

# Rare, or simply overlooked? Practical notes for survey and monitoring of the small glow-worm *Phosphaenus hemipterus* (Coleoptera: Lampyridae)

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**ABSTRACT.** *Phosphaenus hemipterus* (Fourcroy, 1785) is considered a very rare glow-worm and has consequently been studied very little. This paper unites the scattered data on the known distribution of *P. hemipterus* and gives descriptions of habitat use, phenology and activity patterns at recently discovered sites in Belgium. Adult males were found from mid-June to mid-July and were most abundant on warm days, with a clear diurnal activity pattern. Only a few adult females were found, mainly around dusk and in or near crevices. Larvae are mainly nocturnal and glow spontaneously as do most lampyrid larvae, but many were also found during the day. The larvae appear to feed only on earthworms. Typical features of the habitat of *P. hemipterus* are loamy soils and abrupt transitions from dense vegetation into bare patches. Apparently many of these features are present in areas with severe human disturbance such as in gardens, parks, car parks and at field edges. However, most survey studies on glow-worms are carried out in nature reserves, which may explain why *P. hemipterus* is mostly missed. The species may actually be not as rare as presumed, and, moreover, it occurs in areas that are not considered important for conservation management.

**KEY WORDS:** distribution, phenology, habitat use, diurnality, behaviour, survey studies, conservation, Lampyridae

## INTRODUCTION

For over thirty years, many warnings have been given about the decline of glow-worm populations (WOOTTON, 1971; TYLER, 1982-84, 1994). Recently, survey projects for the common glow-worm *Lampyris noctiluca* L. have been started in Great Britain (TYLER, 1994) and in the Benelux (DE COCK, unpubl.) to enable assessments of the species' distribution and state of decline. In these countries another species occurs, the small glow-worm *Phosphaenus hemipterus* (Fourcroy, 1785), which has been little studied. In Great Britain *P. hemipterus* is listed as a Red Data Book species (SHIRT, 1987). Records are confined to a few localities in Sussex and Hampshire (WOOTTON, 1971). The suggestion in TYLER (1994) that *P. hemipterus* might be extinct proved to be wrong (DENTON, 1995(1996)). Although the species no longer seems to

occur on the site described by DENTON (1995(1996)), it is quite likely to survive on the site from which rubble was taken to DENTON's site (TYLER, pers. com.). In Belgium the known distribution of *P. hemipterus* is extremely scattered and limited when compared to other lampyrid species (MAGIS, 1977). However, the species might be more common but simply overlooked (TYLER, 1994). One reason may be its assumed diurnal behaviour (JENNER, 1883; WEBER, 1909; AIRY-SHAW, 1961; MAGIS, 1977; TYLER 1994), with the consequence that it cannot be located by its glowing behaviour, the usual detection method for nocturnal glow-worm surveys. Secondly, females are extremely rarely found since they appear to hide in the soil or under stones (WEBER, 1909) whereas males can easily be confused with staphilinid beetles as they bear shortened wing cases. Finally, the species may just be overlooked because of its small size (< 10 mm). Furthermore, as a unique case among Lampyridae, both sexes are flightless, which restricts their dispersal and in turn may result in a more localised distribution.

Most of the descriptions of habitat of *P. hemipterus* are obsolete and rather superficial, such as: the sunny face of a loamy potato-field (MÜLLER, 1805), a wall in a town garden (JENNER, 1883; BUTLER, 1880), pavement in a garden (MORRIS, 1893), on stones in a rock garden (AIRY-SHAW, 1961), the border of a lettuce field and gardens (WEBER, 1909), an earthen path in a park, on bare plots, a town centre, in an orchard (MAGIS, 1977), in detritus around tombstones in a churchyard (CRIBB, 1991). Information on the geographic distribution of *P. hemipterus* is also fragmented and vague. A literature survey shows that *P. hemipterus* is roughly distributed from the Iberian peninsula in the southwest to the western part of Russia in the east, and from Romania and North Italy in the south, to southern England in the northwest and Sweden, Finland and Karelia in the north (Table 1). This suggests that among glow-worm species, *P. hemipterus* has the second largest distribution in Europe after *Lampyris noctiluca* (TYLER, 1982-1984).

In order to gain a more profound insight into the opportunities for conservation of *P. hemipterus*, one should first know where and when to search for it. In this paper, I present data on the phenology, habitat use and behavioural patterns on several sites in Belgium, which arose from searches for populations of *P. hemipterus* since 1995. These data are an example of what can be collected and may be of practical use for planning survey studies, e.g. when to start studies, habitats of interest and behavioural patterns to consider.

TABLE 1

References to the occurrence of *P. hemipterus*  
in different countries and regions

Country, region	Authors
Belgium	JACOBSON (1911), MAGIS (1977)
Denmark	JACOBSON (1911), LUNDBERG (1995)
England	JACOBSON (1911), WOOTTON (1981), TYLER (1994), DENTON (1995)(1996)
Estonia	JACOBSON (1911), HABERMAN (1960), REMM (1967), ELEBERG (1989), LUNDBERG (1995)
Finland	JACOBSON (1911), LUNDBERG (1995)
France	PERRIER (1971)
Karelia (NW Russia)	JACOBSON (1911), LUNDBERG (1995)
Latvia	TELNOV (1997)
Lithuania	LUNDBERG (1995)
The Netherlands	EVERTS (1903), JACOBSON (1911), DE KEER (1930), BRAKMAN (1966)
North Italy	JACOBSON (1911)
Poland	RAZOWSKI (1991), BURAKOWSKI <i>et al.</i> (1985)
Quebec & Nova Scotia (introduced)	BOUSQUET (1991), TYLER (1994)
Saint-Petersburg gouv., Russia	JACOBSON (1911)
Spain	MAGIS (1977), JACOBSON (1911)
Sweden	JACOBSON (1911), LUNDBERG (1995), BJÖRCK (1998)
West Russia	MAMAEV <i>et al.</i> (1976)

## MATERIAL AND METHODS

Following from MAGIS' (pers. comm.) initial work, searches for *P. hemipterus* populations were started in a park south of Brussels called 'Tervurenpark' in 1995 and 1996, and in the adjacent forest 'Zoniënwoud' where the species has been previously recorded (MAGIS, 1954). These areas were carefully scoured for populations of *P. hemipterus*. In 1997, the species was also discovered by chance and studied at our home campus of the University of Antwerp (U.I.A.) in Wilrijk. From experience I learned that males are best detectable along paths and walls, and while searching for new populations special attention was paid to such places. When one male was found, usually many more were detected in its vicinity.

*P. hemipterus* has accidentally been caught in pitfall traps (LUC CREVECOEUR, BAS DROST, BERND FRANZEN, KONRAD H. MACIEJEWSKI, pers. comm; see further). Pint glasses or plastic beakers (0.5 litre) filled with a 1 to 5% formaldehyde or glycerol solution, sunk to the rim in the soil and placed (in a row) at distances of 5 metres, will do as pitfalls. The use of pitfall traps seems to be a successful method for a survey, but might be too drastic if the studied population is in danger of extinction as nothing is known about its effect on population dynamics. The data presented here are therefore based on simple visual counts. A promising technique to capture live specimens is to use pitfalls with drain bottoms and covered with a funnel to avoid escape.

The phenology data are based on the numbers of adult males found daily during a systematic search at the UIA campus in June and July 1997. The daily activity pattern of males was studied in detail on two different days (26.VI.1996 and 28.VI.1996) and at two sites in the Tervuren park, by counting males several times per day. Activity was expressed as the number of individuals found per unit of searching time, in order to compare between search sessions. Air temperature at the surface and moisture were recorded immediately after each sample session with a mercury thermometer and hair hygrometer (Lufft) in 1996, and a digital thermo-hygrometer (TFA) in 1997. If captured, males were marked with a dot of correction fluid or nail varnish to avoid double counts. The behaviour of some males was also observed in captivity. Following WEBER's (1909) suggestion, females were sought under stones, clods of earth and in the soil up to 10 cm depth, under leaf litter (CHINERY, 1988), and in crevices and openings in walls. Special attention was paid to spots with high male density. During the night, larvae could easily be located by their spontaneous glowing behaviour. Since there is some uncertainty on the diurnal activity of females and larvae (WEBER, 1909; CHAPPELL, 1879-80; MORRIS, 1893), environmental light intensity was measured whenever a female or a larva was found during the day.

Since *P. hemipterus* seems to prefer loamy soils, soil samples were taken at sites where the species was found and compared with samples from sites where *L. noctiluca* was found. The proportions of sand and silt/clay fractions were determined by baking the samples for three hours at 300°C to destroy all organic matter, weighing the sample and sifting it over a sieve of 50 µm to wash out silt and clay. The remaining sand fraction was dried and weighed.

## RESULTS

### Phenology

Fig. 1 shows the daily abundance of adult males. Moderate numbers of males were already found from the start of the census on 16.VI.1997, but they were most abundant towards the end of June. Few males were found by the start of the second week of July. In comparison with MAGIS' (1977) study on material from Belgian collections, the maximum abundance was observed about one week later. This may be explained by the weather, which was unusually wet and cold during this period, as shown by the below-average daily temperatures from 19.VI.1997 till 07.VII.1997 (KMI, 1997). The number of males was positively correlated with temperature within the peak period of abundance, i.e. from 21.VI.1997 to 31.VI.1997 (Spearman rank correlation,  $r_s = 0.68$ ,  $t_9 = 2.9$ ,  $P < 0.01$ ).

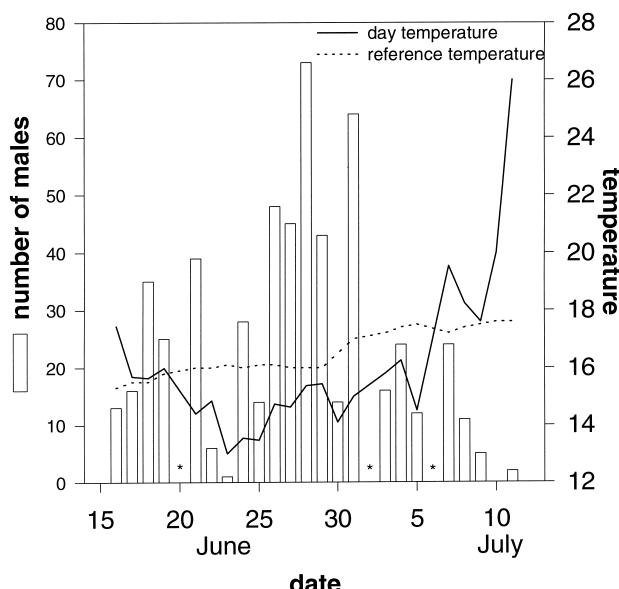


Fig. 1. – Seasonal activity pattern of *P. hemipterus* males at the UIA-campus site in 1997, with daily maximum temperatures and reference mean temperature in June calculated from data between 1921 and 1993 (KMI, 1997). \* = no observations done.

### Habitat use

*P. hemipterus* was found on three sites, the habitat of which is described below. Examples of habitats are illustrated in Fig. 2.

**Tervurenpark (A):** This public park, which houses the Museum of Central Africa, is situated south of Brussels. It contains a mixture of patches of beech forest, mixed forest, ponds and canals, broad strips of lawn and asphalted access roads. Between the Museum buildings and the main park there is a French garden laid out in a stair-like fashion. The soil in these parts of the park is strongly mixed, though the texture would be comparable to the adjacent parts, which have loam soils with a strongly-stained B horizon (DUDAL, 1956). This whole area was searched for *P. hemipterus*, which was found in three separate sites:

**French garden (A.1; Fig. 2a, 2b):** Males were found in an isolated shrubbery of the French garden. The site is surrounded by lawn and on two sides borders on hardened paths. The spot has a dense vegetation of indigenous shrubs such as hazel (*Corylus avellana*), hawthorn (*Crataegus monogyna*) and elder (*Sambucus nigra*), and exotic shrubs like snowberry (*Symporicarpos albus*), Oregon grape (*Mahonia neubertii*), *Rhododendron* spp. and at the borders some herbs, especially ground ivy (*Glechoma hederacea*) and stinging nettle (*Urtica dioica*) and mosses. At the edges and among the vegetation there are bare plots of crumbly loam with many cracks and holes in the soil, which contains no obvious litter layer (Fig. 2b). At less than forty metres from the site there is beech woodland. In 1995, 42 ♂♂ were observed in a four day period, and in 1996, 24 ♂♂ were marked during a similar period. Neither ♀♀ nor larvae were found here.

**Car park site (A.2; Fig. 2c, 2d):** This site is situated near one of the museum buildings that has a lawn in front, which in turn is surrounded by an access road, pavement and several parking lots. Next to the pavement and roads there are hedgerows (*Symporicarpos albus*) with a dense thicket behind. Males were mostly found at the transitions of vegetation into more open areas (Fig. 2d). However, most males were found along a low, 60 metre-long wall of concrete blocks, separating a macadam road from shrub and beech woodland on a slope (Fig. 2c). A four-day search period in 1996 resulted in 142 marked ♂♂, three ♀♀ and three day-active larvae. A two-hour search on two days in 1997 resulted in 17 ♂♂ and one day-active larva. A search for larvae by night was impossible because of the confounding light of street lamps spread over the site.

**Agroforestry site (A.3; Fig. 2e):** This site is along an access road of the park with, on one side, plantations of young trees and on the other side a steep, grassy verge. Next to this verge lay a moist field with overgrown rubbish-heaps, a small afforestation of horse-chestnut (*Aesculus hippocastaneum*) and a somewhat bigger, mixed wood of sweet chestnut (*Castanea sativa*), common and sessile oak (*Quercus robur*, *Q. petraea*), locust tree (*Robinia pseudo-acacia*), hornbeam (*Carpinus betulus*), and especially maple (*Acer pseudoplatanus*). The horse-chestnut wood has a 5 to 10 centimetre thick leaf-litter layer, whereas in the mixed wood up to 60% of bare patches of loamy soil are visible between areas of the thin

litter layer. On open spots and on an overgrown path between the woodlots there are dense patches of nettles (*Urtica dioica*) and brambles (*Rubus fruticosus*). Behind these afforestations there is a beech forest. In 1995, 6 ♂♂



a

were found on the road. In 1996, none was seen, though in both years over 20 larvae were found in the horse-chestnut and mixed wood.



b



c



d



e



f

Fig. 2. – Examples of habitats for *P. hemipterus*. (a) French garden. Overview of the shrubbery. (b) French garden. Microhabitat with crumbly loam soil. (c) Car park site. Low wall of concrete blocks. (d) Car park site. Transitions of vegetation into more open areas. (e) Agroforestry site. (f) adult male of *P. hemipterus*. (photograph taken by Dr. F. Adriaensen, UIA)

The common glow-worm *L. noctiluca* also occurs in this park, the highest densities being found along verges and in vegetation on a pond shore. They were also found on clear places in the beech forests and even in or very close to *P. hemipterus* sites, but always in grassy or leaf litter habitats.

**Zoniënwoud (B):** This beech forest is situated south of Brussels on typical löss soils with moist loamy depressions surrounded by alfisol on the interfluvia (DUDAL & BAEYENS, 1959). Undergrowth consists of ferns in the wood and sparse vegetation along paths and forest roads. Depending on the slope the soil is completely bare or covered by a thick litter and humus layer (up to 10 cm). Some wood clearings with pasture occur throughout the forest. No males or females were discovered during a day of searching in 1995. In October 1996, 11 larvae were found glowing by night on and next to a sunken path at the forest edge near Watermael-Bosvoorde. Another two were found on the same spot in July 1997, during field work on another glow-worm *Lamprohiza splendidula*, which also occurs in these forests.

**Antwerp University, U.I.A.-campus site (C):** *P. hemipterus* was found by chance on the U.I.A.-campus site near Antwerp. It has never been reported before in this region. The site is situated in a closed park landscape with garden-like features. The buildings, parking lots, roads and paths are for the greater part surrounded by dense shrub woods, hedges and lawns. The terrain has been severely dug up, but formerly it had moderate to strongly gleyey sandy loam soils with a strongly stained texture B horizon (BAEYENS, 1971). Sites where the species was recorded are spread over the whole campus, but are separated by roads and paths, so that one might envisage at least five (sub)populations. These populations mostly occur at the edges of small low woods. The leaf litter layer is very thin here and more than 50% of the soil is uncovered. In June 1997, two ♀♀ were found and 159 ♂♂ were marked on 23 days. During the same period 20 day-active larvae were found. Over 20 larvae were seen glowing in wooded parts on a damp night in September. *L. noctiluca* occurs in a less managed, adjacent part of the campus where *P. hemipterus* has not been recorded yet.

### Microhabitats

In all areas, the males mostly crawled on roads, paths and especially along kerbs and road borders (Fig. 2d) or at the base of walls (Fig. 2c), either in the sun or in shadow. In woodland, along hedgerows, beneath shrubs, etc., they were found on bare spots or on loamy soil with a thin leaf-litter cover (Fig. 2b). Occasionally they crawl a few centimetres high on stems, twigs or other elevations.

Only three ♀♀ were found in 1996 and another two in 1997. Three were found in front of very thin fissures (<2 mm wide) at the base of a wall, one in an excavation of a wooden log and another one on top of a fallen branch. No ♀♀ were found in the soil or under leaf litter, wood, stones or lumps.

Larvae were mostly found on leaf litter in the more wooded or densely vegetated parts of sites, but also crawling over bare moist surfaces, for example along kerb stones, patches of bare earth or at the base of walls.

Table 3 shows data on soil samples taken from sites where glow-worms have been found. *P. hemipterus* was never found on pure sand soils, whereas *L. noctiluca* was found on sandy as well as more colloidal soils. A Mann-Whitney test shows that in general soil samples from *P. hemipterus* sites contain more silt and clay than those of exclusive *L. noctiluca* sites ( $P < 0.01$ ).

### Other recent records in the Benelux

There is a recent record on 09.VI.1990 from Ekeren, north of Antwerp (K. JANSSENS, pers. comm.) where a male was found in a bathroom. In Genk (Limburg, Belgium), *P. hemipterus* has been trapped in pitfalls since 1995, on a southeast facing, steep slope between fields and the border of a canal. The stony, chalk-loamy soil shows many bare patches. At about 10 metres from the pitfall traps there is a woodlot and on top of the slope there is a path (L. CREVECOEUR, pers. comm.). Over three years more than 100 ♂♂ have been trapped at Lingedijk (area between the rivers Maas and Rijn in Gelderland, the Netherlands) in a frequently-pruned afforestation of ash (*Fraxinus excelsior*) with intermediate rows of poplar and willow, and dense hawthorn bushes at the edges. The rich clay soil grows nettles, but among the vegetation there are bare spots, which contain many crevices (B. DROST, pers. comm.).

### Activity pattern and behaviour

Fig. 3 shows the diurnal activity pattern of males on two days and in two parts of the car park site. On 26.VI.1996, males were most abundant in the early afternoon shortly before temperatures reached a maximum. However, the observations -particularly on the street side-suggest that male activity declined when the air became too dry. This site received more direct sunlight for a longer period, which explains the lower moisture level. On 28.VI.1996, when both temperature and moisture fluctuated less than on 26.VI.1996, male activity also fluctuated less markedly, except for a notable increase after an evening shower, which may be explained by the sudden rise in moisture at a fairly high temperature. After this peak male activity declined rapidly as dusk set in (Fig. 3).

When crawling, the males sometimes stop abruptly or climb on stems or twigs and start scanning the air by turning their heads and waving antennae, and continue in the same or a new direction. Males mostly aggregated on places where females were present or were observed shortly after. In captivity, males became inactive just after sunset and tended to hide under lumps of loam, leaf litter or in cracks in the soil until the next morning.

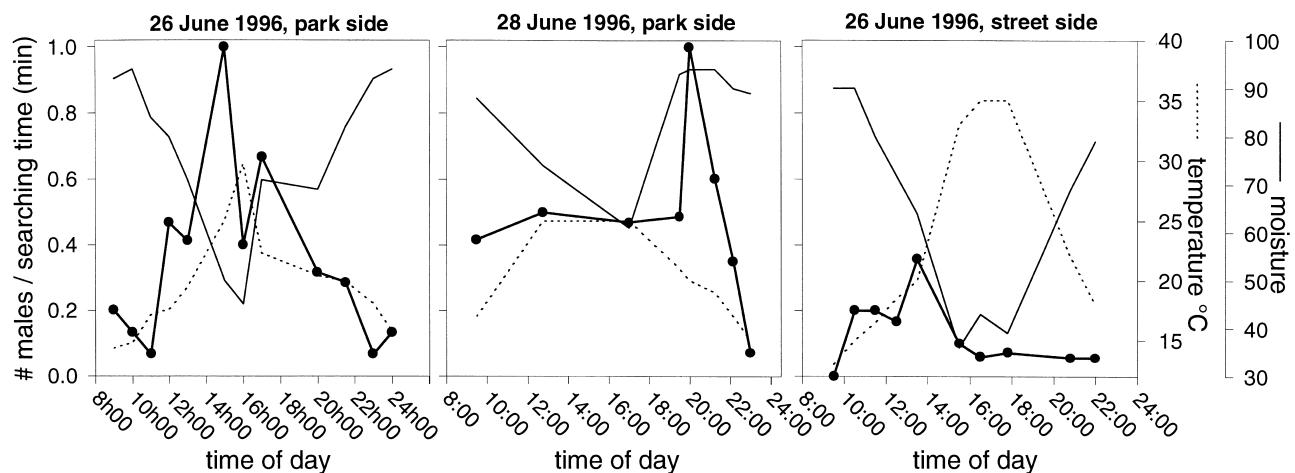


Fig. 3. – Diurnal activity patterns of male *P. hemipterus* and environmental measures at the car park site on two different days.

Two ♀♀ were found crawling at night in copula in front of very thin fissures at the basis of a wall, at respectively 23:11 p.m. (26.VI.1996; 0.5 lux) and 21:28 p.m. (27.VI.1996; 170 lux). When disturbed, they fled into these fissures. Two others were found at noon on drizzly days, in front of a wallcrack (27.VI.1996; 1000-2000 lux), and in a niche of a wooden log (25.VI.1997; 1480 lux). A fifth one was found sitting on top of a fallen branch surrounded by searching males in a dense thicket at 18:30 p.m. (28.VI.1997). Neither the females nor the males were seen glowing spontaneously. They only glowed for a few seconds when disturbed.

In captivity larvae would readily attack earthworms, but always ignored the offered snails and slugs (*Oxylilus spp.*, *Helix rotundatus*, *Succinea* sp., *Cepaea nemoralis*, *Deroeras* sp. and *Arion* sp.), which are however the favourite prey of other European species (SCHWALB, 1961; TYLER, 1994). Also in natural conditions larvae were seen feeding on earthworms, which indicates that *P. hemipterus* specialises on this type of prey. As in other European glow-worm species, the adults do not seem to feed (MIŠKIĆ, 1981).

TABLE 2

The number of observations of diurnal larvae of *P. hemipterus* in relation to light intensity in lux

lux	# observations
500-1000	3
1000-2000	8
2000-3000	1
3000-4000	2
4000-5000	1
5000-6000	0
>6000	2

A final observation is that in total more than 20 larvae were found in broad daylight, up to light intensities of

10774 lux. However, Table 2 shows that most of 17 diurnal larvae appeared at environmental light intensities between 1000-2000 lux, thus in shadowy places or on cloudy days. These larvae mostly crawled very fast along borders. Most larvae have been found during the night when they glowed spontaneously.

## DISCUSSION

Surveys for *P. hemipterus* should best be planned from June till the beginning of July when the adults are most abundant. Occasionally a few males can still be found in August and even September (MAGIS, 1977). Larvae can be found throughout the year, except of course in winter when they hibernate, probably in the soil. However, the chance to come across adult males is likely to be higher, firstly because they are day-active, secondly because they seem to be more mobile and readily move from patches where they developed as larvae, and thirdly they often aggregate when searching for a female. The data suggest that males will be most abundant on afternoons of sultry days or after a thunder-storm when it is hot and damp. If one surveys in these conditions and on places with appropriate habitats, undiscovered populations can easily be detected visually. When one is solely interested in finding this species, it would be more time consuming to put pitfalls than simply searching visually for it. On the other hand, if *P. hemipterus* occurs in an area where a pitfall study is going on, then it is very likely that males will be trapped. For a monitoring study I presume that the use of pitfalls is the most successful if they are put in rows along walls, road borders or other such edges where males and (diurnal) larvae were frequently found. However, females are very difficult to find since they seem to hide most of the time. Their appearance does not seem to be restricted to certain parts of the day. The easiest way to locate an emerged female is by following a congregation of males. Frequently males crawl on the same spot for several days, which suggests that a female is hidden in their vicinity. However, it appears to be nearly

impossible to find such hidden females. Females of *P. hemipterus* were found at environmental light intensities ranging from 0.5 to 2000 lux, while females of other glow-worm species only start activity when light intensity dips under 1.4 lux after sunset (DREISIG, 1971). A possible non-disturbing way to monitor a known population is by counting the number of glowing larvae at night. However, we do not know yet if this larval glowing is strongly correlated with habitat type, season, activity pattern or other environmental variables that may affect this method.

*P. hemipterus* is a unique glow-worm species in several respects. Its most striking feature is that both sexes are flightless and that at least the male adults are diurnal. The behaviour and morphology of males, with their long, broad antennae and small eyes, and the fact that they appear to be attracted to and assemble on places where females are hiding, strongly suggest that this species uses pheromones rather than light signals in sexual communication, as in other diurnal lampyrids (LLOYD, 1972; MATSUDA & OHBA, 1991). Another unique feature of *P. hemipterus* is that the larvae seem to be specialised in feeding on earthworms. The larvae of some North American *Photinus* and *Photuris* spp. also feed on earth worms, though not exclusively, and also possess more hooked mandibles, which contrast with the curved, scythe-like ones of specialised snail predators (McDERMOTT 1964; WING, 1989; BUSCHMANN, 1984).

In spite of its remarkable features and large geographic distribution, knowledge about *P. hemipterus* remains restricted because of its assumed rarity. However, this scarceness may be the result of the interest of today's entomologists in habitats not favoured by *P. hemipterus*. Characteristic habitats for *P. hemipterus* are places with a considerable amount of human disturbance like parks, gardens, (forest)roads and paths, which are mostly encountered in (sub)urban habitats. Apparently, such places were surveyed more often in the past. Another common feature is the presence of compact, loamy or clayey soils (see Table 3). Even the Antwerp population occurs on loam, while sand is the prevalent soil type in this region. This preference can be explained by two factors. Firstly, loam is also preferred by earthworms (EDWARDS et al., 1972), which are prey to *P. hemipterus* larvae, and secondly, the colloidal nature of these soil types helps it to keep moist and crumbly with many cracks and openings, which are ideal hiding places. Another recurring feature of *P. hemipterus* sites is an abrupt transition from dense vegetation or humus layer towards open, bare terrain, e.g. pavement, roads, walls, stones, fields. The preference of *P. hemipterus* for such

human designed environments suggests that the species might originate from rocky or at least partly bare, but humid habitats with sufficient vegetated patches. Other European glow-worm species usually live between the vegetation or on leaf litter in moist forests, edges of wood, grasslands, along river banks, lake shores and verges (SCHWALB, 1961; TYLER, 1994; WUNSCH, 1995). Most of these habitats are present in nature reserves, which until now have received most attention concerning glow-worm survey studies (e.g. WUNSCH, 1995). This difference in habitat use is noticeable as *P. hemipterus* and other glow-worms occur sympatrically in our study areas. It is possible that *P. hemipterus* occurs in some nature reserves, but as it has such a particular habitat preference, it is more likely to be found in areas with more disturbance. Since such habitats are plentiful, the species might be not as rare as presumed. However, this can only be ascertained with further survey studies.

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TABLE 3

Sand fractions after sifting (50 µm) and fractions of washed out silt and clay, and soil texture for soil samples from 22 sites where glow-worm species occur (LN = *Lampyris noctiluca*, LS = *Lamprohiza splendidula*, PH = *Phosphaenus hemipterus*). A, B, C refer to sites described in the text. Soil classes were determined with Bradshaw & Weaver's (1993) soil texture diagram

site	% sand	% silt/clay	soil texture	species
A.1 FrG	20	80	silt	PH
A.2a ISOa	59	41	sandy loam	PH
A.2b ISOb	54	46	(sandy) loam	LN, PH
A.3 ZW	18	82	silt	LN, PH
A. lake	51	49	sandy/silt loam	LN
A. wood	58	42	sandy loam	LN
B. Zoniënwoud	65	35	sandy loam	LS, PH
C. UIA P3	39	61	silt loam	PH
C. UIA Stele	41	59	silt loam	PH
C. UIA D	56	44	sandy loam	PH
C. UIA Anim.	55	45	sandy loam	PH
C. UIA Fort	47	53	silt loam	LN
C. UIA Home	80	20	loamy sand	LN
Wijnegem kloof	87	13	sand	LN
Wijnegem Np	87	13	sand	LN
Wijnegem oever	86	14	sand	LN
Wijnegem Vp	89	11	sand	LN
Wijnegem KAST	86	14	sand	LN
Wijnegem Bp	88	12	sand	LN
Hoboken bos	71	29	loamy sand	LN
Hoboken pad	88	12	sand	LN
Hoboken oever	96	4	sand	LN

Vlaams Instituut ter bevordering van het wetenschappelijk-technologisch onderzoek in de Industrie (I.W.T.).

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