THE NATURE AND POSSIBLE FUNCTIONS OF LUMINESCENCE IN COLEOPTERA LARVAE

John Sivinski

Department of Entomology and Nematology, University of Florida,
Gainesville, FL 32611

Abstract

Continuous aposematic displays can attract the attention of naive or unrepulsable predators to individuals that would otherwise escape notice. In some cases, they may also be metabolically expensive to produce. Warnings emitted when the likelihood of encountering and discouraging predators is high minimizes these disadvantages.

Bioluminescence in juvenile Coleoptera may be a warning signal ("coloration") whose presence and intensity is under larval control. Light organ locations and the conditions that elicit glows suggest that luminescence is directed at interspecific receivers and that emission and risk are correlated.

The perception by a larva of another facultative aposematic display increases the probability that an undetected predator is nearby. This may account for numerous observations of lampyrid larvae glowing in response to the lights of other larvae and adults.

There are several intraspecific contexts for larval luminescence. Self-illumination could explain the correlation of two uncommon phenomena, red lights and luminous organs on the head. Glows have been proposed to be spacing or aggregation signals. The timing and social context of luminescence is, in many cases, inconsistent with such an interpretation.

Introduction

The function of luminescence in beetle larvae is a mystery (Lloyd 1971, 1978). Proposed solutions include density information, startle warning coloration, detoxification, camouflage (mimicry of fungi and bacteria), self-illumination, and luring of prey (Lloyd 1966, 1973a and refs.). Aposematism has attracted the greatest number of proponents (Darwin 1874; Wallace 1878; Seaman 1891; Maxwell-Lefroy 1909; McDermott 1910; Balduf 1935; Bianchi 1937; Kiichiro 1961; Tiemann 1967, 1970; Crowson 1972; Ghiselin 1974) but, like the others, suffers from a dearth of supportive evidence. This paper suggests that a substantial proportion of juvenile glowing can be explained as facultative defensive signals. Several other possibilities are considered. It is conceivable that multiple selective pressures have molded some luminous repertoires (see Lloyd 1977; Buck 1978).

The occurrence and form of light organs

Luminescent larvae occur among Elateridae (principally the Pyrophorinae and Campyloxeninae) and in four families of the Cantharoidea: Lampyridae, Phengodidae, Homalisidae, and Telegeusidae (Crowson 1972; Costa 1975a; Lloyd 1978).

Elateridae: *Pyrophorus punctatissimus* luminesces on thoracic and abdominal segments through round lateral spots and dorso-ventral transverse

bands (Costa *ex. sp.* 1970). Intersegmental transverse bands glow in the North American *Deilelater (=Pyrophorus s.l.,* see Costa 1975a) *atlanticus* with light strongest posteriorly. The prothorax or a band occupying the anterior portion of the prothorax emits a green light (pers. obs.). *Pyroptesis gilvus* has a similar luminescent pattern (Costa 1975b). The prothorax of *Deilelater bellamyi* may glow dorsoventrally over its entire width or from a restricted anterior band (Bianchi 1937). Mature *Pyrearinus* larvae have 2 green spots on the prothorax and rows of lateral and dorsal lights on the abdomen. Early instars bear only thoracic lights (Costa 1978). In addition to prothoracic luminous organs, *Fulgeochlizus* carries a complement of dorsomedian lights, and a *Hapsodrilus* sp. glows dorso-ventrally from transverse bands. A second *Hapsodrilus* sp. and *Opselater pyrophanus* have only prothoracic lights (Costa 1975a).

Lampyridae: Bioluminescence is universal in lampyrid larvae (Crowson 1972) though not in adults (McDermott 1964). Larval lights are normally distinct from those of the adult and their number and form more homogeneous (Harvey 1952; Lloyd 1971). Typically, 2 small organs emitting a greenish or yellow light are located on the venter of the penultimate (8th) segment. In *Lucidota atra, Pterotus obscuripennis, Luciola aphrogenia (=near L. scintillans), Ellychnia corrusca,* and *Pyrophanes indica,* the surrounding tissue allows the lights to shine through dorsally (Williams 1917; pers. obs.; Lloyd 1973b, pers. comm.; Raj 1947). The luminous bodies are situated dorsally in *Luciola cruciata* and *L. lateralis* (Okada 1928), and in *Phaenolis abdita* (?) protrude from the articulation of the last 2 abdominal segments (Barber 1923). *Lamprohiza delarouzei* has 2 pairs of luminous spots (Balduf 1935) and *L. splendidula* 3 to 12 (Schwalb 1960).

Phengodidae: Larvae and larviform females are often arrayed with numerous light organs. *Phengodes* and *Zarhipis* bear lateral spots on segments 2-12 and glow from transverse bands (Harvey 1952; Tiemann 1967; Lloyd 1978). In addition to 11 pairs of thoracic and abdominal spots *Rhagophthalmus* has lampyrid-like caudal lights (Raj 1957). *Diplocladon hasselti* bears a mid-dorsal as well as 2 lateral blue-green or whitish luminous organs on every segment except the head and ultimate abdominal segment (Halverson *et al.* 1973; Harvey 1952; Haneda 1955). *Phrixothrix* bears red headlights, and yellow-green lights are present from the mesothorax to the 9th abdominal segment (Harvey 1952; Tiemann 1970; Halverson *et al.* 1973). The light arrangement in *Stenophrixothrix* is similar (headlights plus lateral spots on last 8 abdominal segments) but white throughout (Halverson *et al.* 1973); *Stenophrixothrix*-like individuals have green or yellow lights (Lloyd 1978, unpubl. field notes). *Ceratophengus* has a kindred luminous topography (Schwarz and Barber, unpubl. ms.). *Mastinocerus* spp. possess cephalic or post cephalic lights and a dim row of nine medio-dorsal abdominal spots (Schwarz and Barber, unpubl. ms.; Schwarz 1889). A single ventral light is present in *Dioptoma adamsi* (an adult larviform female described by Green 1912); larvae may have multiple spots similar to *Phengodes* (McDermott 1964).

Telegeusidae: Crowson (1972) has suggested that a larviform individual described as *Astraptor* by Barber (1907) may have been a telegeusid. It bore a ruby light on its head. In a later unpublished manuscript Schwarz and Barber refer to the single specimen as *Microphengus gorhami,* a phengodid.

Homalisidae: *Homalisus fontisbellaguei* has lateral light organs on the abdominal segments (Bertkau 1891; Crowson 1972).

Defense in luminous Coleoptera

Lampyrids are distasteful to a number of predators (Lloyd 1973a and refs.). Sydow and Lloyd (1975) demonstrated avoidance of adult *Photinus umbratus* (Lampyridae) by experienced fence lizards. Eisner *et al.* (1978) have extracted toxins (termed lucibufogins) similar to toad poisons from the blood of adult *Photinus* spp. (see Blum and Sannasi 1974). The larvae of *Photuris* sp. (Lampyridae) bleed readily and are rejected by birds and Lycosid spiders (Thomas Eisner, pers. comm.), and by the tiger beetle, *Megacephala virginica* (pers. obs.). When stimulated, *Luciola cruciata* and *L. lateralis* larvae evert glands that smell of resin and peppermint (Okada 1928; Kiichiro 1961). *Phrixothrix* discharges a reddish oily substance from the anus when disturbed; this frequently covers the anterior segments due to the curling of the larvae (Harvey 1952). Burmeister (1873) observed a larva turn the end of its body toward a source of disturbance and swing it from side to side while ejecting the anal fluid. It had a corrosive effect on his skin. Tiemann (1970) was bitten on the hand by a *Phrixothrix* larva. He noted a brown secretion in the region of the wound and the surrounding area remained inflamed for several days (see also Burmeister 1873). On abdominal segments 2-9 of *Zarhipis integripennis,* U-shaped pores excrete a clear amber fluid when the larvae are roughly handled (Tiemann 1967). A *Phengodes laticollis* secreted an anal fluid when handled (pers. obs.). The same individual was attacked but not eaten by a scolopendromorph centipede that then completely devoured a large mealworm. A caustic odor is characteristic of *Rhagophthalmus* (Raj 1957). Luminous elaterid larvae regurgitate a brown liquid when disturbed (Costa 1970, 1975; pers. obs.). *Deilelater bellamyi* bites vigorously if harassed (Bianchi 1937; see Dubois 1886). The bite of *Deilelater atlanticus* can draw blood from a finger (pers. obs.).

Facultative aposematism

Few, if any, animals are completely unpalatable and without enemies (Cott 1957). On occasion, the advertising of an aposematic animal will invite attack. Individuals whose display can be modified to suit different states of risk may save energy and avoid the attentions of predators undeterred by the display. Among Carabidae, for example, metallic warning coloration due to diffraction grating is amplified when its bearer is exposed to view (in direct sunlight) and the probability of attracting notice inherently high. When the risk of discovery is low (under cover, out of direct sunlight) the danger is further reduced by a non-reflective cryptic cuticle (Hinton 1973).

Consider an insect with some degree of unpalatability that may signal aposematically or not. Its predators fall into 3 categories: 1) specialist predators and those unaffected by the unpalatability factor will attack whether the display is given or not but are more likely to attack if it is given; 2) naive predators adversely affected by the unpalatability factor will attack and be repulsed, but some damage is possible in the process. Such a predator will be more likely to attack if the display is given; 3) experienced or innately repulsed predators will attack only if the signal is

withheld, and if they should attack the damage is similar to that inflicted by a naive predator before repulsion.

Under such conditions, if an individual is physically contacted or "purposefully" approached by a predator, it should signal, since the danger of attracting attention is nil and the possibility of repulsion exists. When experienced or innately repulsed predators are more frequently encountered than specialist and naive predators, spontaneous signals (emissions in the absence of contact) to undetected predators should be given (repulsable predators need to be greatly in excess of unrepulsable since the average damage inflicted by specialist and non-affected predators is higher).

Environmental clues, some of which are discussed in the following section, might be used to adjust the duration, frequency, and intensity of the display to local risks.

Buck (1978) questions aposematism as the function of lampyrid luminescence by supposing kin selection to be necessary for its evolution (see Fisher 1958). Facultative aposematism diminishes the danger of attracting naive predators and could mitigate the requirement that warning displays evolve through relatives sharing predators.[1]

An emission itself can be repulsive. Nocturnal or negatively phototropic animals might shun or be startled by luminescence (Nicol 1962; Lloyd 1973c; Buck 1978). When a noxious signal in combination with an active defense is encountered by a predator capable of remembering the display, it may become serendipitously aposematic. In such a case the emission could be molded by multiple receivers.

For a display to be consistent with facultative defensive signals, it must be directed at interspecific receivers (unless evolved in the context of cannibalism) and correlated with risk.

Interspecificity of the signal

Light organ locations may give clues as to the intended recipients of their emissions. The preponderance of luminous spots in Lampyridae are latero-ventral, at the posterior end of the body, and illuminate regions away from the direction of movement. They are unobscured laterally and are particularly visible during locomotion when looping motions lift the abdomen from the ground. Thus the major plane of emission agrees with the level of other larvae and probably the majority of their nocturnal predators. In *Luciola cruciata* and *L. lateralis* the lights are dorsal (Kiichiro 1961). Both are bottom-dwelling aquatic species (Okada 1928). As in terrestrial relatives, conspecific larvae are likely to be present in a single plane, but

---

[1]The necessity of kin selection could be eliminated under some circumstances. Over time a maturing unpalatable population "trains" an increasing number of predators. Individual emissions could be positively correlated to the number of repulsable predators in the environment. The signal of a young or early season animal might be issued only when threatened, that of a late season or older individual broadcast continuously. Spontaneous luminescence in *Luciola cruciata* is most common in hatchlings (Kiichiro 1961) and so is counter to the expectations of the above. Individual selection can also generate Mullerian mimics. Numerous species could converge on a "seed" kin selected coloration. Kin selection, however, is not excluded from turning on the lights of Coleoptera. There are, to my knowledge, no relevant studies of population structure.

potential predators such as fish and birds are overhead, the direction from which a dorsal organ would be most visible. Annandale (1900) found a Malaysian aquatic species having ventral lights that rests dorsal side down on near surface vegetation, resulting in a similar glow orientation.[2] *Luciola aphrogenia* lives on coral reefs where it can be found in deep pits, crevasses, and occasionally underwater (Lloyd 1973b). Tissue transparency allows the light to emerge dorsally (J. E. Lloyd, pers. comm.). Elaterid and many Phengodid larvae inhabit opaque, 3-dimensional environments (rotting wood, underground). Such taxa frequently bear multiple organs on several body aspects and numerous encircling transverse bands. These patterns increase the direction from which luminescence can be perceived and minimize the proportion of the insect that need be exposed for glows to be discerned. The lampyrids *Lucidota atra* and *Ellychnia corrusca* frequent similar habitats and their lights are visible dorsally (Williams 1917; Lloyd 1973c).

Correlation to risk

Mechanical stimulation results in glowing in all the luminescent elaterid larvae examined (Dubois 1886; Bianchi 1937; Costa 1970, 1975a; pers. obs.; however, all but Dubois note that disturbance does not inevitably lead to luminescence.) Among the Phengodidae, *Phrixothrix, Zarhipis, Stenophrix-othrix, Diplocladon, Phengodes laticollis,* and *P. nigromaculata* (?) glow when disturbed (Tiemann 1970, 1967; Halverson *et al.* 1973; Atkinson 1887; pers. obs.). Lampyrids lighting up in response to contact include *Photuris* sp. (Hess 1920; McLean *et al.* 1972; *Luciola lateralis* and *L. cruciata* (Kiichiro 1961); *Pyractomena ecostata* (Wenzel 1896); *Lucidota atra* (Williams, 1971); *Ellychina corrusca* (Lloyd 1973c); and *P. lucifera, P. barberi, P. limbicollis, Micronaspis floridana, Pterotus obscuripennis,* and a marsh inhabiting *Photinus* sp. (pers. obs.).

The disturbance threshold to obtain a glow is comparatively low in some species. A football in the vicinity of *Pleotomus* and *Photuris* sp. will turn on their lights (McDermott 1964). *Lamprohiza (=Phausis) splendidula* glows in reaction to gunfire (Schwalb 1960). Captive *Pterotus obscuripennis* and *Phrixothrix* sp. are sensitive to slight disturbances, e.g. the opening or closing of doors in the room in which they are kept (pers. obs.; Tiemann 1970). Both *Zarhipis integripennis* and *Phrixothrix* occasionally light up in response to a flashbulb (Tiemann 1967, 1970).

In a predator is not deterred by a display, further location clues are maladaptive. Spontaneously glowing larvae might stop emitting if disturbed. Darwin (1860) examined a larva that ceased shining at the slightest touch. *Luciola discicollis* turns off its light and drops to the ground when exposed to a flashlight beam (Kaufmann 1965). A footfall or beam of light caused glowing *L. cruciata* and *L. lateralis* to darken (Kiichiro 1961). When

---

[2]Annandale interpreted the larval orientation as a means of attracting prey into the water. It is interesting that the lights are described as blue, an unusual hue in insects. The blue emissions of mycetophilid (Diptera) glowworms have long been suspected of drawing victims into their sticky webs (Fulton 1941). Since insects tend to be more sensitive to shorter wavelengths of light, blueness may be a predatory adaptation.

irritated, an aquatic species discovered by Annandale (1900) sometimes brightened but more frequently extinguished its light.

Contrary to the expectation of facultative aposematism, *Lampyris noctiluca* does not luminesce when roughly handled (Schwalb 1960). Subterranean *Photinus floridanus* only occasionally glowed when repeatedly prodded (pers. obs.).

The duration, frequency, and intensity of spontaneous luminescence varies between species. *Pterotus obscuripennis* is bright (pers. obs.) while the glow of *Hotaria parvula* is hardly recognizable (Kiichiro 1961). *Micronaspis floridana* seldom luminesces in the absence of stimulation (McDermott 1954; pers. obs.), but Bess (1956) estimated that 1 larva of *Lamprigera (=Lamprophorus) tenebrosus* in 5 was glowing at any one time.

Disturbance thresholds, signal intensities, and amount of spontaneous luminescence may be related to the degree of larval unpalatability. Signals broadcast over greater distances and emitted more frequently and at slighter disturbance are more likely to intercept potential predators. Simultaneously, there is the risk of attracting dangerous predators (naive or unaffected by unpalatable factor) who would have remained ignorant of the emitter had the signal not been given. The consequence of the communication depends on the nature of the receivers. Larval toxicity influences the proportion of local predators apt to find a species repugnant. If *Micronaspis* (high disturbance threshold, relatively dim light) and *Pterotus* (low threshold, bright light) face predators with similar tolerances to larval toxins, the *Pterotus* would be predicted to be the least palatable.

Compromising positions and environments might encourage increased advertisement. In species where movement entails exposure, glowing should be related to locomotion. *Pyractomena lucifera* (on aquatic vegetation, and *Photuris* spp. (among leaf litter and terrestrial vegetation) luminesce more often when moving (Buschman 1977; McLean *et al.* 1972; pers. obs.). *Luciola cruciata* and *L. lateralis* glow when leaving the water to pupate. In the former, synchrony of maturation results in up to 200 larvae per m^2 of bank (Kiichiro 1961). Coordinated exposure itself is thought to serve an antipredation end through a number of means: increased intensity of aposematic displays (Cott 1957); pooled defenses (Henry 1972; Tostowaryk 1972); predator swamping (M. Lloyd and Dybas 1966; Janzen 1976). Rapid movements by *Deilelater atlanticus* (Elateridae) in the presence of its prey, termites, were often accompanied by 1-55 second prothoracic glows.

Subterranean larvae of *Photinus floridanus* glow only when stationary (pers. obs.). If the environment is totally opaque the probability of discovery by a searching predator is independent of larval motion. Unless immobility increases nonvisual apparency (e.g. by local accumulation of metabolic products), luminescence only when stationary does not seem consistent with facultative aposematism. Lloyd and Buschman (in Lloyd 1973c) proposed that negatively phototropic soil inhabitants may be repelled by the glow of hypogean lampyrids. The luminescence of burrowing marine invertebrates has been explained in similar terms (Nicol 1962; see Buck 1978). Perhaps mimicry of an interface is most realistic in a quiescent organism.[3]

---

[3]Lloyd (1966) proposed mimicry of bacteria and fungi as a rationale for luminescence. Considering the stationary nature of the models, this form of

Lampyris noctiluca locates snails by tracking slime trails. After im-
obilizing its prey, it often goes off in search of a refuge and drags the snail
to it before feeding. Larvae glow when crossing slime trails and on return to
dead snails (Schwalb 1960). Trail-following occurs in other predaceous in-
sects (Greany and Hagen, in press). The potential for trails and temporarily
abandoned prey to attract other predators could account for *L. noctiluca's*
glow when encountering these regions of high risk. *Phrixothrix* larvae glow
when attacking millipedes and adults luminesce during, but not prior to,
copulation. The vulnerability inherent in these activities may make warn-
ing displays adaptive (Tiemann 1970).

The warning display of another individual may be a clue to the presence
of an undetected predator. To the extent that the signal is the result of
perceiving a predator, the signal itself becomes evidence of a potential
danger to nearby individuals. The longer the display is perceived (i.e. the
longer the survival of the emitter) the more likely it is that the predator is
repulsable. Facultative aposematists might respond to a warning display
by displaying themselves, perhaps after monitoring the fate of the emitter
(he cost of hesitancy may be attack by the predator repelled by the initial
emitter).

Glowing in response to the increased intensity of another larva occurs in
an aquatic Malaysian species (Annandale 1900). *Luciola cruciata, L.
lateralis,* and *Pyractomena* sp. lit up when neighboring larvae luminesced
(Kiichiro 1961; pers. obs.). McLean *et al.* (1972) noted a similar phenomenon
in *Photuris* sp. but were unable to confirm it experimentally.

To the extent that emitters are spatially adjacent and share predators,
their ontogenic and phylogenetic relationships are unimportant to the
quality of information gleaned from a display. Larval and adult lampyrids
can be spatially adjacent (grounded males, copulation pairs, females
responding to male signals). *Photuris "pennsylvanica"* larvae "answer" the
signal patterns of adult males of their own and a congeneric species (Kieper
and Solomon 1972). Larvae of *Luciola aphrogenia* appear to be stimulated
by the flashes of a penlight and flying males (Lloyd 1973b). A *Pyractomena*
sp. was discovered by Minnick and Lloyd (unpubl. ms.) through its
response to a penlight. Lloyd (pers. comm.) has seen *Photuris* spp. larvae
seemingly reply to low flying males.

An unidentified Malaysian species and *Luciola cruciata* glow several
seconds after a neighbor luminesces (Annandale 1900, Kiichiro 1961). They
could be pausing to monitor the survival of the emitter. *Photuris* sp. larvae
glow within a fraction of a second when electrically stimulated, suggesting
that the delay is not due to physiological inertia (see Carlson 1965).

Possible intraspecific contexts for luminescence

Self illumination: Light organs on the head are rare in Coleoptera larvae,
occurring to my knowledge only in genera of the carnivorous Phengodidae:
hrixothrix, Stenophrixothrix, Ceratophengus, and *"Astraptor"*
=*Microphengus* Schwarz and Barber = telegeusid, Crowson 1972). Red

imicry's applicability to mobile glowers is limited. Luminous pathogens occa-
onally afflict insects (Harvey 1952). Predators avoiding contagion might evade
owing arthropods (see also Janzen 1977).

lights are found only in 2, *Phrixothrix* and *"Astraptor,"* and are located on the head. Self-illumination may explain the cooccurrence of these uncommon phenomena. Arthropods are generally, but not inclusively, insensitive to red light (Menzel 1975). A carnivore capable of searching through channel invisible to its prey would be at an advantage. The deep-sea fish *Pachystomias* bears red photophores behind the eyes which may be used in capturing abyssal organisms unable to perceive red light (Denton 1971).

The behavior of *"Astraptor"* is unknown. Barber (1907) noted that its light was not easily seen from above and was best observed through its reflection from objects in front of the larva. Conflicting reports exist for the luminous behavior of *Phrixothrix*. Murray (1868) described the red lights as glowing continuously. Reinhart (1854) noted that some lights, but not all, were on at any one time. Later studies dealing with larger samples reported that luminescence in the larvae was elicited primarily by disturbance (Harvey 1944; Tiemann 1970) and during attacks on millipedes (Tiemann 1970). Halverson *et al.* (1973) found rare spontaneous lighting in larviform females (which do not feed) and Tiemann (1970) occasionally saw luminescing individuals at a distance. The red lights were the first to come on and the last to go out among Harvey's (1944) specimens, and could be used to illuminate a source of disturbance or a line of retreat. *Stenophrixothrix's* green, yellow, or white headlights glow continuously, unlike the abdominal organs (Halverson *et al.* 1973; Lloyd 1978).

Some luminous elaterid larvae possess lateral ocelli, organs which are otherwise hardly known in the Elateroidea (Crowson 1967). Vision is not necessary in the emitter of a defensive signal (e.g., blind geophilid centipedes secrete a glowing material when disturbed, Harvey 1952). However, there may be advantages in perceiving similar warning displays.

Spacing: Halverson *et al.* (1973) proposed that phengodid luminescence preserves distance between the predaceous larvae. Territoriality can occur in immature carnivorous insects (e.g. Edmunds 1976). Individuals actively repelling and retreating from each other would generate uniform rather than random or clumped spatial patterns in homogeneous environments.

Phengodid dispersal does not lend itself easily to such an analysis. Most are difficult to obtain and apparently rare (see Harvey 1952; Tiemann 1967, 1970).[4] Clumped distributions have been found among lampyrid larvae. Williams (1917) described overwintering aggregations of *Lucidota atra.* Several *Photuris versicolor* will construct and occupy the same molting chamber in captivity (Minnick and Lloyd, unpubl. ms.). *Luciola cruciata* migrate en masse toward pupation sites (Kiichiro 1961). The above aggregates occur in apparently non-competitive contexts (see section on correlation to risk). However, gregarious feeding has also been observed in several lampyrids: *Lampyris noctiluca* (Wootton 1971); *Lamprigera tenebrosus* (Hutson 1924); *Pyropyga nigricans* (=*P. fenestraus)* (Hess 1920); *Photuris pennsylvanica* (Williams 1917); and *Pyractomena gamma* (?) (McDermott 1953). Lloyd (1973c) proposed that luminous signals attracting aid to subdue difficult prey might account for such aggregates

---

[4]Their typically nocturnal habits and subterranean, litter, and decaying wood habitats may lead to underestimations of population densities. Arboreal *Stenophrixothrix* (?) were commonly encountered by J. E. Lloyd in Colombia (Lloyd 1978; pers. comm.).

(see Wootton 1971). Killing of large snails by a *Photuris* sp. does not seem to result in an unusual amount of luminescence (pers. obs.). *Phrixothrix* sp. lights up when attacking millipedes but Tiemann (1970) gives no indication that the glow is related to the magnitude of the struggle.

Balduf (1935) suggested that a larva could assemble conspecifics (kin, to make the argument genetically plausible) to share a capture. The rarity or absence of glows emitted while feeding in a Malaysian species (Maxwell-Lefroy 1909), *Luciola discicollis* (Kaufmann 1965) and *Photuris* sp. (McLean *et al.* 1972) does not support such an explanation for these species. The dangers of attracting conspecifics to a feeding site in a *Photuris* sp. (fights resulting in the exclusion of one participant and theft of the snail by one of the larvae, pers. obs.), may explain the lack of glows while eating in this and other species. Such an argument assumes that competitors, including conspecifics, monitor and are attracted to larval signals. The apparent causality between feeding and decreased emission may be spurious. In *Photuris* spp. and *Pyractomena lucifera*, glowing is positively correlated to movement (McLean *et al.* 1972; pers. obs.; Buschman 1977). A feeding, immobile larva is less likely to glow.

Environmental opacity and signal duration

Given a metabolic cost to signalling, a display could more cheaply consist of a series of events rather than a sustained transmission. An aposematic display in which the off time between display units is less than the time a predator requires for orientation and attack is as effective as a continuous signal. The energetically less expensive off time might exceed the maximum time required for an attack if the probability of encountering a predator is low (the cumulative cost of rapid signaling outweighs the risk of damage by a predator completing an attack during a dark non-signaling window). As the probability of an encounter increases, the off time might approach the minimum attack period.

An important factor determining the time a predator requires to orient and attack is the opacity of the environment. Where the opacity in the display channel is high, then the time between orientation of the predator through this channel and attack is necessarily low. The space between signal units should then decline and duration of each unit increase.

Short spontaneous glows are encountered among surface-dwelling lampyrids. In a sample of 308 *Photuris* sp. glows, 90% were 3 seconds or less in duration. Long glows (up to 5 minutes) are rare (see also McLean *et al.* 1972). *Micronaspis floridana* glows are a few seconds long. Several *Pyractomena* spp. luminesce for 5-12 seconds or less, as does a marsh-inhabiting *Photinus* sp. (Minnick and Lloyd unpubl. ms.; pers. obs.).

Subterranean larvae of *Photinus floridanus* seldom spontaneously luminesced for less than 1 minute and often glowed up to 30 minutes (limit of observation time, pers. obs.). The emissions of amphibious *Pyractomena lucifera* are several seconds long above water but are often continuous below the surface (Buschman 1977).

A relationship between environmental opacity to glow duration does not necessarily support facultative aposematism. Many (if not all) signals, regardless of the intended receiver, might exhibit the same correlation. A moving emitter illuminating stationary objects or a stationary emitter at-

tempting to cast a light on moving objects could evolve an identical luminescence pattern.

Implications of aposematism

Immature luminous Coleoptera are poorly known. Even the small body of information harbors incongruities that seem to confound generalization. It is probable, however, that defense is involved in some proportion of displays.

In many lampyrids, eggs, larvae, pupae, and adults are luminous (Harvey 1952; Lloyd 1978). The environs of these stages are diverse, but predation is a common danger and light production may serve now or have served historically a similar end in each. If aposematic displays differ between species due to palatability and to predators encountered and within species because of individual resources and perception of risk, a body of self-revelation is contained in an adult aposematic display. Females could make sexual choices, males gauge potential competitors and direct their searches by distinguishing between signals. Sexual information transmitted by contemporary adults may be the secondarily evolved patterning of an older and ontogenetically common adaptation.

BIBLIOGRAPHY

ANNANDALE, N. 1900. Observations on the habits and natural surroundings of insects made during the "Skeat Expedition" to the Malay peninsula, 1899-1900. VI Insect luminosity: an aquatic Lampyrid larva. Proc. Zool. Soc. London. pp. 862-865.

ATKINSON, G. F. 1887. Observations on the female form of *Phengodes laticollis* Horn. Am. Nat. 21(9):853-856.

BALDUF, W. V. 1935. The bionomics of entomophagous Coleoptera. John S. Swift and Co., St. Louis.

BARBER, H. S. 1907. The glowworm *Astraptor.* Proc. Entomol. Soc. Wash. 9:41-43.

BARBER, H. S. 1923. A remarkable wingless glowworm from Ecuador (Coleoptera, Lampyridae). Insec. Inscit. Menst. 11:191-194.

BERTKAU, P. 1891. Beschreibung der larve und des Weibchens von *Homalisus suturalis.* Dt. Z. Nerv. Heilk 1:37-42.

BESS, H. A. 1956. Ecological notes on *Lamprophorus tenebrosus* (Walker) (Coleoptera: Lampyridae), an enemy of the giant African snail. Proc. Haw. Entomol. Soc. 16(1):24-29.

BIANCHI, F. A. 1937. Notes on a new species of *Pyrophorus* introduced into Hawaii to combat *Anomala orientalis* Waterhouse. Haw. Pl. Rec. 41:319-333.

BLUM, M. S. AND A. SANNASI. 1974. Reflex bleeding in the Lampyrid *Photinus pyralis:* defensive function. J. Insect Physiol. 20:451-460.

BUCK, J. 1978. Functions and evolutions of bioluminescence. Pp. 419-460 *in* P. J. Herring, ed. Bioluminescence in action. Academic Press, London.

BURMEISTER, H. 1873. Observations on a light giving Coleopterous larva. J. Linn. Soc. (Zool.) 11:416-421.

BUSCHMAN, L. L. 1977. Biology and bioluminescence of selected fireflies in the genera *Pyractomena, Photinus* and *Photuris* (Coleoptera: Lampyridae). Unpubl. Ph.D. dissert., Univ. of Florida.

CARLSON, A. D. 1965. Factors affecting firefly larval luminescence. Biol. Bull. 129:234-243.

COSTA, C. 1970. Genus *Pyrophorus.* 3. Life-history, larva, and pupa of *Pyrophorus punctatissimus* Blanchard (Col. Elateridae). Pap. Aval. Zool., S. Paulo 23(8):69-76.

COSTA, C. 1975a. Systematics and evolution of the tribes Pyrophorini and Heligmini with description of Campyloxeninae, new subfamily (Coleoptera, Elateridae). Pap. Dep. Zool., S. Paulo 26:49-190.

COSTA, C. 1975b. Notas sobre o genero *Pyroptesis* con descricao e dados biologicos de *P. gilvus* sp. n. (Coleoptera, Elateridae, Pyrophoridae). Pap. Aval. Zool., S. Paulo 29(1):1-6.

COSTA, C. 1978. Sistematica e bionomis de *Pyrearinus,* 1975 (Coleoptera, Elateridae). Vol. 29, fasc. 4, Museu de zool. de Univ. de Sao Paulo.

COTT, H. B. 1957. Adaptive coloration in animals. Methven and Co. Ltd., London.

CROWSON, R. A. 1967. The natural classification of the families of Coleoptera. E. W. Classey Ltd., Middlesex, England.

CROWSON, R. A. 1972. A review of the classification of Cantharoidea (Coleoptera) with the definition of two new families, Cneoglossidae and Omethidae. Pub. Rev. de la Univ. Madrid 21(82).

DARWIN, C. 1860. The voyage of the Beagle. Doubleday and Co. Inc., Garden City, N.Y.

DARWIN, C. 1874. The descent of man and selection in relation to sex. 2nd ed. Hurst, New York.

DENTON, E. J. 1971. Reflectors in fishes. Sci. Am. 224(1):64-72.

DUBOIS, R. 1886. Contribution a l'etude de la production de la lumiere par les etres vivants. Les elatrides lumineux. Bull. Soc. Zool. Fr. 11:1-275.

EDMUNDS. M. 1976. The defensive behavior of the Ghanaian praying mantids with a discussion of territoriality. Zool. J. Linn. Soc. 58:1-37.

EISNER, T. E., D. F. WIEMER, L. W. HAYNES AND J. MEINWALD. 1978. Lucibufogins: defensive steroids from the fireflies *Photinus ignitus* and *P. marginellus* Coleoptera: Lampyridae). Proc. Nat. Acad. Sci. 75(2):905-908.

FISHER, R. A. 1958. The genetical theory of natural selection. Oxford The Clarendon Press. (2nd. ed.). Dover, New York.

FULTON, B. B. 1941. A luminous fly larva with spider traits (Diptera, Mycetophilidae) Ann. Entomol. Soc. Am. 34:289-302.

GHISELIN, M. T. 1974. The economy of nature and the evolution of sex. Univ. of Calif. Press. Berkeley, Calif.

GREANY, P. AND K. S. HAGEN. Prey selection. *in* D. A. Nordlund, R. L. Jones, and W. J. Lewis, eds. Semiochemicals: their role in pest control. John Wiley and Sons. (in press)

GREEN, E. E. 1912. On some luminous Coleoptera from Ceylon. Trans. Roy. Entomol. Soc. London (ser. 4) 60:717-719.

HALVERSON, R. C., J. F. CASE, J. BUCK AND D. TIEMANN. 1973. Control of luminescence in phenogodid beetles. J. Insect Physiol. 19:1327-1339.

HANEDA. Y. 1955. Luminous organisms of Japan and the Far East. Pp. 335-386 *in* F. H. Johnson, ed. The luminescence of biological systems. Am. Assoc. Adv. Sci. Wash., D.C.

HARVEY, H. E. 1944. The nature of the red and green luminescence of the South American railroad worm. J. Cell. Comp. Physiol. 23:31-38.

HARVEY, H. E. 1952. Bioluminescence. Academic Press Inc., New York.

HENRY, C. S. 1972. Eggs and repugula of *Ululodes* and *Ascaloptynx* (Neuroptera: Ascalophidae): a comparative study. Psyche 79(1,2):1-22.

HESS, W. N. 1920. Notes on the biology of some common Lampyridae. Biol. Bull. 38:39-76.

HINTON, H. E. 1973. Natural deception. Pp. 96-159 *in* R. L. Gregory and E. H. Gombrick, eds. Illusion in nature and art. Chas. Scribner's Sons, New York.

HUTSON, J. C. 1924. Notes on the habits and life history of the Indian glow-worm, an enemy of the African or Kalutara snail. Bull. Dept. Agric. Ceylon 69:1-15.

JANZEN, D. H. 1976. Why bamboos wait so long to flower. Annu. Rev. Ecol. Syst. 7:347-391.

JANZEN, D. H. 1977. Why fruits rot, seeds mold, and meat spoils. Am. Nat. 111:691-713.

KAUFMANN, T. 1965. Ecological and biological studies on the West African firefly *Luciola discicollis* (Coleoptera: Lampyridae). Ann. Entomol. Soc. Am. 58(4):414-426.

KEIPER, R. R., AND L. M. SOLOMON. 1972. Ecology and yearly cycle of the firefly *Photuris pennsylvanica* (Coleoptera: Lampyridae). J. N.Y. Entomol. Soc. 80:43-47.

KIICHIRO, M. 1961. Hotaru no Kenkyu (a study of fireflies). (In Jap.) Published by the author, Moriyama Shigu prefecture, Japan. (Translated by H.Q. Dept. Army).

LLOYD, J. E. 1966. Studies on the flash communication system in *Photinus* fireflies. Misc. Publ. Mus. Zool. Univ. Mich. No. 130.

LLOYD, J. E. 1971. Bioluminescent communication in insects. Annu. Rev. Entomol. 16:97-122.

LLOYD, J. E. 1973a. Firefly parasites and predators. Coleopts. Bull. 27(2): 91-106.

LLOYD, J. E. 1973b. A firefly inhabitant of coastal reefs in New Guinea (Coleoptera: Lampyridae). Biotropica 5(3):168-174.

LLOYD, J. E. 1973c. Fireflies, commonplace beetles and larvae by day, but tiny flashing lanterns on summer evenings. Animals May:220-225.

LLOYD, J. E. 1977. Bioluminescence and communication. Pp. 164-183 *in* T. A. Sebeok, ed. How animals communicate. Univ. Ind. Press, Bloomington, Ind.

LLOYD, J. E. 1978. Insect bioluminescence. Pp. 241-272 *in* P. Herring, ed. Bioluminescence in action. Academic Press, London.

LLOYD, M., AND H. S. DYBAS. 1966. The periodical cicada problem: I population ecology. Evolution 20(2):133-149.

MAXWELL-LEFROY, H. 1909. Indian insect life. Thacker Spink and Co., Calcutta and Simla.

McDERMOTT, F. A. 1910. A note on the light emission of some American Lampyridae. Can. Entomol. 42:357-363.

McDermott, F. A. 1953. Glowworms in a marine littoral habitat in Jamaica. Entomol. News. 64:89-90.

McDermott, F. A. 1954. The larva of *Micronaspis floridana* Green. Coleopts. Bull. 8:59-62.

McDermott, F. A. 1964. The taxonomy of the lampyridae (Coleoptera). Trans. Am. Entomol. Soc. 90:1-72.

McLean, M., J. Buck and F. E. Hanson. 1972. Culture and larval behavior of Photurid fireflies. Am. Mid. Nat. 87(1):133-145.

Menzel, R. 1975. Colour receptors in insects. Pp. 121-153 *in* G. A. Horridge, ed. The compound eye and vision of insects. Clarendon Press, Oxford.

Minnick, D. R. and J. E. Lloyd. Observations on the rearing, natural history, and behavior of four genera of Lampyridae: Coleoptera (Micronaspis, Pyractomena, Photinus and Photuris). Unpubl. ms.

Murray, A. 1868. On an undescribed light giving Coleopterous larva (provisionally named *Astraptor illuminator*). Entomology 4:281-289.

Nicol, J. A. C. 1962. Animal luminescence. Adv. Comp. Physiol. Biochem. 1:217-273.

Okada, Y. K. 1928. Two Japanese aquatic glowworms. Trans. Roy. Entomol. Soc. London. 76:101-108.

Raj, J. S. 1947. Two species of undescribed lampyrid larvae from S. India. Proc. Indian Acad. Sci. (B) 25:188-194.

Raj, J. S. 1957. An undescribed luminous beetle from southern India. J. Bombay Nat. Hist. Soc. 54:788-789.

Reinhardt, J. 1854. Phosphorescence of the larva of an insect. Trans. Roy. Entomol. Soc. London 3(2):5-8.

Schwalb, H. H. 1960. Beitrage sur biologie der einheimeschem Lampyriden. Dissertation Johanes-Gutenberg-Universitat, Maniz.

Schwarz, E. A. 1889. Proc. of the Ent. Soc. of Wash. 4:348.

Schwarz, E. A. and H. S. Barber. A revision of the coleopterous family Phengodidae. Unpubl. ms.

Seaman, W. H. 1891. On the luminous organs of insects. Proc. Am. Soc. Microsc. 13:133-162.

Sydow, S. L., and J. E. Lloyd. 1975. Distasteful fireflies sometimes emetic but not lethal. Fla. Entomol. 58(4):312.

Tiemann, D. L. 1967. Observations on the natural history of the western banded glowworm *Zarhipis integripennis* (LeConte) (Coleoptera: Phengodidae). Proc. Calif. Acad. Sci. 35(12):235-264.

Tiemann, D. L. 1970. Nature's toy train, the railroad worm. Nat. Geogr. 138(1):56-67.

Tostowaryk, W. 1972. The effect of prey density on the functional response of *Podisus modestus* (Hemiptera: Pentatomidae) to the densities of sawflies *Neodiprion swainei* and *N. pratti banksianae* (Hymenoptera: Neodiprionidae). Can. Entomol. 104:61-69.

Wallace, A. R. 1878. Tropical nature, and other essays. MacMillan and Co., London.

Wenzel, H. W. 1896. Notes on Lampyridae with the description of a female and larva. Entomol. News 7:294-296.

Williams, F. X. 1917. Notes on the life history of some North American Lampyridae. J. N.Y. Entomol. Soc. 25:11-33.

Wootton, A. 1971. A dim future for glowworms (Lampyridae). Country life (London) 150(3874):604-605.