate (Tricaine), or a control solution of aged well water (Control). Each treatment was replicated four times in the activity experiment (a) and six times in the predation rate experiment (b). Each replicate initially contained 12 tadpoles. Error bars represent 1 SE.

predators (Woodward 1983; Lawler 1989; Azevedo-Ramos et al. 1992; Chovanec 1992). In this case, however, differences in activity were not confounded by other potential discrepancies between species. The results of these experiments strongly suggest that activity of tadpoles is associated with risk of predation, and also suggest that factors other than activity may also be associated with predation risk. *Anax* struck at and consumed tadpoles in three of six tricaine treatment replicates (by comparison *Anax* in all six control replicates consumed at least one tadpole). Larval odonates are generally thought to require movement, detected either visually or via mechanosensory hairs, in order to elicit a predatory strike (Pritchard 1965; Richards & Bull 1990a). A previous study (Kanou & Shimozawa

1983) found that tadpoles immobilized using carbon dioxide were not attacked by larvae of the Aeschnid dragonflies, *Aeschna nigroflava* and *Aeschna juncea* over periods of 30 min. In this study anaesthetized tadpoles showed virtually no movement and remained sedated for over an hour after the experiment was completed. While it is possible that highly infrequent movements accounted for predatory strikes by *Anax* in tricaine treatment containers, it is also possible that *Anax* have some additional ability to detect prey (e.g. chemical or visual detection of non-moving prey). Resolution of these possibilities will require continuously monitoring behaviour of predator and prey (e.g. using video cameras).

Several species of larval anuran are known to reduce activity in the presence of predators, or other cues associated with predation risk (Lawler 1989; Skelly & Werner 1990; Werner 1991; Skelly 1992). The decrease in risk of predation associated with lowered activity implied by the results of this study can come about in at least two ways. Theoretical models of predator-prey interactions typically predict that reducing time spent moving will reduce encounter rate with predators (e.g. Abrams 1984). Activity can also have more subtle effects where prey are cryptic or where predators require movement to elicit an attack. In these cases proximity does not guarantee detection and even when rates of movement have little or no influence on rates of encounter, they could have a large influence on rates of detection and attack. The results of this study may actually understate the advantages of facultative reductions in activity. Dragonfly larvae are frequently unsuccessful in capturing tadpole prey (capture success can be < 50%), and the abilities to avoid strikes and escape the grasp of predators can be important determinants of predation risk (Richards & Bull 1990b; Chovanec 1992). While tricaine treated tadpoles might have been less likely to be encountered or detected than control individuals, they may have been more likely to be captured once detected because of their inability to evade predatory strikes or shake free from a predator's grasp once caught.

Activity-based trade-offs may be a common feature of aquatic communities. Evidence of similar conflicts between resource acquisition and predation risk exists for aquatic insects (McPeck 1990a), and crustaceans (G. A. Wellborn, personal communication). Where applicable, such trade-offs can be an effective means of predicting the

consequences of behaviour to performance (e.g. survivorship, growth), and ultimately patterns of distribution (McPeck 1990b). Facultative responses to food and predators have been found in a great variety of taxa and it is becoming apparent that animals are highly sensitive to alterations in these factors (Werner & Anholt, in press). It is equally apparent that even closely related species often differ markedly in their responses to the environment; these differences may offer important clues related to the mechanisms of ecological performance (e.g. McPeck 1990a, b). Experimental manipulations of behaviour offer a direct means of testing hypotheses concerning behavioural mechanisms. Such studies may provide a means of understanding the underpinnings of species' attributes and their consequences to patterns at larger scales such as distribution and community composition.

Discussions with Mark McPeck, Earl Werner and Gary Wellborn were helpful in the formulation of the experiment. I thank Mark McPeck, Earl Werner and an anonymous referee for their comments on previous versions of the manuscript. Access to the E. S. George Reserve was provided by Ron Nussbaum, associate director, and Jack Haynes, caretaker. I was supported by a block grant from the Department of Biology at the University of Michigan during the research and by a grant from the Australian Flora and Fauna Research Program at the University of Wollongong during preparation of the manuscript.

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