Bulletin of Insectology **63** (1): 21-30, 2010
ISSN 1721-8861

Phytophagous insects captured in carrion-baited traps in central Spain

Arturo Baz[1], Blanca Cifrián[1], Daniel Martín-Vega[1], Manuel Baena[2]
[1]*Departamento de Zoología y Antropología Física, Universidad de Alcalá, Alcalá de Henares, Madrid, Spain*
[2]*Departamento de Biología y Geología, I.E.S. Trassierra, Córdoba, Spain*

Abstract

We present a list of 114 different species of phytophagous insects (Hymenoptera Apoidea, Lepidoptera and Heteroptera) that were collected in carrion-baited traps in central Spain. We discuss the feeding habits of these insects as found in previously published literature, especially in tropical environments. In each group studied, the reasons for their attraction appear to be different, but in any case, we demonstrated that many species of phytophagous insects exploit this resource, at least on an occasional basis and that it is a regular activity in temperate and not only tropical latitudes.

Key words: Apoidea, Lepidoptera, Heteroptera, necrophagy, carrion.

Introduction

The arthropod fauna that come to dead animal bodies varies considerably in relation to habitat and environmental conditions. Their mode of action may be affected by the type of body that they find. In general, when they discover dead invertebrates, they can be disaggregated or buried very quickly. However, when it comes to bodies of vertebrates, there are a wide variety of arthropods species that exploit this resource as it is of high quality. Moreover, there is a sequential pattern of carrion-feeding species that will colonize and remove carrion along a specific decomposition process. Insects visiting carrion exploit this resource in many different ways, which allows a number of trophic groups or categories according to the criteria of Leclercq (1978) and Braack (1987) as follows:

1 - Necrophagous: They feed directly from the bodies and usually complete their life cycle on them. These include sarcophagous species, where they feed on the flesh and soft tissue, and dermatophagous, if they feed the skin.
2 - Necrophilous: Those that eat the carrion-feeding and are predators. Predators capture and feed on the other arthropods in the environment (mostly Diptera larvae). Parasites use the larvae of flies or other insects to complete their life cycle.
3 - Saprophagous: In general, they feed on decomposing organic matter; in this case, those that feed upon the fluids and tissues of rotting corpses. They do not usually complete their life cycle on the body, and sometimes simply are attracted to odors of putrefaction. Therefore they are not strictly necrophagous.
4 - Opportunistic or casual: Those species that use the body as a refuge or simply in passing, or have a diet completely different from necrophagous but occasionally can obtain nutrients from the bodies as a food supplement.

Many insect species belong to this last category. Some are insects with strictly phytophagous diets that occasionally feed on non-plant material, or insects that are strictly phytophagous in the larval stage and may feed at other sources as adults. These alternative food sources, including bird droppings, dung and carrion. Many examples are known in Heteroptera (Adler and Wheeler, 1984) and tropical butterflies (see Molleman *et al*., 2005 for a recent review of this behaviour). Among bees (Apoidea) there is the remarkable well-known case of *Trigona hypogea* Silvestri, an obligate necrophage, that uses carrion instead of pollen as a protein source (Roubik, 1982) and other Meliponinae (stingless bees) that occasionally collect faeces and carrion (Silveira *et al*., 2005). The reasons behind this behaviour are still not clear and depend largely on the type of insect involved. In this paper we present a compilation of species of phytophagous insects (Lepidoptera, Heteroptera and Hymenoptera Apoidea) that have been collected, in recent surveys in central Spain, in carrion-baited traps. We also discuss, based on the previously published literature, the meaning of this unusual behaviour for each of the insect groups considered.

Materials and methods

To capture carrion visiting insects we used carrion-baited traps modified from the design of Morón and Terrón (1984) (for more details see also Baz *et al*., 2007). Although the study of necrophagous insects through the use of Wing Oriented Traps (WOT) is more frequent (Martínez-Sánchez *et al*., 1998), we prefer to use a more robust trap that can remain installed for longer periods of time. Traps were baited with squid. The use of squid as a bait has been shown to be very effective in such ecological studies because it maintains a moist state of decay for much longer periods than other baits (e.g., chicken or liver, Newton and Peck, 1975). The bait was place inside a perforated plastic jar that prevents access to the bait by insects, and prevents accidental falling of insects into the bait. Traps were semi-buried into the ground so that there was 8-10 cm between the edge of the trap and the ground surface. Finally, traps were protected with a perimeter of stones to avoid destruction by wild animals that were attracted by the carrion. Data were collected in different surveys conducted in the centre of the Iberian Peninsula designed to study the necrophagous fauna. Each survey was designed to address a different objective, and the data cannot then be compared between sites from a quantitative point of view. A brief description of the three surveys follows.

Survey 1

Designed to study the variation of the assemblages of necrophagous insects along an altitudinal gradient (Baz *et al*., 2007). Samples were collected between the localities of Lozoya and Puerto de Navafría (Madrid province). Nine trapping sites were selected along an altitudinal gradient at 100 m intervals between 1100 and 1900 m a.s.l. (both included), with one trap at each site. Traps were maintained during June, July and August of 2003 and were visited every 15 days. On each visit, the specimens were collected and the bait replaced, so that traps were operating without interruption for 90 days. At the end, 53 samples were taken as one sample at site 8 was destroyed, probably by a wild animal.

Survey 2

Designed to study the habitat associations of necrophagous insects on a regional scale. Traps were set up at sites throughout the province of Madrid. Twenty one sites were selected, providing sampling of 7 habitat types. To cover the environmental heterogeneity of each sampling site, three traps at each site were installed. So, a total of 63 traps were installed in the study area and were maintained from June 2006 to May 2007. Traps were operated for a period of seven days within each month. A total of 756 samples were obtained (63 traps x 12 times), although samples obtained during the winter provided virtually no insects. If we consider only the favourable period of April to September, there were 378 samples.

Survey 3

We determined the necrophagous insects of the "Hoces del rio Riaza" Natural Park (Segovia province). A total of 10 sites were selected as representative of 5 habitat types. Traps operated 15 days each month (June to September 2007). At the end, 36 samples had been obtained as four samples were destroyed. Moreover, despite all the precautions taken, it is possible to find individual insects caught accidentally that were not attracted to carrion. So, in this last survey we attempted to avoid this problem. Next to each active trap, we are installed a control trap, similar to the carrion-baited trap, except for the fact that control traps were not baited with carrion. Thus, by examining catches of the control traps, we could determine which species were caught occasionally and not attracted to carrion. In these samples we did not find any Apoidea, Lepidoptera or Heteroptera in the control traps. Therefore we assume that in the other samples, the species were attracted by the carrion. Therefore, in this paper, we only take into account those species that are really attracted to carrion and we have eliminated the species that were trapped accidentally.

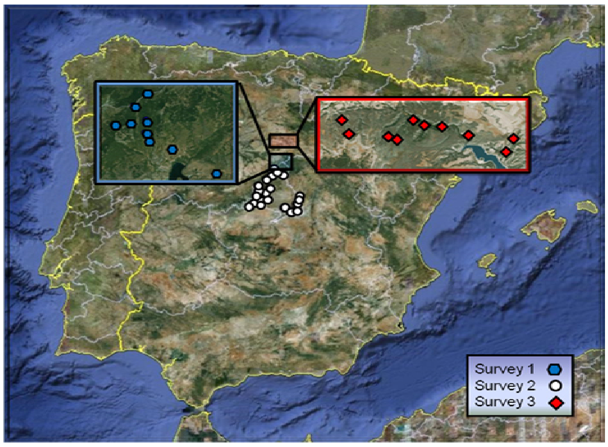

Figure 1. Map of the Iberian Peninsula with the location of the sampling sites.

A brief description of the localities sampled, together with their geographical locations, is provided in table 1 and a map with the location of sampling sites can be found in the figure 1.

Results and discussion

Together for the three different surveys, we trapped a total of 918 individuals of 114 different phytophagous insect species (see table 2 for a detailed overview of trap catches). Also, detailed data about the number of species, number of individuals, occurrences and sex-ratio, can be found in table 3.

Hymenoptera-Apoidea

A total of 276 individuals belonging to 19 species are bees. In addition to *T. hypogea* and other Meliponiinae (Roubik, 1982; Silveira *et al*., 2005), other records of non-plant food by bees are those of the honey bee (*Apis mellifera* L.) and *Bombus impatiens* Cresson which fed on the fluids at a pig carcass (Payne, 1965), the tropical *Bombus ephippiatus* Say feeding on mammalian faeces and the temperate *Bombus terrestris* (L.) feeding on bird droppings, human urine and carrion (Herrera, 1990). Apoidea have been recorded (without a specific identification) at carrion on the Iberian Peninsula by Arnaldos *et al*., (2004) and Castillo-Miralbes (2002). Our data are consistent with those found in the scientific literature. The most common bee species in our traps was the honey bee, which was caught in all 3 of the surveys. Seven different species of bumbles bees were trapped in our studies. Of these, *Bombus pascuorum* (Scopoli) and *Bombus humilis* Illiger were the most common. Anthophoridae and Megachilidae bees have not been recorded prior to now as attracted to carrion. Several species of *Amegilla* and *Anthophora*, as well as different genera of Megachilidae were taken for first time in relation to non-plant food. By instance, *Megachile pilidens* Alfken was trapped with carrion in all three surveys. The only Halictidae trapped was *Nomiapis diversipes* (Latreille), and only in Survey 3. However, the abundance and site frequency of this species in traps suggest that it may use

Table 1. Description of the localities sampled. Climatic data have been obtained from Ninyerola *et al*. (2005) and they represent the annual Maximum, Minimum, and Mean Temperature as well as the total rainfall.

Localities	UTM coordinates	m a.s.l.	Main vegetation type	Temperature °C mean	max.	min.	Total rainfall mm
SURVEY 1							
1) Lozoya-1	(30T 432653, 4538581)	1900	*Cytisus oromediterraneus* shrublands in a cleared pinewood of Scot's pine (*Pinus sylvestris* L.)	8	14	1	707
2) Lozoya-2	(30T 431902, 4537778)	1800	Scot's pine forest (*Pinus sylvestris)*	8	14	2	710
3) Lozoya-3	(30T 430781, 4536716)	1700	Scot's pine forest (*Pinus sylvestris)*	8	14	2	770
4) Lozoya-4	(30T 432498, 4536918)	1600	Scot's pine forest (*Pinus sylvestris)*	9	15	3	660
5) Lozoya-5	(30T 432493, 4536585)	1500	Mixed forest of Scot's pine (*Pinus sylvestris*) and oaks (*Quercus pyrenaica*)	11	17	4	662
6) Lozoya-6	(30T 432556, 4536203)	1400	Oakwood (*Quercus pyrenaica*)	10	16	3	688
7) Lozoya-7	(30T 432736, 4535458)	1300	Oakwood (*Quercus pyrenaica*)	10	16	4	629
8) Lozoya-8	(30T 433707, 4535206)	1200	Cleared Oakwood (*Quercus pyrenaica*)	10	16	4	638
9) Lozoya-9	(30T 436602, 4533374)	1100	Cleared Holm Oakwood (*Quercus ilex* ssp. *ballota*) with scattered oaks (*Quercus pyrenaica*)	11	17	5	682
SURVEY 2							
10) Pezuela de las Torres	(30T 480340, 4472921)	730	Mesomediterranean Holm Oakwood (*Quercus illex* ssp *ballota*) on limestones	13	20	6	404
11) Olmeda de las Fuentes	(30T 485437, 4467550)	810	Mesomediterranean Holm Oakwood (*Quercus ilex* ssp *ballota*) on limestones	13	20	6	467
12) Orusco	(30T 480996, 4460577)	730	Mesomediterranean Holm Oakwood (*Quercus ilex* ssp *ballota*) on limestones	13	20	7	446
13) Valdaracete	(30T 480896, 4461005)	730	Mesomediterranean Holm Oakwood (*Quercus ilex* ssp *ballota*) on gypsum and marlstones	14	20	7	468
14) Valdelaguna	(30T 468149, 4443709)	750	Mesomediterranean Holm Oakwood (*Quercus ilex* ssp *ballota*) on gypsum and marlstones	14	20	7	454
15) San Martín de la Vega	(30T 456182, 4453188)	620	Mesomediterranean Holm Oakwood (*Quercus ilex* ssp *ballota* on gypsum and marlstones	14	21	8	443
16) Villaviciosa de Odón	(30T 419855, 4473962)	540	Mesomediterranean Holm Oakwood (*Quercus ilex* ssp *ballota*) on sands	14	21	8	537
17) Villanueva de Perales	(30T 406526, 4467450)	596	Mesomediterranean Holm Oakwood (*Quercus ilex* ssp *ballota*) on sands	15	21	9	559
18) Villamanta	(30T 404260, 4464245)	610	Mesomediterranean Holm Oakwood (*Quercus ilex* ssp *ballota*) on sands	15	21	9	528
19) Villa del Prado	(30T 386567, 4459281)	660	Mesomediterranean Holm Oakwood (*Quercus ilex* ssp *ballota*) on granites	15	21	9	589
20) Chapineria	(30T 397145, 4465864)	515	Mesomediterranean Holm Oakwood (*Quercus ilex* ssp *ballota*) on granites	16	21	11	573
21) Fresnedillas de la Oliva	(30T 399023, 4482478)	922	Mesomediterranean Holm Oakwood (*Quercus ilex* spp *ballota*) on granites	12	18	6	661
22) Puentes Viejas	(30T 452686, 4529060)	905	Supramediterranean Holm Oakwood (*Quercus ilex* ssp *ballota*) on granites	12	18	6	550
23) Lozoya A	(30T 436780, 4533579)	1121	Supramediterranean Holm Oakwood (*Quercus ilex* ssp *ballota*) on granites	11	17	5	652
24) Hoyo de Manzanares	(30T 424771, 4497334)	1020	Supramediterranean Holm Oakwood (*Quercus ilex* ssp *ballota*) on granites	12	18	6	677
25) Lozoya B	(30T 436732, 4533732)	1295	Supramediterranean Oakwood (*Quercus pyrenaica*) on granites	10	16	4	696
26) La Morcuera	(30T 428653, 4525428)	1440	Supramediterranean Oakwood (*Quercus pyrenaica*) on granites	9	15	3	776
27) El Escorial	(30T 399940, 4481102)	971	Supramediterranean Oakwood (*Quercus pyrenaica*) on granites	12	18	6	863
28) Puerto de Navafría	(30T 431060, 4536202)	1810	Oromediterranean Scot's pine forest (*Pinus sylvestris)* on granites	8	14	2	791
29) Puerto de Navacerrada	(30T 419976, 4519462)	1711	Oromediterranean Scot's pine forests (*Pinus sylvestris*) on granites	8	13	2	968
30) Collado de la Mina	(30T 403507, 4506344)	1710	Oromediterranean Scot's pine forests (*Pinus sylvestris*) on granites	8	14	2	752
SURVEY 3							
31) Montejo de la Vega	(30T 446440, 4599328)	996	Herbaceous and shrub vegetation	12	18	5	521
32) Montejo de la Vega	(30T 446756, 4598380)	1050	Herbaceous and shrub vegetation	11	18	5	451
33) Valdevacas de Montejo	(30T 449536, 4598040)	1081	Juniper forest (*Juniperus thurifera*)	11	17	5	517
34) Valdevacas de Montejo	(30T 449212, 4598128)	1057	Juniper forest (*Juniperus thurifera*)	11	17	5	499
35) Montejo de la Vega	(30T 450328, 4599426)	901	Holm Oakwood (*Quercus ilex* ssp *ballota*)	12	18	6	520
36) Montejo de la Vega	(30T 451196, 4599034)	902	Holm Oakwood (*Quercus ilex* ssp *ballota*)	12	18	6	521
37) Maderuelo	(30T 456652, 4598028)	973	Lusitanian Oakwood (*Quercus faginea*)	12	18	5	454
38) Maderuelo	(30T 456171, 4597179)	930	Lusitanian Oakwood (*Quercus faginea*)	12	18	5	453
39) Maderuelo	(30T 452051, 4598944)	903	Riparian forest (*Populus nigra*)	12	18	5	476
40) Maderuelo	(30T 453316, 4598375)	899	Riparian forest (*Populus nigra*)	12	18	6	468

Table 2. List of species caught on carrion-baited traps in each survey. OCC: number of occurrences; IND: total number of individuals; MAX: maximum n. of individuals per trap. Numbers that identify the localities are the same as reflected in table 1.

	Survey 1			Survey 2			Survey 3			Localities
	OCC	IND	MAX	OCC	IND	MAX	OCC	IND	MAX	
HYMENOPTERA - APOIDEA										
Family APIDAE										
Apis mellifera L. 1758	2	2♀	1	16	32♀	12	13	48♀	12	3, 4, 10, 13, 14, 16, 19, 23, 31, 32, 34, 37, 38, 39, 40
Bombus hortorum (L. 1761)	3	3♀	1	-	-	-	-	-	-	1, 2, 5
Bombus humilis Illiger 1806	1	3♀	1	2	2♀	1	-	-	-	7, 23, 26
Bombus laesus Morawitz 1875	-	-	-	-	-	-	1	1♀	1	40
Bombus magnus Vogt 1911	-	-	-	1	1♀	1	-	-	-	30
Bombus pascuorum (Scopoli 1763)	9	39♀	10	-	-	-	1	1♀	1	1, 2, 4, 5, 6, 7, 31
Bombus sylvarum (L. 1761)	-	-	-	-	-	-	2	6♀	5	40
Bombus terrestris (L. 1758)	1	2♀	2	-	-	-	-	-	-	6
Family ANTHOPHORIDAE										
Amegilla albigena (Lepeletier 1841)	-	-	-	1	1♀	1	-	-	-	14
Amegilla ochroleuca (Perez 1879)	-	-	-	1	2♀	2	-	-	-	14
Amegilla quadrifasciata (de Villers 1789)	-	-	-	1	1♀	1	-	-	-	13
Anthophora furcata (Panzer 1798)	1	1♀	1	-	-	-	-	-	-	1
Family MEGACHILIDAE										
Megachile pilidens Alfken 1924	1	1♀	1	4	4♀	1	3	4♀	2	3, 10, 14, 17, 32, 39, 40
Megachile willughbiella (Kirby 1802)	-	-	-	-	-	-	2	1♂, 3♀	3	36, 40
Anthidium florentinum (F. 1775)	-	-	-	-	-	-	1	1♀	1	40
Anthidiellum strigatum (Panzer 1805)	-	-	-	-	-	-	1	4♀	4	37
Trachusa interrupta (F. 1781)	-	-	-	2	3♀	2	3	3♂, 1♀	2	10, 12, 32, 34, 37
Chalicodoma pyrenaica (Lepeletier 1841)	-	-	-	1	1♀	1	-	-	-	22
Family HALICTIDAE										
Nomiapis diversipes (Latreille 1806)	-	-	-	-	-	-	9	10♂, 95♀	52	31, 32, 33, 34, 35, 39
LEPIDOPTERA										
Family NOCTUIDAE										
Catocala conjuncta (Esper 1787)	-	-	-	6	7♀	2	-	-	-	13, 14, 17, 19, 20
Catocala conversa (Esper 1783)	-	-	-	5	5♀	1	-	-	-	10, 14, 17, 20
Catocala dilecta (Hübner 1808)	6	13♀	4	10	17♀	4	-	-	-	6, 7, 8, 10, 17, 18, 19, 20, 27
Catocala nymphagoga (Esper 1787)	-	-	-	9	3♂, 16♀	6	-	-	-	10, 11, 12, 13, 14, 16, 19, 21
Catocala nymphaea (Esper 1787)	-	-	-	14	2♂, 17♀	4	-	-	-	10, 11, 15, 17, 12, 19, 20, 21, 23
Minucia lunaris (Denis et Schiffermüller 1775)	-	-	-	3	2♂, 1♀	1	-	-	-	11, 15, 22
Lygephila craccae (Denis et Schiffermüller 1775)	1	1♂	1	-	-	-	-	-	-	5
Acronicta psi (L. 1758)	1	1♂	1	-	-	-	-	-	-	8
Tyta luctuosa (Denis et Schiffermüller 1775)	-	-	-	2	2♂	1	-	-	-	12, 13
Caradrina noctivaga Bellier 1863	-	-	-	1	1♂	1	-	-	-	15

(Continued)

(Table 2 Continued)

	Survey 1			Survey 2			Survey 3			Localities
	OCC	IND	MAX	OCC	IND	MAX	OCC	IND	MAX	
Polyphaenis sericata (Esper 1787)	-	-	-	1	1♀	1	-	-	-	10
Olivenebula xanthochloris (Boisduval 1840)	1	1♂	1	-	-	-	-	-	-	4
Thalpophila matura (Hufnagel 1766)	-	-	-	-	-	-	1	3♂	3	32
Dicycla oo (L. 1758)	1	1♂	1	-	-	-	-	-	-	8
Apamea arabs Oberthür 1881	-	-	-	1	1♂	1	-	-	-	21
Agrochola meridionalis (Staudinger 1871)	-	-	-	1	1♀	1	-	-	-	27
Omphaloscelis lunosa (Haworth 1809)	-	-	-	1	1♂	1	-	-	-	20
Conistra rubiginosa (Scopoli 1763)	-	-	-	1	1♂	1	-	-	-	14
Jodia croceago (Denis et Schiffermüller 1775)				1	1♀	1				25
Dryobota labecula (Esper 1788)				1	1♂	1				15
Ammopolia witzenmanni (Standfuss 1890)				1	1♀	1				14
Trigonophora crassicornis (Oberthür 1918)				3	3♂, 1♀	2				20, 24
Aporophyla nigra (Haworth 1809)				1	2♂	2				14
Polymixis argillaceago (Hübner 1822)				2	2♂	1				15
Orthosia cruda (Denis et Schiffermüller 1775)				1	1♂	1				25
Noctua comes Hübner 1813							1	1♂	1	33
Chersotis anatolica (Draudt 1936)	1	1♂	1							1
Xestia kermesina (Mabille 1869)				1	1♂	1				14
Xestia xanthographa (Denis et Schiffermüller 1775)				1	1♂	1				16
Euxoa temera (Hübner 1808)				2	2♂	1				10, 28
Euxoa tritici (L. 1761)	1	1♂	1							1
Agrotis ipsilon (Hufnagel 1766)				1	1♂	1				13
Family ARCTIIDAE										
Eilema palliatella (Scopoli 1763)	1	1♂	1							4
Family NYMPHALIDAE										
Nymphalis polychloros (L. 1758)	1	1♂	1	4	6♂	2				5, 19, 25, 26
Polygonia c-album (L. 1758)	1	1♀	1							7
Melitaea phoebe (Denis et Schiffermüller 1775)				1	1♂	1	1	1♂	1	10, 37
Argynnis aglaja (L. 1758)				2	1♂, 1♀	1				25, 26
Argynnis niobe (L. 1758)				1	1♂	1				21
Boloria dia (L. 1767)							1	1♂	1	40
Family SATYRIDAE										
Brintesia circe (F. 1775)	1	1♂	1	5	9♂	3	2	1♂, 1♀	1	8, 21, 22, 23
Pararge aegeria (L. 1758)	1	1♂	1							4
Maniola jurtina (L. 1758)				1	1♂	1				25
Hyponephele lupinus (O. Costa 1836)				5	2♂, 3♀	1	2	2♂	1	10, 11, 14,16
Coenonympha dorus (Esper 1782)				1	1♂	1	5	5♂, 2♀	2	30, 32, 33, 36
Hipparchia alcyone (Denis et Schiffermüller 1775)							2	3♂	2	37, 38

(Continued)

(Table 2 Continued)

	Survey 1			Survey 2			Survey 3			Localities
	OCC	IND	MAX	OCC	IND	MAX	OCC	IND	MAX	
Hipparchia semele (L. 1758)				1	1♂	1	2	2♂	1	19, 34, 38
Neohipparchia statilinus (Hufnagel 1766)				1	1♀	1	4	12♂, 1♀	4	10, 33, 34, 39
Pseudotergumia fidia (L. 1767)				2	4♂	2	5	8♂, 7♀	4	12, 33, 37
Family HESPERIDAE										
Spialia sertorius (Hoffmannsegg 1804)							4	3♂, 1♀	1	32, 35, 40
HEMIPTERA - HETEROPTERA										
FAM. ALYDIDAE										
Alydus calcaratus (L. 1758)	8	22♂	12	7	12♂	4	1	1♂	1	1, 6, 7, 9, 20, 25, 26, 27, 28, 40
Camptopus lateralis (Germar 1817)	2	4♂	2	31	52♂, 5♀	6	11	25♂	5	6, 9, 10, 11, 12, 13, 16, 18, 20, 21, 22, 23, 25, 26, 28, 31, 32, 33, 34, 37, 38, 39, 40
Family COREIDAE										
Bothrostethus annulipes (Herrich-Schaeffer 1835)				7	40♂	25				12, 26
Centrocoris variegatus Kolenati 1845				2	2♀	1				18, 20
Ceraleptus gracilicornis (Herrich-Schaeffer 1835)				4	8♂	5				16, 22, 25, 27
Ceraleptus lividus Stein 1858				6	10♂ ,1♀	5				16, 25, 26, 27
Ceraleptus obtusus (Brullé 1839)	1	1♂	1	3	7♂	4				9, 16, 26, 27
Coriomeris affinis (Herrich-Schäffer 1839)	4	4♂	1	24	35♂	4	10	36♂	16	8, 9, 10, 11, 12, 13, 15, 16, 18, 20, 21, 23, 24, 25, 27, 31, 33
Coriomeris denticulatus (Scopoli 1763)				2	5♂	4	2	2♂, 2♀	2	25, 27
Loxocnemis dentator (F. 1794)				7	9♂	2	4	5♂	2	10, 12, 13, 15, 31, 32, 34
Syromastus rhombeus (L. 1767)				1	2♂	2				11
FAM. LYGAEIDAE										
Beosus maritimus (Scopoli 1763)				2	4♂, 6♀	8				11
Emblethis verbasci (F. 1803)				4	4♂	1				25, 26, 28
Eremocoris abietis (L. 1758)	3	1♂, 4♀	2							2
Eremocoris fenestratus (Herrich-Schaeffer 1839)							1	1♀	1	38
Gonianotus galactodermus Fieber 1861				2	3♂	2	7	60♂, 1♀	21	10, 13, 31, 32, 33, 34
Heterogaster artemisiae Schilling 1829							3	1♂, 2♀	1	31, 33
Horvathiolus guttatus (Rambur 1839)							1	1♀	1	33
Macroplax fasciata (Herrich-Schaeffer 1835)							1	1♀	1	34
Melanocoryphus albomaculatus (Goeze 1778)				1	1♀	1	1	2♀	2	22, 34
Pezocoris apicimacula (A. Costa 1853)				1	2♂	2				20
Raglius confusus (Reuter 1886)	2	1♂, 1♀	1	5	6♂, 1♀	2				6, 7, 20, 25, 27
Raglius tristis (Fieber 1861)				1	1♀	1				30
Rhyparochromus phoeniceus (Rossi 1794)				2	2♀	1				26
Rhyparochromus vulgaris (Schilling 1829)	2	2♀	1							7
Trapezonotus dispar Stål 1872				1	1♀	1				28
Xanthochilus minusculus (Reuter 1885)							1	1♀	1	33

(Continued)

(Table 2 Continued)

	Survey 1			Survey 2			Survey 3			Localities
	OCC	IND	MAX	OCC	IND	MAX	OCC	IND	MAX	
FAM. MIRIDAE										
Capsodes flavomarginatus (Donovan 1798)				2	1♂, 2♀	2				28, 29
Miridius longiceps Wagner 1955							1	1♂	1	33
Miridae sp.				1	1L	1				27
Phytocoris sp.				1	1L	1				29
Rhabdomiris striatellus (F. 1794)	1	1♂	1							7
Thiomiris sulphureus (Reuter 1879)				1	1♂	1				22
Family NABIDAE										
Himacerus apterus (F. 1798)	3	1♂,2♀, 1L	2							5
Himacerus mirmicoides (O. Costa 1834)	1	1♂	1	1	1♀	1				8, 23
Family PENTATOMIDAE										
Acrosternum heegeri Fieber 1861				1	1♀	1				14
Dolycoris baccarum (L. 1758)							1	1♀	1	34
Dyroderes umbraculatus (F. 1775)	1	1♂	1							8
Eurydema ornata (L. 1758)				1	1♀	1				13
Holcostethus strictus (F. 1803)				1	1♂	1				21
Picromerus nigridens (F. 1803)				1	1♀	1				23
Piezodorus lituratus (F. 1794)				1	1♀	1				14
Sciocoris maculatus Fieber 1851				1	1♂, 1♀, 1L	3	1	1♂	1	12, 33
FAM. REDUVIIDAE										
Rhynocoris cuspidatus Ribaut 1921				1	1♀	1				27
FAM. RHOPALIDAE										
Rhopalus conspersus (Fieber 1837)				1	1♂, 2♀	3				26
Rhopalus distinctus (Signoret 1859)							4	7♂, 2♀	6	31, 33

Table 3. Summary of the results obtained in the different samples. Also included is the proportion of sexes for each group of insects in each survey.

	Survey 1				Survey 2				Survey 3			
	Apoidea	Lepidoptera	Heteroptera	Total	Apoidea	Lepidoptera	Heteroptera	Total	Apoidea	Lepidoptera	Heteroptera	Total
N. species	7	12	11	30	9	35	33	77	10	12	16	38
N. individuals	51♀	10♂, 14♀	37♂, 9♀, 1L	122	47♀	54♂, 72♀	202♂, 33♀, 3L	411	14♂, 164♀	42♂, 12♀	139♂, 14♀	385
Occurrences	13	15	20	37	26	67	83	117	19	18	17	30
Sex-ratio ♂/♀	0	0.72	4.11	--	0	0.75	6.12	--	0.086	3.5	9.93	--

carrion generally. The causes of attraction to carrion in bees remain unclear. Carrion has been considered as an important food source for social stingless bees in the Neotropical region (Silveira *et al*., 2005). Many species have been reported collecting meat or juices from carcasses. Some of them, such as *T. hypogea* and related species, are obligatorily necrophagous. In these stingless bees, pieces of meat are not transported to the nest but are masticated and consuming at the feeding site and are subsequently regurgitated to other workers in the nest to be used in larval nutrition (Noll *et al*., 1997; Serrão *et al*., 1997). In temperate regions, however, data on bees responses to or uses of carrion are very scarce. Nevertheless, it has been suggested that bees using carrion, faeces and urine as alternative sources of nitrogenous substances (Herrera, 1990). Bees use pollen as the usual source of nitrogen. So, this behaviour could be related to a shortage of flowers or low production of pollen. However, the catches of bees in our carrion traps were fairly evenly distributed between different sites and the different dates during the summer months. It is not very probable that floral resources were scarce simultaneously everywhere. From this point of view, we can consider that bees use the carrion, not as an alternative source, but as a regular and complementary source of proteins.

Lepidoptera

A total of 204 moths and butterflies were trapped, belonging to 49 species. The feeding behaviour of adult Lepidoptera is a somewhat neglected topic in the study of butterfly biology. In temperate regions butterflies most commonly obtain nutrients from floral nectar, and it is this behaviour which has received the most attention (Watt *et al*., 1974; Baz, 2002; Tudor *et al*., 2004). However, in the tropics, adult Lepidoptera (namely butterflies) are known to supplement their nectar diet by feeding on a much wider diversity of substrates, including decaying fruit and animal matter, and moist surfaces (a behaviour known as 'puddling') (Adler, 1982; Downes, 1973; Boggs and Jackson, 1991; Austin *et al*., 1993; Sculley and Boggs, 1996). However, Lepidoptera that feed on rotting carrion are less well known, although rotting carrion seems to be an important lepidopteran food source. Many authors have recorded adult Lepidoptera feeding on rotting carrion or attracted to carrion baits. For example, Austin and Riley (1995) recorded numerous species of butterflies on carrion baits and Hall and Willmott (2000) found more riodinid species attracted to rotting carrion than to any other substrate in Equatorian forests, and Hamer *et al*. (2006) found the same pattern in a tropical lowland rain forest in Sabah, Borneo. These taxa are butterflies of tropical latitudes, and examples of Lepidoptera in temperate regions feeding on rotting carrion are virtually unknown. The responses of 49 species to carrion that are summarized in this paper represent the most comprehensive data on the carrion habits of Lepidoptera in Europe. Most species that we collected belong to the moth family Noctuidae (32 species). The frequency and abundance of species in the genus Catocala that we trapped with carrion is remarkable. This is a genus that consists of large species with powerful flight. In addition to noctuid moths, all other species collected (with the exception of one species of Arctiidae) were butterflies belonging to the families Nymphalidae, Satyridae and Hesperidae. The causes of this behaviour are still controversial but, in light of recent work two hypotheses have been developed.

First, in most butterfly species, puddling is exclusively a male behaviour. A possible explanation for this division in feeding behaviour is that nutrients derived from puddling are transferred to the female in the spermatophore during mating as a nuptial gift (Smedley and Eisner, 1995; 1996). Secondly, in species in which both sexes puddle, nutrients might be used for neuromuscular activity in both males and females and may therefore correlate with flight morphology (Hall and Willmott, 2000).

While species that puddle are searching for minerals, we assume that species on carrion are searching for protein. Hall and Willmott (2000) found that those species attracted to rotting carrion seemed to have relatively large thoraces, while those species not recorded feeding from any substrate often had relatively small thoraces. Thus, it appears that there might be a general relationship between adult feeding behaviour and morphology in relation to flight and resultant metabolic rate. That is, Lepidoptera that are active and powerful flyers may have larger thoraces, and are active feeders as adults to support the high metabolic demands of flight. On the other hand, Beck *et al*. (1999) have experimentally investigated the attraction of adult butterflies to different bait types in two species-rich tropical communities on the island of Borneo and found that butterfly families differed consistently in their resource preferences. Representatives of the families Papilionidae and Pieridae more often visited NaCl solutions, but still accepted albumin, whereas representatives of the Nymphalidae, Hesperiidae and, in particular, Lycaenidae preferred the protein resource.

Our findings agree well with this mobility hypothesis. First, the sex-ratios of moths and butterflies that we captured indicate that both sexes of many species visit carrion (table 3). In some cases (i.e. the species of *Catocala*), this behaviour seem to be restricted to females. Second, almost all moths captured belong to the family Noctuidae, a family that consists of mobile and powerful flight species. With respect to butterflies we only found representative of the families Nymphalidae, Satyridae and Hesperiidae. No species of Papilionidae, Pieridae and Lycaenidae has been attracted to carrion-baited traps. Although in tropical latitudes, Lycaenidae preferred protein sources, in temperate zones they are more frequently observed at mud-puddles (see for instance Nieves-Aldrey, 2009). These results support the notion of a distinctive carrion-feeding fauna of Lepidoptera comprising more mobile species, which may use carrion to meet additional nitrogen requirements resulting from greater flight musculature and flight muscle use (Hamer, 2006) not only in tropical regions, where this behaviour is best studied, but also in temperate zones.

Heteroptera

We captured 438 individuals belonging to 46 species of bugs in the carrion traps Species such as *Camptopus lateralis* (Germar), *Alydus calcaratus* (L.), *Coriomeris affinis* (Herrich-Schaeffer) and *Gonianotus galactoder-*

mus Fieber are particularly frequents in the samples. True bugs are known to feed on non-plant sources such as bird droppings, dung and carrion (Adler and Wheeler, 1984). These authors reported eighteen species of Heteroptera, belonging mainly to the Coreidae and Alydidae, feeding on various extra-phytophagous foods. According to these authors, some of these bug species collected at carrion or excrement may have been preying on the other insects or may have been feeding on fungi. For example, Payne *et al*. (1968) observed the seed-feeding lygaeid *Myodocha serripes* Olivier preying on a dipteran larva in pig carrion. Several instances involved aggregations of individuals, especially at carrion. Numbers of bugs at carrion are not unheard of, with about 40 individuals of *Alydus eurinus* (Say) (Bromley, 1937) and 12 individuals of *Merocoris distinctus* Dallas (Engelhardt, 1912) seen at one carrion source. Such numbers suggest the possibility of long-distance orientation to carrion odour, although this has not been studied. Our results included some similar observations [i.e. *Bothrostethus annulipes* (Herrich-Schaeffer) 25 individuals in a sample; *Coriomeris affinis* (Herrich-Schaeffer) 16 and *Gonianotus galactodermus* Fieber 21]. Any gregarious behaviour at such food sources could be adaptative as a means of bringing together the sexes. Again, Payne *et al*. (1968) observed mating pairs of *A. eurinus* and *Megalotomus quinquespinosus* (Say) on pig carrion. The presence of mating pairs at extra-phytophagous food sources raises the question of the sex of individuals involved in feeding. Unfortunately, the information available is scanty. The results of our surveys indicate that most bugs visiting or arriving at carrion (and trapped) were males (see table 1). This strongly skewed sex ratio suggests that females of the species that we trapped generally are not feeding at carrion, if they are not arriving at carrion. Considering all the catches of Heteroptera as a whole, the overall sex ratio in the three surveys is 4.11, 6.12 and 9.93 respectively (table 3). It seems clear therefore that in the case of the Heteroptera, the use of carrion as an alternative source of food has a strong sexual component. This may be related with the cost of mating for males. There may be a number of costs of mating for males, the most universal being the time and energy devoted to mate-finding and courtship and the energetic costs of gamete production (Daly, 1978; Dewsbury, 1982). It is difficult to generalize when it comes to 46 species, but there is some evidence suggesting that mating may involve high costs for males of some species. By instance, Krupke *et al*. (2008) found that in the pentatomid bug *Euschistus conspersus* Uhler, males transfer a significant percentage of their body mass during the initial mating. Mating was also found to reduce male longevity by 37.8% but had no significant effect on female longevity or fecundity. From this point of view, we can speculate on the possibility that carrion feeding in males of some species may serve to supplant or add to proteins used that are part of the cost of mating. Obviously, it would be necessary to test this hypothesis experimentally, but in any case, our data have the interest of revealing a little known aspect of the biology of the Heteroptera.

Concluding remarks

Perhaps the most interesting aspect of our findings is how carrion appears to be a significant resource by many species of insects with strictly phytophagous diets, and potentially an additional source of protein that can be used in different aspects of their biology. Carrion-visiting was observed in all types of habitats, suggesting that it is an activity common in temperate latitudes. The ways in which this resource is exploited probably depends on the group of insects considered. Thus, in the case of the Apoidea, this activity was mainly by the workers of the colony. In the Lepidoptera, carrion appears to be used by both males and females, but maybe only by species with a large capacity for flight. In the case of the Heteroptera, this behaviour appears primarily in males and may have a strong sexual or reproductive component. Lastly, regardless of the reasons why phytophagous insects feed on carrion, it certainly constitutes an important resource for adults of many species in temperate latitudes, not only in the tropics, from where most of the information on the use of carrion as food for phytophagous insects originated.

Acknowledgements

This work has been funded by the Spanish Ministerio de Ciencia y Tecnologia (Research Project BOS2003-00400) and by the University of Alcala (Research Project PI2003/016). We also thank to Dr Francisco Sanchez-Aguado, director of the Natural park “Hoces del río Riaza”, for the facilities provided during the field-work.

References

ADLER P. H., 1982.- Soil-and puddle-visiting habits of moths.- *Journal of the Lepidopterists Society*, 36: 161-173.

ADLER P. H., WHEELER A. G., 1984.- Extra-phytophagous food sources of Hemiptera Heteroptera: Bird droppings, dung, and carrion.- *Journal of the Kansas Entomological Society*, 57 (1): 21-27.

ARNALDOS M. I., ROMERA E., PRESA J. J., LUNA A., GARCÍA M. D., 2004.- Studies on seasonal arthropod succession on carrion in the southeastern Iberian Peninsula.- *International Journal of Legal Medicine*, 118: 197-205.

AUSTIN G. T., RILEY T. J., 1995.- Portable bait traps for the study of butterflies.- *Tropical Lepidoptera*, 6 (1): 5-9.

AUSTIN G. T., BROCK J. P., MIELKE O. H. H., 1993.- Ants, birds, and skippers.- *Tropical Lepidoptera*, 4 (Suppl. 2): 1-11.

BAZ A., 2002.- Nectar plant sources for the threatened Apollo butterfly (*Parnassius apollo* L. 1758) in populations of central Spain.- *Biological Conservation*, 103 (3): 277-282.

BAZ A., CIFRIÁN B., DÍAZ-ARANDA L. M., MARTÍN-VEGA D., 2007.- The distribution of adult blow-flies (Diptera: Calliphoridae) along an altitudinal gradient in Central Spain.- *Annales de la Societe Entomologique de France*, 43 (3): 289-296.

BECK J., MUHLENBERG E., FIEDLER K., 1999.- Mud-puddling behavior in tropical butterflies: in search of proteins or minerals?- *Oecologia*, 119 (1): 140-148.

BOGGS C. L., JACKSON L. A., 1991.- Mud puddling by butterflies is not a simple matter.- *Ecological Entomology*, 16 (1): 123-127.

BRAACK L., 1987.- Community dynamics of carrion-attendant arthropods in tropical African woodland.- *Oecologia*, 72: 402-409.

BROMLEY S. W., 1937.- *Alydus* on carrion.- *Bulletin of the Brooklyn Entomological Society*, 32: 213.

CASTILLO-MIRALBES M., 2002.- *Estudio de la entomofauna asociada a cadáveres en el Alto Aragón (España)*.- Monografías S.E.A., 6. Sociedad Entomológica Aragonesa, Zaragoza, Spain.

DALY M., 1978.- The cost of mating.- *The American Naturalist*, 112: 771-774.

DEWSBURY D. A., 1982.- Ejaculate cost and male choice.- *The American Naturalist*, 119: 601-610.

DOWNES J. A., 1973.- Lepidoptera feeding at puddle-margins, dung and carrion.- *Journal of the Lepidopterists Society*, 27: 89-99.

ENGELHARDT G. P., 1912.- A hemipteron on carrion.- *Journal of the New York Entomological Society*, 20: 294.

HALL J. P. W., WILLMOTT K. R., 2000.- Patterns of feeding behaviour in adult male riodinid butterflies and their relationship to morphology and ecology.- *Biological Journal of the Linnaean Society*, 69: 1-23.

HAMER K. C., HILL J. K., BENEDICK S., MUSTAFFA N., CHEY V. K., MARYATI M., 2006.- Diversity and ecology of carrion- and fruit-feeding butterflies in Bornean rain forest.- *Journal of Tropical Ecology*, 22 (1): 25-33.

HERRERA C. M., 1990.- Bumble bees feeding on non-plant sources.- *Bee World*, 71: 67-69.

KRUPKE C. H., BRUNNER J. F., JONES V. P., 2008.- Factors Influencing Mate Choice in *Euschistus conspersus* Uhler (Heteroptera: Pentatomidae).- *Environmental Entomology*, 37 (1): 192-197.

LECLERCQ M., 1978.- *Entomologie et Médecine Légale. Datation de la mort*.- Ed. Masson, París, France.

MARTÍNEZ-SÁNCHEZ A. I., ROJO S., ROGNES K., MARCOS-GARCÍA M. A., 1998.- Califóridos con interés faunístico en agroecosistemas de dehesa y catálogo de las especies ibéricas de Polleniinae (Diptera: Calliphoridae).- *Boletín de la Asociación española de Entomología*, 22 (1-2): 171-183.

MOLLEMAN F., GRUNSVEN R. H. A., LIEFTING M., ZWAAN B. J., BRAKEFIELD P. M., 2005.- Is male puddling behaviour of tropical butterflies targeted at sodium for nuptial gifts or activity?- *Biological Journal of the Linnean Society*, 86: 345-361.

MORÓN M. A., TERRÓN R. A., 1984.- Distribucion altitudinal y estacional de los insectos necrofilos en la Sierra Norte de Hidalgo, Mexico.- *Acta Zoologica Mexicana*, 3: 1-47.

NEWTON A., PECK S. B., 1975.- Baited pitfall traps for beetles.- *The Coleopterists Bulletin*, 29 (1): 45-46.

NIEVES-ALDREY J. L., 2009.- Bebederos de mariposas.- *Quercus*, 276: 52-55.

NINYEROLA M., PONS X., ROURE J. M., 2005.- *Atlas Climatico Digital de la Peninsula Iberica. Metodologia y aplicaciones en bioclimatologia y geobotanica*.- Universidad Autonoma de Barcelona, Bellaterra, Spain.

NOLL F. B., ZUCCHI R., JORGE J. A., MATEUS S., 1997.- Food collection and maturation in the necrophagous stingless bee, *Trigona hypogea* (Hymenoptera: Meliponinae).- *Journal of the Kansas Entomological Society*, 69: 287-293.

PAYNE J. A., 1965.- A summer carrion study of the baby pig *Sus scrofa* Linnaeus.- *Ecology*, 46 (5): 592-602.

PAYNE J. A., MEAD F. W., KING E. W., 1968.- Hemiptera associated with pig carrion.- *Annals of the Entomological Society of America*, 61: 565-567.

ROUBIK D. W., 1982.- Obligate necrophagy in a social bee.- *Science*, 217: 1059-1060.

SCULLEY C. E., BOGGS C. L., 1996.- Mating systems and sexual division of foraging effort affect puddling behaviour by butterflies.- *Ecological Entomology*, 21 (2): 193-197.

SERRÃO J. E., CRUZ-LANDIM C., SILVA-DE-MORAES R. L. M., 1997.- Morphological and biochemical analysis of the stored and larval food of an obligate necrophagous bee, *Trigona hypogea*.- *Insectes Sociaux*, 44: 337-344.

SILVEIRA O. T., ESPOSITO M. C., SANTOS JR. J. N., GEMAQUE JR. F. E., 2005.- Social wasps and bees captured in carrion traps in a rainforest in Brazil.- *Entomological Science*, 8: 33-39.

SMEDLEY S. R., EISNER T., 1995.- Sodium uptake by puddling in a moth.- *Science*, 270 (5243): 1816-1818.

SMEDLEY SR., EISNER T., 1996.- Sodium: A male moth's gift to its offspring.- *Proceedings of the National Academy of Sciences of the United States of America*, 93 (2): 809-813.

TUDOR O., DENNIS R. L. H., GREATOREX-DAVIES J. N., SPARKS T. H., 2004.- Flower preferences of woodland butterflies in the UK: nectaring specialists are species of conservation concern.- *Biological Conservation*, 119. 397-403.

WATT W. B., HOCH P. C., MILLS S. G., 1974.- Nectar resource use by Colias butterflies chemical and visual aspects.- *Oecologia*, 14: 353-374.

Authors' addresses: Arturo BAZ (corresponding author, arturo.baz@uah.es), Blanca CIFRIÁN, Daniel MARTÍN-VEGA, Departamento de Zoología y Antropología Física, Universidad de Alcalá, 28871 Alcalá de Henares, Madrid, Spain; Manuel BAENA, Departamento de Biología y Geología; I.E.S. Trassierra; c/Avenida Arroyo del Moro s/n; 14011 Córdoba, Spain.

Received June 8, 2009. Accepted October 7, 2009.