Animal Behaviour 83 (2012) 81–86

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Firefly flashing and jumping spider predation

Skye M. Long [a], Sara Lewis [b], Leo Jean-Louis [c], George Ramos [a], Jamie Richmond [c], Elizabeth M. Jakob [c,*]

[a] *Graduate Program in Organismic & Evolutionary Biology, University of Massachusetts Amherst, Amherst, MA, U.S.A.*
[b] *Department of Biology, Tufts University, Medford, MA, U.S.A.*
[c] *Department of Psychology, University of Massachusetts Amherst, Amherst, MA, U.S.A.*

ARTICLE INFO

Article history:
Received 5 April 2011
Initial acceptance 27 May 2011
Final acceptance 14 September 2011
Available online 4 November 2011
MS. number: A11-00290R

Keywords:
aposematic
firefly
flashing
jumping spider
learning
Phidippus
Photuris
predation
startle response

Bioluminescent flashing in fireflies, while primarily a sexual signal, is known to deter some predators while attracting others. We tested whether flashing serves an antipredator function against two species of diurnal, visually hunting jumping spiders, *Phidippus princeps* and *Phidippus audax*. To confirm anecdotal reports that fireflies flash during the day in a nonmating context, we documented that adult fireflies (*Photuris* sp.) of both sexes flash when disturbed in daylight. We also confirmed that activity periods of *Phidippus* and fireflies overlap, and that spiders attack fireflies and elicit flashing behaviour. We conducted three experiments to examine the influence of flashing on spider behaviour. (1) We tested whether the sudden onset of a flashing LED startled spiders that had initiated attacks on crickets, and found no evidence that it did so. (2) We used choice tests to determine whether flashing lights attracted or deterred spiders from attacking palatable prey. Spiders more often attacked crickets positioned next to a flashing LED versus an LED that was either off or glowed steadily. (3) Many firefly species are distasteful. Therefore, we tested whether flashing lights facilitate avoidance of unpalatable prey with experience. Spiders were given seven encounters with unpalatable prey (nonluminescent *Ellychnia corrusca* fireflies) associated with either flashing or unlit LEDs. Spiders in the two treatments were equally likely to attack the prey during their first encounter, but spiders exposed to flashing LEDs were significantly less likely to attack unpalatable prey by their seventh trial. Spiders tested with palatable prey showed no decline in attacks after exposure to flashing LEDs. We conclude that, although bioluminescent flash signals may increase attack rates by predatory jumping spiders, they may also facilitate learning about unpalatable prey. Thus, the costs and benefits of flashing may depend on the prevalence of firefly palatability.

Fireflies (Coleoptera: Lampyridae) are well known for bioluminescent signalling, which is used for species recognition and mate choice (reviewed in Lewis & Cratsley 2008). Firefly signals may also have important consequences outside the arena of sexual communication. Bioluminescence is not always only a sexual signal. Larval fireflies are also bioluminescent, and adult fireflies flash in other contexts besides mating, such as flashing when disturbed during the day (McDermott 1964; De Cock & Matthysen 1999; reviewed in: Sivinski 1981; De Cock 2009). In particular, firefly signals are likely to influence interactions with potential predators. Potential predators of larval and adult fireflies include both vertebrates (birds, mammals, amphibians) and invertebrates (spiders, mantids and other firefly species) (Lloyd 1965, 1973).

Firefly flashing may affect interactions with predators in several ways. First, flashes may act as a cue to eavesdropping predators, increasing the risk of detection. For example, flashing by the firefly *Photinus* sp. is detected by the predaceous firefly *Photuris* sp. (Woods et al. 2007). Laboratory-reared house mice, *Mus musculus*, that have never encountered fireflies are more likely to select prey next to a flashing light than prey next to a light that is off (Underwood et al. 1997). The little brown bat, *Myotis lucifugus*, preferentially attacks flashing over nonflashing lures (Moosman et al. 2009).

On the other hand, firefly bioluminescence may function to protect against predators (reviewed in: Lloyd 1973; Sivinski 1981; Buschman 1988; De Cock 2009). Bioluminescence serves as an antipredator defence in numerous marine organisms, including dinoflagellates, jellyfish, squid and crustaceans (reviewed in: Widder 2010; Haddock et al. 2010). Recent phylogenetic analyses support the idea that firefly bioluminescence originated in larvae as an antipredator defence, and only later became exapted into an adult courtship signal (Branham & Wenzel 2001; Bocakova et al. 2007; Sagegami-Oba et al. 2007).

Firefly flashing may reduce the risk of predation via at least three mechanisms. First, naïve neophobic or photophobic predators that rarely encounter fireflies may be reluctant to attack flashing prey

* Correspondence: E. M. Jakob, Department of Psychology, Tobin Hall, University of Massachusetts, Amherst, MA 01003, U.S.A.
E-mail address: ejakob@psych.umass.edu (E. M. Jakob).

0003-3472/$38.00 © 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2011.10.008

(reviewed in Sivinski 1981). Second, a sudden flash may startle an approaching predator long enough to allow escape, similar to the way io moths, *Automeris io*, startle predators by suddenly exposing the eyespots on their hindwings (Blest 1957). There are anecdotal reports that larval and adult fireflies readily flash when they are physically disturbed either during the day or night (reviewed in: Lloyd 1973; Sivinski 1981; De Cock 2009). Lloyd (1973) summarized casual observations on startle behaviour in response to firefly flashes: horses, raptorial insects, rats, geckos, and a chicken were reported to startle, but toads, frogs, spiders and bats were not. To our knowledge, startle responses of terrestrial, invertebrate predators to sudden flashes of light have not yet been tested.

Third, in firefly species that are chemically defended and thus distasteful, firefly flashing may serve as an aposematic signal (De Cock & Matthysen 1999). Distasteful prey often advertise chemical defences with conspicuous visual signals that deter predators (Ruxton et al. 2004). Many (but not all) fireflies are distasteful to numerous vertebrate and invertebrate predators (reviewed in Lewis & Cratsley 2008). Some firefly genera contain defensive steroidal pyrones known as lucibufagins, which have been shown to deter predation by *Phidippus* jumping spiders (Eisner et al. 1978). Thus, bioluminescent signals may reduce predatory attacks by increasing predator recognition and avoidance of distasteful prey (Guilford 1986; reviewed in De Cock & Matthysen 1999). For example, wild-caught big brown bats, *Eptesicus fuscus*, were less likely to attack flashing compared with nonflashing aerial lures (Moosman et al. 2009). Similarly, when presented with glowing dummy prey resembling glow-worm larvae, wild-caught toads (*Bufo bufo*) showed lower attack rates and longer latencies to attack (De Cock & Matthysen 1999).

Aversion to aposematic signals may be innate or learned (reviewed in Lindström et al. 1999). Visual aposematic signals enhance learned avoidance in avian (reviewed in Rowe & Guilford 2000), aquatic (Aguado & Marin 2007) and invertebrate predators (Prudic et al. 2006). Bioluminescent signals in particular may help predators learn and retain information that signalling prey are distasteful (Guilford & Cuthill 1989). In terrestrial ecosystems, the role of learning has been tested only in vertebrate predators. House mice, *M. musculus*, learn to avoid unpalatable food more rapidly when it is positioned next to a glowing light (Underwood et al. 1997). Toads (*B. bufo*) exposed to distasteful, glowing firefly larvae (*Lampyris noctiluca*), become more reluctant to attack glowing (but not nonglowing) dummy prey (De Cock & Matthysen 2003).

Diurnal and nocturnal spiders are known predators of fireflies (reviewed in Lloyd 1973). Here we investigate the effect of bioluminescent flashes on the behaviour of jumping spiders in the genus *Phidippus* (Araneae: Salticidae), specifically *Phidippus princeps* and *Phidippus audax*. These North American spiders have a broad geographical range that overlaps that of many firefly species (Lloyd 1966; Edwards 2004). Jumping spiders have excellent vision and are able to see colour, motion and image detail (reviewed in Richman & Jackson 1992). Instead of using a prey-capture web, jumping spiders stalk and tackle prey. Members of the genus *Phidippus* prey upon a wide variety of insects (Freed 1984; Edwards & Jackson 1993). *Phidippus audax* have been used in bioassays for firefly chemical defences, as they readily attack these insects (Eisner et al. 1978, 1997). However, the relationship of firefly flashing to spider behaviour was not recorded during these studies. Furthermore, spiders are capable of learning to avoid aversive stimuli (reviewed in Jakob et al. 2011). In particular, *P. princeps* has been shown to reduce its attacks on toxic prey after repeated experiences (Skow & Jakob 2006).

Fireflies begin sexual signalling at dusk, whereas jumping spiders are generally diurnal. However, firefly flashing might be important to jumping spiders both during daylight and at dusk. We had noticed that fireflies resting on vegetation during the day flashed when disturbed, such as when we brushed against their plants while walking. Thus, during daylight, a spider might sometimes see a flashing firefly that had been disturbed, or might itself induce flashing by touching or attacking a firefly. We conducted daytime trials to more rigorously quantify flashing in response to gentle disturbance. We also observed interactions between fireflies and spiders at dusk under natural light in order to examine whether their activity periods overlapped, and whether interactions resulted in flashing. We tested three hypotheses about the role of bioluminescent flash behaviour in predator–prey interactions between fireflies and jumping spiders: (1) jumping spiders will be startled by sudden light flashes and stop their attack, (2) flashing light affects the prey choice of spiders, and (3) after multiple encounters, spiders are less likely to attack unpalatable prey associated with a flashing versus an unlit light.

METHODS

Study Organisms

The spiders used in these experiments were female *P. princeps* and *P. audax*, collected in western Massachusetts (Quabbin Reservoir, Hampshire County, U.S.A.) in the late summer and autumn of 2009 and 2010. These two species co-occur in the same fields and we routinely capture them in the same microhabitats (see Skow & Jakob 2006 for habitat description). We used *P. princeps* in all experiments except for dusk activity trials where *P. audax* were used. Dusk activity trials were conducted in late spring of 2011 before *P. princeps* could be collected in large numbers. We housed spiders individually in plastic cages enriched with leaves of plastic plants and wooden dowels painted green (Carducci & Jakob 2000) and fed them *Acheta domesticus* house crickets weekly. Crickets were also used as a palatable prey item in the experiments described below. Before each experiment, spiders were starved for 5–9 days to ensure they were hungry.

For firefly disturbance and dusk activity trials, we collected adult male and female *Photuris* sp. in early summer 2010 and 2011 from three locations in Massachusetts (Greenfield, Franklin County and Quabbin Reservoir and University of Massachusetts Amherst, Hampshire County). We housed fireflies in clear plastic cups with ventilated lids and gave them a wet piece of filter paper and a piece of apple to maintain humidity in the cage and a piece of vegetation from plastic plants to rest on.

To examine avoidance of unpalatable prey with experience, we used the diurnal firefly, *Ellychnia corrusca*, which our preliminary observations showed to be unpalatable to *P. princeps*. Overwintering adult fireflies were collected in January 2010 on oak trees, *Quercus rubra* (Cadwell Forest, Pelham, Hampshire County, MA). Fireflies were housed communally in a plastic container outfitted similarly to those for *Photuris* sp.

Firefly Disturbance and Flash Behaviour

Previous reports indicated that adult fireflies flash when disturbed by contact with potential predators (reviewed in: Lloyd 1973; Fu 2006). To confirm these reports, we recorded the response of female and male *Photuris* sp. to physical disturbance. During daylight trials in the laboratory, we placed individual fireflies in a clear plastic, open-topped vial (3 cm diameter × 5.7 cm long). We observed undisturbed fireflies for 3 min and scored whether they flashed. We then gently tapped each firefly with a paint brush and again scored whether they flashed. We compared flashing before and after disturbance using McNemar's exact test, appropriate for paired samples (Daniel 1978).