Research signpost
37/661 (2), Fort P.O., Trivandrum-695 023, Kerala, India

Bioluminescence in Focus - A Collection of Illuminating Essays, 2009: 161-200
ISBN: 978-81-308-0357-9 Editor: Victor Benno Meyer-Rochow

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Biology and behaviour of European lampyrids

Raphaël De Cock
Associate Researcher, Evolutionary Ecology Group, University of Antwerp
B-2610 Antwerp, Belgium

Abstract

Firefly research already started a couple of centuries ago in Europe. Nevertheless recent research on the behaviour and the ecology of European species seems to leap behind compared to the other continents. Possible explanations for being less studied may be that European fireflies are just less eye-catching. This may be due to a more northern latitudinal position by which Europe has a relative lower biodiversity compared to other continents. Also because of this more northern position, sunset occurs late in summer and firefly displays are only seen late at night. The high degree of urbanisation, industrialisation and intensive agriculture may have

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Correspondence/Reprint request: Dr. Raphaël De Cock, Associate Researcher, Evolutionary Ecology Group
University of Antwerp, B-2610 Antwerp, Belgium. E-mail: rdecock@hotmail.com

had negative impacts on numbers of fireflies making them relatively rare in many European countries. Last but not least, the far less spectacular bioluminescent displays of European fireflies may explain their lower success as a study species. The information about European fireflies is quite scattered and within this chapter I try to summarize what is known about behaviour, ecology, some peculiarities and especially about bioluminescence and latest discoveries. A most updated overview of European firefly taxa and a general review about the types of communication systems used by these taxa are presented. This resulted in a presumption that many sympatrically living species of some taxa may experience quite some confusion in recognising a right mate resulting in the possibility of multiple hybridisations (in the past), which in turn may explain the problem of classifying and species description without the involvement of genetic markers. Also other topics are discussed. Synchronous flashing is known from American and Asian species but does it also occur in Europe? What types of bioluminescent displays do the larvae show and why do they glow? Over the whole, a lot of questions remain unresolved and I conclude with several topics that may deserve research in some near future.

1. Introduction

In general few Europeans can tell they witnessed fireflies in their surroundings. Mediterraneans usually have dinner when the adult insects show their bioluminescent displays, while more to the North where the sun sets at about 10 or even 11.30 pm people usually prepare to go to bed when the glow-worm starts to shine [1]. Yet glow-worms and fireflies play some role in the mind of European people. They are often associated with remembrance of childhood, romantic summer evenings, mystic legends, holidays, or in the past even with Saints, more in particular Saint John whose holyday (24th June), the longest day of the year when in many European countries at midsummernight fires are lit, falls in the peak season of some firefly species. Probably because of this association of fire and light the shiny insect was named after Saint John (or St. Jan, Johan, Johannis, Hans) in many countries: Sankthansorm (Danish, Norwegian), Szent-Jánosbogár (Hungarian), Świetlik świętojański (Polish), Lu mohe de Sint Tch'han (Walloon: Belgium), Jonvabalis (Estonian), Johanniskäfer (German). During the last few decades, a lot of effort has been spent in some European countries and regions (UK, Portugal, Switzerland, Germany, Normandy, Benelux, Denmark, Zurich, Turin, etc.) in popularising fireflies and making them known to the general public [2], in order to organise volunteer surveys and monitor glow-worm populations. Indeed, more and more anecdotal evidence suggests a decline in populations [1-6]. Possible factors for a decline are habitat destruction and decline as well as fragmentation due to intensified agriculture, industrialisation and urbanisation, drainage and overconsumption of water, light pollution, and pesticides [1,6]. Recently also climate change and global warming have come up as likely future threats.

Depending on the geographical region there seems to exist quite some misunderstanding and confusion about the use of the english terms “glow-worm” and “firefly”. In Europe, The term “glow-worm” is commonly used in connection with the flightless larviform females of lampyrid fireflies and with lampyrid larvae. In other parts of the World however, a glow-worm might belong to a totally different taxon (Table 1). For instance, in some parts of the United States, New-Zealand and Austalia, “glow-worms” are luminous larvae or even the adults of certain fungus gnats beloging to the subfamilies Arachnocampinae, Keroplatinae and Macrocerinae [7] or the bioluminescent larvae and larviform females of phengodid beetles. Therefore one often has to specify “lampyrid glow-worms” or “firefly glow-worms“ in order to prevent misunderstandings when addressing an international audience. Further down this text we will always refer to lampyrid species when mentioning “glow-worms”. Fireflies then, are the winged and flying bioluminescent forms, i.e., exclusively males on our Continent. As a matter of fact, using these terms, the British Isles are only home to glow-worms!

Europe is not particularly famous for its high biodiversity of firefly species. It lies almost entirely in the temperate climate zone where biodiversity is generally lower than in more (sub)tropical regions. In the early eighties only about 35 species were known [8], but at present about 64 European lampyrid taxa, divided over only 8 genera (see Table 2), have been described in the literature [9]. Recent fieldwork proves that yet many more new species are to be discovered [10,11] especially in the southern and eastern parts of the continent where many species seem to have been misidentified in the past or stayed overlooked up till now.

In contrast to the Americas [12-18] and Asia [19-39], research on the ecology, bioluminescent behaviour and communication systems of European lampyrids in mate location, attraction and identification has been rather scarce

Table 1. Regional distribution of fireflies and glow-worms in English terminology.

Region	**Lampyridae**	**Phengodidae**	**Keroplatidae (Diptera, Mycetophilidae)**
Europe	Firefly & Glow-worm	absent	No common name (*Keroplatus* sp.)
USA	Firefly & Lightning bug	Glow-worm	Glow-worm (*Orfelia* sp.)
Australia & New-Zealand	Firefly	absent	Glow-worm (*Arachnocampa* sp.)

Table 2. Updated list of European Lampyrid species and subspecies (with the kind permission of Dr. Michael Geisthardt,[9]).

SUBFAM.	TRIBE	GENUS	SPECIES/ SUB-SPEC	AUTHOR	GEOGRAPHIC DISTRIBUTION
Lampyrinae	**Lampyrini**	*Lampyris*	*ambigena*	Jacquelin du Val, 1860	Italy, Sicily
			angustata	Motschulsky, 1854 (Lampronetes)	Georgia; Caucasus
			angustula	Fairmaire, 1895	Syria; Asia Minor: Turkey, Anatolia; Mesopotamia
			brevicollis	Motschulsky, 1854	Georgia, Caucasus
			brutia	Costa, 1882	Italy, Calabria
			caspica	Motschulsky, 1854 (Lampronetes)	Georgia, Caucasus; Turkey?; Iran?
			costalis	Motschulsky, 1854	Armenia
			depressiuscula	Motschulsky, 1854	Georgia, Caucasus
			fuscata	Geisthardt, 1987	Italy, Abruzzi
			fuscata subsp. apuliae	Geisthardt, 1987	Italy
			germariensis	Jacquelin du Val, 1860	Jugoslav countries
			hellenica	Geisthardt, 1983	Greece
			lareynii	Jacquelin du Val, 1859	France, Corsica
			lareynii subsp. maculata	Geisthardt, 1987	Italy, Giglio
			limbata	Motschulsky, 1854	Georgia, Caucasus
			membranacea	Motschulsky, 1854 (Lampronetes)	Georgia, Caucasus
			monticola	Geisthardt, 2000	Greece
			noctiluca	Linnaeus, 1758	Europe
			orientalis	Faldermann, 1835	Georgia, Caucasus; Turkmenistan
			pallida	Geisthardt, 1987	Malta, Gozo
			pseudozenkeri	Geisthardt, 1999	Turkey, W-Turkey
			raymondi	Mulsant & Rey, 1859	France, West-Alps; Italy; Spain
			sardiniae	Geisthardt, 1987	Italy, Sardinia
			sardiniae subsp. brunnea	Geisthardt, 1987	Italy, Asinara
			vesuvius	Geisthardt, 2007	Italy, Campania
			vesuvius subsp. insularis	Geisthardt, 2007	Italy, Pontic Isles
			zenkeri	Germar, 1817	Jugoslav countries, Kroatia; Greece; Bulgaria; Romania
			zenkeri subsp. liebegotti	Geisthardt, 1985	Greece, Kyra Panagiá
			zenkeri subsp. sulpuri	Geisthardt, 1999	Greece
		Nyctophila	*anatolica*	Geisthardt, 1982	Turkey, Anatolia
			bonvouloirii	Jacquelin du Val, 1860 (Lampyris)	Italy, Sicily
			calabriae	Geisthardt, 1983	Italy, Calabria
			caucasica subsp. lenkorani	Geisthardt, 1982	Caucasus, Azerbaijan
			colorata	Geisthardt, 1983	Greece, Santorini
			graeca	Geisthardt, 1990	Greece
			heydeni	E. Olivier, 1884 (Lampyris)	Spain, Balearic Isles
			libani	Laporte, 1833 (Lampyris)	Syria; Turkey, Anatolia; Cyprus (?); Libanon
			maculicollis	Fairmaire, 1866 (Lampyris)	Turkey, Anatolia; Iran; Persia; Syria
			molesta	Jacquelin Du Val, 1860 (Lampyris)	Italy, Liguria
			pseudocaucasica	Geisthardt, 1982	Caucasus
			reichii	Jacquelin Du Val, 1859 (Lampyris)	France; Spain; Jugoslav countries; Turkey, Anatolia Portugal
			reichii subsp. brullei	Reiche, 1863 (Lampyris)	Greece
			riegeri	Geisthardt, 1990	Greece
			scabripennis	Olivier, 1907	Asia Minor
		Pelania	*mauritanica*	Linnaeus, 1767 (Cantharis)	S-Europe, France, Portugal, Spain; N-Africa, Algeria, Morocco, Tunisia
	Photinini	*Lamprohiza*	*boieldieui*	Jacquelin Du Val, 1859	France
			delarouzei	Jacquelin Du Val, 1859	France
			foliacea	Baudi, 1871	Italy, Sardinia
			germari	Küster, 1844 (Lampyris)	Croatia, Dalmatia
			morio	Baudi, 1875: (Lamprorhiza)	Italy, Etruria
			mulsanti	Kiesenwetter, 1850	Pyrenees (France, Spain)
			paulinoi	Olivier, 1884	Portugal
			splendidula	Linnaeus, 1767 (Lampyris)	Europe
		Phosphaenopterus	*metzneri*	Schaufuss, 1870	France; Portugal
			montandoni	Bourgeois, 1900	Romania
		Phosphaenus	*hemipterus*	Goeze, 1777 (Lampyris)	Europe; North Italy; Spain; Portugal; Baltic states; Latvia; Denmark; Slovenia; Croatia;

Table 2. Continued

					Bosnia; France; Sweden; Finland; Denmark; England; Belgium; Netherlands; Switzerland; Poland, Hungary; Check Rep.; Slovakia; West Russia, Karelia; Canada, Nova Scotia [49]
Luciolinae	**Luciolini**	*Lampyroidea*	*achaiaca*	Geisthardt, 1999	Greece
			dispar	Fairmaire, 1857 (Luciola)	Turkey; Bulgaria
			greaca	Laporte, 1833 (Luciola)	Greece, Naxos; Turkey (?)
			quadrinotata	Wittmer, 1935	Greece
			quadrinotata subsp. binotata	Wittmer, 1935	Greece
		Luciola	*italica*	Linnaeus, 1767 (Lampyris)	Europe; Italy; Romania; Jugoslav countries, Croatia, Slovenia; Turkey; Switzerland
			lusitanica	Charpentier, 1825 (Lampyris)	Greece; Bulgaria; France; Corfu; Italy; Turkey; Caucasus; South Russia; Portugal
			novaki	Müller, 1946	Jugoslav countries

and restricted to few species. Geisthardt [9], who seems to be the only taxonomist working on European lampyrids over the last few decades, has described and (re-)classified most of our species (see Table 2). The behaviour and ecology have been studied more or less thoroughly only in four lampyrid species, i.e. *Lampyris noctiluca*, *Lamprohiza splendidula*, *Phosphaenus hemipterus* and *Luciola lusitanica* [5-6,40-55]. Probably this is also due to the fact that these are the most widely distributed and most common species in Europe. The first three species are as a matter of fact the only species occurring above a latitude of 48°N (north of the line defined by southern France, Switzerland, Austria, Slovenia).

In this chapter we will focus on the bioluminescent behaviour, sexual communication systems and some particular features of the general biology of the best-studied European species.

2. General aspects and peculiarities of European firefly biology

None of the adults of European fireflies are able to feed and few will survive for more than a week or two. Instead they must rely on the internal fatbody, built up during their larval stage, which can last from one to three years depending on the species region and/or climate zone. The larvae differ in their tastes. As with the majority of fireflies, most species actively hunt slugs and snails [6,41]. The tiny larvae are capable of overcoming prey a hundred times larger than themselves by using their sharp, hollow jaws to inject a powerful toxin that paralyses the victim and digests it from within [41]. O'Donald [56] set up an experiment to test for any preference of larval *Lampyris noctiluca* for particular phenotypes of the snail *Cepaea nemoralis* (brown, banded yellow, unbanded yellow) as he observed lower frequencies of the brown variant in part of a population where also glow-worms occurred. And indeed, the preference for brown and unbanded yellow to banded snails was statistically highly significant. Up till now it stays unclear why *Lampyris noctiluca* shows this strong preference for certain prey phenotypes. *Phosphaenus hemipterus*, in many features an exception to the rule (read further below), prefers a diet of earthworms [49], a habit which it shares with just a handful of its American (e.g. *Photinus* spp.) and Oriental (e.g. *Stenocladius* spp., *Lucidina* spp.) relatives. The larvae spend their entire life hunting and eating prey and after about six to eight moults, most species (*Lampyris noctiluca, L. sardiniae, Nyctophila reichii, Phospaenus hemipterus, Luciola lusitanica*) pupate under leaf litter, stones, pieces of bark, in cracks in the soil or in moss [6,41,49]; pers. obs. in captvity), or even in ants nests (*Pelania mauritanica*, [57]). Except for *Luciola* species that build pupal mud chambers in the soil, and *Lamprohiza* species that seem to make a cell of little pieces of dead leaf litter (pers. obs., unpublished), other European lampyrids do not seem to make any special structure in which they spend pupation; they just shed skins in a hiding place with the right ambient conditions. No aquatic larvae are known to Europe. Semi-aquatic larvae are known from the New World [58] and species with fully aquatic larvae seem to be exclusively limited to the Asian region while some uncertain cases were reported from Africa [36].

The larvae of some species show some conspicuous colour patterns, usually combinations of whitish, pinkish or yellowish-orange lateral spots on a jet-black velvety background (Figure 1; *Lampyris* spp. [10,53]; *Pelania mauritanica* [56]; *Phosphaenopterus metzneri* [59], or a jet-black velvety background with almost fluorescent-like magenta or fuchsia lateral sides (*Lampyris sardiniae* [10]; *Nyctophila reichii*, pers. obs.). Similar dotted colour patterns are also known from genera in Asia (e.g. *Pyrocoelia* spp. [33]; *Diaphanes* spp. (pers. obs.)) or even more consipucous colour patterns combining white and black with orange or even red stripes or dots (e.g. *Stenocladius* spp. [34]). Such conspicuous colour patterns often seem to occur in species with so-called “walkabout larvae” that exhibit a change to diurnal activity and in mature larvae display exposed behavioural patterns, which probably accompany the search for a suitable pupation site [6,10,50,53]. “Walk-about” larvae are know in *Lampyris noctiluca, Lampyris sardiniae, Phosphaenus hemipterus* and *Pelania mauritanica* [6,10,50,53,57]. It seems that glow-worm larvae evolved such colour patterns to advertise to diurnal and visually guided predators that they are distasteful or even toxic [53]. This defensive or anti-predator strategy is better known under the name colour aposematism. Yet the other European firefly taxa in general have a more cryptic lifestyle and show duller and usually brown camouflage colours

Figure 1. Larvae of different species of European firefly; *Luciola lusitanica* (top left; photo YA), *Nyctophila reichei* (top right; photo YA), *Lampyris sardiniae* (middle left; photo YA), *Lampyris noctiluca* (middle right photo; JM), *Lamprohiza splendidula*, (down left; photo RV), *Phosphaenus hemipterus* (down right; photo JM). YA: Yves Adams; RV: Rollin Verlinde; JM: Jeroen Mentens.

blending with the leaf litter or soil backgrounds (*Phosphaenus hemipterus* contrary to its walkabout behaviour; *Lamprohiza* spp; *Luciola spp.* Figure 1).

2.2. Introduction to European species

Details of the adult bioluminescent behaviour will be dealt with further below. Since reviews about European fireflies are rather scarce I will first shortly introduce the best-known species.

Lampyris noctiluca, the Common Glow-worm, one of the first lampyrid species described by Linnaeus [60], is without doubt the best-studied

European species. Studies have been performed on its life cycle and general biology [6,41], sexual development [61,62], adult and larval anatomy [63,64], larval ecology in the lab [41] and in the field [65], feeding preferences [10,41,56], onset of circadian bioluminescent activity in adults [43,46], sexual communication [41], system of colour vision in males and evidence for a green-blue chromatic mechanism [66], larval bioluminescent displays and activity period [44], the use of aposematic coloration and bioluminescent defensive displays [52-54], its defensive chemicals [67], light emission spectrum [41,51,68], the structure of its luciferase gene [68], and its distribution worldwide and within countries and regions ([3,10] and ongoing glow-worm surveys). If no misidentifications have been made, this species is the most widespread lampyrid with an almost complete Palaearctic distribution, occuring from Portugal to Northern China from West to East, and from halfway Scandinavia to the Caucasus from North to South [10,8].

Pelania mauritanica has been reported from Southern parts of Europe, like South France, South Portugal and Spain [57], but recent sightings are lacking in spite of renewed search actions for instance in Portugal [11]; pers. comm. Gonçalo Appleton Figueira). The species seems to be more typical of North-African Maghreb countries [57,69]. These authors are the only sources about this species' behaviour and ecology, which is quite unusual for European species. Previously, only normally winged males were known, since they were caught using light traps which are often the standard method to hunt for lampyrid males. However, both Cros [57] and Lhéritier [69] discovered males with shortened wings and wingcases (brachelytrous males) in copula when collecting glowing females. These brachelytrous males also seem to show some other adaptations compared to the normally winged ones, such as shortened legs, more distant coxae, less developed eyes and they are vaguely reminiscent of *Phosphaenopterus* or *Phospaenus* males (see further below) or the American *Pyropyga nigricans* [17]. The female always resides in a burrow and only comes out for a short period during the night in order to attract males with a constant glow [57,69]. This behaviour is also known from *Photinus collustrans*, a Florida firefly with females that reside in burrows [70].

Yet more remarkable is that *Pelania* larvae and females not only like to hide in burrows and cracks in the soil just like many other species but often reside inside an ant's nest. This turns them into non-obligatory myrmecophiles. The frequency of myrmecophile individuals seems to depend on the region as Cros [57] found 77% associated with ants nests in Mascara, Algeria, and Lhéritier [69] 14% in Chella, Morocco. They usually seem to associate with "friendly" granivorous ants (*Messor barbara* L., *Messor instabilis* var. *maroccana*, *Pheidole sinaitica* Mayr). All life stages are left unharmed and probably some chemical defence protects *Pelania* from being removed or even touched by the ants. Lhéritier [69] noticed a strong smell vaguely reminiscent to elder (S*ambucus nigra*) and this might be associated with toxicity and chemical aposematism [50]. Probably the species prefers ant's nests as the temperature and humidity are highly regulated here and being protected from ant attacks by their chemical defenses the nests are the best choice in the arid conditions of the outside world [71]. Moreover this makes it an ideal environment for the development of eggs, larvae and pupae and even food sources seem to be available (snails reside inside the nests as well: *Rumina decollata*; [69]) Myrmecophile or ant-associated fireflies are also known from other continents, i.e. *Pleotomodes needhami* from Florida, North America that shows a very similar lifestyle and inhabits equally harsh and dry environments like *Pelania mauritanica* [71]. It is yet unclear if these are cases of convergent evolution or if continental drift separated a myrmecophile common ancestor into Old and New World demes [71]. Then recently, Fu & Ballantyne [19] discovered a possibly new and unusual species, *Pygoluciola qingyu,* from mainland China which is not only remarkable for its semi-aquatic mode of life and luminous activity including synchronous flashing and sexual dimorphism in adult colour of bioluminescence, but even more because its larval predacious activity on large mandibulate ants.

The fact that females, after their nightly glow activity, always find the 20 to 30 cm way back to their own preferred burrow suggests that they use some kind of pheromone track [69]. This author also supposed that especially the flightless males use olfactory cues in order to locate females, but rough, on the spot experiments with crushed females were fruitless.

Lamprohiza splendidula is the best studied European species after *Lampyris noctiluca.* It has a more central European distribution. Larval and adult morphologies were compared with those of *L. noctiluca* [72]. Schwalb [41] studied its larval behaviour and ecology and the courtship behaviour and importance of the light organ patterns in the adults. *Lamprohiza delarouzei* is described thoroughly by Bugnion [40] with notes on its general biology and behaviour.

Phosphaenus hemipterus - also known as the Lesser Glow-worm -, is apart from its appetite for earthworms quite exceptional. In fact at first sight it hardly looks like a glow-worm at all. The males are tiny, no more than 10 mm from head to tail, and have relatively large antennae, running about half the length of the body. What makes the males particularly unusual - and possibly unique – amongst fireflies is that they are always flightless: there are plenty of firefly species in which the female is wingless but as yet the Lesser Glow-worm is the only known species in which neither sex is able to fly. The wings are reduced to small vestiges covered by equally small wing-cases. This makes the male similar in appearance to numerous species of common rove beetles (Staphilinidae) and, together with its diminutive size, causes the Lesser Glow-worm to be easily missed [49]. Being also present in Nova Scotia, Canada (Table1,[50]), it seems to be the only European firefly that, probably occasionally, got imported into another continent [6].

The poorly documented genus ***Phosphaenopterus*** counts two species, *Phosphaenopterus montandoni* from Romania [73] and *Phosphaenopterus metzneri* from Portugal and the French Pyrenees [74]. Since their descriptions these species have not been reported again (except for some recent and vague rumours from Portugal; Gonçalo Appleton Figueira pers. comm.). Mikšić [8] suggests they might just be macropterous forms of their short-winged look-alike *Phosphaenus hemipterus.* Interestingly these species occur at the outer borders of the distributional range of *Phosphaenus* which in turn suggests that the latter species possibly evolved from a winged *Phosphaenopterus*-like ancestor that spread back to North and Central Europe from refugia in the Pyrenees and Portugal, as well as the Balkans after the last glaciation. Assuming such a scenario there could have been strong selection for flightless forms through isolation of founder populations and/or habitat fragmentation (e.g. [17]). Further genetic analysis and study of male genitalia may reveal the phylogenetic relationship these taxa but first we will have to wait for new specimens. Yet, one fact differentiating *Phosphaenopterus metzneri* from *Phosphaenus* is that -at least if no misidentification happened-, its larva seems to look quite different with a dull brown-blackish colour and orange spots on the hind corner of each segment, (i.e. this sounds more like the description of larval *L. noctiluca*).

Luciola lusitanica is the third best-studied European firefly after *L. noctiluca* and *L. splendidula*. Especially Bugnion [40] delivered excellent descriptions about the adult and larval morphology. Papi [42] and Bialdaccini et al. [75] cautiously analysed the rather complicated courtship behaviour and flash dialogues between and within sexes (details see below). I did not find any studies about the behaviour or ecology of *Luciola italica*. Also, there seems to exist some unreliability of the taxonomic characters commonly chosen for discriminating between these *Luciola* species and Bonaduce & Sabelli [76] retain some doubts regarding the real status of *L. italica* and *L. lusitanica* (often still called *L. mingrelica* in Russia), a doubt expressed by other authors who have stated “that *L. italica* and *L. lusitanica* in reality form two quite distinct geographic races of one unique species” [42,47]. The coastal Montenegro endemic *Luciola novaki* has never been caught again since its description [8] and no information is available on its flash behaviour.

3. Bioluminescent displays & signalling systems in European fireflies: Perfumes, glow-shows and flashing

Table 3 summarizes the bioluminescent displays, light organ patterns and signalling systems used by European lampyrid taxa.

3.1. Who is who? Glow confusions!

Europe harbours mostly lampyrids that rely on the simplest bioluminescent courtship signals, involving flying males attracted to the seemingly continuous (but see below) glow emitted by flightless sedentary females. These generally have enlarged abdomens, but may be larviform, brachypterous, or apterous; [77]. Typical genera that use this signalling system are *Lampyris, Nyctophila, Pelania* and *Lamprohiza*. Lloyd [15] classifies it as System I and Ohba [30] as the (modified) PR system (Table 3).

The onset of adult activity is induced by a reduction of ambient illumination under ca. 1 lux (for *L. noctiluca*: [43,45,46]. The females leave their hiding places around the end of sunset, choose a display spot –either climbing in the vegetation or sitting on the ground or on the litter-, and start to glow continuously [43,45]; Figure 2). The males begin to fly and when they spot a female's light they just fly to her, hover above her and then simply drop down right near her to begin with the copulation [41]. Females stop to glow when mated, so the female glow activity in the field stops earlier, depending on the density of males around [43]. Male activity occurs during the first part of the activity period of the females and lasts about 1 hour, while unmated females continue to glow for 3 to 4 or even more hours. The activity of the males, and therefore indirectly that of females, depends on environmental factors, especially temperature and wind [43].

There is good evidence that location of mates by lampyrid beetles is achieved by a single spectral class of photoreceptor, whose spectral sensitivity is tuned to the bioluminescent spectrum emitted by conspecifics, and is achromatic [35,78,79,80]. However, two spectral classes of photoreceptor seem to be involved in male *Lampyris noctiluca* phototaxis to their bioluminescent mates [66]; binary choice experiments with artificial light stimuli showed that the normal preference for a green stimulus (λmax=555 nm), corresponding to the female bioluminescence, was significantly reduced by adding a blue (λmax=485 nm) component to the signal. This implies an antagonistic interaction between long- and short-wavelength sensitive photoreceptors, suggesting colour vision based on chromatic opponency [66]. Cryosections also showed a band of yellow (blue-absorbing) filter pigment in

Table 3. Summary of adult and larval light organ patterns, bioluminescent diplays and sexual communication systems in European lampyrid taxa (based on [8,40-42,57,88,141] and pers. obs.).

Species group	Sexual communication system	Colour of bioluminescence	Female light organ	Female bioluminescent displays	Male light organ	Male bioluminescent displays	Larval light organ	Larval bioluminescent displays
Lampyris spp.; Nyctophila spp.; Pelania mauritanica*	System I [15] or modified PR system [30]: Sedentary flightless females attract males with continuous glow display	Yellow-green (λmax = 546-550 nm: [41,51,68])	transversal band on sternite VI & second band one on VII + 2 larval dots on sternite VIII; yellow-green light	Sexual display continuous glowing & induced glowing	Larval light organs	induced glowing (spontaneous glows are extremely rare)	Paired, lateroventral ovally shaped dots on sternite VIII	Spontaneous glows & induced glowing
Lamprohiza splendidula	System I [15] or modified PR system [30]: Sedentary flightless females attract males with continuous glow display	Yellow-green (λmax = 546-550 nm: [41,51])	Broken transversal band on sternite VI & transversal band on sternite VII + larval light organs	Sexual display continuous glowing & induced glowing	transversal band on sternite VI & second band one on VII + larval light organs in freshly pupated individuals only	Spontaneous continuous glowing & induced glowing	Highly variable, often asymmetric number and pattern; usually bright lateral spots in abdominal segments II and VI + lateral smaller dots in the segments in between (all dorsally translucent)	induced glowing
Lamprohiza mulsanti, L. paulinoi, L. delarouzei & other Lamprohiza spp.	System I [15] or modified PR system [30]: Sedentary flightless females attract males with continuous glow display	Yellow-green; most probably like *Lamprohiza splendidula*	transversal band on sternite VI & second band one on VII + larval light	Sexual display continuous glowing & induced glowing	Vestigial or no light organs or larval light organs in freshly pupated individuals only	No glowing (needs confirmation for *L. foliacea*)	Highly variable, often asymmetric number with pattern depending on the species; usually lateral spots from abdominal segments I to VI or even VIII	induced glowing

Table 3. Continued

							(dorsally translucent)	
Phosphaenus hemipterus	LB system [30]: chemical communication by pheromones (males are diurnal)	Yellow-green (λmax = 546 nm: [51])	Larval light organ	induced glowing	Larval light organ (dorsally translucent)	induced glowing	Paired, lateroventral ovally shaped dots dots on sternite VIII; yellow-green light	Spontaneous glows & induced glowing
Phosphaenopterus	Unknown; probably like *Phosphaenus*	Unknown; most probably like *Phosphaenus*	unknown	unknown	unknown	unknown	Unknown; most probably like Phosphaenus sp.	unknown
Luciola spp.	HP system [30]; Flash dialogues between male and female;	All stages yellow (pers. obs.)	Transversal more or less broken band on sternite VI (= ventrite V)	Sexual display flashes & induced glowing	Sternite VI + VII (= ventrite V+VI)	Sexual display flashes & induced glowing	Paired, lateroventral ovally shaped dots dots on sternite VIII	Spontaneous glows & induced glowing
Lampyroidea spp.	Unknown; probably a form of flash dialogues between male and female	unknown	unknown	Unknown; probably sexual display flashes & probably induced glowing	Sternite VI + VII (= ventrite V+VI) some species lack light organs [72]	Unknown; probably sexual display flashes & probably induced glowing	unknown	unknown

Figure 2. Displaying *Lampyris noctiluca* female. Note the turned upward abdomen tip with the segments containing light organs (photo: Marek Kozlowski).

the fronto-dorsal region of the male compound eye [66]. This presents an intriguing paradox because the resultant reduction in photon catch would tend to restrict green-blue colour vision still further. Although their precise flight patterns have not been studied, male glow-worms are believed to mate-search by flying low over the vegetation [6], so the ventral retina probably plays a vital role in the initial stage of mate location. The primary function of these filter pigments in nocturnal lampyrids may therefore be more concerned with shielding the sensitive eye from skylight than with signal discrimination [66]. In this regard the distinction should be made between nocturnal species, such as *L. noctiluca*, and crepuscular fireflies: the latter possess filter pigments that are quite different in both spectral absorbance properties and location within the eye [81], and it has already been suggested that the role played by filter pigments may differ between nocturnal and crepuscular species [80].

From what is described in literature, the general aspects of glow and courtship behaviour of *Pelania mauritanica* seem very similar, if not identical, to that of *Lampyris noctiluca* [57,69]. The same is true for *Nyctophila reichii* (pers. obs., [11]). Pheromones are probably not involved at larger distances. However, when the male arrives at the female contact pheromones may be important [41], maybe in the form of cuticular hydrocarbons [82]. However, from personal observations in Portugal in 2007, it seems that species recognition is not only difficult for taxonomists, but even for males belonging to different taxa. On several occasions males of *Nyctophila reichii* were seen trying to copulate with *Lampyris sp.* females, and vice versa. Such observations suggest that contact pheromones are quite inefficient as species discriminatory cues – at least in nocturnal species [82] -, and their purpose may rather be finding the right copulatory position, as proposed by Schwalb [41]. Moreover, the female (and male) light organ patterns and the spectral emissions of *Lampyris, Nyctophila* and *Pelania* are as good as identical (see Table 3, Figure 4; [10,57,69]. All these factors suggest that species recognition is very poor within and amongst these genera.

Currently, there is no information whatsoever on whether sympatric species evolved, adapted certain behaviours (e.g. female choice), selected different activity periods at night or shifted their appearance during the season in order to prevent mistakes and such forms of interspecific male competition. Such misidentifications by the males themselves may also form the basis for numerous hybridisations. The possibility of multiple hybridisations may in turn explain why the identification of European species within these taxa is so difficult, based on the high levels of variation in coloration and morphology as testified by taxonomists [57,83].

Sometimes *Lampyris* males, but only very rarely, also glow continuously and spontaneously in flight from tiny light organs they inherited from the larval stage [84]; pers obs. only once). Why would they do so? Adult lampyrids, as well as the other life stages, almost always react with distress-glowing (or flashing) when handled or when disturbed. This suggests a defensive function. Maybe the spontaneous glowing indicates stress, either in the form of disease or possibly as an anti-predator reaction if they were able to perceive bat echolocation (either adaptive as "facultative aposematism" or "startle signal")? In that case we would expect to see more of such behaviours in the field, especially in areas with high bat densities, unless the glows are to weak to notice down below from the ground. The hypothesis, "do male lampyrids react with bioluminescent displays when stimulated with infrasonic impulses" could be easily tested.

Figure 3. Female light organ patterns of *Lampyris sardiniae* (left) and *Lampyris noctiluca* (right) (from [10]).

3.2. Nature's mini disco light shows: Selection for more spots?

The female light organ in *Lamprohiza* species (and their North-Amercan close relatives of the genus *Phausis* from the Appalachian Mountains; [13] is completely different from that of other lampyrid genera and is somewhat reminiscent of Phengodid or Rhagophtalmid species. It consists of quite a normal looking adult lampyrid-like light organ in ventral segments V and VI, also called "ventrites" (Tergites VI+VII) and depending on the individual or species an additional number of 4 to 12 smaller lateral light spots in the abdominal segments that are "inherited" from the larval stage (details check Table 3). Females of the genus *Lamprohiza* often show a great deal of individual variation in the number of lateral light organs (pers. obs.; [41]). In contrast to females of the other continuously glowing genera, they rarely climb up plants or grasses to broadcast their glow-display sites but rather stay on the ground or on dead leaf litter. They also do not curl up their abdomen sideways in order to let the light shine upward, but rather raise their abdomen, fully equipped with light organs, dorsally upward (Figure 4 & 5).

In his lab experiments with models of female light organ patterns Schwalb [44] discovered that *Lamprohiza splendidula* males are attracted to any colour of light he presented (red, yellow, green, blue), but with a supernormal preference for blue light. Interestingly, *Lampyris noctiluca* males showed a very pronounced preference for yellow shining models (ca. 571 nm) and preferred these over their own yellow-green shining females (ca. 550 nm). Schwalb [44] also found that *Lampyris noctiluca* males prefer models with similar intensity and the same light organ pattern as natural females, whereas the *Lamprohiza splendidula* males select for more intensely shining lures, be it larger scale, stronger shining models or models with more light dots regardless of the configuration. This last observation shows that there exists a strong male selection for stronger light emissions and it may explain why we

Figure 4. Female light organ pattern in *Lamprohiza splendidula.* (photo: Raphaël De Cock).

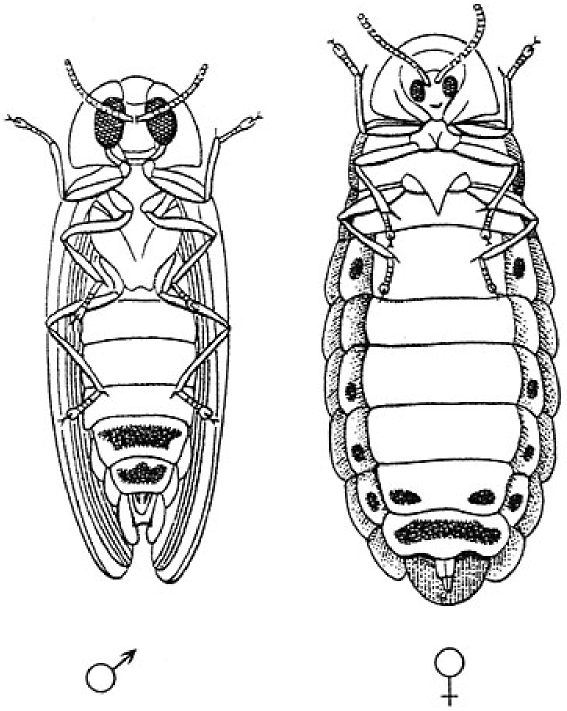

Figure 5. *Lamprohiza splendidula* male and female light organ patterns (indicated as dark areas on the abdomen).

observe such individual variation in the number of light dots and their size in *Lamprohiza* female light organs. The same is true for *Lampyris* males, yet that they select for models with a fixed light organ pattern, natural light intensity and colour of emission, and that is exactly what we see in the field.

However, own field and lab observations contradict Schwalb's [44] findings. In the field *Lampyris* males seem to be far less choosy for colour and intensity of light traps (6V light bulbs, green or yellow LED, glow-stick tubes, *Lamprohiza* females all work fine), while *Lampohiza splendidula* males (contrary to *L. paulinoi* and *L. mulsanti*: see [11]) are very difficult or impossible to lure with whatever kind of light trap (unpublished results, R. De Cock). It should be noted that although his findings look convincing, Schwalb used few males (10 to 60) in his experiments, did not repeat experiments per treatment and did not apply statistics. Another suspect fact is that the success rates of attracting males by natural females are quite low in Schwalb's experiments (*Lampyris*: 40%-65%; *Lamprohiza*: 25%-40%), while in natural conditions and high male densities it is very difficult to find unmated (and per definition glowing) females, since they are found almost immediately by the males [6,85].

An additional peculiarity of *Lamprohiza splendidula* is that also the males glow continuously or show minute-long glows of variable intensity in flight from two ventral bands in the last abdominal segments (Figure 5). They start activity at sunset and first fly short distances low over the forest floor or show short lasting glows. When it gets darker they fly higher (1.50m to just under the canopy), glow continuously and also fly in more open spaces like forest edges and over fields and orchards [41]. These displays look like fairytale sceneries full of slowly air-drifting little lights. After about 45 minutes to one hour male activity gradually decreases to stop completely two hours after sunset. Similar behaviour is seen in *Phausis reticulata* males from North-America [13]; pers. comm. Lynn Frierson Faust) and *Diaphanes* and *Pyrocoelia* species from Asia ([30,86], pers. obs.). Noteworthy is also that all these genera know species with males lacking functional light organs. For instance, the males of the other *Lamprohiza* species often show pale areas on the segments where one would expect adult light organs; yet, no luminescence is observed [40]. So why did some nocturnally active species apparently lose the male's ability to glow in the course of evolution, or why do they start glowing only when getting disturbed (e.g., the *Lampyris–Nyctophila-Pelania*-group), while other taxa glow in full glory and conspicuously in flight?

Male bioluminescence does not seem to be involved in courtship signalling, as *Lamprohiza splendidula* females glow spontaneously and do not answer to overhead flying glowing males. Closely related American

Phausis reticulata females seemingly respond to glowing males later at night; yet it remains doubtful that male glowing is evolutionary adaptive for courtship, since females glow spontaneously without the need of a male's glow during the normal male activity period [13]. *Lamprohiza splendidula* males land at a distance from the female and crawl the last few centimeters to her, without glowing or only weakly glowing [41]. Thus, the male's glowing is probably not involved in female choice either especially if several males arrive at once. So what is the adaptive value or function of male glowing in these cases? The males seem to fly quite dispersed, but it is difficult to decide if this effect or impression has to do with spacing on the basis of the light of nearby flying males. Moreover, what would be the biological significance of such behaviour? Or is it used for illumination [14] in dark environments like in the dense forests, which these species with glowing males seem to prefer as a habitat? However, most probably it is involved in sort of an anti-predator display against bats or night hawks (Caprimulgidae) as suggested earlier [16,50]? Favouring this hypothesis are anecdotal reports of bats that approach fireflies, but then turn away from the shiny target at a distance of ca. 1 m. Future experiments analysing male behaviour in relation to the glow of nearby males, or bioassays and predation experiments with bats and nighthawks might tell what is going on.

3.3. A handful of species flash simply or in synchrony!

In Europe probably only 2 genera, *Luciola*, and less certain *Lampyroidea*, counting altogether for about 8 species (12% of European taxa), show flash bioluminescence. All of these "flashy" species, occur south of the line southern France, South slopes of the Alps, Slovenia, South Ukraine, South Russia (see Table 2), and are, thus, restricted in their distribution to only about 30% of Europe. Up till now there are no published studies on the (bioluminescent) behaviour or ecology of *Lampyroidea.* From personal communication with local informants it seems they use flash communication, but this needs to be confirmed yet.

Neither the flash behaviour nor the communication system of *Luciola italica* and *L. novaki* have been described yet. Papi [42], Mikšić & Mikšić [48] and Bialdaccini et al. [75] provide the only European studies on the flash and courtship behaviour of *L. lusitanica* (Figure 6). These reports are rare and excellent examples of studies describing and analysing the flash behaviour of a species in such detail. We will summarize here most of their findings.

One of the most exciting findings for Europe is that also from this continent, more exactly from Sarajevo, Bosnia-Herzegovina (former Yugoslavia) we have reports on synchronously flashing fireflies! They probably

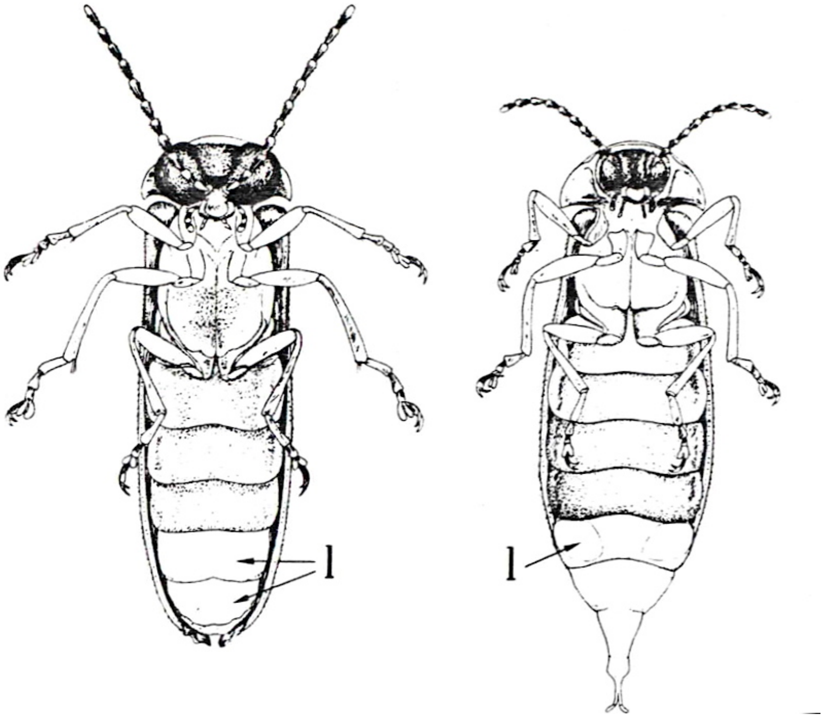

Figure 6. *Luciola lusitanica*, male (left) and female (right) light organs are indicated [42].

belong to some regional form or maybe a still unidentified sibling species of *Luciola lusitanica* since posterior wings are missing in the females [42,48,75]. After their discovery these synchronized flashing populations have not been studied again, but this could have been a side effect of the recent turbulent political situation in that region.

Papi [42] reports that there seem to be local variations or “dialects” in the flash displays (i.e flash frequencies, flash and interflash lengths and variability here within) with differences observed between populations from Nice (France), Bologna (Italy) versus Pisa and Genoa (Italy). This suggests that flash behaviour could perhaps be used as a taxonomic character in order to classify and identify species, just as was done for *Photuris* or *Photinus spp.* in the Americas where identically looking species seem to be isolated and are recognisable by their flash courtship behaviour [18]. Since for the moment we only have information about the situation near Pisa we will stick to Papi’s [42] findings.

It is typical of females of many species of flashing Lampyridae to respond with steady latency to the “on” of a light stimulus and interspecific differences in latency times at the same temperature can often be used as taxonomic characters [87]. Yet, *Luciola lusitanica* communication systems can be classified as the *HP* system of Ohba [30] or System II according to Lloyd [15]. Here males fly and flash with an unfixed frequency and females just respond to male flashes with a fixed delay response and their own peculiar and recognisable flash display which differs in flash length, form and/or rate from male flashes. However, in most (New World) species the female seems to be the discriminating partner, checking for and responding to the right male flash length, flash number and pulse interval length. In *Luciola lusitanica*, however the male is the discriminator leading the flash dialogue by changing the flash frequency and checking whether the female is able to respond to his changes with a response flash of the right length and at the right response delay.

In both sexes of *L. lusitanica* the bioluminescent displays may consist of both clear flashes as well as dim light emitted for variable time periods. Flying males emit an average 1.8 flashes per second at 17°C with occasional dim light emissions during interflash periods (Figure 7). These dim emissions might be adaptive for illumination [14] and consist of either a close sequence of short irregular flashes or a more regular flicker [42]. Females are never seen flying. They have a thicker and heavier body and shorter wings and wingcases than males.

Females regularly respond with a typical flash (see Figure 8) to each light stimulus of steeply rising intensity, regardless of stimulus intensity, length, or

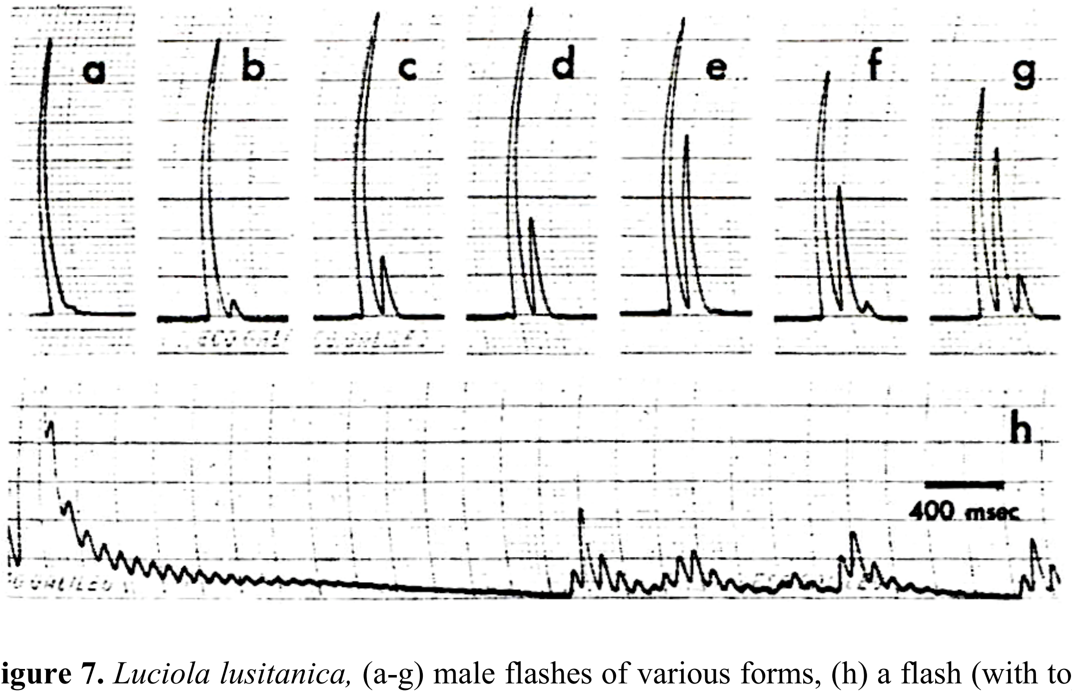

Figure 7. *Luciola lusitanica,* (a-g) male flashes of various forms, (h) a flash (with top part cut out on the left side) slowly dying out with a flicker and dim light emissions [42].

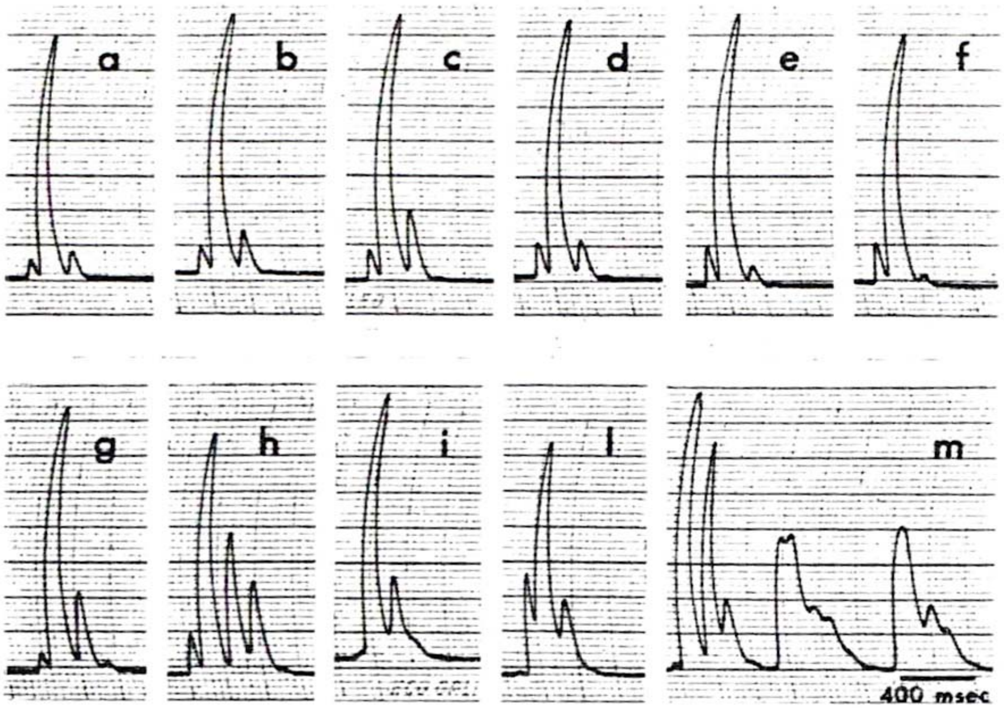

Figure 8. *Luciola lusitanica*, female flashes (a-g) dialogue response flashes, (h-m) irregular flashes when disturbed or when flash dialogues are interrupted [42].

spectral range (at least between 413 nm (violet) and 682 nm (red)). The response flash is emitted at a specific delay time after the stimulus with a delay that increases exponentially at lower temperatures. When the stimulus frequency increases progressively above a rate of 2 flashes per second, the female at first responds 1:1 for brief periods or else flashes once every other stimulus, and subsequently fails to respond regularly. In rhythmical stimulation by light pulses with slowly rising intensity females don't respond or respond irregularly, sometimes flashing at rates almost equal to the stimulus flashes but with no fixed temporal relation between stimuli and response flashes.

Mechanically stimulated males or females whose flash dialogues with males have been interrupted show irregular flashing with longer flash lengths composed of many peaks of which the flicker can be seen by the human eye.

The scheme in Figure 9 summarises the general flash communication protocol for *L. lusitanica* based on Papi [42]. Flying males upon receiving a female response to their own flashing, will fly toward the female, make an inspection-dialogue flight of variable duration, then land and approach the female by crawling on the ground. The substrate where the female is flashing seems to play a role as the inspection-dialogue phase may be lengthened

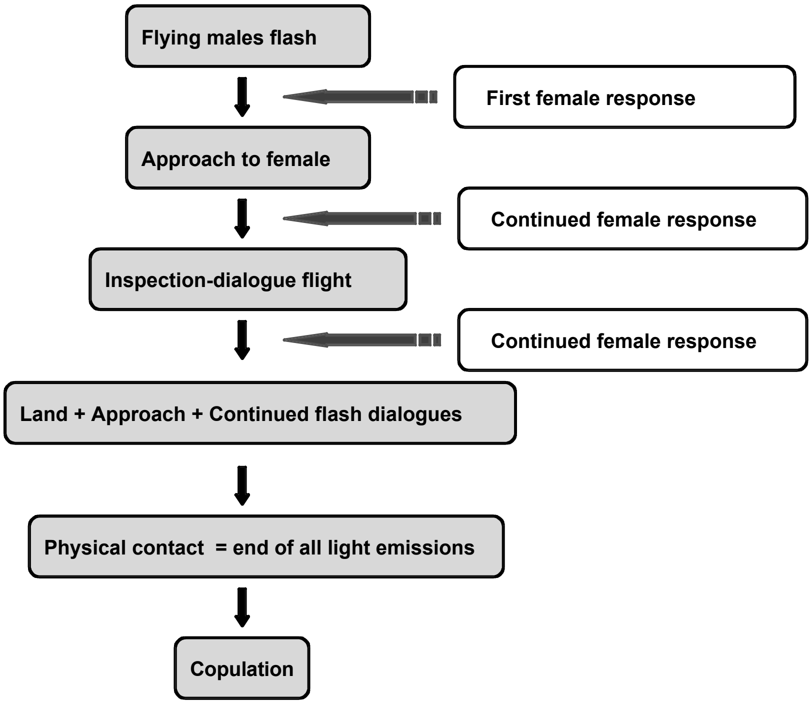

Figure 9. Generalized flash communication protocol of *Luciola lusitanica* from Pisa, Italy, based on Papi [42].

depending on the characteristics of the female surroundings. Flash dialogues take place during all phases of the approach to the female, but all, or nearly all light emission ceases immediately after the partners make physical contact. The spectral characteristics of the female light signal don't seem to play an important role as flashes of different colours ranging from 473nm to at least 644nm can attract males. Features of the female response that play an important role in male recognition and positive responses (resulting in landing or abandoning a female) are flash length and flash response latency. The female flash form (the triple flash) does not seem to have a major influence on male behaviour.

Male-to-male responses

Males on the ground flash irregularly and sometimes show female type responses to light stimuli. Such behaviour is frequently seen in males which are engaged in unsuccessful dialogues with females. With their flashes these males induce the other overhead flying males to engage in inspection-dialogues with them and occasionally even to land. Male-to-male dialogues may take several forms. Perching males may engage in flash exchanges according to certain rules. The most common type (a-b, a-b, ... type dialogues) simulates a heterosexual dialogue, with one of the two males (A, leader) leading the dialogue and the other (B, follower) responding after a fixed delay as a female. The mimicking male very often flashes irregularly in response to a rhythmical light stimulus maintaining a frequency very close to the stimulation rate, or he even delivers regular 1:1 responses. The response latency of female simulating males is more variable than the actual female latency. In another type of dialogue the leader emits two flashes for each follower's flash (a1-b-a2, a1-b-a2, ... dialogues). The second flash seems to be a response to the follower's flash, thus the leader subsequently shifting"role", while the follower seems unable to act like a leader due to the high frequency rate of flashes. Yet in a third and less frequent type (a-b-a-b... dialogues) no role difference is discernible between the males.

According to Papi [42] the biological significance of such male-to-male flash dialogues is to induce other males to inspect an area where a difficult to approach female is to be found and as such in improving her chances for fertilization. It seems more likely that such behaviour is rather involved in complex intra-sexual competitive strategies which are yet not fully understood. Similar female-mimicking of rejected males have also been observed in the American *Photinus carolinus* (pers. comm. Lynn Frierson Faust).

Table 4. Major characteristics of bioluminescent behaviour of male and female *Luciola lusitanica*.

Male

- Light organs on entire ventrites 5 and 6 (Figure 6)
- Spontaneous flashes
- Occasional dim light emissions during interflash periods
- Flashrate: at flight 1.8 flashes/second at 17°C; decreases with temperature; variable in landed or perched males
- Flash form and length: at flight 200-250 msec, usually very intense peak accompanied by a series of minor ones (Figure 7); variability is higher in males landed or perched males than in free flying individuals.
- Disturbance flash flickers

Female

- Light organ on ventrite 5, consisting of a transversal band with highest light intensities coming from spots on the lateral sides (Figure 6)
- Occasionally spontaneous flashes
- Occasional dim light emissions during interflash periods
- Flash form and length: composed of three peaks with the interval between the first two peaks increasing exponentially at decreasing temperatures (ca. 77 msec at 26°C; 245 msec at 10°C). Second peak most intense, while first equal, smaller or larger than third one. The latter may be missing or is replaced by other peaks of decreasing intensity. Flash length depends on temperature and number of peaks, but the time interval between the first and second peak is remarkably constant at a given temperature (Figure 8).
- Response flash delay: 160-590 msec depending on temperature (respectively 26-10°C)
- Disturbance flash flickers

3.4. Day-active species

For a long time it stayed unclear whether adult *Phosphaenus* show day-active courtship behaviour [74] or rather are nocturnal [4,8] since both sexes are weakly bioluminescent. But recent evidence established that the males are indeed diurnally active and use olfactory cues to locate their mates [49,55]. Male *Phosphaenus hemipterus* like those shown in Figure 10, are extraordinary, at least within the European fireflies, not only in being flightless and active during the day, but also in using its large, sensitive antennae to sniff out the airborne scent – or pheromones -, produced by the even more inconspicuous female. No more than 13 mm long, she looks like a miniature version of a *Lampyris noctiluca,* but lacks the well-developed light organs that make the latter so visible. Whatever feeble light she can muster comes from two small dots at the tip of her abdomen which, like those of the male, are inherited from the larval stage and are switched on if she is disturbed. This makes her extremely difficult to find (at least for humans), so in most places the majority of sightings are of males, which often roam about on bare surfaces such as footpaths, pavements and the bases of walls on sultry June afternoons [49].

Figure 10. A day-active male *Phosphaenus hemipterus.* Note the large antennae, short wings and wingcases and the pale translucent dorsal spots in the last segment that permit that the light produced in the more ventrally situated light organs is also visible from above (Photo: T. Tolasch).

3.5. Larval glowing

It is a well-established fact that adults of nocturnal fireflies use light signals for sexual communication, but surprisingly little is known about the functions of glowing behaviour of the larvae. Defence is the most cited function [see 89]. Many other plausible functions of luminescence have been proposed, but most of these reflected the inventiveness of the observers rather than being based upon any supporting evidence [89,90,91,92]. Examples of prey attraction are known from Elaterid beetles like *Pyrearinus* sp. larvae that probably use luminescence to attract flying termites as prey [93], or the famous "femmes fatales" of *Photuris spp*. which mimic courtship flashes of other firefly species in order to lure males and to acquire additional chemical defences [94-97]. One may also think of the and luminous larvae of fungus gnats, Mycetophilidae, which attract insects into their sticky webs [7,98,99]. However, in all these examples the predator stays immobile whereas lampyrid larvae actively hunt for prey. Therefore, prey attraction seems an unlikely function.

Illumination and communication have been proposed as alternative possibilities [89,97,100,101]. Some phengodid beetles, like the railroad-worms, *Phrixothrix spp*. have continuously shining red headlights and a preliminary electroretinogram study (V. R. Viviani, E. J. H. Bechara, D. Ventura and A. Lall unpublished data; [100]) revealed red-shifted vision in these larvae, implying that they might use a visual channel not used by their prey.

Dreisig [44] suggests that they act as a competitive signal since lampyrid larvae seem to be evenly spaced in the field. Unfortunately, he never presented data on the spatial distribution of lampyrid larvae, nor did he test the effect of glow signals on the behaviour of the larvae to support his view. Kaufmann [102] also proposed a competitive signal in which egg-laying females use the spontaneous larval glowing as a cue to avoid densely populated areas. Even when kin selection is involved, it remains difficult to see how such complex communication could have evolved, especially when the larvae have a very poorly developed visual system of simple ocelli.

Even if bioluminescence is used for such non-defensive functions it is difficult to explain how it could have evolved without protection against visually guided predators. Moreover, Dreisig [44] argues that deterring predators is not the primary function of luminescence in lampyrid larvae because they do not only emit light when attacked but glow in a regular way for several hours in exposed places, making them more conspicuous to predators and abolishing any possible startling effect. However, Dreisig apparently overlooked the possibility of the luminescence being an aposematic display. It seems logical that visual patterns that catch the attention of predators should have an anti-predatory function, unless the organism has other adaptations to evade predation. From the point of view of predation, light emission could have evolved under similar selective pressures as other visually conspicuous signals, such as colour patterns. Surprisingly, bioluminescence has rarely been mentioned as a warning signal in studies concerned with the principles or the evolution of aposematism. Recent evidence firmly supports the hypothesis of bioluminescent aposematism [52-54,103].

3.5.1. Induced glowing

Disturbance-induced glowing is a typical type of luminescent display in lampyrid larvae [16,58,89,104]. Hereby larvae –but also all other life stages, from hatch-ready eggs to adults- glow continuously several seconds or minutes in response to several types of disturbance and usually stay motionless or act dead [44,89,104]. In European taxa this display is known from *Lampyris, Phosphaenus, Lamprohiza, Luciola, Nyctophila* (pers. obs.) and *Pelania* [57], and probably occurs in all species. In *Lampyris*, *Lamprohiza* and *Phosphaenus* larvae the disturbance intensity threshold to respond to with induced glows varies between individuals from slight disturbance, such as weak sounds (e.g. rustling of dead leaves), over surface vibrations, to rough handling such as grasping with forceps. The disturbance-intensity threshold seems to decrease with feeding status, whereby recently moulted and slender larvae tend not to glow, whereas larvae that get ready to moult or pupate begin already to glow at sudden sounds [50]. Noteworthy is that *Lamprohiza splendidula* does not react with glowing to any disturbance except for one to two weeks prior to moulting and then usually already to acoustic stimuli. However, Portuguese *Lamprohiza* larvae (either *L. paulinoi* or *L. mulsanti*) always respond with glowing (pers. obs.). I assume that, when in danger and being less mobile and more vulnerable due to their well-fed status, larvae that prepare to moult instead of fleeing choose the best of a bad job, which is trying to deter or confuse a possible predator by showing the induced luminescence display instead, in order to startle the predator or as a facultative aposematic display.

3.5.2. Weak body glow

It should be noted that apart from light organs (at least in European taxa like *Lampyris*, *Phosphaenus* and *Nyctophila*) larvae, but also eggs, pupae and even adults, show a very faint overall body glow from all body parts that are not pigmented (pers.obs.). This is visible with dark-adapted eyes in a darkroom or even recordable with specialized light-sensitive gadgets (pers.

comm. Laurence Tisi). This effect has also been described from other species by several authors [cf.,105].

3.5.3. Spontaneous bioluminescent displays in larvae

Apart from disturbance-induced luminescence, glow-worm larvae often show spontaneous glows, emitted intermittently at night without any indicative reason. Spontaneous glowing has been observed in European *Lampyris spp., Phosphaenus, Nyctophila reichei* and *Luciola lusitanica* (pers. obs.,[44]. Although Schwalb [41] described spontaneous luminescence in *L. splendidula* from laboratory observations, it seems very doubtful that this species shows the display, since I never observed it in the field in neither this nor any other species of the genus. Schwalb's [41] recorded luminescence was probably a disturbance-induced rather than spontaneous display. The absence of spontaneous glowing behaviour is only known from some aquatic species, but these seem to show spontaneous glows once they leave the water [89,104].

The spontaneous display is especially seen in crawling larvae (Figure 11; [31,41,44,50,58,89,91,94,102,104,106]. This coincidence of spontaneous glowing and locomotion as seen in Figure 11, is one of the key predictions for the possibility of luminescent aposematism in glow-worm larvae. Obviously, locomotion renders the larvae more conspicuous to visually-guided predators that are adapted to hunt at night, such as amphibians. In that manner, the spontaneous glow display could be considered more a context-dependent or facultative form of aposematism [52,54].

Almost no detailed studies have been performed on the behavioural characteristics of the spontaneous display, i.e. the lengths of glow pulses and extinguished intervals, pulse frequencies, or the proportion of time that individuals spent glowing, and interspecific differences. Some data found in the literature suggest that the length of glow pulses and pauses between glows vary within individual larvae [44,89,102,104], but that averages may differ between species [89,102,104]. Preliminary results of ongoing analyses suggest that the duration of glow pulses and the amount of time spent glowing differ between *L. noctiluca* and *P. hemipterus*, and that ambient light suppresses the amount of time that is spent glowing (Figure 12, [50]. Kaufmann [102] also reported that ambient factors seem to influence the characteristics of the display. Further studies could test whether the perceptible interspecific variation in pulse frequency is associated with the detectability of the signal within certain microhabitats, whereby lower frequencies are expected in open habitat and higher frequencies in denser vegetation [58,89]. Sometimes *Lampyris noctiluca* larvae show periods of more intensive glowing, which gives the impression of some sort of synchrony

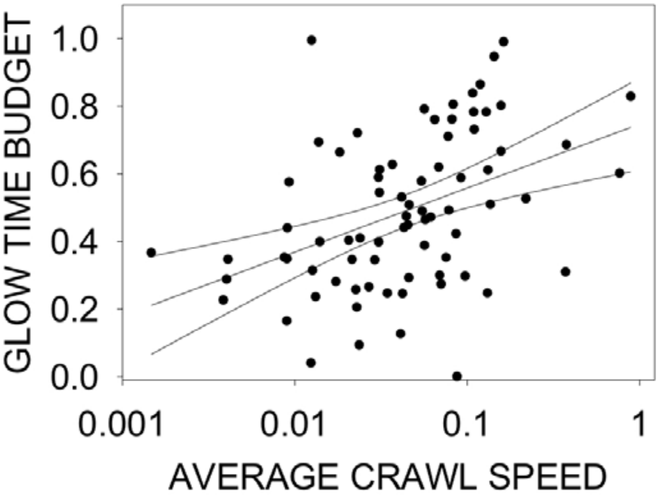

Figure 11. The amount of time spent glowing in larval *Lampyris noctiluca* increases with crawl activity (mm/sec) ($r^2 = 0.18$) [50].

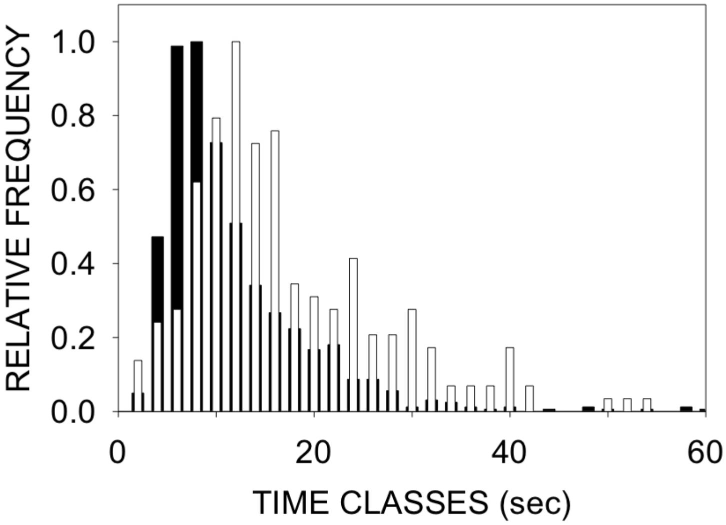

Figure 12. Preliminary data on glow pulse lengths in larvae. Histogram showing the relative frequencies of pulse lengths in *L. noctiluca* (black bars) and *P. hemipterus* (open narrow bars). [50].

of larval spontaneous glow displays [84]. Also Sivinski [89] and Viviani [58] report that in some species, larvae seemingly glow in response to the glow of nearby individuals and the possibility that larvae are able to perceive each other's light signals.

An important question that needs more attention is why the larvae signal intermittently and not continuously. Given a metabolic cost to signalling a most likely explanation is that the display is cheaper when it consists of a series of glows rather than a sustained glow [89]. Although it is possible to calculate the biochemical cost of light production, which seems to be low indeed compared to other metabolic reactions [107], it remains difficult to evaluate the total cost of luminescent signalling. Firstly, most metabolic processes involve a more complex chain of several enzymatic reactions while only one enzyme is involved in bioluminescence (apart from the metabolic cost of the biosynthesis of luciferin). The cost of light production, therefore, may in the end be relatively low [107,108]. On the other hand, in order to control light production and signalling, glow-worm larvae invest extra metabolic costs producing specialised innervated light organs with an adapted tracheolar network for the supply of sufficient oxygen [105,109]. Species with less control over bioluminescence, glowing continuously, usually do not develop such extra costs (e.g. *Phengodes*; [105,110]. Apart from metabolic costs, there might be strategic predator related reasons to produce intermittent luminescence. Tests with LEDs have shown that continuous glows make better targets than intermittent, short flashes, and that staying dark is safest [111]. From this follows that intermittent luminescence in fireflies probably evolved under predation pressure, as the trail of a flashing prey is more difficult to track [112]. This mechanism is vaguely reminiscent of “flash coloration” [113] whereby individuals are cryptic at first, but once detected, move suddenly flashing bright colours (e.g. in moths, butterflies and grasshoppers).

It is hypothesised that predators are either startled or get distracted and search for the brightly coloured prey, which have disappeared when the prey settles again [113]. However, the larval glow is much slower and longer than a flash [104], and hence it does not seem adapted for such a tactic. Though, in addition to the warning function of luminescence, the pulsing of the signal may be selectively advantageous in another way by interfering with the predator's visual performance. Visually hunting nocturnal predators, such as toads, need to focus long at low ambient light conditions in order to receive enough information about the location of their prey [114,115]. Moreover, these predators normally snap at the prey's front and need to correct the direction of their attack for the delay in the visual information they obtain at low light levels, which they seem to learn by experience [115]. Hence it seems likely that the predator might get blinded or fooled by the afterimage of the glow pulses and snaps at these or to the rear end where the light organs are located, rather than to the exact location of the extinguished prey, which by then already has moved further. Such a tactic would obviously not work with continuously emitted light. Future experiments on the visual performance and prey catching accuracy of predators (toads/frogs), using glow-pulsing prey models, may resolve whether such anti-predator strategy works and under what conditions (e.g. only at extreme low light levels, or depending on pulse rate and lengths). Of course experienced predators can adapt their prey catching technique and then the advantage is lost. However, the initial adaptive advantage provided by such a mechanism could have been important for the evolution of (spontaneous) bioluminescence as an aposematic signal, much in the same way as innate biases and novelty effects of birds are often cited as processes that might have facilitated the initial evolution of conspicuous warning colours [116].

In the literature no details are found about when exactly larvae show spontaneous glowing, while such knowledge may particularly explain when or why the display may be of adaptive importance. *L. noctiluca* and *P. hemipterus* glow spontaneously throughout the night, but the moments of peak activity seem to differ significantly between species, respectively at dusk and between midnight and dawn [50]. Further it seems that the amount of spontaneous glowing observed in natural populations depends on ambient factors, such as temperature, humidity, rainfall, and also on the season, with more glowing in autumn. At first sight this could be ascribed to the emergence of a new generation of larvae by the end of summer. However, at least in *Lampyris noctiluca,* it generally are later instar larvae that are seen glowing. "Autumn glowers" like *Phosphaenus hemipterus, Nyctophila reichei, Lampyris sardiniae* hardly glow spontaneously in spring, while other species like *Lampyris noctiluca, Lampyris iberica* and *Luciola lusitanica* show spontaneous glows from spring to autumn ([50,10,11], pers. obs.). Explanations for this seasonality in spontaneous larval glowing should come from further research.

3.5.4. Ecology of larval bioluminescence colours

Lampyrid larvae typically emit green coloured light [51]. However, intraspecific differences in the colour of bioluminescence between adults and larvae do exist in quite many species (e.g. orange vs. green; [58,79,108]. *Luciola* larvae seem to be an exception and produce yellowish light like the adults. Ecological reasons, more especially the spectral properties of ambient light, explain why adults produce light shifted to the yellow. The colour-shift appears to be an adaptation to overcome the noise-to-signal effect from green reflected light of foliage on courtship signalling during twilight in adults of species predominantly active shortly after sunset [81,117,118] while their larvae are active later at night. According to Viviani [58] the conservancy of green bioluminescence in lampyrid larvae agrees with the lack of an intra-specific function, for instance reproduction, and the increased importance of an interspecific function like defence. However, selection for visibility of the emitted light provides a more proximate explanation for this conservancy

[119]. This idea is supported by the fact that most terrestrial vertebrates and arthropods have eyes with highest spectral sensitivity in the green region of the light spectrum [35,118,120-126], which strongly suggests that the green colour of bioluminescence was selected for maximal visibility of the emitted light [50]. Some evidence for strong selection for the colour of bioluminescence comes from Viviani and Bechara [127], who discovered enzymes with luciferase-like action in non-luminescent beetles, which produce weak red light instead of green when firefly luciferin is added as a substrate.

3.5.5. Luminescent aposematism in a "multimodal" context

Next to warning flashes and glows, Lampyridae show several other features that support the hypothesis of protection through aposematism. The literature harbours numerous references on the unpalatability of lampyrids [16,41,89,94,103,128,129]. In addition, own experiments show that lampyrid glow-worm larvae are unpalatable to different species of lizards (*Lacerta vivipara, L. muralis, L. viridis*), frogs (*Rana temporaria* and *R. esculenta),* starlings (*Sturnus vulgaris*) and toads, and they are rejected to a high extent by insectivorous arthropods, such as carabid beetles, centipedes and spiders (R. De Cock, B. De Weirdt and E. Matthysen, unpublished graduate thesis; pers. obs.). In these and other predation experiments [95,130,131] lampyrids experience very low attack rates. Eisner et al. [95] found direct evidence for chemical defences in *Photinus* and *Photuris* fireflies, in the form of cardiotoxic steroids or so-called lucibufagins and other toxins [96]. The fact that lampyrids show chemical defences strongly suggests that their aposematism functions through avoidance learning. The numerous descriptions of plant-like, musky, cabbage-like, fungus, peppermint and resin odours in several lampyrid species [16,89] are reminiscent of the description of pyrazine smells and suggest the possibility that they may also use warning odours [132,133]. Blum and Sannasi [129] describe reflex bleeding in lampyrids and its effects on predators, which is another feature usually associated with aposematism [134].

Recently, defensive gland-like organs have been described in larval *Lampyris noctiluca,* which seem to facilitate reflex bleeding and which become exposed in certain cases of danger, e.g. in the presence of ants [67,135,136]. In Asian species with aquatic larvae similar eversible glands produce possibly defensive volatile products [20]. Yet, bio-assays should still show if these odours and volatiles function as direct predator repellents or are used as another aposematic signal to warn for toxicity. Experiments with lizards showed that the colour patterns with combinations of black, red and yellow of some species of adult lampyrids act as warning colours [131]. Many lampyrid species also have conspicuously coloured larvae that seem to be aposematically defended against bird attacks [53,67]. In some species the larvae become diurnal before pupation [2,6,10,50,53]; Raphaël De Cock, unpublished data), and in these cases colour aposematism may be a useful adaptation. Lloyd [112] further suggested the possibility of Batesian mimicry within the Lampyridae and of mimicry complexes with moths, roaches (e.g. non-luminescent Firefly roach, *Schultesia lampyridiformis*), luminescent beetles, and soldier beetles, as these often show firefly-like colour patterns or luminescence [16,130,137]. This may also apply to the only known species of staphilinid beetle which is luminous in the larval stage [138] and emits light of the same spectral properties and from light organs in the same position as in lampyrids. There is also anecdotal evidence in support of chemical defences in other luminous beetles, Phengodidae and Elateroidea [89,100,101], which suggests the existence of Müllerian mimicry (different noxious species using similar signals to advertise their defencive abilities), or even Batesian mimicry (undefended species "lie" by copying warning signals of truly defencive species) between and within taxa of luminescent beetles. The fact that the adults of many firefly species emit yellow light as opposed to the green light produced by larval stages of all species [139], may also be an indication of mimicry in the larvae of different species.

Finally, a more physiological support that glowing may be involved in defencive activities is that the neurophysiological onset of larval glowing is controlled by specialized neurons and the transmitter octopamine, which in other insects are involved in stressful situations, e.g. encounters with predators [109]. In some species of fireflies this neural system also triggers reflex bleeding in larvae (A.D. Carlson, pers. comm.). Taken together, this knowledge not only supports the possibility of luminescent aposematism, but also suggests that lampyrids may use multimodal signals in which olfactory and visual components co-operate to enhance the aposematic signal [134,140-143].

Conclusion

From the previous paragraphs it must have become obvious that we possess quite a lot of information about European fireflies, but most of it stems from the first half of the 20th century with additional inputs from the sixties and seventies. Unfortunately numerous studies were discontinued, not followed up, or led to outcomes that contradicted what we would have expected on the basis of what we observe in the field nowadays. Many of the observations or experiments could and actually should be repeated, since we can now use our greater knowledge of experimental set-ups and statistic methods. Although the study of lampyrids started very early in Europe, especially in the Central and Northern European countries with their low lampyrid biodiversity, it remains puzzling why so few studies have been performed as a whole and why fireflies have so seldomly been chosen as study subjects compared with other regions of the world. For instance, only one taxonomist has been specialising on European lampyrids for the last 50 years. Beyond doubt, there is still plenty more to be discovered about the ecology and luminescent behaviour of European species; details of their communication systems and especially the fine-tuning of their phylogenetic relations need to be investigated. Yet there is hope, for European fireflies lately became sufficiently "sexy" and popular enough, even to non-scientists, and are the topic of volunteer surveys and in artistic, environmental, and educational projects. The following list provides a summary of some challenging ideas and research topics, some more general and some more specifically based on European species:

- What are the effects and what is the importance of light pollution on the bioluminescent behaviour and survival of firefly and glow-worm populations? How do artificial lights and more indirectly cloud-reflected city lights interfere with courtship signals or defensive glows?
- Is the male and female partner choice based on bioluminescent displays and light organ patterns and what is the importance of pheromones and contact pheromones in our nocturnal species? What is the role of nuptual gifts (spermatophores) and multiple mating and how are these involved in sexual competition?
- To what extent is the system of sexual communication and partner discrimination related to the isolation of species and state of speciation especially in Southern European lampyrids, where males seem to have problems to distinguish their own females within and between genera, and what is the possibility of recent or past multiple hybridisations? Such questions call for multidisciplinary research, combining genetic and etho-ecologic analyses.
- Why do some species in which male bioluminescence does not seem to be involved in sexual communication, nevertheless show spontaneous and continuous glowing, while other closely related species have lost this characteristic during evolution?
- Are European *Luciola* species a complex of sibling species and how can differences in flash characteristics offer possibilities for species isolation and identification?
- What is the principle of synchronous flashing in the Bosnian *Luciola* species and what can this tell us about the system, ecology and multiple

evolution of synchronous flashing? Indeed, synchronous flashing seems to have evolved often in isolated species within certain genera (*Pygoluciola, Luciola, Pteroptyx, Photinus, Atyphella*)?

- Are *Phosphaenopterus spp.* and *Pelania mauretanica* still present in Europe?
- What about the general biology and communication systems of *Phosphaenopterus* and *Lampyroidea*?
- To what extent do the larval glow characteristics differ between species and how are they related to differences in ecology and (micro)habitat? Does the glow have an anti-predator function (e.g. relationship to the predator community, density and presence of other model species)?
- Did lampyrids evolve Müllerian or even Batesian mimicry (see text) between species? Only an international multidisciplinary approach can answer such questions by combining more detailed descriptions about bioluminescent displays, the presence of other possible aposematic signals, the performance of bioassays with analyses of chemical defences and mapping of these characteristics on the phylogeny.
- Why do many lampyrids show pink or magenta colouration on non-melanised bodyparts? Depending on their absorption spectrum, many pigments reflect the complementary colour of the wavelengths they absorb. The complementary colour of pink is yellow-green, which is exactly the colour of bioluminescence of most lampyrid species. So, did lampyrids evolve pinkish absorption pigments in order to conceal an unwanted overall weak body glow as much as possible? Is this pigment a derivative of orange and red pigments that are, or were, 'pre-adaptive' as aposematic colours?

Acknowledgements

I thank Dr. V. Benno Meyer-Rochow for inviting and convincing me to contribute to this book about one of my most favourite topics in Biology. Warm thanks go to Dr. Sara Lewis and my former PhD supervisor Dr. Erik Matthysen for their support and enthusiasm for my quest for firefly research. Dr Michael Geisthardt receives special thanks for his encouragement and the sharing and kind permission for the use of the most updated information about the current biodiversity of European Lampyrids.

References

1. Nuss, M., and Seidel J. 2008, Sächsische Entomologische Zeitschrift, 3, 30-38.
2. Tyler, J. 2004, Luminescence, 19(6), 358.
3. Wootton, A. 1971, Country Life, 150, 604-605.
4. Björck, M. 1998, Körmacken, 9, 8-15.

5. Tyler, J. 1982-1984, Alatala, 10-12, 17-19.
6. Tyler, J. 2002, The glow-worm, Sevenoaks, Lakeside Printing Ltd., 76 pp.
7. Meyer-Rochow, V. B. 2007, Luminescence, 22 (3), 251-265.
8. Mikšić, R. 1982, Acta Entomologica Jugoslavica, 17(1-2), 19-26.
9. Geisthardt, M. 2007, Lampyridae, In: Löbl, I., and Smetana, A. (Eds.): Catalogue of Palaearctic Coleoptera, Vol. 4. Stenstrup, Apollo Books, 46-47.
10. De Cock, R., and Geisthardt, M. 2007, Entomologische Zeitschrift, 117(3), 99-102.
11. Geisthardt, M., Figueira, G., Day, J. C., and De Cock R. 2008, Heteropterus Rev. Entomol., 8(2), submitted.
12. Lewis, S.M., and Cratsley, C.K. 2007, Annu. Rev. Entomol., 53, 293–321.
13. Lloyd, J. E. 1965, Ann. Entomol. Soc. Am., 58, 588-591.
14. Lloyd, J. E. 1968, Entom. News., 10, 265–268.
15. Lloyd, J.E. 1971, Ann. Rev. Entomol., 16, 97-112.
16. Lloyd, J.E. 1973, Coleops. Bull., 27, 91-106.
17. Lloyd, J.E. 1999, Florida Entomologist, 82(2), 165-179.
18. Lloyd, J.E. 2003, Florida Entomologist, 86(2), 99-113.
19. Fu, X., and Ballantyne, L.A. 2008, Zootaxa, 1733, 1-44.
20. Fu, X., Vencl, F.V., Ohba, N., Meyer-Rochow, V. B., Lei, C., and Zhang, Z. 2007, Chemoecology, 17, 117-124.
21. Fu X., Wang Y., Lei C., and Ohba N. 2005, Coleopterist Bulletin, 59(4), 501-504.
22. Fu X., Ohba N., Vencl, F.V., and Lei, C. 2005, Canadian Entomologist, 137, 83-90.
23. Ohba, N. 1980, Sci. Rept. Yokosuka City Mus., 27, 13-18.
24. Ohba, N. 1983, Sci. Rept. Yokosuka City Mus.,30, 1-62, pls.1-6
25. Ohba, N. 1983, , Sci. Rept. Yokosuka City Mus., 31,1-8.
26. Ohba, N. 1984, Sci. Rept. Yokosuka City Mus, 32, 23-33, pl.8.
27. Ohba, N. 1985, , Sci. Rept. Yokosuka City Mus., 33, 13-17.
28. Ohba, N. 1999, Sci. Rept. Yokosuka City Mus. 46, 33-40.
29. Ohba, N. 2003, SICB 2003 Annual Meeting and Exhibtion Final Program and Abstract, 264.
30. Ohba, N. 2004, Integr. Comp. Biol., 44, 225-233.
31. Ohba, N., and Sim, S.H. 1994. Sci. Rept. Yokosuka City Mus., 42, 1-11.
32. Ohba, N., and Sim, S.H. 2000, Sci. Rept. Yokosuka City Mus., 47, 23-30.
33. Chen, T.R. 1999, An Ecological Guide to Taiwanese Firelies, Field Image Publisher, Taipei, 199.
34. Ohba, N., Y. Goto, and Kawashima, I. 1996, Sci. Rept. Yokosuka City Mus., 44, 21-31.
35. Eguchi, E., Nemoto, A., Meyer-Rochow, V. B., and Ohba, N. 1984, J. Insect Physiol., 30, 607-612.
36. Jeng, M.-L., Lai, J., and Yang, P.-S. 2003, Lampyridae: a synopsis of aquatic fireflies with description of a new species (Coleoptera), In: Jäch, M.A., and Ji, L. (Eds.), Water Beetles of China. Vol.III. Zoologisch Botanische Gesellschaft in Österreich and wiener Coleopterologenverein, Vienna, Austria, 539–562 pp.
37. Suzuki, H. 1997, Tokyo met. Univ. Bull. Nat. Hist., 3, 1-53.
38. Suzuki, H., Sato, Y., Fujiyama, S., and Ohba, N. 1996, Genetics, 34(5/6), 191-200.

39. Suzuki, H., Sato, Y., Ohba, N., Base, Jin-Sik, Jin, Ryung-Raae, Sohn, Hung-Dae, and Kim, Sam-Eun 2004, Biochemical Genetic, 42(9/10), 284-300.
40. Bugnion, E. 1929, Association des naturalistes de Nice et des Alpes-Maritimes. Imprimerie “Association Typographique”, Nice. pp. 131.
41. Schwalb, H.H. 1961, Zool. Jb. Syst., 88, 399-550.
42. Papi, F., 1969, Monit. Zool. Ital. (N.S.), 3, 135–184.
43. Dreisig, H. 1971, J. Zool. Lond., 165, 229 -244.
44. Dreisig H, 1974, Ent. Scand., 5, 103-109.
45. Dreisig, H. 1975, Oecologia,. 18, 85-99.
46. Dreisig, H. 1978, Behav. Ecol. Sociobiol., 3, 1-18.
47. Mikšić, R. 1969, Bollettino della Associazione Romana di Entomologia, 24(2), 43-46.
48. Mikšić, R., and Mikšić, S. 1965, Entomol. Nachr. 9, 76-77.
49. De Cock, R. 2000, Belgian Journal of Zoology, 130(2), 93-101.
50. De Cock, R. 2004, The adaptive value of bioluminescent behaviour in glow-worms (Coleoptera: Lampyridae), [Ph.d. dissertation]. University of Antwerp, Belgium, 193 pp.
51. De Cock, R. 2004, Photochemistry and Photobiology 79(4), 339–342.
52. De Cock, R., and Matthysen, E. 1999, Evol. Ecol., 13, 619-639.
53. De Cock, R., and Matthysen, E. 2001, Ethology ,107, 1019-1033.
54. De Cock, R., and Matthysen, E. 2003, Behavioural Ecology, 14(2003), 103-108.
55. De Cock, R., and Matthysen, E. 2005, Anim. Behav., 70(4), 807-818.
56. O’Donald, P. 1968, Nature, 217, 194.
57. Cros, A. 1924, Bull. Soc. Hist. Nat. Afr. Nord, 15, 10-52.
58. Viviani, V.R. 2001, Annals of the Entomological Society of America, 94, 129-145.
59. Olivi*er,* E. *1884,* L’Abeille, 22, 1-55.
60. Linnaeus, C. 1767, Systema naturae, Tom. I. Pars II. Editio duodecima, reformata. Holmiae. (Laurentii Salvii)., 533-1327.0
61. Naisse, J. 1966, Archives de Biologie (Liège), 77, 139-201.
62. Maas, U., and Dorn, A. 2005, Gen. Comp. Endocrinol., 143(1), 40-50.
63. Vogel, R. V. 1912, Zool. Anz., 39, 515-519.
64. Vogel, R. 1913,. Zool. Anz., 41, 325-332.
65. Wunsch, E. 1995, Mitteilungen des Internationalen Entomologischen Vereins, 20(1/2), 1-14.
66. Booth, D., Stewart, A.J.A., and Osorio, D. 2004, J. Exp. Biol., 207, 2373-2378.
67. Tyler, J., McKinnon, W., Lord, G, and Hilton, P. 2008, Physiological Entomology, 33(2), 167-170.
68. Sala-Newby, G.B., Thomson, C.M., and Campbell, A.K. 1996, Biochem. J., 313, 761-767.
69. Lheritier, G. 1955*,* Société des Sciences Naturelles et Physiques du Maroc, 35, 223-233.
70. Wing, S.R. 1989, J. Insect Behaviour, 2(6), 841-847.
71. Sivinski, J. M., Lloyd, J.E., Beshers, S.N., Davis, L. R., Sivinski, R.G., Wing, S.R., Sullivan, R.T., Cushing, P.E., and Petersson, E. 1998, Coleops. Bull., 52, 23-30.

72. Geisthardt, M. 1979, Zool. Jb. Anat., 101, 472-536.
73. Bourgeois, J. 1900, Bull. Soc. Ent. Fr., 1900, 337-338.
74. Olivier, E. 1907, Genera Insectorum, 53, 74 pp.
75. Bialdaccini, N.E., Fiaschi, V., and Papi, E. 1970, Monitore Zool. Ital. (N.S.), 3, 239-245.
76. Bonaduce, A., and Sabelli B. 2006, Bollettino del Museo Civico di Storia Naturale di Verona, 30, Botanica Zoologia, 155-159.
77. Branham, M.A., and J.W. Wenzel. 2003, Cladistics, 19(1), 1-22.
78. Lall, A. B. 1981, J. Insect Physiol. 27, 461-468.
79. Lall, A. B., Seliger, H. H., Biggley, W. H., and Lloyd, J. E. 1980, Science, 210, 560-562.
80. Lall, A. B., Strother, G. K., Cronin, T. W., and Seliger, H. H. 1988, J. Comp. Physiol. A, 162, 23-33.
81. Cronin, T. W., Järvilehto, M., Weckström, M., and Lall, A. B. 2000, J. Comp. Physiol. A186, 1-12.
82. South, A., K. LeVan, L. Leombruni, C. Orians, and S.M. Lewis. 2008, Ethology, 114, 916–924.
83. Grandi, G. 1907, Osservazioni sulla variabilità delle Lampyris. Il Naturalisto siciliano, anno XIX, n° 9.
84. Campbell, A.K. 2008, Luminescence, 23, 187-190.
85. De Cock, R. 1997, Preliminary etho-ecological study of three glow-worm species. [in Dutch: Inleidende gedragecologische studie van drie soorten glimwormen; (Coleoptera: Lampyridae). m.s. thesis], University of Antwerp, Belgium, 99 pp.
86. Jeng, M.-L., and Yang, P.-S. 2003, Journal of the Kansas Entomological Society, 76(3), 477–483.
87. Lloyd, J.E. 1981, Scientific American, 245, 138-145.
88. Geisthard, M. 1979, Familie: Lampyridae, In: Freude, H., Harde K.W., and Lohse, G.A. (Eds.), Die Käfer Mitteleuropas, Band 6, Diversicornia, Goecke and Evers, Krefeld, pp. 14-18.
89. Sivinski, J. 1981, Coleops Bull, 35, 167-179.
90. Buck, J.B. 1978, Academic Press, London, pp. 419-460.
91. Bushman, L.L. 1988, Coleops. Bull., 42, 94-97.
92. Hastings, J.W., Morin, J.G. 1991, Bioluminescence. In: Prosser, C.L., (Ed): Neural and integrative animal physiology, Wiley Interscience, New York, 131-170.
93. Redford*, K. H. 1982,* Coleopt. Bull., 35, 167-179.
94. Carlson, A.D., and Copeland, J. 1985, Q. Rev. Biol., 60, 415-436.
95. Eisner, T., Goetz, M.A., Hill, D.E., Smedley, S.R., Meinwald, J. 1997, Proc Natl Acad Sci USA, 94, 9723-9728.
96. Gonzales, A., Schroeder, F.C., Attygalle, A.B., Svatos, A., Meinwald, J., and Eisner. T. 1999, Chemoecology, 9, 105-112.
97. Lloyd, J. E. 1983, Annu. Rev. Entomol., 28, 131-160.
98. Richards, A.M. 1960, Trans. R. Soc. N.Z., 88,559-574.
99. Sivinski, J. 1982, Ecological Entomology, 7, 443-446.
100. Viviani, V.R., and Bechara, E.J.H. 1997, Annals of the Entomological Society of America, 90, 389-398.

101. Lloyd, J.E. 1978, Insect bioluminescence. In: Herring, P.J. (Ed.), Bioluminescence in Action, New York, Academic Press, 570 pp.
102. Kaufmann, T. 1965, Ann. Entom. Soc. Am., 58, 420.
103. Underwood, T.J., Tallamy, D.W., and Pesek, J.D., 1997, J. Insect. Behav., 10, 365-370.
104. Hasama, B. 1942, Annot. Zool. Japan, 21(2), 59-76.
105. Buck, J.B. 1948, Ann. N.Y. Acad. Sci., 49, 397-482.
106. Ballantyne, L.A., and Buck, E. 1979, Trans. Am. Entomol. Soc. 105: 117-137.
107. Woods, W.A., Hendrickson, H., Mason, J., and Lewis, S.M. 2007, Am. Nat., 170(5), 702-708.
108. Wood, K. V. 1995, Photochem. Photobiol., 62, 662-673
109. Christensen, T.A., and Carlson, A.D., 1982, J Comp. Physiol., 148, 503-514.
110. Halverson, R.C., Case, J.F., Buck, J., and Tiemann, D. 1973, J. Insect Physiol. 19, 1327-1339.
111. Lloyd, J.E., and Wing, S.R. 1983, Science, 222, 634-635.
112. Lloyd, J.E. 1989, Coleops. Bull. 43, 83-91.
113. Cott, H.B.1940, Adaptive Coloration in Animals. Menthuen & Co Ltd, London
114. Aho, A.-C., Donner, K., Hydén, C., Larsen, L.O., and Reuter, T. 1988, Nature 334, 348-350.
115. Aho, A.-C., Donner, K., Helenius, S., Larsen, L.O., and Reuter, T. 1993, J. Comp. Physiol. A, 172, 671-682.
116. Lindström, L. 2000, Evolution of Conspicuous warning Signals, Academic Dissertation, Jyväskylä Studies in Biological and Environmental Science, 81, University of Jyväskylä, Finland.
117. Lall, A. B. 1993, J. Insect Physiol., 39, 123-127.
118. Seliger, H.H., Lall, A.B., Lloyd J.E., Biggley, W.H. 1982, Photochem. Photobiol., 36, 673-680.
119. Herring, P. J. 1983, Proc. R. Soc. Lond. (Ser. B), 220, 183–217.
120. Granit, R. 1943, Nature, 151, 11-14.
121. Donner, K.O., and Rushton, W.A.H. 1959, J. Physiol., 149, 303-317.
122. Koskelainen, A., Hemilä, S. and Donner, K. 1994, Acta. Physiol. Scand. 152, 115.
123. Goldsmith, T.H., and Bernard, G.D. 1974, The physiology of Insecta, Vol. 2. (Edited by R.M. Rockstein), Academic press, London, 165 pp.
124. Jacobs, G.H. 1981, Comparative Color Vision. Academic Press, New York.
125. Barth, F.G., Nakagawa, T., and Eguchi, E. 1993, J. Exp. Biol., 181, 63-79.
126. Meyer-Rochow ,V.B., and Eguchi, E. 1983, N.Z. Ent., 8, 111-119.
127. Viviani, V.R., and Bechara, E.J.H. 1996, Photochem. Photobiol., 63, 713-718.
128. Sydow, S.L., and Lloyd, J.E. 1975, Fla. Ent. 58, 312
129. Blum, M.S., and Sannasi, A. 1974, J. Insect Physiol., 20, 451-460.
130. Jones, F.M. 1932, Trans. Ent. Soc. London, 80, 345-385.
131. Sexton, O.J. 1966, Anim. Behav., 12, 101-110.
132. Rothschild, M. 1961, Trans. R. Ent. Soc. Lond., 113, 101-121.
133. Guilford, T., Nicol, C., Rothschild, M., and Moore, B. 1987, Biol. J. Linn. Soc. 31, 113-128.

134. Marples, N.M., van Veelen, W., and Brakefield, P.M. 1994, Anim. Behav., 48, 967-974.
135. Tyler, J. 2001, The Coleopterist, 10, 38.
136. Tyler, J., and Trice, E. 2001, The Coleopterist, 10, 75-78.
137. McDermott, F.A. 1964, Trans. Am. Entom. Soc., 90, 1-72.
138. Costa, C., Vanin, S.A., and Colepicolo-Neto P. 1986, Rvta. Bras. Ent., 30, 101-104.
139. Viviani, V.R., and Bechara, J.H. 1995, Photochemistry and Photobiology, 62, 490-495.
140. Marples, N.M., and Roper, T.J. 1996, Anim. Behav., 51, 1417-1424.
141. Geisthardt, M., and Day, J. 2004, Zootaxa, 427, 1-6.
142. Rowe, C., and Guilford, T. 1996, Nature, 383, 520-522
143. Roper, T.J., and Marples, N.M. 1997, Anim. Behav., 53, 1241-1250.