

Differential use of visual and chemical cues in predator recognition and threat-sensitive predator-avoidance responses by larval newts (*Notophthalmus viridescens*)

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Abstract: For prey under the threat of predation, the ability to distinguish between different levels of danger can have important fitness consequences. Larval central newts, *Notophthalmus viridescens louisianensis*, distinguished between predatory (*Ambystoma tigrinum tigrinum* larvae) and nonpredatory (*Hyla chrysoscelis/versicolor* complex tadpoles) heterospecifics, but only when chemical cues were available. When only visual cues were present, larvae responded to both predatory and nonpredatory stimuli by reducing activity (fright response), but did not distinguish between the two types. Fine-scale discrimination of visual stimuli may have failed to develop because larval newts typically live in aquatic habitats in which chemical cues may be more reliable than visual cues, owing to large amounts of sediments and vegetation or possibly to myopia. Late-stage newt larvae that were approaching metamorphosis were unpalatable to *A. t. tigrinum*, and histological examination of the skin revealed that granular (poison) glands were present in the skin of late-stage but not early-stage larvae. Late-stage larvae did not distinguish between chemical stimuli from predators and nonpredators, which suggests that fright responses of larval newts are plastic and can be modified according to the level of perceived threat.

Résumé : Pour des proies menacées de prédation, la capacité de distinguer divers degrés de danger peut avoir d'importantes conséquences sur le fitness. Des larves du triton *Notophthalmus viridescens louisianensis* sont capables de faire la distinction entre des espèces prédatrices (larves d'*Ambystoma tigrinum tigrinum*) et des espèces non prédatrices (têtard de complexe d'*Hyla chrysoscelis/versicolor*), mais seulement en présence de stimulus chimiques. En présence de stimulus visuels seulement, les larves réagissaient de la même façon aux prédateurs et aux non prédateurs, en réduisant leur activité (une réaction de peur), mais ne pouvaient faire la distinction entre les deux. Les larves du triton n'ont pas acquis la capacité de discrimination fine entre des stimulus visuels probablement parce qu'elles vivent surtout dans l'eau où les stimulus chimiques sont sans doute plus fiables que les stimulus visuels à cause de l'abondance des sédiments et de la végétation, ou alors parce que ces larves sont myopes. Les larves de stades avancés à l'approche de leur métamorphose ne sont pas recherchées par les *A. t. tigrinum* et l'examen histologique de leur peau a révélé la présence de glandes granulaires (à poison) dans la peau des larves avancées, glandes absentes chez les jeunes larves. Les larves des stades avancés ne pouvaient pas faire la distinction entre les stimulus chimiques provenant des prédateurs et ceux provenant d'espèces non prédatrices, ce qui semble indiquer que les réactions de peur des larves du triton sont variables et peuvent être modifiées en fonction du degré de menace perçu.

[Traduit par la Rédaction]

Introduction

Prey animals often respond to the threat of predation by decreasing the frequency or efficiency of behaviour associated with foraging, reproduction, or other activities (Lima and Dill 1990; Lima 1998). Minimizing the negative effects of such trade-offs requires prey to discriminate between high-threat and low-threat situations and to adjust their behaviour accordingly. For individuals that can match their predator-

avoidance responses to the level of threat, the long-term payoffs should be greater than for individuals that are less flexible.

The ability to distinguish between predatory and nonpredatory heterospecifics is a basic component of threat assessment. Animals that exhibit fright responses to inappropriate stimuli are expending time and energy that could be better used in other activities, while animals that fail to respond appropriately to dangerous stimuli have a decreased probability of survival. For aquatic vertebrates, visual (Krapf and Algom 1981) and chemical (Chivers and Smith 1993) cues may both be important for predator recognition. However, relatively few studies have examined the independent contributions of both visual and chemosensory systems (Mathis et al. 1993; Stauffer and Semlitsch 1993; Kiesecker et al. 1996).

Once a predator is identified as potentially dangerous, other factors may modify the perceived level of threat. Miti-

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gating factors may depend on environmental features such as the time of day (Fraser and Mottolese 1984) or the presence or proximity of cover (Dill 1990; Babbitt and Tanner 1997). Other influences may be characteristics of the individual prey and predator, such as relative size differences (Foster and Ploch 1990; Anholt et al. 1996; Bridges and Gutzke 1997), the effect of body condition on prey running speeds (Dowdey and Brodie 1989; Watkins 1996), prey hunger levels (review in Lima 1998), and the level of protection provided by morphological features such as spines and defensive armour (Godin and Clark 1997).

Newt (*Notophthalmus viridescens*) larvae occupy pond habitats in which they are vulnerable to a wide range of vertebrate and invertebrate predators (e.g., Formanowicz and Brodie 1982; Freda 1983; Fauth and Resetarits 1991). An interesting predator-prey dynamic occurs in ponds where newts coexist with tiger salamanders, *Ambystoma tigrinum*. Adult newts are aquatic and consume eggs of *A. tigrinum*, but the surviving salamander larvae grow rapidly and soon prey upon the newt larvae (Morin 1983). Newt larvae that survive through metamorphosis transform into a highly toxic terrestrial stage ("eft") that has relatively low vulnerability to predation (Brodie 1968). Glands typically develop in amphibian larvae prior to metamorphosis (e.g., Formanowicz and Brodie 1982), and we hypothesize that the presence of granular (poison) glands may protect late-stage larvae from predation by tiger salamanders.

We examined the following hypotheses in laboratory experiments. (i) Early-stage central newt (*Notophthalmus viridescens louisianensis*) larvae reduce their activity (fright response) following exposure to visual stimuli from tiger salamander (*Ambystoma tigrinum tigrinum*) larvae in the absence of chemical stimuli. Control visual stimuli were an empty tank or a tank containing grey tree frog (*Hyla chrysoscelis/versicolor* complex) tadpoles (a familiar "neutral" stimulus). (ii) Early-stage newt larvae reduce their activity following exposure to chemical stimuli from tiger salamander larvae in the absence of visual stimuli. Control chemical stimuli were obtained from brine shrimp (*Artemia* sp., a familiar feeding stimulus) and grey tree frog tadpoles. (iii) Early-stage newt larvae are palatable and late-stage larvae are unpalatable to tiger salamander larvae. (iv) Granular glands are present in the skin of late-stage but not early-stage newt larvae. (v) Late-stage newt larvae do not exhibit the same fright responses to stimuli from tiger salamander larvae as were exhibited by early-stage newt larvae.

Ethical considerations

In experimental studies of predation, special consideration should be given to reducing the pain and suffering that must inevitably be experienced by study animals (Huntingford 1984). In accordance with the guidelines of the Canadian Council on Animal Care, we minimized pain and suffering in several ways. First, the most extensive experiments (chemical and visual stimuli trials) involved no physical contact between predators and prey. Second, when predation was necessary (palatability study), we used the minimum number of individuals that we felt to be necessary to demonstrate palatability. Third, exposure to predatory stimuli was short (5–10 min). Fourth, when the sacrifice of some individuals was required for histological work, we killed the animals

with a topical anaesthetic followed by decapitation. Decapitation leads to rapid death and is listed as an acceptable method of euthanasia of small amphibians by the American Veterinary Medical Association's panel on euthanasia (1993).

Collection and maintenance

We collected central newt larvae and tiger salamander larvae from a fishless farm pond in Webster County, Missouri, on 6 July and 26 August 1994. Larvae from the first collection ("early-stage larvae") were several weeks post hatching and had total lengths ranging from 2.5 to 4.9 cm (mean \pm 1 SD = 3.9 \pm 0.64 cm). Larvae from the second collection ("late-stage larvae") were within several weeks of metamorphosis and had total lengths ranging from 4.1 to 5.0 cm (4.5 \pm 0.26 cm). In the laboratory we immediately separated the larvae into individual plastic holding chambers. Chambers (8 \times 8 cm, 8 cm deep) for newt larvae held approximately 400 mL of dechlorinated tap water and chambers (13 \times 16 cm, 8 cm deep) for tiger salamander larvae held approximately 1000 mL of dechlorinated tap water. We fed newt larvae with frozen brine shrimp (*Artemia* sp.) and tiger salamander larvae with earthworms (*Lumbricus* sp.) every other day. We collected gray treefrog tadpoles from the same pond to serve as a control stimulus. Both tiger salamander larvae and gray treefrog tadpoles were considered to be "familiar" heterospecifics because they occurred in the same pond as the newt larvae. We considered the tadpoles to be "neutral" stimuli because they are herbivores and therefore neither predators nor competitors of the newts. We housed tadpoles in groups of six in plastic containers (13 \times 16 cm, 8 cm deep) that held 1000 mL of dechlorinated tap water and fed them commercial *Spirulina* discs. The laboratory was kept at 20 \pm 1°C on a 14 h light : 10 h dark cycle under fluorescent lights and tests were conducted throughout the light period.

Response to visual stimuli

Methods

We tested early-stage newt larvae (collected in early July) at the end of July 1994. Test chambers were 9-L aquaria that were divided in half widthwise by a permanent clear glass barrier that was sealed with silicone. We placed a removable opaque barrier adjacent to the permanent barrier and filled each side of the chamber with 1000 mL of dechlorinated tap water. At the beginning of each trial we placed a newt larva in one randomly selected side of the chamber and one of three treatments in the opposite side: no stimulus (blank), one tiger salamander larva (predator stimulus; snout-vent length 6.3–7.2 cm), or six tadpoles (nonpredator control; total length 2.7–4.8 cm). Six tadpoles occupied approximately the same volume as one tiger salamander larva. The purpose of the tadpole treatment was to determine whether the newt larvae would discriminate between a familiar predator (tiger salamander larva) and a familiar nonpredator (gray treefrog tadpoles). Although it would have been ideal to use individual nonpredators similar in size to the predator, none of the animals in the pond met this criterion. Assignment of treatment and order of testing were determined randomly and each newt larva was tested only once. After a 15-min habituation period we recorded the time spent moving by the newt larva over a period of 5 min to determine base-line levels of activity. Activity was defined as any movement made by the larva except for gill flicks. We then removed the opaque barrier and continued to record the movements of the newt for the next 5 min. A response

index was calculated as post-stimulus activity minus prestimulus activity. Decreased activity in the presence of predators has been observed for many taxa and can decrease the risk of predation (Azevedo-Ramos et al. 1992; Skelly 1994). Activity indices for the three treatments were compared using a Kruskal-Wallis non-parametric analysis of variance by ranks followed by nonparametric multiple-comparison tests (Zar 1984).

Results

Activity responses by the newts differed among the three treatments ($H_2 = 9.23$, $p < 0.01$, $n = 7$; Fig. 1). Newts decreased their activity more in response to the visual stimulus of both the tiger salamander larva ($q = 3.81$, $p < 0.025$) and the tadpoles ($q = 3.59$, $p < 0.05$) than to the blank. There was no significant difference between responses to the tiger salamander larva and to the tadpoles ($q = 0.21$, $p > 0.50$).

Response to chemical stimuli: early stage larval newts

Methods

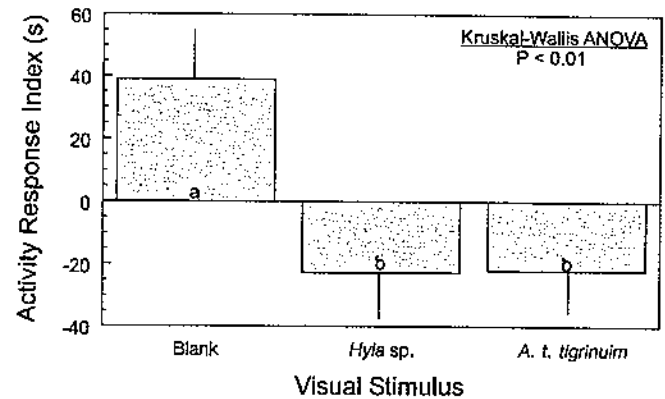
We tested newt larvae collected on 6 July 1994 and conducted the trials on 14–21 July 1994. We tested the responses of newt larvae to water from aerated chambers (13 × 16 cm, 8 cm deep, holding 1000 mL of dechlorinated tap water) containing either a tiger salamander larva (predator stimulus), six grey treefrog tadpoles (nonpredator stimulus), or 3.25 g of frozen brine shrimp (familiar feeding stimulus). The brine-shrimp treatment was included because changes in activity can result from exposure to chemical stimuli from either predators (e.g., Chivers and Smith 1993) or prey (e.g., Lemly and Smith 1985), therefore it is important to demonstrate that newt larvae respond to a predator stimulus differently from a feeding stimulus. Exposure to a chemical blank ("plain" water) produced no significant change in the activity of central newt larvae (A. Mathis, unpublished data). Stimulus chambers were set up approximately 12 h before the start of each trial; frozen brine shrimp were added to the stimulus chamber only 30 min prior to the trial to reduce decomposition that might negatively influence feeding responses. The tiger salamander larva and the tadpoles were not fed during the treatment period.

Testing chambers were plastic boxes (13 × 16 cm, 8 cm deep) containing 1000 mL of dechlorinated tap water. At the beginning of each trial we placed an individual newt larva in a testing chamber for a 25-min habituation period and then recorded the time spent moving by the larva (as defined above) for 10 min. At the end of the base-line observations, we injected 30 mL of water from one of the stimulus tanks into the testing chamber via a plastic tube that was attached to the side of the chamber and ended 3–4 cm above the surface of the water. We recorded activity for an additional 10 min. We also recorded a posture in which the larva pointed its snout toward the substrate ("snout down"); this posture is often observed during feeding (A. Mathis, personal observations) and is presumably a searching or chemosensory behaviour. The snout-down posture was relatively infrequently observed during the prestimulus period, so only post-stimulus occurrences were included in the analysis. Statistical analysis was as described in the visual-recognition experiment. Treatments were assigned randomly and each larva was tested only once. All chemical-stimulus trials were conducted blind.

Results

Activity-response indices varied among the three treatments ($H_2 = 18.34$, $p < 0.001$, $n = 12$; Fig. 2A). Decreases in activity were greater in response to the tiger salamander stimulus than to either the tadpole ($q = 4.63$, $p < 0.005$) or

Fig. 1. Activity-response indices (mean ± 1 SE) for central newt (*Notophthalmus viridescens louisianensis*) larvae exposed to the visual stimulus of tiger salamander (*Ambystoma tigrinum tigrinum*) larvae (predator), grey tree frog (*Hyla chrysoscelis/versicolor* complex) tadpoles (nonpredator), or a blank control. The index was calculated as post-stimulus activity minus prestimulus activity; a positive value indicates an increase in activity and a negative value indicates a decrease in activity. Different lower-case letters indicate a significant difference according to nonparametric multiple-comparison tests.



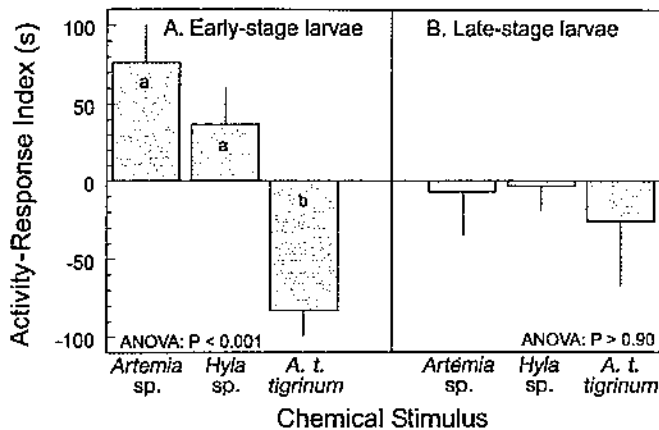
brine shrimp ($q = 5.73$, $p < 0.001$) stimulus. Activity responses to the tadpole and brine shrimp stimuli were not significantly different ($q = 1.13$, $p > 0.50$).

The frequency of occurrence of the snout-down posture during the post-stimulus period varied significantly among the treatments ($H_2 = 11.96$, $p < 0.01$; Fig. 3A). The snout-down posture occurred significantly more often in response to the brine shrimp stimulus than to either the tiger salamander ($q = 4.411$, $p < 0.01$) or the tadpole ($q = 3.890$, $p < 0.025$) stimulus. Responses to the tiger salamander and tadpole stimuli were not significantly different ($q = 0.521$, $p > 0.50$).

Palatability of early- and late-stage newt larvae

The purpose of this portion of the study was to confirm that early-stage newt larvae were palatable but late-stage larvae were not palatable to predatory tiger salamanders. Because of ethical considerations (see above), we felt that only a small number of prey individuals would be necessary to demonstrate this point. In mid-July 1994 we placed an early-stage newt larva in the home container with a tiger salamander larva in four separate trials, approximately 2 days after the tiger salamander larva had last been fed. The newt was consumed within 2 min. On 14 September we repeated the trials with four recently collected late-stage newt larvae and four different tiger salamander larvae. Two of the tiger salamander larvae did not attempt to eat the newt larva. To ensure that the tiger salamander larva had detected the newt larva, we then held the newt larva with forceps approximately 2 cm from the snout of the tiger salamander larva. The newt larvae were ignored but the tiger salamander larvae subsequently consumed earthworms presented on forceps. In two cases the tiger salamander larva took the newt larva into its mouth but immediately spat it out, shaking its

Fig. 2. Activity-response indices (mean \pm 1 SE) for newt larvae exposed to chemical stimuli from tiger salamander larvae (predator), grey tree frog tadpoles (nonpredator), or *Artemia* sp. (familiar food stimulus). The index was calculated as post-stimulus activity minus prestimulus activity; a positive value indicates an increase in activity and a negative value indicates a decrease in activity. Different lower-case letters indicate a significant difference according to nonparametric multiple-comparison tests.



head violently. Although the sample size was small, the proportion of early-stage newt larvae that were consumed (100% of four) was significantly different from the proportion of late-stage newt larvae that were consumed (0% of four) (Fisher's exact-probability test, $p = 0.014$, one-tailed).

Skin histology: early- versus late-stage newt larvae

We compared the skin histology of selected early-stage newt larvae (captured in mid-July 1994), late-stage newt larvae (captured in mid-August 1994), and recently metamorphosed laboratory-reared eft (terrestrial juvenile stage). We decapitated the newts and removed sections of skin and associated muscle tissue from the dorsal surface of the head, trunk, and tail. We fixed the samples in alcohol – formaldehyde – acetic acid solution, embedded them in paraffin, and cut them into 8- μ m sections. Samples were stained with haematoxylin, Birich scarlet–orange, and fast green FCF.

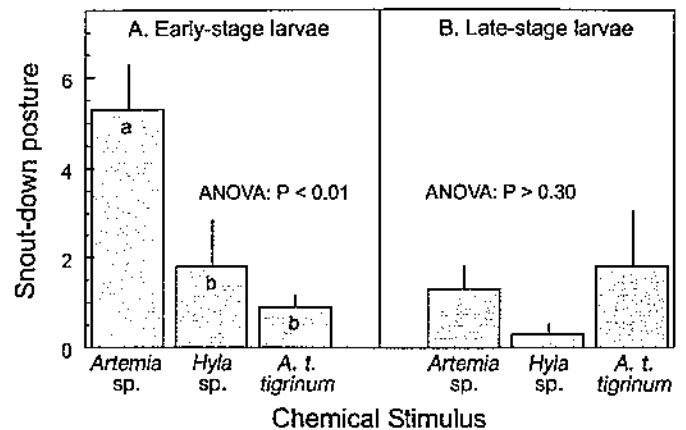
There were no visible granular glands on any of the samples from early-stage newt larvae. Granular glands were visible on the head, body, and tail of the samples from late-stage newt larvae. These glands were similar in size and frequency to those seen in the fully metamorphosed eft.

Retention of the fright response: response of late-stage newt larvae to chemical stimuli

Methods

We tested the responses of late-stage newt larvae to chemical stimuli from tiger salamanders to determine whether they retained the fright response that was present in younger larvae. Tests were identical with those for young larvae except that we tested larvae collected on 26 August and conducted the trials between 28 August and 9 September. Any larvae that showed signs of the onset of metamorphosis (reduction in either the gills or the keel of the tail) were not tested. The late-stage newt larvae that we tested in this experiment had all begun to develop the small dark pigment spots

Fig. 3. Frequency of occurrence of the snout-down posture (mean number \pm 1 SE) exhibited by larval newts following exposure to chemical stimuli from tiger salamander larvae (predator), grey tree frog tadpoles (nonpredator), or *Artemia* sp. (familiar food stimulus). Different lower-case letters indicate a significant difference according to nonparametric multiple-comparison tests.



(dermal melanophores) that are characteristic of larvae just prior to metamorphosis (Forbes et al. 1973). All the larvae metamorphosed in the laboratory approximately 1–3 weeks after testing.

Results

There were no significant differences in the activity-response indices among the three treatments ($H_2 = 0.141$, $p > 0.90$, $n = 12$; Fig. 2B). There also were no significant differences among treatments in the frequencies of occurrence of the snout-down posture during the post-stimulus period ($H_2 = 2.30$, $p > 0.30$, $n = 12$; Fig. 3B).

Discussion

Early-stage newt larvae distinguished between heterospecifics that were predatory (tiger salamander larvae) and nonpredatory (gray treefrog tadpoles), but only when chemical cues were available. In tests with visual stimuli alone, newt larvae reduced their activity in response to both predatory and nonpredatory heterospecifics, but not to a blank control. The blank treatment also incorporated disturbance (removal of the opaque barrier), so the decrease in activity was not simply a general disturbance response. Therefore, the newt larvae visually detected the presence of “something” on the other side of the tank but were apparently unable to correctly identify the predator. This lack of visual discrimination is particularly noteworthy given the size difference between predatory (tiger salamander larvae) and nonpredatory (tadpoles) individuals. Amphibian larvae are typically myopic (Manteuffel et al. 1977; Mathis et al. 1988), so even short-distance visual cues may be inadequate for fine-scale discrimination. The lack of visual acuity could explain the fright response to both predatory (tiger salamander larvae) and neutral (tadpoles) stimuli and the failure to discriminate between these two stimuli. If the larvae are unable to distinguish between classes of visual stimuli, a decrease in activity may be the best response to the presence of any “unknown” stimulus. Although this approach has obvious benefits for predation avoidance, decreasing in activity in response to neutral stimuli may unnecessarily limit foraging opportuni-

ties. The consequences of reduced foraging success may be severe because populations of newt larvae often experience intense intraspecific competition (Morin 1983; Harris et al. 1988).

In contrast to visual cues, chemical cues alone were sufficient for predator identification. The use of chemical cues for predator recognition has been documented for a number of aquatic taxa (for reviews see Dodson et al. 1994; Kats and Dill 1998), but only a few studies have compared the relative importance of the two classes of stimuli. For example, the preferential use of chemical cues over visual cues has been reported for anuran amphibian larvae (Stauffer and Semlitsch 1993; Kiesecker et al. 1996). Small freshwater fishes may also rely particularly heavily on chemical cues. For example, although fathead minnows (*Pimephales promelas*) can use visual cues for predator recognition (Mathis et al. 1993; Chivers and Smith 1994), predator-naïve minnows learned to recognize chemical cues from predators several days faster than they did visual cues (Brown et al. 1997). Newts may rely heavily on chemical cues because their aquatic habitats are typically turbid and heavily vegetated, which greatly restricts visibility. Newt larvae tend to occupy vegetation and litter during the day (Morin 1983; A. Mathis, personal observations) and restrict their activity in more open water to nighttime (Morin 1983), further limiting visibility.

It is possible that differences in diet between the two types of stimulus animals (tiger salamander larvae and gray treefrog tadpoles) played a role in discrimination by the newt larvae (e.g., Mathis and Smith 1993; Laurila et al. 1997; Lefcort 1998). Because tiger salamanders are carnivores and gray treefrogs are herbivores, it was not practical to feed them identical diets. However, our experimental design somewhat mimicked natural conditions, in which dietary cues from predators are available for assessment by prey.

Vulnerability to predation by tiger salamander larvae decreased as the newt larvae approached metamorphosis. The explanation is not size-related because the tiger salamanders were large enough to easily consume prey the size of the metamorphosing newts. Instead, the newts appeared to have become unpalatable to the predatory salamanders. Although these data should be interpreted with caution because of the small sample size, our inference is in agreement with the conclusions drawn from some other studies of amphibian larvae. Late-stage new larvae have also been reported to be unpalatable to the predatory larvae of diving beetles (*Dytiscus verticalis*; Formanowicz and Brodie 1982). The change from palatable to unpalatable was associated with the development of granular epidermal (poison) glands. Chadwick (1950) reported that the development of numerous "acinous glands" preceded metamorphosis of newt larvae, but he did not specifically refer to granular glands. Development of granular glands is also correlated with unpalatability of wood frogs (*Rana sylvatica*; premetamorphic tadpoles were palatable and had small granular glands with little or no secretion, while metamorphic tadpoles were unpalatable and had larger glands with visible secretion; Formanowicz and Brodie 1982). Similar changes in palatability have also been reported for other anuran larvae (Brodie et al. 1978; Garton and Mushinsky 1979; Brodie and Formanowicz 1987). Premetamorphic development of granular glands could have important conse-

quences for survival during metamorphosis for a number of amphibian species.

For the newts in our study, a decreased response to chemical stimuli from tiger salamanders was associated with the development of unpalatability. Ontogenetic changes in vulnerability to predation have also been correlated with changes in predator-avoidance responses by toad (*Bufo americanus*) tadpoles (Anholt et al. 1996) and California newt (*Taricha torosa*) larvae (Kats et al. 1994), although in these studies the decrease in vulnerability was apparently achieved by outgrowing a gape-limited predator. In contrast, ontogenetic changes in predator-avoidance behaviour of Pacific (*Hyla regilla*; Watkins 1997) and red-eyed (*Agalychnis callidryas*; Warkentin 1999) tree frog tadpoles do not appear to be associated with changes in vulnerability to predation for either *H. regilla* (E.D. Brodie, Jr., personal communication) or *A. callidryas* (Warkentin 1999) tadpoles. For *N. v. viridescens*, an additional ontogenetic change in predation-avoidance behaviour occurs between the highly toxic eft stage and the less toxic adult stage: efts are more likely to respond with high-intensity, high-visibility antipredator postures and are less likely to flee than adults (Ducey and Dulciewicz 1994). Therefore, behavioural responses to predators may be highly plastic over the life of an individual of this species.

The failure of late-stage newt larvae to respond to chemical stimuli from predators may indicate a general decrease in response to chemical stimuli during the period immediately preceding metamorphosis. Early-stage newt larvae performed the snout-down posture more frequently in response to a feeding stimulus than to the tadpole or the tiger salamander stimulus, but this differential response did not occur in the late-stage newt larvae. Because the snout-down posture occurred more frequently in response to prey stimuli than in response to nonprey stimuli, we infer that it is associated with searching for food. Consumption of prey typically declines in the laboratory as larvae begin metamorphosis, but complete cessation of feeding may occur only 1–2 days prior to transformation, if at all (Kuzmin 1997). It seems unlikely that the reduction in response to chemical cues was due to an increased reliance on visual cues. Immediately prior to metamorphosis, a number of physical changes in the structure of the eye begin and changes continue throughout metamorphosis (Duellman and Trueb 1986). These ongoing morphological changes suggest a decrease in visual function during this period. Therefore, it seems unlikely to us that visual cues would have become more important than chemical cues during the period just prior to metamorphosis. Even so, a test of the response of late-stage newt larvae to visual cues would be of some interest. We did not perform these tests because we only had time to do one set of trials during the short period preceding metamorphosis, and we felt that the tests with chemical stimuli would be more informative.

The reduction in predation-avoidance behaviour by Pacific tree frog tadpoles undergoing metamorphosis was associated with overall lower levels of activity (Watkins 1997). However, reductions in overall activity cannot explain the lack of a fright response by the late-stage newt larvae in our study; prestimulus levels of activity were almost identical for early-stage (mean \pm 1 SD = 193.6 \pm 73.7 s) and late-stage (197.9 \pm 120.8 s) larvae.

Vulnerability to predation has typically been considered to increase during metamorphosis (e.g., Wassersug and Sperry 1977; Arnold and Wassersug 1978). However, our data are in agreement with Formanowicz and Brodie's (1982) findings indicating that premetamorphic development of granular glands protects newt larvae from some predators during this period of vulnerability. Moreover, changes in the occurrence of the fright response appear to be correlated with changes in vulnerability to predators.

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