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### Satellite flies (*Leucophora personata*, Diptera: Anthomyiidae) and other dipteran parasites of the communal bee *Andrena agilissima* (Hymenoptera: Andrenidae) on the island of Elba, Italy

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## Satellite flies (*Leucophora personata*, Diptera: Anthomyiidae) and other dipteran parasites of the communal bee *Andrena agilissima* (Hymenoptera: Andrenidae) on the island of Elba, Italy

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### Abstract

Solitary and presocial aculeate Hymenoptera are parasitized by a range of dipteran species in the families Anthomyiidae, Bombyliidae, Conopidae, Phoridae, and Sarcophagidae that are likely to impact on their hosts. We undertook a study over several years of a univoltine and communal bee, *Andrena agilissima*, and its main dipteran parasites, in particular the satellite fly *Leucophora personata* (Diptera: Anthomyiidae). Behavioural and ecological data were collected from one nesting aggregation of the host bee on the island of Elba, Italy, from 1993 to 2003, and from a foraging site of the bee, ca 5 km from the nesting aggregation. Other Diptera associated with *A. agilissima* at the field site were the bee fly *Bombylius fimbriatus* (Bombyliidae), the conopid fly *Zodion cinereum* (Conopidae), and the scuttle fly *Megaselia andrenae* (Phoridae). The phenology of the Diptera broadly overlapped with that of their host across the season of activity (end of April and all of May). Diurnal activity patterns differed slightly; *L. personata* in particular was active at the host's nesting site before *A. agilissima*. Female satellite flies also showed a range of behaviours in gaining entry to a host nest. We summarize published data on this and other *Leucophora* species that parasitize *Andrena* host bees. Host bees returning to their nests occasionally undertook zig-zag flight manoeuvres if followed by a satellite fly that were generally successful in evading the fly. Satellite flies that entered a nest, presumably to oviposit, were less likely to remain therein if another host bee entered the same nest, suggesting that one advantage to communal nesting for this host is a reduction in brood cell parasitism by *L. personata*. We provide the first clear evidence for parasitism by a *Zodion* of any *Andrena* host. Both *L. personata* and *M. andrenae* concentrated their parasitic activities in the zone of the host nesting aggregation with highest nest densities. Three of the Diptera, *L. personata*, *B. fimbriatus*, and *Z. cinereum*, seemed to have extremely low rates of parasitism whilst that of *M. andrenae* appeared low. Though they have refined parasitic behaviour that allows them to gain entry into host nests (*L. personata*, *B. fimbriatus*, and *M. andrenae*) or to parasitize adults (*Z. cinereum*), these parasites seem not to impact upon the dynamics of the host *A. agilissima* at the nesting aggregation, and the host possesses traits to reduce parasitism.

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## Introduction

Solitary and presocial Hymenoptera (Apoidea, Vespoidea) are often hosts to many families of parasitic flies (Diptera) such as Anthomyiidae, Bombyliidae, Conopidae, Phoridae, and Sarcophagidae (e.g. Bohart and Menke 1976; Coville and Griswold 1983, 1984; Wcislo 1990; Paxton et al. 1996; Andrietti et al. 1997; Polidori et al. 2001). Particularly noteworthy for their host searching behaviour are so-called satellite flies of the genus *Leucophora* (Diptera: Anthomyiidae) that fastidiously track host insects, often aculeate Hymenoptera, in flight with great precision. They are known to feed on brood cell stores (pollen and nectar) of a variety of species of solitary, ground-nesting bees, including members of the families Andrenidae, Anthophoridae, and Halictidae; they also feed on the prey items of some species of fossorial, solitary wasps in the family Crabronidae (Collin 1920; Krombein 1963; Batra 1965; Eickwort et al. 1996; Barthell et al. 1998).

Despite their refined and easily observed satellite behaviour, the biology of satellite flies is poorly known. Commonly *Leucophora* species are included in the ecological guild of satellite flies, parasites that typically find host nests by directly following host females in flight at a fixed distance behind them. Once they have entered a host nest in pursuit of a host, they are thought to lay their own egg or eggs on the food stores of the host's brood cell (Copeman 1921; Davis and LaBerge 1975). However, differences in their parasitic behaviour have been reported. For example, Michener and Rettenmeyer (1956) state that *Leucophora obtusa* (Zetterstedt) oviposits in the tumulus surrounding the nest entrance of its host bee *Andrena bipunctata* Cresson.

*Leucophora personata* Robineau-Desvoidy was previously recorded in association with *Andrena scotica* Perkins, *Andrena labialis* Kirby, *Andrena nigroaenea* Kirby, and *Andrena trimmerana* Kirby (Collin 1920; Paxton et al. 1996). This largely solitary bee genus is therefore one putative host of *L. personata*. Seemingly the fly has an even broader host range that includes the andrenid bee *Panurgus banksianus* (Meyer-Holzappel 1986).

Bee flies (Diptera: Bombyliidae) are a family of parasitic flies that commonly parasitize the brood of aculeate Hymenoptera within host brood cells; females flick eggs into host nest entrances at high speed (Andrietti et al. 1997). Conopid flies (Diptera: Conopidae) lay eggs into the abdomens of other insects, where the conopid offspring acts as an endoparasitoid (e.g. Paxton et al. 1996). Scuttle flies (Diptera: Phoridae), on the other hand, eat brood cell provisions, though the biology of this large family is generally poorly known (Disney 1994).

Here we report on the parasitic behaviour and other aspects of the biology of *L. personata* that we recorded at a large nesting aggregation of *Andrena agilissima* (Scopoli) (Hymenoptera: Andrenidae), a bee recently described in Italy as nesting in communal societies (Giovanetti et al. 1999, 2003; Paxton et al. 1999). Communalism is a form of social organization in which females share a common nest entrance, though each is reproductively active and provisions its own brood cells (Michener 1974). In addition, we present data on other dipteran parasites of *A. agilissima* at the same site, and evaluate the impact of dipteran parasitism on the host bee.

## Material and methods

Our study site is at Colle Palombaia (Campo nell'Elba), on the island of Elba, Italy. Here, we have observed an aggregation of the fossorial *A. agilissima* that has nested in an earth

wall of 16 m × 3 m for at least the last 11 years (Andrietti et al. 1997). The host bee is univoltine, with adults seen from late April to late May each year. Giovanetti et al. (1999) give further details about the site and the host bee. Based on data in Giovanetti et al. (1999) and Paxton et al. (1999), we estimate that >2000 *A. agilissima* females nest in the earth wall every year. We divided the earth wall into 11 zones; within each zone nest density was relatively uniform. Nest entrance density per zone was recorded accurately to relate it to dipteran parasite activity.

#### Diptera: Anthomyiidae

Observations of *Leucophora personata* at the field site were made across 6 years (Table I). In 1997, 2000, and 2002, flies were marked on the thorax with non-toxic paints to facilitate observation (Figure 1). All behaviours of female *L. personata* at the nesting aggregation were then recorded directly onto tape.

On every non-rainy day in the 1997 flight season of *A. agilissima*, the presence of *L. personata* was recorded in the central part of the host nesting aggregation from 08:00 to 16:00 h, where host nests were dense. We simultaneously recorded the activity of *A. agilissima* entering nests at the same central part of the aggregation. In 2000 and 2003,

Table I. Summary information concerning the dipteran parasites associated with a nesting aggregation of *Andrena agilissima* on the Island of Elba, Italy.

Species	Years recorded	Evidence for association
<i>Leucophora personata</i>	1993, 1997, 1998, 2000, 2002, 2003	Enters <i>A. agilissima</i> nests
<i>Bombylius fimbriatus</i>	1993 <sup>a</sup> , 1995, 1997, 1998, 2000, 2002	Oviposits into <i>A. agilissima</i> nests; callow offspring emerge from <i>A. agilissima</i> nest entrances
<i>Megaselia andrenae</i>	1992, 1993, 1997 <sup>b</sup> , 2002 <sup>c</sup> , 2003 <sup>c</sup>	Mates close to <i>A. agilissima</i> nest entrances; enters <i>A. agilissima</i> nests
<i>Zodion cinereum</i>	1997, 2002, 2003	Callow offspring emerge from <i>A. agilissima</i> nest entrances

Publication of observations: <sup>a</sup>Andrietti et al. (1997); <sup>b</sup>Disney et al. (2000); <sup>c</sup>Polidori et al. (2004).

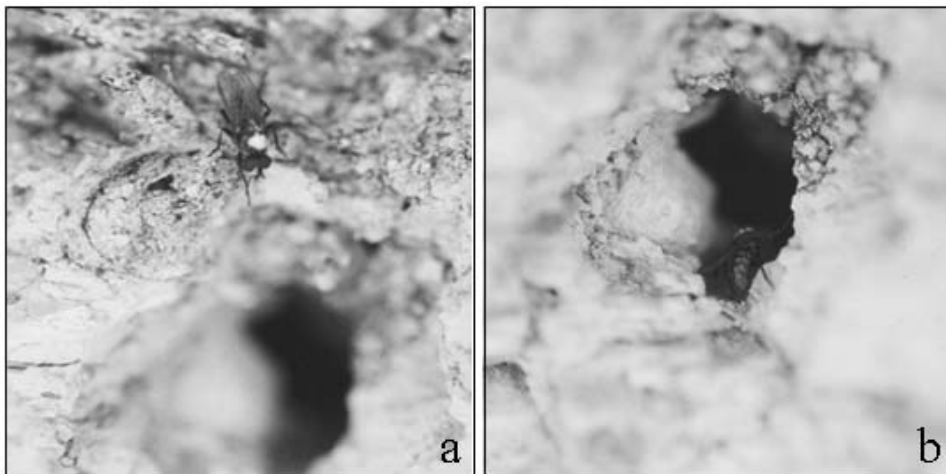


Figure 1. A *Leucophora personata* female, paint-marked on its thorax, waits for the exit of a host bee (a) and then enters its nest (b). Note the head directed towards the nest entrance in (a).

periodic scans of the whole nesting area (in 2003: 5 min per hour for each zone of the aggregation, from 07:00 to 17:00 h) allowed us to relate *L. personata* activity to host nest density.

#### *Diptera: Bombyliidae*

Andrietti et al. (1997) have reported on this bee fly's oviposition behaviour at the nesting aggregation in 1993. Observations of *Bombylius fimbriatus* (Meigen) (Diptera: Bombyliidae) were made across six other years (Table I) at the nesting aggregation, using the methods described above for *L. personata*. Occasional observations were also made of *B. fimbriatus* feeding at flowers at 5 km from the nesting aggregation, in a field containing *Sinapis arvensis* and *Raphanus raphanistrum* in bloom. Flowers of these two plant species are regularly visited by foraging *A. agilissima* (M. Giovanetti, personal observations), and we have recorded numerous *A. agilissima* females at the same field that had been marked at the nesting aggregation.

#### *Diptera: Conopidae*

A sample of *A. agilissima* females ( $n=19$  in 2002 and  $n=52$  in 2003) was collected from the nesting aggregation and from the foraging site of the host bee described above (5 km from the aggregation) to determine the frequency of infection by conopid flies. We collected and dissected bees that were visiting flowers as well as bees that were flying to their nest, either with or without pollen. At the same time and at the same foraging site of *A. agilissima* we also collected and dissected 12 female *Andrena congruens* Schmiedeknecht. Occasional observations were made of the conopid fly *Zodion cinereum* (Fabricius) (Diptera: Conopidae) at the nesting aggregation across 3 years (Table I).

#### *Diptera: Phoridae*

The scuttle fly *Megaselia andrenae* (Diptera: Phoridae) was recorded at the entrance to *A. agilissima* nests at the aggregation across 5 years (Table I). Polidori et al. (2004) report on its reproductive behaviour. Their small size did not permit us to individually mark *M. andrenae* with paint. However, we recorded scuttle fly abundance in 2000 and 2003 during periodic scans of the nesting aggregation, as described for *L. personata* above.

In order to estimate rates of parasitism by satellite flies, bee flies, and scuttle flies, we excavated 85 host brood cells at the aggregation at the end of the flight season of *A. agilissima* in 1997 and 1998, when brood cells were fully provisioned.

Observations relate to an independent event when a fly or bee was recorded once. However, as insects were not always individually marked, two or more observations across different times may relate to the same individual. Thus our observations indicate the relative amount of activity of different species and not the absolute number of individuals. Time is given throughout as solar hours, and means are presented  $\pm$  standard error.

## Results

### *Leucophora personata*

In 1997, the seasonal activity of *L. personata* females ( $n=32$  observations) was concentrated around the peak of *A. agilissima* activity ( $n=1284$  observations), in the early part of May

(Figure 2). Though *L. personata* was active from 08:00 through to 16:00 h, satellite flies were more active in the morning whilst host bees were more active later in the day (Figure 3).

In 2003, *L. personata* females ( $n=11$  observations) were most abundant in zones of the host aggregation with highest nest densities (Spearman rank correlation,  $r_s=0.620$ ,  $n=11$  zones,  $P=0.05$ ; see Figure 4). This satellite fly therefore concentrates its seasonal and spatial activity, but not diurnal activity, to parts of the nesting aggregation with the greatest encounter rates with hosts.

In 1997, 2000, and 2002, we marked a total of 11 *L. personata* females, of which only five were observed again at the aggregation, often far from where they had been marked. Only one marked individual (marked in 1997) was seen to enter the same host nest entrance twice or more ( $n=17$  visits to host nest entrances by this marked individual in 1997). In this same year, we only observed two other, marked *L. personata* (once each) and made five independent observations of unmarked individuals, suggesting that very few *L. personata* females were present at the host nesting aggregation. This view is supported by data from 2003, when we recorded only a maximum of four *L. personata* females simultaneously at the nesting site that contained >2000 female host bees.

*Behaviour at the nesting site.* Female satellite flies were often observed to sit quite close to a host nest entrance (within 1–10 cm), from where they flew up to intercept an incoming bee,

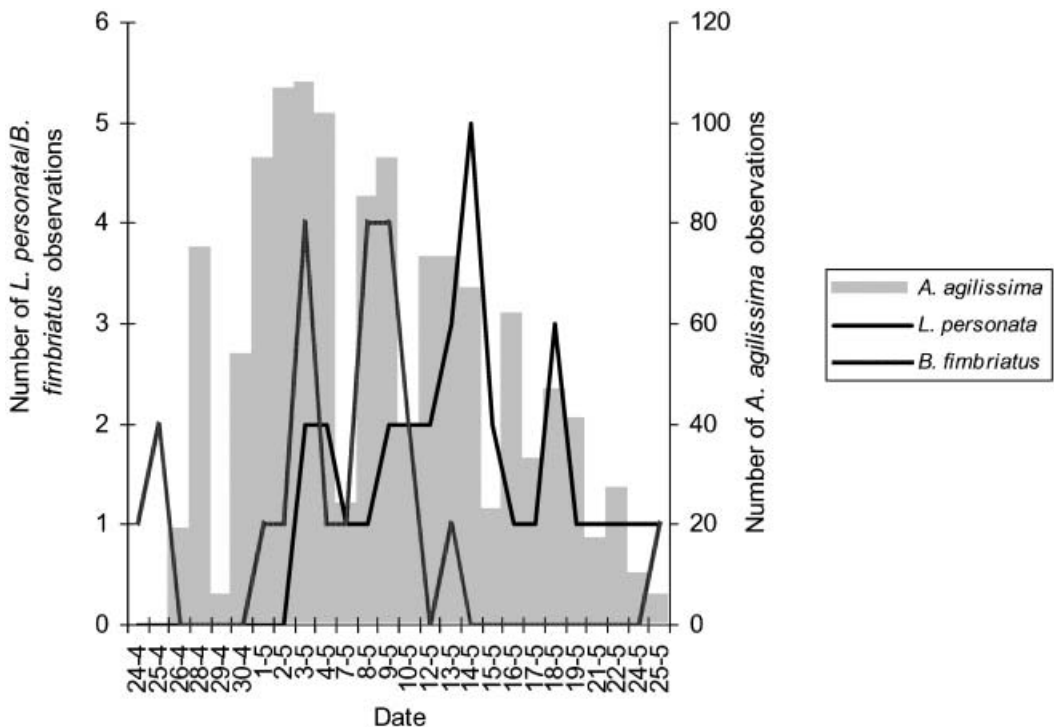


Figure 2. Seasonal activity of the parasitic flies *Bomblyus fimbriatus* and *Leucophora personata* and their host bee *Andrena agilissima* in 1997. For the Diptera, the left ordinate gives the total number of observations, whilst for *A. agilissima* the right ordinate gives the number of marked bees that were observed on one day. Rainy days, when neither flies nor bees were active, are omitted.

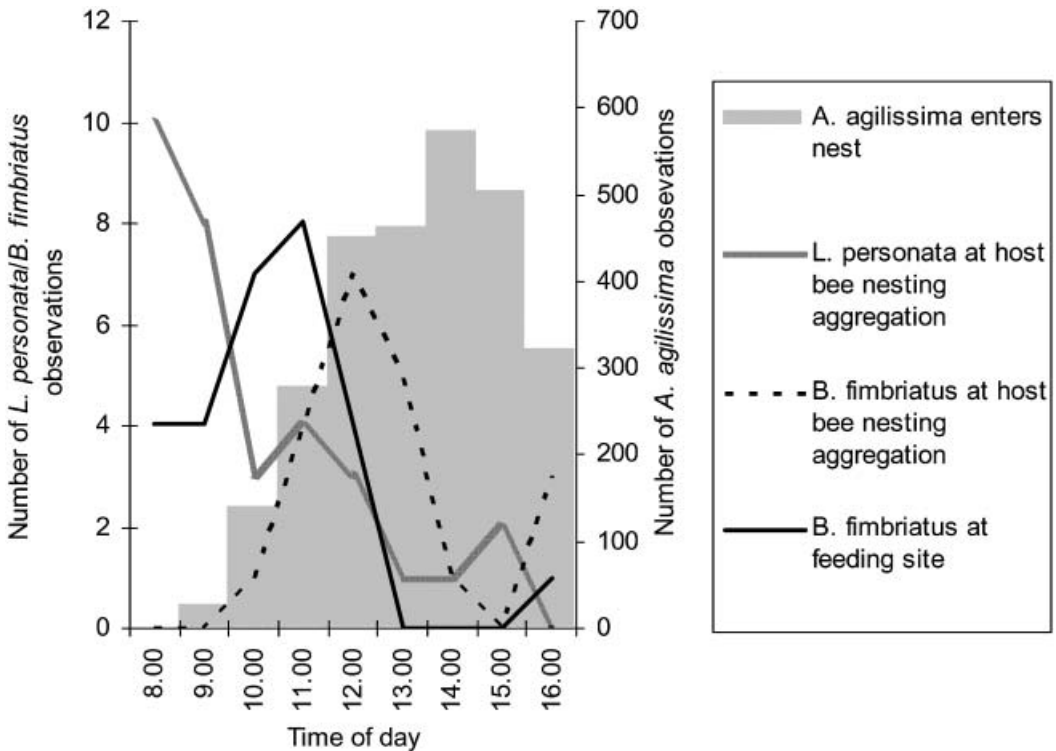


Figure 3. Daily activity patterns of the parasitic flies *Bombylius fimbriatus* and *Leucophora personata* and their host bee *Andrena agilissima* in 1997. For the Diptera, the left ordinate gives the total number of observations per hour, whilst for *A. agilissima* the right ordinate gives the number of marked bees that were observed to enter nests over the same time period.

generally when the bee was 40–70 cm distant from the fly (78% of  $n=23$  observations). The fly would follow behind the host at a fixed distance of 3–4 cm. Once the bee reached its nest entrance, the fly either followed the bee directly into the nest or stopped close to but outside the entrance, waiting for the bee exit before finally entering the nest. The duration of a successful satellite flight from initiation of the flight to final landing near the bee's nest was generally short, averaging  $6 \pm 2$  s ( $n=23$  observations).

*L. personata* females followed bees back to their nests that were both with (39 out of 63 observed satellite flights) and without (24 out of 63 flights) pollen in their scopal and floccal hairs. They appeared to enter nests in pursuit of a bee more often if the bee was carrying pollen (17 of 39 observations) than if it was not carrying pollen (five of 24 observations), though this difference is not significant (Fisher exact test,  $P=0.102$ ).

Host bees often took evasive action when returning to their nest and pursued by a satellite fly. In 35% of  $n=66$  observed satellite flights, the pursued bee performed large zig-zag flights, taking it away from its nest. Satellite flies were more successful at entering a host nest if the host had not undertaken evasive manoeuvres (26 successful entries of 43 pursuits without host evasion) than if the host had engaged in zig-zag flights (four successful entries of 23 pursuits with host evasion), a significant difference (Fisher exact test,  $P<0.01$ ; each observation is taken as an independent point. As many flies were not individually marked, sample sizes may be slightly inflated).



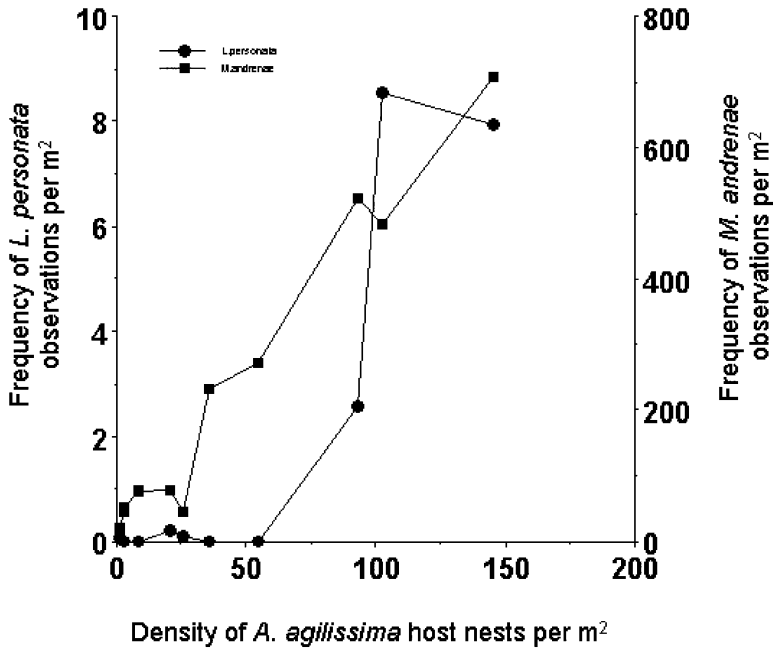


Figure 4. The frequency of observations of the parasitic flies *Leucophora personata* ( $n=11$  observations) and *Megaselia andrenae* ( $n=2384$  observations) across a nesting aggregation of their host bee *Andrena agilissima* in relation to variation in the density of host nests.

We observed three different methods by which satellite flies successfully entered a host nest after tracking a bee in flight: (1) *L. personata* pursued a bee directly into its nest (behaviour 1); (2) *L. personata* stopped close to the entrance of a nest in which a host bee entered, constantly observing the entrance (Figure 1), and only entered the nest after the exit of the same or another bee (behaviour 2); and (3) *L. personata* stopped halfway into a nest, then it exited completely, waited some moments outside the nest entrance, then eventually re-entered completely into the nest, occasionally entering in reverse (behaviour 3). Of the 87 observations of *L. personata* females following their host bees (years 2000–2003), in 37 cases the fly successfully pursued its host into a nest. Of these 37 cases, seven (19%) were of behavioural category 1, 11 (30%) of behaviour 2, and 19 (51%) of behaviour 3. In six of the latter 19 events, the fly reversed into the nest rather than entering head first.

After entering a host nest, one satellite fly remained therein for over 12 min (Table II), presumably ovipositing, whereas others exited after only 2 s. Interestingly, satellite flies spent a shorter time inside a host nest when no other host bee entered the same nest after them (Mann Whitney  $U$  test,  $U=498.5$ ,  $n=38$  and 19,  $P<0.05$ ; see Table II; as flies were often not marked and could therefore not be individually identified, each observation is

Table II. Time spent by *Leucophora personata* females in various behavioural events after following a host bee back to its nest (1997, 2000–2003).

Event	Mean duration $\pm$ SE (s)	Range (s)	$n$ observations
Waiting outside the nest	222 $\pm$ 36	30–540	19
Inside a nest, no other host entry to nest	143 $\pm$ 28	2–740	38
Inside a nest, another host enters the nest	56 $\pm$ 20	2–290	19

treated as an independent event, which may slightly inflate the degrees of freedom; differences are, however, profound). This suggests that one advantage to communal nesting for *A. agilissima* at this site is defence against *L. personata* parasitism.

### *Bombylius fimbriatus*

We have occasionally observed the bee fly *B. fimbriatus* at the *A. agilissima* nesting site. Females oviposited in flight by flicking eggs into nest openings, as reported by Andrietti et al. (1997). *Bombylius fimbriatus* was active throughout May at the field site, which was approximately towards the middle and end of the flight season of *A. agilissima* (Figure 2). However, the number of *B. fimbriatus* individuals observed at the nesting aggregation at any one time was low. Of six females that were individually marked at the nesting aggregation in 1997, one was seen repeatedly across the following 12 days at the site, and it accounted for 14 of the 19 independent observations of this species in 1997. In 2002, we rarely saw *B. fimbriatus* and it was not recorded at the site in 2003 despite the many hours of observation that we undertook in that year.

In 1997 we observed many times ( $n=28$  observations) *B. fimbriatus* feeding on flowers of *Sinapis arvensis* at the field that was also visited by the host bee. Across a day, *B. fimbriatus* seemed to forage a little earlier than it was observed ovipositing (Figure 3), yet its diurnal schedule of appearance at the host nesting aggregation roughly coincided with host bee activity.

On 17 April 1995, when *A. agilissima* adult activity had already commenced, we observed two callow *B. fimbriatus* emerging from *A. agilissima* nest entrances. We never recorded other potential host species using the nest entrances. Therefore this observation strongly supports the notion that *A. agilissima* is a host of *B. fimbriatus*.

### *Zodion cinereum*

In mid-May 1997, two callow *Z. cinereum* emerged from *A. agilissima* nest entrances; the ptilinum between the compound eyes of each was still being inflated rhythmically, indicating that they were freshly emerged adults. In mid-May 2002, one callow *Z. cinereum* emerged from a nest entrance and another callow was collected from the earth bank of the nesting aggregation. Probably the latter had, undetected by us, emerged from a nest entrance. These observations provide strong evidence for the role of *A. agilissima* as a host of *Z. cinereum*.

Only two of 71 *A. agilissima*, collected and dissected in 2002 and 2003 from the nesting aggregation and the flowering field, were found to contain a conopid larva. One conopid larva was also found in one of 12 *A. congruens* females collected at the same flowering field in 2003. Though we could not identify the conopid larva to species, *Z. cinereum* adults were present at the flowering field and one was observed to attack and presumably lay an egg into a foraging female *A. agilissima* in 2002 (C. Papadina, personal communication).

### *Megaselia andrenae*

*Megaselia andrenae* was the most common fly parasite at the *A. agilissima* nesting site, being present usually as pairs but sometimes as tens of individuals. Its larvae exploit the bee's brood cell provisions (pollen and nectar, see Disney et al. 2000). Copulations were frequently observed, after which the female, usually alone though occasionally with the

male, entered a host nest. The abundance of *M. andrenae* ( $n=2384$  observations) increased with host nest density across the nesting aggregation (Spearman rank correlation,  $r_s=0.936$ ,  $n=11$  zones,  $P<0.01$ ; see Figure 4).

#### *Nest dissections*

Of 85 brood cells excavated at the end of the adult flight season in 1997 and 1998, 10 contained soil and one a dead adult; these 11 cells had presumably been provisioned in a previous year. Of the remaining 74, four (5%) were mouldy, two (3%) contained small dipteran larvae, probably of *M. andrenae*, and the remaining 68 (92%) contained an egg, larva or prepupa of *A. agilissima*. The two brood cells assumed to have been parasitized by *M. andrenae* contained two and eight dipteran larvae, yet the pollen provisions and host bee larva in each were still intact, suggesting that *M. andrenae* larvae may not kill host offspring.

### Discussion

Bees of the genus *Andrena* are very commonly host to a suite of dipteran parasites in the families Anthomyiidae, Bombyliidae, and Conopidae, as was our study population of *A. agilissima*. For example, *Andrena scotica* studied in Sweden by Paxton et al. (1996) was associated with *L. personata*, *Bombylius major* Linnaeus, and *Myopa buccata* Linnaeus, respectively. *Andrena fulva* in France and the UK was associated with *L. obtusa* and *B. major* (Litt 1988; Paxton and Pohl 1999). We additionally detected a fourth dipteran family associated with *A. agilissima*, the Phoridae (*M. andrenae*).

#### *Anthomyiidae*

Many species of *Andrena* have been found to be associated with the genus *Leucophora*; Table III summarizes published information on dipteran parasitic behaviour and host-parasite associations. Other satellite fly-host associations of congeners for which no behavioural data have been reported are: *L. sericea* Robineau-Desvoidy with *A. haemorrhhoa* (F.) and *A. fulva*; *L. unistriata* Zetterstedt with *A. labialis* (O'Toole 1978), *L. fusca* Hockett with *A. carlini* Cockerell (Schrader and LaBerge 1978), and *L. personata* with *A. labialis* and *A. nigroaenea* (Collin 1920).

*L. personata* has already been observed in association with other species of *Andrena* (Table III; Collin 1920; Paxton et al. 1996). Our observations reported here represent a new host record for this satellite fly species.

The mode of entry of *L. personata* to *A. agilissima* nests after a satellite fly has followed a host back to its nest is variable. It may either pursue the bee directly into the nest (behaviour 1), await the exit of a bee before entering the host nest (behaviour 2), or it may enter half its body into the nest, retreat, then re-enter in pursuit of the bee (behaviour 3). Schrader and LaBerge (1978) observed that *Leucophora fusca* employs behaviours 1 and 2 at nests of its host *Andrena regularis*. For *L. obtusa* parasitizing *A. fulva*, Paxton and Pohl (1999; see also Paxton et al. 1996) commonly observed a variation on behaviours 2 and 3, in that in both situations the satellite fly reversed into the host's tunnel, abdomen first, when entering for up to 10 min, presumably to oviposit. Reverse entry to a nest was occasionally observed in *L. personata* at Elba, too.

The function of the preliminary tunnel inspection, the first component of behaviour 3, is unclear. It is unlikely to serve in the inspection of brood cell contents, as brood cells are

Table III. Summary of observed behaviours of the satellite flies *Leucophora personata*, *Leucophora obtusa*, *Leucophora grisella* Hennig, and *Leucophora fusca* Huckett in parasitizing their *Andrena* spp. hosts.

	<i>L. personata</i>			<i>L. obtusa</i>		<i>L. grisella</i>	<i>L. fusca</i>	
Author(s)	Present work	Paxton et al. (1996)	Paxton et al. (1996); Paxton and Pohl (1999)	Copeman (1921)	Davis and LaBerge (1975)	Michener and Rettenmeyer (1956)	Huie (1916)	Schrader and LaBerge (1978)
Host(s)	<i>A. agilissima</i> , Italy	<i>A. scotica</i> , Sweden	<i>A. fulva</i> and <i>A. nitida</i> , Cardiff, Wales	<i>A. fulva</i> , London, England	<i>A. erigeniae</i> , USA	<i>A. bipunctata</i> , USA	<i>A. tarsata</i> , Scotland	<i>A. regularis</i> Malloch, Canada
Pursue only pollen-laden bees	No	Probably not	Probably yes			Probably yes	Yes	Probably yes
Behaviour category <sup>a</sup>	1, 2 and 3	1	1 and 2	1	1		2	1 and 2
Fly- <i>bee</i> pursuit distance	3–4 cm	5–10 cm	5–10 cm					
Bee evasive manoeuvres	Often	Yes						Yes
Head-pointing towards the nest entrance (behaviour category 2) <sup>a</sup>	Yes (see Figure 3) (5–15 cm distance)		Yes (2–6 cm distance)				Yes	Yes
Re-enter host nest abdomen-first	Rarely		Yes	Yes			Yes	
Time spent inside the nest	143.4 s (average)		Up to 10 min				Usually <1 m	
Site of oviposition						At the tumulus close to the nest entrance	1.25 cm deep in the nest burrow, but not in host brood cells	
Rate of parasitism of host cells	Very low	2%	3%					

<sup>a</sup>Behaviour categories: 1, fly enters nest in pursuit of host; 2, fly awaits exit of a bee before entering host nest; 3, fly inspects host nest, withdraws, then re-enters host nest in pursuit of a host (see text for further details).

generally deeper underground (Giovanetti et al. 1999). Alternatively, the preliminary inspection may serve to indicate the presence of host bees in the tunnel; *A. agilissima* nests communally, and tunnels at the Elba nesting aggregation interconnect just below the soil surface (Giovanetti et al. 1999, 2003). Thus a satellite fly might need to avoid not only the pursued host bee but also its other nestmates when entering a host tunnel to parasitize brood cells. This hypothesis is supported by our data showing that *L. personata* spends less time in an *A. agilissima* nest if another host bee enters the nest.

Huie (1916) states that satellite flies only pursue pollen-laden hosts. We and others (Paxton et al. 1996) observed that *L. personata* pursues both pollen-laden and unladen host bees, and even other passing insects of similar size to the host (e.g. a potter wasp, Hymenoptera: Eumenidae). The evasive zig-zag flight of a host bee as it returns to its nest with a satellite fly in pursuit has been occasionally recorded (Schrader and LaBerge 1978; Paxton et al. 1996). *Andrena agilissima* at our study site often undertook similar behaviour and was then more successful in evading a pursuing satellite fly.

In summary, the methods employed by satellite flies to enter host nests (Table III) demonstrate plasticity in the behaviour of these species, which may relate to the social biology of the host, its nesting architecture, and nest density. However, *L. personata* was rare at our study site, and rates of parasitism were probably very low. Similarly, a rate of parasitism of only 2% has been recorded for *L. personata* at a large aggregation of *A. scotica* (Paxton et al. 1996), and of 3% for *L. obtuse* parasitizing an aggregation of *A. fulva* (Paxton and Pohl 1999).

### *Bombyliidae*

*Bombylius* are commonly considered parasites of *Andrena* bees. A shortlist of *Andrena*–*Bombylius* associations is given by Andrietti et al. (1997). To that list can be added *B. major* with *A. scotica* in Sweden (Paxton et al. 1996), and with *Andrena bicolor* Fabricius, *Andrena chrysoseles* (Kirby), *Andrena clarkella* (Kirby) (O'Toole 1978), *Andrena haemorrhoa* (Fabricius), possibly *Andrena similis* Smith and/or *Andrena wilkella* (Kirby) (Knight 1968) in the UK. Most data relate to the widespread *B. major*. Cases in Italy include *Bombylius canescens* Milkan parasitizing *Andrena humilis* Imhoff (Bonelli 1964) and *B. fimbriatus* parasitizing *A. agilissima* (Andrietti et al. 1997).

It is generally thought that bee flies emerge from the ground through their own self-constructed tunnels rather than using host tunnels (e.g. Paxton et al. 1996). Our observations suggest that *B. fimbriatus* rather emerges through host *A. agilissima* tunnels, a difference that may reflect the texture and hardness of the host nesting substrate. Given the scarcity of *B. fimbriatus* at the aggregation of *A. agilissima*, its rate of parasitism was probably very low. Low rates of parasitism have been determined through host nest excavations for *B. major* parasitizing *A. scotica* (6.1%, Paxton et al. 1996) and *A. fulva* (3%, Paxton and Pohl 1999).

### *Conopidae*

Many conopids parasitize adult aculeate Hymenoptera. Their larvae consume host haemolymph and internal organs. After host death, conopids pupate and, for temperate species, typically overwinter before emerging the following spring (Paxton et al. 1996). These generalizations match with our observation of *Z. cinereum* parasitizing *A. agilissima*.

Members of the genus *Zodion* often parasitize bees. *Zodion fulvifrons* Say has been described as a parasite of the honey bee *Apis mellifera* L. (Severin 1937) and of the solitary halictid ground-nesting bee *Dieunomia triangulifera* (Pierce 1904) (quoted in Wcislo et al. 1994). *Z. obliquefasciatum* (Macq.) is a parasite of the halictid *Nomia melanderi* Ckll. (Howell 1967). A *Zodion* sp. has been found in another halictid, *Halictus ligatus* Say (Knerer and Atwood 1967). As far as we are aware, ours is the first record of a member of the genus *Zodion* associated with the genus *Andrena*.

Conopids can be frequent parasites of aculeate Hymenoptera. For example, Paxton et al. (1996) found 40% of *A. scotica* to be parasitized by the conopid *Myopa buccata*. However, the rate of conopid parasitism based on dissection of *A. agilissima* was low, at 3% for 2002 and 2003.

### Phoridae

Many species of phorid flies are associated with aculeate Hymenoptera, though most are thought to have little host specificity (Wcislo 1990). The genus *Megaselia* includes species associated with members of the Hymenoptera: Vespidae, Sphecidae, Pompilidae, Crabronidae, and Megachilidae (e.g. Collart 1933; Krombein 1963, 1967; Polidori et al. 2001). The recently described *M. andrenae* (Disney et al. 2000) represents the first case of a scuttle fly associated with an andrenid bee. Its reproductive biology is given in Polidori et al. (2004). The large numbers of *M. andrenae* at our host nesting aggregation and the probable presence of their larvae in host cells suggest that this phorid has a measurable rate of parasitism of *A. agilissima* brood cells (estimate: 3%).

### Parasitism and the host bee

Our study aggregation of *A. agilissima* has maintained approximately the same dimensions from 1993 through to 2003, both in terms of the area in which nest entrances are constructed or reused and in terms of the approximate number of adult bees active per year. The data we report here, combined with emergence data in 1998 (127 bees emerged from nests, but no parasites, see Paxton et al. 1999), suggest that the four dipteran parasites, *L. personata*, *B. fimbriatus*, *Z. cinereum*, and *M. andrenae*, have little if any impact on the population dynamics of the host bee. This is all the more surprising given the low rate of reproduction of *A. agilissima* (Giovanetti and Lasso 2005). In addition to the above four Diptera, we only detected two individuals of the cleptoparasitic bee *Sphecodes* across 7 years of observation, which were anyhow not associated with *A. agilissima* nests. Westrich (1989, p 469) states that *Nomada melathoracica* and *Nomada lineola* are cleptoparasites of *A. agilissima* in SW Germany (Baden-Württemberg). We never detected any *Nomada* cuckoo bees at Colle Palombaia.

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