Zoological Studies **48**(2): 141-150 (2009)

Zoological Studies

Searching for the Right Target: Oviposition and Feeding Behavior in *Bombylius* Bee Flies (Diptera: Bombyliidae)

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(Accepted July 10, 2008)

Roberto Boesi, Carlo Polidori, and Francesco Andrietti (2009) Searching for the right target: oviposition and feeding behavior in *Bombylius* bee flies (Diptera: Bombyliidae). *Zoological Studies* **48**(2): 141-150. Bee flies (Diptera: Bombyliidae) are ectoparasitoids of larval stages of insects, often digger bees and wasps. We studied the behavior of 4 species of the genus *Bombylius* at a nest aggregation of their host bee, *Lasioglossum malachurum* Kirby, and at an adjacent feeding site. Although eggs were frequently thrown on vegetation patches, the number of eggs oviposited and the time spent in hovering flight were higher at host nest entrances. *Bombylius* females fed essentially on 3 (2 Caryophyllaceae and 1 Asteraceae) of 9 blooming plant species found in the area. Oviposition and feeding activities had different daily distributions. In general agreement with optimal foraging theories, *Bombylius* females exhibited the strongest interest in the predicted target, i.e., the host nest, and fed essentially on a few but highly exploited plants in the close vicinity of the host nesting site. http://zoolstud.sinica.edu.tw/Journals/48.2/141.pdf

Key words: Bee fly, Parasitoid, Nectar feeding, Host searching, Halictidae.

Bee flies (Diptera: Bombyliidae) have a virtually cosmopolitan distribution and are commonly found in warm arid to semi-arid habitats (Hull 1973, Evenhuis and Greathead 1999), where they can form a conspicuous part of the flower-visiting insect fauna (Toft 1983). Adults of larger species are powerful and agile fliers, rivaling hoverflies (Syrphidae) in their ability to hover and move in all directions while in flight. With many species possessing colorful patterns of stripes and spots on the wings and bodies, bee flies are often some of the most striking in appearance of all the Diptera. Larvae of all reared species of Bombyliidae are parasitoids (most often ectoparasitoids) or predators of other insects, primarily the immature stages of the large endopterygote orders of Coleoptera, Hymenoptera, Lepidoptera, Orthoptera, and Diptera. Despite their widespread and common occurrence at host aggregation sites, few studies have been carried out on the behavior of females during host searching activities, oviposition, and flower visitations. The genus *Bombylius* (one of the richest in the family with 278 recognized species (Evenhuis and Greathead 1999)) seems to be specialized in attacking bees, and much less commonly, wasps (Table 1). Brief descriptions of the oviposition patterns were reported for some species of the genus (reviewed in Andrietti et al. 1997 and Polidori et al. 2005). Past research showed that bee fly females apparently shoot their eggs toward any naturally occurring dark spot resembling a nest entrance at host nesting sites. For example, *Bombylius fimbriatus* Meigen parasitizing *Andrena agilissima* (Scopoli) was found to be unable to discriminate available targets at a bee nesting site (Andrietti et al. 1997). However, no statistical analysis was made to support those

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More information is available on flower visitation and feeding habits. Adults are nectar feeders, and females are obligate pollen feeders, obtaining pollen from anthophilous plants as a necessary requirement for nourishing developing eggs. The evolution of the family is considered to be connected to the evolution of spermatophytes (Ren 1998), and bombyliids are often the major pollinators of many flowering plants, especially those occurring in deserts. Some bee flies (in particular belonging to the tribe Anthracini) have been found to be specialists, feeding on a single species of plant (e.g., El-Moursy et al. 1999) (also *Bombylius anthophoroides* Hall & Evenhuis on *Trichostema lanceolatum* in California (Hall and Evenhuis 1980, Evenhuis, 1983)).

Bombylius bee flies are an important component of parasitic guilds found at bee nest aggregations (Paxton et al. 1996, Paxton and Pohl 1999, Polidori et al. 2005). Foraging activities of host and parasitoid populations are seasonally (and often daily) synchronized, particularly in temperate regions (Wcislo 1987); thus co-evolution of attack/defensive strategies are predictable for any association (the so-called “arms race”, Thomson 1994). On the other hand, mutualistic co-evolution between pollinators and plants is also constantly at work (Kevan and Backer 1983).

Herein, we report quantitative data on host-searching, oviposition, and adult feeding behaviors of 4 species of *Bombylius*, namely *B. posticus* Fabricius, *B. cinerascens* Mikan, *B. fulvescens* Wiedemann, and *B. canescens* Mikan, at a large nest aggregation of their host bee, *Lasioglossum malachurum* Kirby (Halictidae) in Italy. Host information is only available for *B. canescens*, including species of *Andrena*, *Lasioglossum*, *Halictus*, and *Odynerus* (Table 1). Considering the intimate relationships of bee flies with both host

Table 1. Review of host associations in the genus *Bombylius*. A, Andrenidae; C, Colletidae; H, Halictidae; V, Vespidae; Anth, Anthoporidae

Species	Host family	Host genera	No. of host species	References
Bombylius albicapillus Loew	H	*Halictus*	1	Cole and Lovett (1921), Eickwort (1985)
B. fimbriatus Meigen	A	*Andrena*	1	Andrietti et al. (1997)
B. posticus Fabr.	H	*Lasioglossum*	1	present work
B. canescens Mikan	H, A, V	*Lasioglossum, Andrena, Odynerus, Halictus*	4	present work, Ebejer (1988), Chapman (1878), Grandi (1957, 1961), Bonelli (1964), Yerbury (1902)
B.cinerascens Mikan	H	*Lasioglossum*	1	present work
B. fulvescens Meigen	H	*Lasioglossum*	1	present work
B. major L.	A, H, C	*Andrena, Halictus, Lasioglossum, Colletes*	15	Chapman (1878), Bishoff (2003), Eickwort (1985), Litt (1988), Paxton et al. (1996), Knight (1968), Paxton and Pohl (1999), Vereecken et al. (2006) Dufour (1858), Imhoff (1834), Perkins (1919), Vleugel (1947), Walrecht (1949, 1950)
B. vulpinus Wiedemann	A	*Panurgus*	1	Seguy & Baudot (1922), Schremmer (1964), Knerer & Plateaux-Quénu (1970)
B. minor (L.)	C, A	*Colletes, Andrena*	2	Neilsen (1903), Oldroyd (1969), Blair (1920), Schmidt-Goebel (1876)
B. pulchellus Loew	H	*Halictus*	1	Batra (1965), Packer (1988)
B. discolor Mikan	A	*Andrena*	3	Müller (1944), Ismay (1999), Perkins (1919), Brauer (1883), Walrecht (1949, 1950)
B. medius Linneaus	A	*Andrena*	1	Westwood (1876)
B. anthophorioides Hall & Evenhuis	Anth	*Anthophorus*	1	Hall and Evenhuis (1980)
B. duncani Painter	H	*Halictus*	1	Hall and Evenhuis (1980)
B. facialis Cresson	Anth	*Anthophora*	1	Hall and Evenhuis (1980)
B. sp. 1.	C	*Colletes*	1	Schmidt-Goebel in Riley (1881)
B. sp. 2.	H	*Halictus*	1	Bohart et al. (1960)
B. sp. 3.	C	*Colletes*	4	Batra (1980)

and plants, a general prediction is that, according to optimal foraging strategies (Krebs and Davis 1987), bee flies save time and energy 1) by discriminating the right target to oviposit and 2) by feeding mostly on flowers in the vicinity of a host's nesting site.

MATERIALS AND METHODS

Study area and focal sampling of activity

The study was carried out in Tuscany, central Italy, next to a little town (Alberese) inside Maremma Regional Park (Tuscany, Italy: 42°40'5''N, 11°6'23''E) from 18 May to 2 June 2004, during the period of foraging activity of the 1st matrifiliar worker phase of *L. malachurum* (Polidori et al. unpubl. data). The area is typically Mediterranean, with an average annual temperature around 14-15°C (7.1°C in Jan. and 23.1°C in Aug.); the average yearly rainfall is about 690 mm, with a maximum in Nov.-Dec. and a minimum in July-Aug.

A collection of 27 females of *Bombylius* spp. gave the following species frequencies: 7% *B. posticus*, 3% *B. cinerascens*, 77% *B. fulvescens*, and 11% *B. canescens*. Although individuals were not marked and observations are not referable to a species (we marked 20 females at the beginning of the study period but none of them was re-collected at the sites), *Bombylius* flies share most ecological traits, all attacking ground-nesting bees, and thus they probably evolved the same host-searching behavior; moreover, the species collected in our study have similar sizes (with a body length excluding the proboscis of about 7-9 mm), thus their feeding behaviors are also probably similar. For these reasons, we pooled the data and referred observations to the genus as a whole.

Through focal animal sampling (25 May-2 June), we followed and recorded the activity and behavior of bee fly females at 2 different sites about 50 m from each other: site A was an area of 100 x 100 m with grass and flowers, while site B corresponded to a large portion (100 x 2 m) of the host nest aggregation; thus, site A represented a feeding area, while site B was a foraging area. Site A was patrolled every day from 09:00 to 17:00 in search of a suitable bee fly to follow on flowers; when a female was detected, the behavior (number of flowers visited, frequency of visits to flowers, and duration of visits) was recorded until the fly disappeared from the observer's view. Data on flowering species present in the area were obtained by sampling the plant species and counting the number of plants per species in 37 random plots (1 x 1 m each). The height of the flowers of each species was also recorded by measuring at least 50 individuals (or fewer if the species was rare, see Table 2). Site B was patrolled from 09:00 to 17:00 in search of individuals engaged in host-searching or oviposition activities; when a female was detected, we recorded the number of eggs oviposited and the corresponding target (a nest, a vegetation patch, an area under a stone, or

Table 2. Availability of flowers and their exploitation by *Bombylius* spp. H, average height in cm (no. of records in parentheses); AB, abundance; [a]data lacking

	Species	H	AB (%)	Percent visits on flowers (N = 575)	Percent visits with feeding	Percent flower component in diet	Flower color
1	*Chrysanthemum clausonis* (Pomel) (Asteraceae)	36.04 (162)	38.21	3.30	26	1.37	yellow
2	*Petrorhagia prolifera* (L.) (Caryophyllaceae)[a]	39.30 (69)	5.29	30.61	64	30.77	violet
3	*Linum bienne* Miller (Linaceae)	20.75 (52)	0.43	4.52	65	4.67	violet
4	*Matricaria inodora* L. (Asteraceae)	15.78 (68)	28.21	1.91	46	1.10	white/yellow
5	*Tuberaria guttata* (L.) (Cistaceae)	28.35 (72)	4.87	5.57	19	1.65	yellow
6	*Hieracium* sp. (Asteraceae)[a]	17.89 (62)	17.15	33.74	70	37.36	yellow
7	*Silene neglecta* Ten. (Caryophyllaceae)[a]	21.80 (54)	1.36	17.74	75	20.88	violet
8	*Centaurium maritimum* (L.) (Gentianaceae)	14.38 (66)	2.26	0	0	0	yellow
9	*Anagallis arvensis* (blue var.) L. (Primulaceae)	7.86 (76)	1.55	0	0	0	blue
10	*Anagallis arvensis* (red var.) L. (Primulaceae)	5.32 (110)	0.10	0	0	0	red
11	*Geranium dissectum* L. (Geraniaceae)	23.26 (46)	0.03	0	0	0	violet
12	*Consolida regalis* Grey (Ranunculaceae)	[a]	0.53	1.57	56	1.37	violet
13	*Sherardia arvensis* L. (Rubiaceae)	[a]	[a]	1.04	50	0.82	blue

a fracture of the ground), and the duration of hovering flights on the targets when possible. The area, where many (> 100) nests of the fossorial bee host were scattered in plots, was divided by a mesh into 24 plots of 3.5 x 2 m. In each plot, we recorded the number of open nest entrances, the vegetative coverage (as a percentage of the entire plot), the number of stones (those with at least one of the dimensions of > 5 cm), and the number of flowers in blossom. All behaviors were recorded on a portable tape-recorder by following a focal individual, until it disappeared from the observer's view. Independent observations were carried out from 09:00 to 17:00 on 10 nests of *L. malachurum*, in order to obtain the daily provisioning patterns of the host bee; during these periods, all the entrances of workers with pollen were recorded.

Statistical analysis

Data analysis was performed using non-parametric statistics (χ^2 test, Spearman correlation test, Mann-Whitney test, Kruskall-Wallis test, and Kolmogorov-Smirnov test) and parametric ones (Student's *t*-test and analysis of variance (ANOVA)). A multiple linear regression analysis (ANCOVA) was performed to test the influence of variables (vegetative cover on the surface of the plots, time of day, the presence of stones on the ground, the number of flowers in blossom per plot, the time of hovering flight on each target, and the number of open host nests) on the frequencies of oviposited eggs on each target. A binary logistic regression was carried out to test which variable (time of day and plant species) affected the probability of a plant being chosen. In the text, average numbers are given as ± standard deviation (SD).

RESULTS

Host searching activity and oviposition behavior

Seventy-six focal observations were performed. Individuals at the host nesting site were observed mostly between 11:00 and 14:00 (71%); between 12:00 and 14:00, we observed the highest average number of oviposited eggs (11.5 ± 13.45/min) (Figs. 1B, C). Host bees provisioned their nests mostly in the late morning and early afternoon (Fig. 1D). Data analysis showed that vegetation was the most chosen target (with 1.19 ± 1.52 hovering flights/min) (Fig. 2A), more than twice those of other targets (Kruskall-Wallis test: $\chi^2 = 28.37$, *d.f.* = 3, $p < 0.001$). Stones were chosen with a frequency of 0.62 ± 0.81, nests of *L. malachurum* with a frequency of 0.51 ± 0.85, and ground fractures with a frequency of 0.37 ± 0.89 (Fig. 2A).

The average number of eggs oviposited in a nest/min was 4.25 ± 9.14, while it was 2.14 ± 2.45 on vegetation, 1.27 ± 1.91 on stones, and 0.76 ± 2.33 in ground fractures (Kruskall-Wallis test: $\chi^2 = 25.43$, *d.f.* = 3, $p < 0.001$) (Fig. 2B).

The probability of a fly ovipositing more than 1 egg when it hovered near a nest entrance was higher than when it hovered near other targets ($\chi^2 = 19.45$, *d.f.* = 1, $p < 0.001$). The average time spent hovering at a nest (average, 23.4 ± 34.4 s) differed from the time spent on the other (pooled) targets (average, 7.6 ± 8.2 s) (Student's *t*-test: $t = 3.52$, *d.f.* = 123, $n_1 = 63$, $n_2 = 62$, $p < 0.001$), and durations were differently distributed between nests and other targets (Kolmogorov-Smirnov test: D = 0.46, $n_1 = 63$, $n_2 = 62$, $p < 0.001$) (Fig. 2C). Considering the 2 most frequently chosen targets, the average number of eggs oviposited during a hovering flight was higher towards nests (7.91 ± 17.16) and lower towards vegetation (2.4 ± 1.9) (Mann-Whitney test: U = 4766, $n_1 = 79$, $n_2 = 95$, $p < 0.01$. Fig. 2D), and the same appeared to occur when considering the number of oviposited eggs/min during a hovering flight (Mann-Whitney test: U = 1235, $n_1 = 79$, $n_2 = 49$, $p < 0.001$. Fig. 2B).

Considering all feasible variables (e.g., vegetative cover of the plot, time of day, stones in the plot, the number of flowers in blossom in the plot, the durations of hovering flight on the 4 targets, and the number of open nests in the plot), we found that the number of oviposited eggs seemed to be correlated with the time of day and the time of hovering flight (model goodness of fit: ANCOVA, *d.f.* = 121, $r = 0.735$, $p < 0.001$; significance of time of day: $p = 0.006$; significance of hovering flight: $p < 0.001$), but was not dependent on other traits. Moreover, considering all variables but the previous significant ones, a positive association was observed between the number of eggs and the target "nest" (model goodness of fit: ANCOVA, *d.f.* = 121, $r = 0.37$, $p = 0.017$; significance oft "nest" category: $p = 0.007$).

Activity on flowers and feeding behavior

During this study, *Bombylius* females were followed 58 times during their feeding activity. Individuals on flowers were observed mostly between 09:00 and 11:00 (38%, *n* = 58) and between 13:00 and 16:00 (26%) (Fig. 1A).

Thirteen plants were observed to be in blossom in the area (Table 2), of which 9 (69%) were observed to be visited by flies. The most frequently visited flowers were *Petrorhagia prolifera* (L.) (Caryophyllaceae) (30.6%, *n* = 575), *Silene neglecta* Ten. (Caryophyllaceae) (17.7%), and *Hieracium* sp. (Asteraceae) (33.7%) (Table 2). All other flowers accounted for < 6% each. Three available species were never observed to be visited by flies: *Centaurium maritimum* (L.) (Gentianaceae), *Geranium dissectum* L. (Geraniaceae), and *Anagallis arvensis* L. (Primulaceae) (the last present in 2 flower varieties of blue and red). The time spent on flowers was analyzed only when all durations of events in a focal sampling were recorded (Fig. 3), and the analysis of weight of each time component on the whole feeding activity (i.e., the time spent on each plant species visited) showed that *P. prolifera* (*n* = 31, average time component of 17%; average, 19.4 s), *Hieracium* sp. (average time component of 10%; average, 35 s), and *S. neglecta* (average time component of 9%; average, 21s) were the species females visited for longer periods (ANOVA,

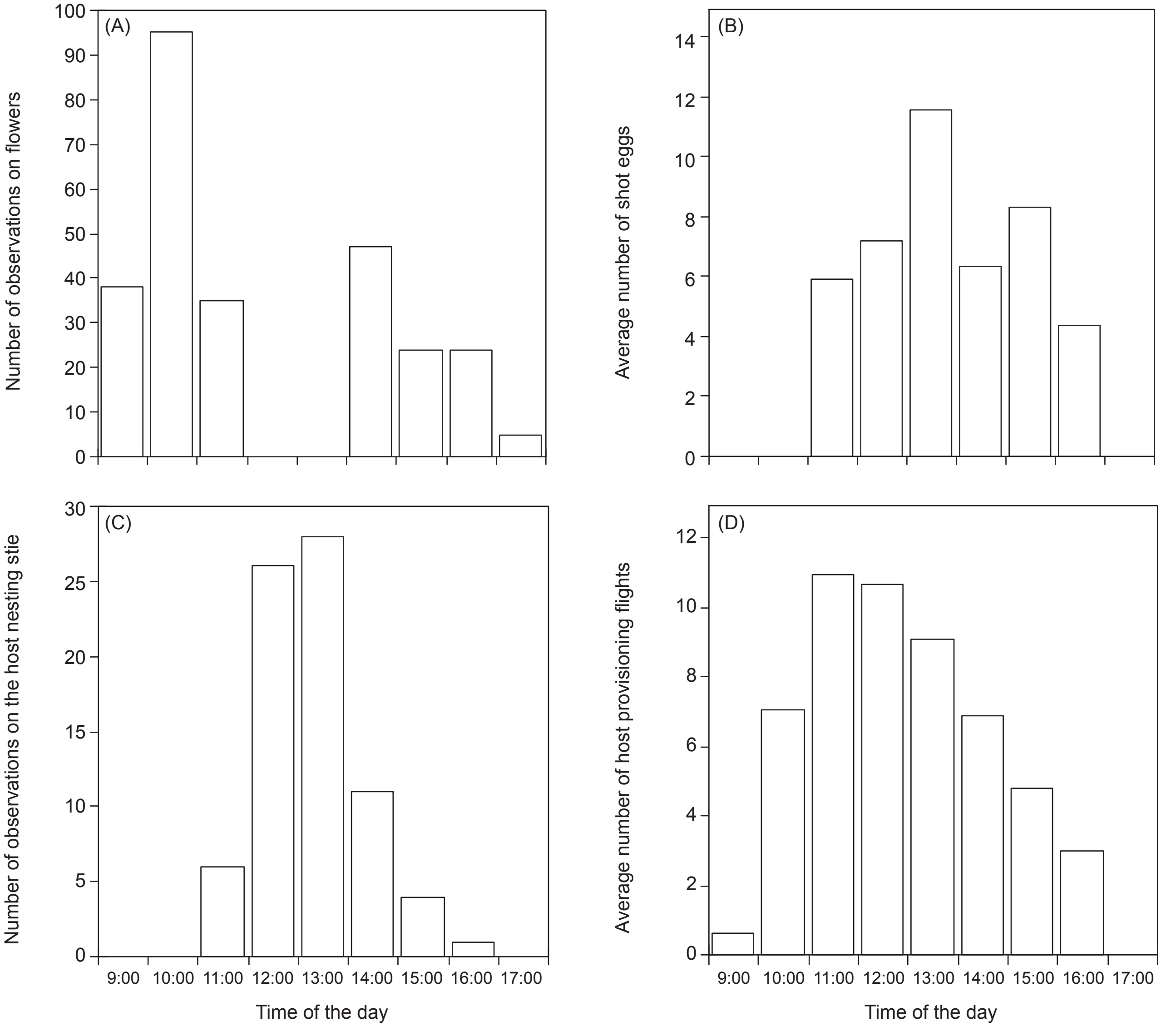

Fig. 1. Daily distribution of records on flowers (A), of the number of ovipositions (B), at the host nesting site (C), and of the provisioning flights of the host bee (D).

$d.f. = 6$, $F = 2.1$, $p < 0.001$) (Table 2).

Considering the most abundant plant species at the site (1-7 in Table 2) and the time of day, we noted a positive correlation between species number 2, 3, 6, and 7 and a positive feeding event (model goodness of fit: logistic regression, $d.f. = 7$, $r^2 = 0.1$, $p < 0.001$; significance of species: *P. prolifera* (2), $p = 0.009$, *Linum bienne* Miller (3), $p = 0.005$, *Hieracium* sp. (6), $p < 0.001$, and *S. neglecta* (7), $p < 0.001$).

When a plant species was chosen much more than 1 time in a sequence, we considered it to be offering a significant nectar reward that eventually led the individual to choose the same species for the next plant visit. Analysis of sequences showed that flowers of *P. prolifera*, *Hieracium* sp., and *S. neglecta* were chosen for most sequences (83%, $n = 93$); the length of these sequences (number of times an individual stopped consecutively on the same species) ranged 2-20 (Fig. 4).

One individual was observed to stop 23 times on a plant, hovering in place until the following flight without feeding. The average time of a visit was 62.14 ± 76.2 s ($n = 22$). One time, at about 09:00, an individual rested on a blade of grass for more than 50 min while on another occasion, at about 17:00, an individual rested on vegetation for 46 min (then the observation concluded for that individual). The average height of points where females rested was 4.35 ± 1.3 cm. Finally, an almost significant positive correlation was found between the average height of flowers per species and the corresponding frequency of visits by flies (Spearman test: $r = 0.56$, $n = 11$, $p = 0.06$).

DISCUSSION

The genus *Bombylius* contains over 270 species found in all biogeographic regions except Australasia (Evenhuis and Greathead, 1999), reaching their highest diversity in and around regions with a Mediterranean climate. Although they represent a very diverse group of flies, their behavioral ecology is poorly known, with most data concerning host associations and flowers visited for nectar feeding (Hull 1973). Thus, any contribution that more-thoroughly analyzes the biology of the species can be useful in ascertaining the behavioral co-evolution between bee flies and their exploited resources (hosts and plants). In fact, both pollination and parasitism are known to evolve accurate adaptations and counter-adaptations (Thompson 1994). Taking

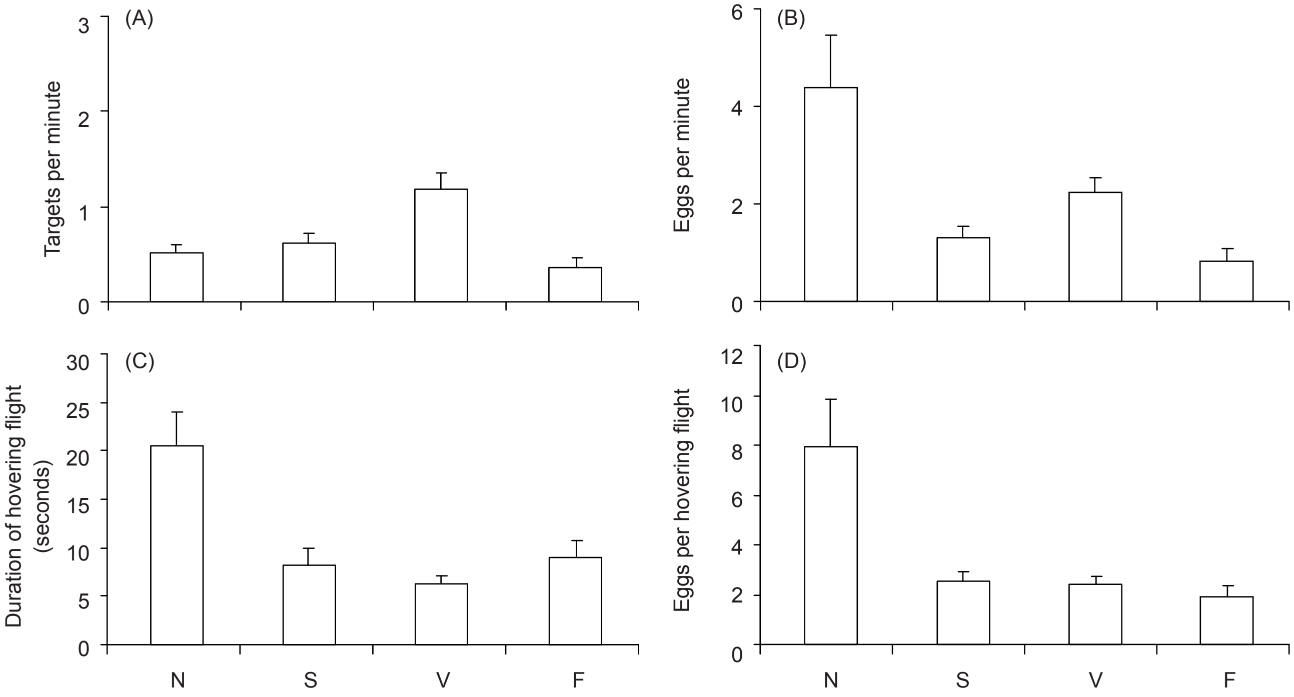

Fig. 2. Average number of chosen targets/min (A), average number of eggs shot/min (B), average length of hovering flight on targets (C), and average number of shot eggs per hovering flight on a target (D). N, nest; S, stones; V, vegetation; F, earth fractures. Bars are drawn as + S.E.

into account both these intimate relationships, as stated above in the “Introduction”, one also could predict that bee flies should discriminate the right target toward which to oviposit and should feed mostly on flowers in the vicinity of a host nesting site (optimal foraging strategies; Krebs and Davis 1987).

All larvae of bee flies parasitize immature stages of other insects. Despite the possibility that competition for nectar and pollen may therefore be unimportant for bee flies, community patterns contradict this hypothesis (Toft 1983 1984a). Although we analyzed the 4 species of *Bombylius* collected at the site as a whole, we have no apparent reasons to predict important differences in their species biology. Toft (1984b) showed that 2 species of *Lordotus* allocated time and energy differently when feeding, but in that study, the species greatly differed in size and in their behavior on flowers; in our study, the sizes of the species were similar, and no differences in behavioral sequences were evident. Moreover, Toft (1984b) showed that adults of *Lordotus* spp. spend a large proportion of time feeding, further supporting the importance of food resources for adult bee flies, of at least some species. In our study, about 1/2 of the daily activity period of the flies seemed to be devoted to feeding on flowers. Interestingly, feeding occurred mostly at hours when females were not engaged in host searching, in this way, probably optimizing the energy to be spent on these 2 main activities of their adult life. Female *Bombylius* individuals visited flowers for nectar early in the morning and late in the afternoon, i.e., when the host bee was not provisioning or scarcely provisioning their nests. In particular, between 09:00 and 11:00 and after 17:00, flies were recorded only on flowers; most records of flower visitations occurred in the morning, when it is known that most flowers (at least those selected by females) produce the most nectar (Kevan and Backer 1983), while later in the afternoon, they may return to flowers perhaps because they represent rendezvous or lekking sites, as occurs in other bombyliids (e.g., Johnson and Dafni 1998). A similar kind of daily distribution of feeding was recorded for *B. fimbriatus* (Polidori et al. 2005), which seemed to forage a little earlier than it was observed ovipositing on the bee host nesting site, and returning, less frequently, to flowers in the afternoon. Contrarily, the overlap between the host searching activity and provisioning activity of the bee host apparently should not be dependent on a higher probability of finding a suitable host at those hours. In fact, bee fly females seem to fly in search of host nests regardless of their actual content (note that despite the fact that most immature bee flies accept only mature larvae, pre-pupae, or pupae, young immature bee flies can also feed on pollen stores (Yeates and Greathead 1997)). During this study period (May) at this latitude, nests of *L. malachurum* consist of a mixture of fresh pollen masses, eggs, larvae, prepupae, and pupae (Polidori et al. unpubl. data, Wyman and Richards 2003). Another hypothesis is that *Bombylius* females use an additional visual cue to select the right target on which to oviposit (the nest), i.e., the bees continuously entering and exiting their nests while provisioning. Other natural enemies seem to use such indirect cues to locate

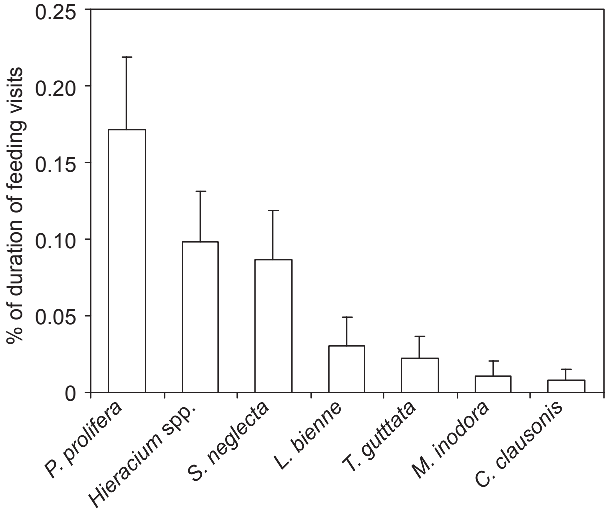

Fig. 3. Duration of feeding visits on flowers, in decreasing order. Bars are drawn as ± S.E.

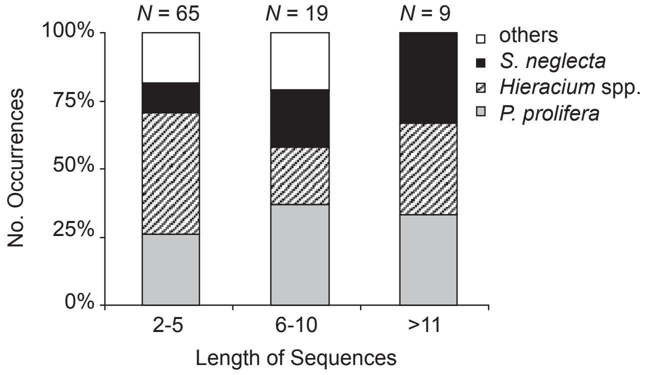

Fig. 4. Number of observations of feeding flights of a given length (number of times an individual stopped consecutively on the same species).

provisioned nests, and return later in the absence of the owners (Rosenheim 1987). At least 1 bombyliid genus, *Antonia*, has been reported to follow closely behind host wasps of the genus *Bembix* and *Sceliphron* (Hesse 1956, Greathead 1967), thus most likely using such visual cues to locate host nests. Moreover, bee flies, which do not physically enter a host nest but simply oviposit eggs near or in the entrance while hovering, should not have problems of direct, agonistic encounters with the hosts. Once an egg is laid near the nest entrance, the 1st instar planidial larva, which is narrow-bodied, actively searches for a host brood cell in the nest (Gerling and Hermann 1976).

Those findings agree with our results, which clearly showed that *Bombylius* females are able to discriminate, although not always with great accuracy, between the right target (the host nest) and other possible, confounding targets present at a nesting site (vegetation, ground fractures, and stones). This is true considering that individuals spent a longer time in hovering flight on the “nest entrance” target, ovipositing a higher number of eggs despite what they did on other targets and, finally, they oviposited a higher number of eggs/min during a focal. To our knowledge, this is the first evidence of such discrimination. For example, *B. fimbriatus* was not found to be capable of discriminating available targets at the nesting site of its host bee, *A. agilissima* (Andrietti et al. 1997), and the same occurred for *Heterostylum robustum* (Osten Sacken), a natural enemy of the alkali bee *Nomia melanderi* Cockerell, which was seen to oviposit into man-made depressions in the ground adjacent to bee nests (Bohart et al. 1960). However, we also found that the number of times vegetation was chosen as target in a focal was highest, suggesting an evidently important confounding effect of such visual stimuli, in agreement with what was previously observed in the above-cited works. Although a better discriminatory power clearly reduces the number of eggs lost far from host nests, it is also true that egg production in the Bombyliidae may be prodigious (up to about 1000-3000 eggs/d (Bohart et al. 1960, Marston 1964, Gerling and Hermann 1976), and thus the percentage of eggs effectively oviposited on wrong targets should not adversely affect the reproductive success of these species. In fact, some bombyliid flies can be the main cause of a decline in host populations (Bohart 1960, Bishoff 2003).

In accordance with what was previously observed in various species of the family (Kastinger and Weber 2001), bee flies in our study visited plants of different families, but preferred groups with hypocrateriform, tubular, disk, and lip flowers. Bee flies seem to use visual cues when selecting a flower: selected experiments on *Usia bicolor* Macquart, for example, showed that flies strongly preferred models with a dissected outline over models with a simple outline, pink models over other colors, and larger models over smaller models (Johnson and Dafni 1998). The preferred colors found in our study differed somewhat from what has been previously observed in other species: in fact, in our study *Bombylius* females chose plants with violet flowers more frequently (already shown to be preferred by most species) but also those with yellow flowers (supposed to be much less attractive according to Kastinger and Weber (2001)). We also observed that a bee fly that visited a given plant tended to make the subsequent visit at another flower of the same plant, suggesting that exploitation of nectar may follow a short-term learning path. Grimaldi (1988) observed that *Bombylius major* L. and *B. pygmaeus* Fabricius, the main pollinators of the distylous *Hedyotis caerulea* (L.) (Rubiaceae) visited most of the flowers in a bluets patch in just 2 d, revealing a great constancy in plant choice.

Finally, preliminary data on the most exploited plant families by *L. malachurum* (Polidori et al., unpubl. data), revealed a relatively weak overlap with those exploited by *Bombylius* spp.: in fact, bee workers mostly visited Asteraceae (also exploited by bee flies) but very rarely Cariophyllaceae (abundantly exploited by bee flies); this contrasts with what was observed in *B. fimbriatus*, which fed on *Sinapis arvensis* L. (Polidori et al. 2005), which was also one of the main species visited by its oligolectic bee host *A. agilissima* (Giovanetti 2007). Bee flies were often recorded visiting the Cariophyllaceae (Kephart et al. 2006), with 2 species of *Silene* (the same genus exploited by *Bombylius* spp. in our study) almost exclusively visited by these flies (Talavera et al. 1996).

In conclusion, our observations show general agreement with optimal foraging theories, of *Bombylius* females exhibiting the strongest interest in the predictable target, i.e. the host nest, and feeding essentially on a few but highly exploited plants in the close vicinity of a host nesting site.

Acknowledgments: Thanks are due to the late D. Greathead, who kindly determined the specimens and gave many suggestions on an early draft of the manuscript, and we dedicate this paper to his memory. Many suggestions came also from N. Evenhuis. We are indebted to A. Ebmer, who determined the host bee, to F. Mosiewicz for help in collecting field data, and to M. Brambilla for help with the statistical analysis. We thank the Maremma Regional Park for kind support. This work was supported by a 3-yr grant (RBAU019H94-001) from Fondo per gli Investimenti della Ricerca di Base (2001).

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