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Glow-worm larvae bioluminescence (Coleoptera: Lampyridae) operates as an aposematic signal upon toads (*Bufo bufo*)

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It is an established fact that the spectacular bioluminescent displays of adult fireflies and glow-worms are used as courtship signals; however, the survival value of the glowing behavior of their larvae remained the subject of speculation for many years. Our study is the first that demonstrates that lampyrid larvae use luminescence to signal unpalatability to nocturnal, visually guided predators. Wild-caught toads (*Bufo bufo*) were more reluctant to attack luminescent artificial prey, and we show that avoidance learning increased this reluctance. After being exposed to glow-worm larvae (*Lampyris noctiluca*), which the toads experienced as disagreeable, attack latencies to luminescent prey increased, but not those to nonglowing prey. Not all toads showed avoidance learning to the same extent, because of either differences in previous experience with glow-worms or differences in memory. *Key words:* aposematism, bioluminescence, *Bufo bufo*, insect defenses, *Lampyris noctiluca*. *[Behav Ecol 14:103–108 (2003)]*

Although its biochemistry is well understood and is applied for various scientific techniques (Campbell et al., 1994; Haddock, 2000), the survival value of bioluminescence to the organisms themselves often remains unclear (Buck, 1978; Hastings and Morin, 1991; Morin, 1983). Even in fireflies, famous for their courtship flashes (Carlson and Copeland, 1985), there has been speculation for many years about the function of the light organs and distinctive glowing behavior of the larvae (Bushman, 1988; Christensen and Carlson, 1982; Dreisig, 1974; Lloyd, 1973; Sivinski, 1981; Tyler, 2002).

Glow-worm larvae typically glow from a paired light organ in the penultimate abdominal segment. Larval luminescence is usually induced by disturbance, but many species also glow spontaneously during the night, especially during locomotion (Christensen and Carlson, 1982; Dreisig, 1974). Hereby, they emit slow glow-pulses of several seconds, which are separated by intervals of variable duration. Antipredator defense is cited as the most possible function (Bushman, 1988; Lloyd, 1973; Sivinski, 1981; Tyler, 2002), but it still lacks convincing experimental support. Aposematism, the use of conspicuous signals to warn predators of unprofitability (Cott, 1940; Edmunds, 1974; Gittleman and Harvey, 1980; Guilford, 1986; Lindström, 2000; Poulton, 1890), seems the most likely strategy (De Cock and Matthysen, 1999; Grober, 1988, 1989; Guilford and Cuthill, 1989; Lloyd, 1973; Sivinski, 1981; Underwood et al., 1997). Plenty of other functions have been proposed for the glowing of lampyrid larvae (Lloyd, 1973; Sivinski, 1981; Tyler, 2002), but many arguments and a lack of supportive data favor against these hypotheses (see De Cock and Matthysen [1999] for an exhaustive discussion).

Recent studies found that larvae of *Lampyris noctiluca* L. are unprofitable to birds (De Cock and Matthysen, 2001; Tyler, 2001a) and wood ants (Tyler, 2001b), and they possess glandular self-defensive organs along either side of the abdomen (Tyler and Trice, 2001). Underwood et al. (1997) showed that laboratory mice also reject lampyrid larvae and are able to learn to avoid luminescent artificial prey. However, the species of larvae used for this study were sufficiently defended by repellent odors from reflex bleeding. Hence, it needs to be shown that spontaneous glow behavior functions as an aposematic display for visually guided predators such as the toads we used for our experiments. Toads must be considered potentially important predators because they occur in glow-worm habitat, are also nocturnal, and consider all small items moving along a longitudinal axis as potential prey, which they attack according to a fixed action pattern (Ewert, 1987). This latter behavior allows the use of artificial prey, which overcomes the problem of different locomotion and activity levels of live prey and, as such, the detectability to and responsiveness of the toads (Aho et al., 1993).

We experimentally tested the role of luminescent behavior in avoidance learning in toads by means of a prey dummy apparatus supplied with glowing or nonglowing artificial prey. In a prelearning experiment, we tested whether wild-caught toads discriminated against glowing prey. We expected them to do this if they had previously experienced aposematic glow-worm larvae in nature or showed innate reluctance to luminescent signals. Next, the toads were subjected to a learning experiment to test whether they showed reluctance and avoidance learning to real glow-worm larvae (*L. noctiluca*). After the learning experiment, the toads were subjected to recognition experiments to test our prediction that the willingness to attack glowing artificial prey would decrease after exposure to glow-worm larvae, as is to be expected of luminescent aposematism.

MATERIALS AND METHODS

Predators

Twenty-seven adult male toads (*Bufo bufo)* were caught from *L. noctiluca* habitat near Antwerp in Belgium during spring migration (March 1999). They were kept in

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terrariums supplied with moist earth, dead leaves, pieces of bark for shelter, and dug-in plastic containers with water that was refreshed every 2 days. The experiments started 2 months later. The month before the start of the first experiment, each individual was put on a daily diet of two prey items (mealworms and crickets) in the test environment to get them (1) used to being in captivity and being handled, (2) adjusted to a similar hunger level without starving them, and (3) motivated to attack prey during the experiments.

Experimental setup: the prey dummy apparatus

Our prey dummy apparatus consisted of a horizontally turning drum. On its surface, black cardboard stripes (prey dummies) were attached at fixed distances and along the same height, in such a way that they moved along their longitudinal axis when the drum turned. Glowing larvae were mimicked by putting a small green light-emitting diode (LED) behind a puncture at the rear end of each black stripe. Nonglowing controls were dummies with the LEDs turned off. The color and intensity of the LEDs approximated, as closely as possible, the luminescence of glow-worm larvae (De Cock and Matthysen, 1999). The main difference between natural and artificial luminescence was that the dummies glowed continuously, whereas larvae usually glow in separate slow pulses or continuously with a superimposed pulsation in intensity. Other differences between dummies and larvae are the manner of locomotion and color pattern. Glow-worm larvae move the rear end of their abdomen in the way of geometrid caterpillars. We used black dummies, as this color closely approximates the jet-black color of larval *L. noctiluca*, except that these have lateral yellowish dots at the caudal side of each segment (De Cock and Matthysen, 2001).

The turning drum was placed in front of a small test terrarium (21 × 38 cm) in such a manner that the prey dummies passed along the lower edge of a horizontal viewing window (50 × 200 mm) on one side of the terrarium. It took each dummy 100 s to move across the window, and only one dummy was visible at any time. A trial consisted of maximum 600 s of prey dummy exposure, and it was stopped if a toad snapped at a dummy; the latency time to the first tongue snap was recorded. If no attack occurred, the maximum possible latency of 600 s was given as the value for that trial. Experiments were conducted at an illumination level of 10 μlux, such as observed at night, and the toads were adapted to the dark at least 1 h before the start of an experiment (Aho et al., 1988). Observations were made by an infrared camera provided with an infrared-light source and connected to a video recorder and monitor. A more elaborate description of this setup can be found in De Cock and Matthysen (2001).

Experiments

Prelearning experiment

Do wild-caught toads show avoidance to light signals? Each toad was tested in the prey dummy apparatus in a session with glowing dummies and in a session with nonglowing dummies, in randomized order and in direct succession. Before each session, the toads had 5 min to accommodate. Each treatment (glowing and nonglowing) was tested on five trials, and individuals were tested on alternate days. When no snapping occurred at either treatment and mealworms were not accepted immediately afterwards, the trial was canceled, as we presumed that the toad was insufficiently hungry or unmotivated.

Results of this experiment are already published (De Cock and Matthysen 1999). We summarize the most important findings here as they are needed for the interpretation of results of the following experiments. Two toads did not respond to the prey dummies at all and were omitted from the statistical analysis. The 25 remaining toads did attack the dummies and discriminated against glowing prey, as attack latencies were significantly longer than those for nonglowing prey dummies ($F_{1,234} = 7.18$; $p = .008$). In De Cock and Matthysen (1999), we accidentally reported the F value and degrees of freedom for the nonintercept solution to obtain parameter estimates. The output presented here is the correct one. We observed considerable variation in attack responses to glowing dummies. Seven toads invariably snapped repeatedly at nonglowing and glowing dummies, seemingly without any difference. The other toads were more reluctant toward the glowing prey and usually oriented but did not approach, and if they did, they withdrew when they saw the light or stayed motionless without approaching or following the glowing dummy.

Learning experiment

Next, the toads were subjected to a learning experiment with real glow-worm larvae (*L. noctiluca*) collected from the same area where we got the toads. The larvae were induced to glow spontaneously by means of the neurotransmitter octopamine (0.1 M; Christensen and Carlson, 1982) applied directly on the glow organs.

Three prey were presented in a trial: one glow-worm larva and two mealworms (bought from a pet shop). Each prey was presented singly and exposed for a maximum of 600 s in the following order: mealworm/glow-worm/mealworm or glow-worm/mealworm/mealworm. The order was assigned randomly to prevent predictability of prey presentation. At least one mealworm was always presented after a glow-worm larva to ensure that toads were hungry and responsive even if they ignored glow-worms. The tests were performed in the same terrarium as the dummy experiments. Individuals were tested over each day until they avoided glow-worm larvae on five successive trials while still accepting mealworms, within a maximum of 25 trials. We defined toads that reached this criterion within the 25 trials as "learners." We used the same 27 individuals of the prelearning experiment and one extra toad, for a total of 28 individuals in this experiment. Two toads escaped during this experiment, and one toad died. Thus, 25 toads were used in the analysis.

Recognition experiment

After the learning experiment, 12 of the 25 toads used in the learning experiment met our criterion of avoidance learning (learners). The procedure of the recognition experiment was exactly the same as described for the prelearning experiment, the only exception being a time lag of 3 to 10 days between trials. The first trial was started within the week that the individual learned to avoid glow-worm larvae.

Extra learning experiment

We hypothesized that the 13 of the 25 toads of the learning experiment that did not learn avoidance during the learning experiment (nonlearners) had poorer learning capabilities and needed more than a single larva each trial to learn avoidance. Moreover, in nature, toads would come across dozens of larvae on a single night. Therefore, we conducted an extra learning experiment that consisted of six trials in which each individual was presented a maximum of five larvae. Each individual got one trial a day. A trial was stopped if the individual neglected glow-worm larvae for a period of 10 min while still accepting mealworms.

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Combination experiment

The same 13 nonlearner toads were presented one session of extra learning just before testing them in the prey dummy apparatus. Each individual got two trials.

Statistical approach

Data for latency times were constrained to lie between a minimum of 0 s and a maximum of 600 s. Because toads snapped at dummies after a relatively short while or not at all, the data behaved in a binomial way. To get proportional data, latency times were divided by the maximum possible latency time of 600 s. Logit-transformed data were analyzed with the GLIMMIX macro of SAS 612 in general mixed model analysis with binomial error structure to estimate and test mean latency times (Littel et al., 1996). Individual identity of the test predators and the interaction term of individual with trial were added as random variables to account for individual variation and individual differences in change of response or slope over trials, thus over time. Degrees of freedom of the F tests were approximated by the method of Satterthwaite (Verbeke and Molenberghs, 1997).

Full models on latency times included Treatment (glow versus nonglow), Experiment (learners, prelearning versus recognition; nonlearners, recognition trial versus combination), and the interaction term.

The same type of logistic regression was used to test for an effect of trial number on attack rates in the learning experiment (yes/no data). Individual identity of the test predators and the interaction term of individual with trial were treated as random variables.

The data for the extra learning experiment were numbers of prey attacked by an individual per trial. These data were log transformed and analyzed with the GLIMMIX macro of SAS 612 in general mixed model analysis with Poisson error structure to test for an effect of trial number. Individual identity of the test predators and the interaction term of individual with trial were added as random variables.

We checked distributional assumptions with the standardized residuals, which are expected to follow an approximately normal distribution (Crawley, 1993): for all models, the Shapiro-Wilks statistic W was higher than 0.9, which indicates that the standardized residuals did follow an approximately normal distribution.

RESULTS

Are glow-worm larvae disagreeable to toads, and do these show avoidance learning?

During the learning experiment, 30% of 463 presented glow-worm larvae were left untouched, 66% were eaten, and 5% of the 323 attacked larvae were spat out; mealworms were always attacked and eaten. The rejected larvae always survived an attack. Typical behavior of dislike—such as puffing, wiping snouts with forelegs, urinating, turning away, or fleeing from the prey—were only shown toward glow-worm larvae, especially during trials of neglect. This indicates that these prey were distasteful, toxic, or unprofitable in some way. The attack rate or willingness to snap at glow-worm larvae decreased significantly, from 80% to almost 40% during the experiment, which indicates that avoidance was learned (Figure 1; $F_{1,606}$ = 33; p = .0001). However, only 12 out of 25 toads avoided glow-worms on at least five successive trials before the end of the experiment, which we classified as learners (Figure 1). The change in attack rate differed significantly between the two groups ($F_{1,24}$ = 76; p = .0001). Although the learners reached total avoidance from about the 12th trial (slope = −0.40; t = 8.12; df = 39; p = .0001), attack rates of non-learners stayed high and even increased slightly (slope = 0.09; t = 2.67; df = 11; p = .02).

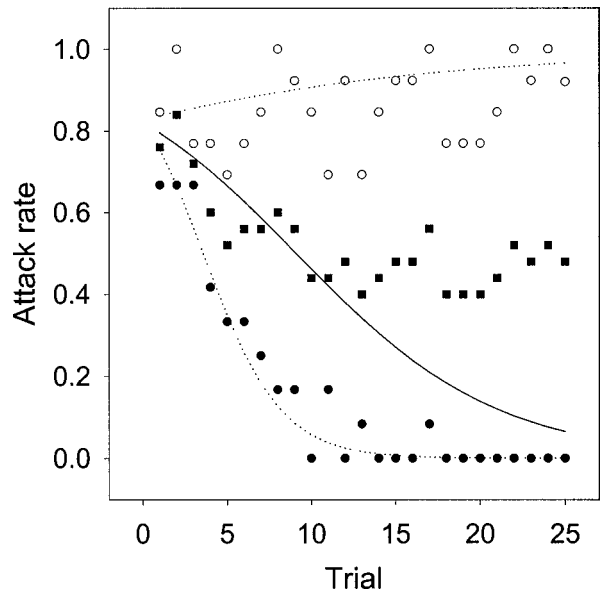

Figure 1
The result of the learning experiment plotted as the attack rate per trial session for all toads together (squares), toads that met the criterion of avoidance learning to glow-worm larvae (learners, n = 12; filled circles), and toads that did not (nonlearners, n = 13; open circles). Symbols represent proportions of individuals that attacked on one trial. Mealworms were attacked and eaten on all trials. The curves are calculated from logistic regressions on the attack response (yes/no).

Do toads show stronger aversion to luminescent prey after avoidance learning?

Although the learner toads already discriminated between glowing and nonglowing prey before the learning experiment (Figure 2; t = 11.1; df = 181; p = .0001), their reluctance to attack glowing prey became even higher in the recognition experiment after experiencing the glow-worm larvae of the learning experiment (t = 4.8; df = 181; p = .0001). Attack latencies to nonglowing prey were short and remained similar (t = 0.01; df = 179; p = ns). One of the 12 learner toads was, in fact, the extra individual added in the learning experiment. Because it was not included in the prelearning experiment, only those 11 individuals tested in both the prelearning and the recognition experiment were used for comparing latencies. The result can only be attributed to the fact that the toads learned avoidance to glow-worm larvae and discriminated by means of the glow signal.

Do nonlearner toads need more frequent encounters to learn avoidance?

Although the nonlearner toads were unable to meet our criterion of avoidance learning, they nevertheless clearly showed signs of disgust and neglect on several trials in the learning experiment. This is also shown in the extra learning trials, as the number of larvae sampled decreased significantly throughout the experiment (Figure 3; $F_{1,9}$ = 24.7; p = 0.001). However, the toads that showed avoidance within each trial continued to sample a few larvae, even at the end of the experiment. The idea that nonlearners had less experience with glow-worm larvae than did learners is supported by their shorter attack latencies toward glowing prey in the

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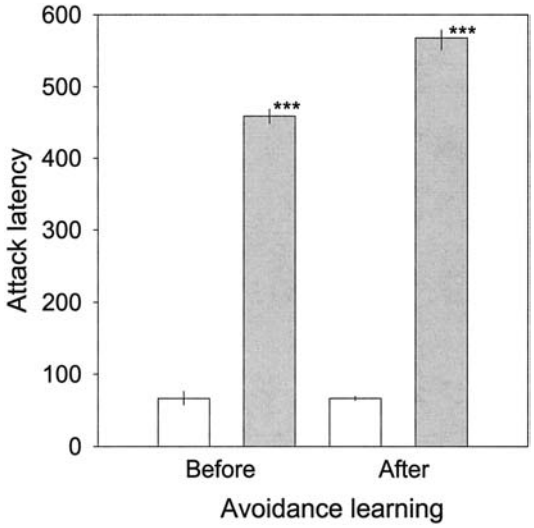

Figure 2
Estimated attack latency times (±SEM) to artificial glowing (filled bars) and nonglowing prey items (open bars) by learner toads before and after learning to avoid glow-worm larvae. Latencies for non-glowing prey are low and did not differ between experiments; however, for glowing prey, latencies have increased significantly after avoidance learning to glow-worm larvae (treatment × experiment interaction: $F_{1,336}$ = 21.3; p = .0001). ***p = .0001

prelearning experiment (t = 2.7; df = 26; p = 0.01), whereas attack latencies to nonglowing dummies did not differ between both groups (t = 0.7; df = 36; p = ns).

Do nonlearner toads discriminate glowing from nonglowing prey after avoidance learning?

The previous probably explains why the nonlearners did not discriminate between glowing and nonglowing dummy prey when tested in a single recognition trial with the prey dummy apparatus (Figure 4; t = 0.65; df = 74; p = ns). When they

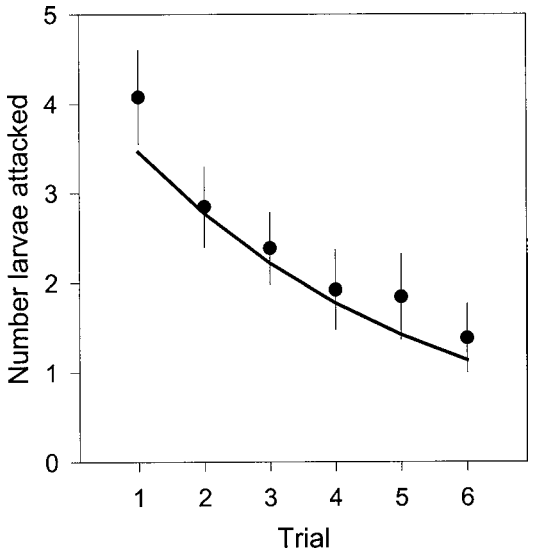

Figure 3
Result of the extra-learning experiment for nonlearner toads (n = 13) plotted as the number of larvae sampled per trial before avoidance occurred (±SEM). The curve calculated from a Poisson regression shows that the toads sampled significantly fewer larvae through the experiment (slope, −0.22; t = 4.9; df = 9; p = .0008).

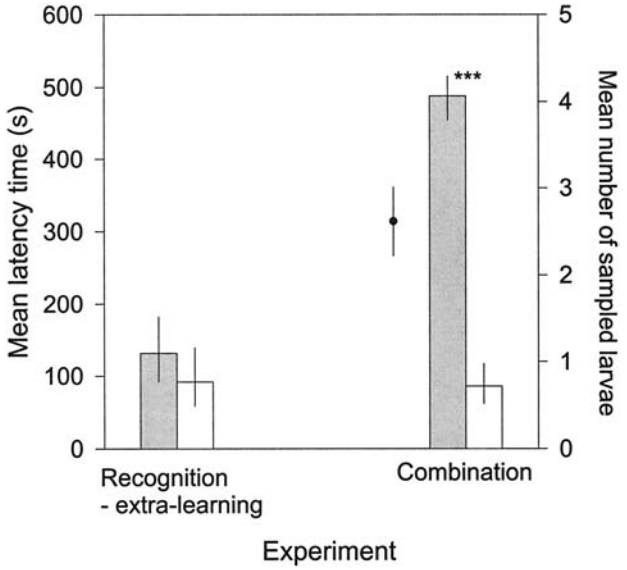

Figure 4
Result of the combination experiment plotted as the mean latency time to the first attack (±SEM). After the extra learning experiment, nonlearner toads (n = 13) did not discriminate between glowing (filled bars) and nonglowing prey (open bars) when tested in one recognition trial. In the combination experiment, latency times to attack glowing prey differed significantly between glowing and nonglowing prey between the experiments with or without extra learning, with a significant interaction effect between these two factors (see text for details). Filled circles indicate mean number of sampled larvae (±SEM). ***p = .0001

were subjected to one extra learning session immediately before the recognition trial in the so-called combination experiment, however, they did discriminate, as indicated by the much longer latency times for glowing prey dummies (Figure 4). Latency times to attack glowing prey differed significantly between glowing and nonglowing prey ($F_{1,74}$=19.7; p = .0001) between the experiments with or without extra learning ($F_{1,74}$=10.1; p = .002), with a significant interaction effect between these two factors ($F_{1,74}$=11.5; p = .001).

DISCUSSION

If bioluminescence plays a role in antipredator defense, one would expect to find that wild-caught predators avoid glowing prey. The prelearning experiment revealed that toads collected from glow-worm habitat indeed show weaker attack responses (De Cock and Matthysen, 1999) and higher attack latencies for luminescent prey compared with the same prey dummies without the light signal. This behavior is compatible with the interpretation that these individuals had more experience with aposematic glow-worm larvae in nature. On the other hand, the reluctance to attack glowing prey could also be attributed to an innate bias, neophobia, or learned avoidance. We (2001), however, have discussed why such mechanisms are less likely to occur in toads. Furthermore, the learning experiment shows that part of the toads learn avoidance to glow-worm larvae. Our definition of learners was used as an operational definition for avoidance learning rather than as a general description of learning capabilities. Therefore, the definition is to a certain level arbitrary because the results are, for instance, dependent on the number of trials performed. The other toads did not meet our criterion of avoidance learning, although they avoided attacking glow-worms on several trials (but not five consecutively), which was

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never the case for perfectly edible mealworms. Although the glow-worm larvae were left untouched in many cases and the toads clearly showed behavior of dislike, only few were spat out after an attack.

It seemed that the toads had difficulties in getting rid of bad prey. We observed that toads that finally ate glow-worms regularly protruded their tongue a couple of times with the larva stuck on it while sometimes moving their forelegs along their snout, seemingly trying to wipe off the prey. If these efforts were without result, they ended up swallowing the prey. Many studies report that Lampyridae have a bad taste and/or smell (for reviews, see Lloyd, 1973; Sivinski, 1981), and some species are even defended by effective cardiotoxins called lucibufagins (Eisner et al., 1978, 1997). It has not yet been determined whether *L. noctiluca* contains such defensive toxins, yet the hemolymph of larval *L. noctiluca* contains substances that kill invertebrates (Schwalb, 1961).

The recognition experiment shows that the learner toads—although they previously already showed reluctance to luminescent prey—show stronger avoidance after having had experience with real glow-worms in the previous experiment. This result clearly shows that the toads learned (stronger) avoidance, which can only be ascribed to luminescent aposematism, as the light signal was the only cue to distinguish between the prey dummies. The outcome of the combination experiment shows that the nonlearners use luminescence as a discriminatory cue, but it also suggests, together with the results of extra learning, that the luminescent aposematism is not always remembered for longer periods. This suggests that part of the toad population, represented here by the nonlearners, may need frequent reinforcement by sampling a few distasteful larvae each night to relearn aposematism, whereas others (the learners) are capable of remembering the warning signal for a much longer time. This difference among toads in learning capabilities and memory could also be explained by a difference in previous exposure to glow-worm larvae, genetic variation in these traits (Marples and Brakefield, 1995), a higher hunger level, or a lower susceptibility to glow-worm defenses. The results indeed suggest that nonlearners had less experience with glow-worm larvae. These findings highlight the importance of dynamics of learning and forgetting, which only recently have been included in theoretical studies on avoidance learning (Turner and Speed, 1996).

A prediction of Guilford and Cuthill (1989) for bioluminescence to have an aposematic function is that predators should learn to reject bioluminescent prey more rapidly than nonbioluminescent ones. The setup of our study, though, did not allow investigating this aspect. In that case, we should have tested if toads showed faster avoidance learning to luminescent than to nonluminescent unprofitable prey when regularly fed similar looking nonluminescent, though edible, prey. One of the criticisms of Guilford and Cuthill (1989) on Grober's (1988) experiment was that it neatly demonstrated that bioluminescence deters predators and that unpalatability deters them, but there is no interactive effect of an association between bioluminescence and unpalatability. This other prediction to conclude for bioluminescent aposematism (Guilford and Cuthill, 1989) was shown by our results because bioluminescence deterred toads more effectively after avoidance learning to unpalatable glow-worm larvae. This can only be explained by the fact that the toads associated bioluminescence to unpalatability. Adaptation implies selective advantage, so the critical prediction of aposematism is that luminescence be a more effective warning signal than no luminescence, and it is generally accepted that, except where avoidance reactions are innate, this must constitute a special ability to enhance the acquisition and maintenance of learned aversions (Guilford and Cuthill, 1989). Also, this critical prediction of aposematism, that luminescence be a more effective warning signal than no luminescence, was confirmed by the results.

We conclude that this is the first study to demonstrate that a potentially important predator learns to avoid larval glow-worms by using the light signals as aposematic cues, without the need for other cues. This does not exclude the possibility that different cues, including color patterns (De Cock and Matthysen, 2001) and odors (Lloyd, 1973), are used in a multimodal aposematic display (Rowe and Guilford, 2001). Although our results cannot show that glow signals primarily evolved for an antipredation function, until now they constitute the only evidence favoring this hypothesis, whereas the other hypothetical functions (see De Cock and Matthysen, 1999) remain unsupported.

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