

Differential distribution of resources for females on a dioecious plant affects the small-scale distribution of male of an oligolectic bee

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Abstract

Differential distribution of resources for females on a dioecious plant affects the small-scale distribution of male of an oligolectic bee. Females of the solitary digger bee *Andrena florea* Fabricius, 1793 (Hymenoptera, Andrenidae) nest in aggregations and collect pollen almost exclusively on dioecious plants of the genus *Bryonia*, making this species a good model to study the relationship between nest density, male density, male behaviour and female lecty. At a study site in the valley of the river Serio, in Italy, an aggregation of this bee showed low density of randomly distributed nests and was closely surrounded by *B. dioica* plants. Female nectar foraging and male feeding and mate-searching activity, confined to the host plants, peaked at similar hours across the day, while female pollen foraging peaked earlier. Males fed on plants of both sexes but seemed to perch waiting for females more frequently on male *B. dioica* leaves. Individual males more often visited only one of the male plants, for up to four days; here they did not interact aggressively with conspecifics, suggesting scramble competition in resource-based home ranges and not territoriality. These findings are preliminarily in accordance with the predicted resource-based rendez-vous sites at low nest density for oligolectic bees and the predicted occurrence of scramble competition in case of high male density. Additionally, males would maximize their mating opportunity by mainly perching on male plants, the only source of the most limited resource for females (pollen).

Key words: Mating strategy, Digger bee, Dioecious plant, *Bryonia*, *Andrena*, Andrenidae

Resumen

Las diferencias en la distribución de los recursos para las hembras, en una planta dioica, afectan a la distribución a pequeña escala de los machos de una abeja oligoléctica. Las hembras de la abeja excavadora solitaria *Andrena florea* Fabricius, 1793 (Hymenoptera, Andrenidae) anidan en agregaciones y recolectan polen casi exclusivamente de las plantas dioicas del género *Bryonia*, lo que hace de esta especie un buen modelo para estudiar la relación entre la densidad de nidos, la densidad de machos y su comportamiento y la especialización trófica de las hembras. En una localidad del valle del río Serio, en Italia, se estudió una agregación de esta abeja con una baja densidad de nidos distribuidos al azar y rodeada muy de cerca por plantas de *B. dioica*. Las actividades de alimentación y de búsqueda de pareja de los machos, que se realiza solo sobre las plantas hospedadoras, y la actividad de recolección de néctar de las hembras alcanzaron su máximo en horas similares a lo largo del día; no obstante, la recolección de polen, realizada por las hembras, alcanzó su máximo en horas más tempranas. Los machos se alimentaban en plantas de ambos sexos, pero aparentemente se posaban con mayor frecuencia en las hojas de las plantas masculinas de *B. dioica* para esperar a las hembras. Los machos visitaron más frecuentemente solo una de las plantas masculinas, donde llegaban a permanecer hasta cuatro días y donde no interactuaron entre ellos de manera agresiva, lo que sugiere competencia por acaparamiento en las áreas de distribución determinadas por los recursos y no territorialidad. En principio, estos resultados coinciden con la predicción de que los encuentros tendrían lugar en sitios donde se encuentran los recursos y la densidad de nidos es baja en el caso de las abejas oligolécticas, y con la predicción de competencia por acaparamiento cuando la densidad de machos es elevada. Asimismo, los machos aprovecharían al máximo su oportunidad de apareamiento principalmente visitando plantas masculinas, que son la única fuente del recurso más limitante para las hembras (polen).

Palabras clave: Estrategia de apareamiento, Abeja excavadora, Planta dioica, *Bryonia*, *Andrena*, Andrenidae

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Introduction

Behaviour of male bees (Apoidea) has been studied in many species, showing that they use a wide range of behavioural strategies to find mates (reviewed in Alcock et al., 1978; Eickwort and Ginsberg, 1980; Ayasse et al., 2001; Paxton, 2005). Such strategies are mainly driven by the fact that females select males to maximise their individual reproductive success, and by the fact that receptive females, which are generally prone to mate only for a short time after emergence, are a major limiting resource (Alcock et al., 1978). According to these considerations, the evolution of mating strategies in bees is expected to be driven, and thus somehow predicted, by three factors: the distribution in space and time of receptive females; the ratio of males over females; and female reproductive life–history (Ayasse et al., 2001; Shuster and Wade, 2003; Paxton, 2005).

Regarding the first factor, if females nest in dense aggregations, males are expected to find a partner at nesting sites, while if females nest in low–density, males should look for a mate on flowers (resource sites) or non–resource sites (Alcock et al., 1978; Ayasse et al., 2001) (fig. 1). In reference to the second, male scramble competition (i.e. patrolling the areas visited by females without establishing territories) would be favoured if male density is high, while male territoriality would be favoured if male density is low (Paxton, 2005), with males in the former showing no fixed home ranges and males in the latter case showing defined territories that are actively defended from conspecific competitors (fig. 1). And in reference to the third factor, if the level of specialization of pollen resource by females is taken into account, at low female (nest) density, males of oligolectic bees would use resource–based rendez–vous sites while males of polylectic bees would use non–resource based sites (Paxton, 2005) (fig. 1). This is because receptive females of oligolectic species more predictably aggregate at their host flowers whereas females of polylectic species are more likely to disperse widely across flowering plant species (but see exceptions in Westrich, 1989; Danforth, 1991; Seidelmann, 1999). Thus, the different combinations of these traits lead to different outcomes in male behaviour: 1) when nest density is high and male density is low, male territoriality is expected at the nesting site; 2) when nest density is low and male density is high, male scramble competition at resource–based sites (in case of oligolectic species) or at other sites is more likely; and 3) when nest density is low and male density is low we can expect male territoriality at resource–based sites (in case of oligolectic species) or in other sites (in case of polylectic species) (fig. 1).

Although these predictions have generally been confirmed by comparative analyses of literature data (see above), particular situations have been poorly studied in detail. For example, it is still little known whether, in the case of oligolectic bee species foraging on plant species presenting individuals of different sexes (dioecious), males would equally patrol/control both male and female plants, or whether there is a bias towards the male plants, because they reward the most limited

resource for females (pollen) (fig. 1). Increasing our knowledge on specialized bee behaviour is important for conservation plans, particularly because pollinators that rely on few plants for their resources have declined impressively in the last years (Memmott et al., 2004).

Here, we report observations on the behaviour of males and females of the solitary digger bee, *Andrena florea* Fabricius (Andrenidae), an oligolectic species whose females collect pollen almost exclusively from the delicate white blossoms of bryony (*Bryonia*, Cucurbitaceae), a genus of dioecious plants (Westrich, 1989; Schröder and Lunau, 2001) and –though more rarely– from species of *Ecballium*, the sister genus to *Bryonia* (Dukas, 1987).

Andrena florea belongs to one of the richest bee genera (roughly 1300 species worldwide, Gusenleitner and Schwarz, 2002; Michener 2007). It is a univoltine species in Central and Southern Europe on flight from May to June, with males emerging some days earlier than females (Westrich, 1989). Females are solitary and dig nests in the soil at variable distances from their plant hosts (Edwards and Williams, 2004). While females are strictly associated with *Bryonia*, males have been observed on this plant but also on plants belonging to other genera, such as *Echium*, *Rubus*, *Crataegus*, *Hieracium* (Gadoum and Didier, 2008) and *Lithospermum* (Baldock, 2008). Because males have been sometimes observed in large numbers on these plants, it has been suggested that they could be mating sites (Baldock, 2008). Although the mating system of a number of species of *Andrena* Fabricius, 1775 was studied in detail (e.g. Westrich, 1989; Paxton and Tengö, 1996; Paxton et al., 1999), as far as we know, no detailed information is available on *A. florea* mating strategy, the object of the present study. Additionally, given the pronounced oligolecty of the studied bee species and the reproductive biology of *Bryonia*, we argue that males would visit the male plants rather than the female plants, because female bee are likely to be more aggregated on plants that offer their most limiting resource (pollen).

The aim of this study was to study behavioural aspects that could be relevant to the better understanding of the mating strategy of *A. florea*, and used for future tests of the predictions presented above on mating strategy. In particular, in order to evaluate the presence of territoriality or scramble–competition, we evaluated: 1) female nest aggregation size and spatial arrangement of nests; 2) female pollen and nectar foraging on plants throughout the day and in relation to the number of flowers; 3) male foraging and perching on leaves of plants throughout the day and in relation to the number of flowers; and 4) behaviour of marked males on plants,

Material and methods

Field data collection

The field study was conducted at the 'Stazione Sperimentale per la Conservazione Della Flora di Pianura', in the 'Castelleone wood', an area of ca. 15 ha, 55–64 m a.s.l. in the valley of the river Serio

(45° 18' 0" N, 9° 46' 0" E). The area has the typical climate of the Padana plain, with cold winters (1.5 °C on average in January), hot summers (24 °C on average in July) and generally high air humidity. Rainfall is 600–1,000 mm/year and rather evenly distributed during the year, with July and February being the months with the least rain and October the wettest month (100 mm). In a path leading into the wood, a small nest aggregation of *A. florea* (21 nests in about 15 m² at the end of the study) was found in the proximity (about 30 m from its far northern edge) of about ten of *B. dioica* plants, arranged in a row.

Field observations were carried out from 28 April to 2 May 2004 at the bee nesting site, and from 3 to 13 May 2004 in front of four *B. dioica* plants, two male plants and two female plants, at about 1–2 m distance from each other.

At the nesting site, the number of nests of *A. florea* was counted and the nest coordinates were recorded in a Cartesian system (error: ± 0.5 cm) with the help of a 1 m x 1 m mesh mounted on the ground (Polidori et al., 2006, 2008).

Regarding the plants, we counted the total number of flowers for each plant on the first and last day of the study. We also calculated the mean and used this as an estimate of plant size. A total of 20 male bees were netted on plants, individually marked on the thorax using a combination of colours with non-toxic paint (Uni-Posca®), and then released. During the observations on plants, consisting of 15-min observations for each plant each hour from 9:00 to 18:00 (GMT), we recorded the following events: 1) male feeding (marked and not marked males landing on a flower and feeding on nectar; 2) male perching (marked and unmarked males landing on a leaf and staying there for at least 5 seconds); and 3) female foraging (females landing on a flower and gathering pollen or nectar). While it was easy to score whether a female bee foraged on pollen because of its presence on the scopae, we could not distinguish whether pollen-foraging bees were also collecting nectar. Thus, we could only separate nectar foraging from pollen or pollen + nectar foraging (hereafter: pollen foraging). For marked males, we recorded the number of days they were recaptured on each of the four plants. In this case all the observations for each male (feeding and perching) were pooled for the analysis.

Statistical analysis

For each nest at the aggregation, we calculated the distance to the nearest nest (nearest neighbour distance, NND). We then obtained nest density by dividing the total number of nests by the nesting area (a rectangle including all nests and a buffer of 10 cm from the extreme nests on all directions). We used Ripley's *K*-distribution (or *K*-function) (Ripley, 1976) to analyse the spatial distribution of nests. The *K*-distribution is the cumulative frequency distribution of observations at a given point-to-point distance (or within a distance class). Because it preserves distances at multiple scales, Ripley's *K* can quantify the intensity of patterns at multiple (different distan-

ces/scales) scales. Ripley's analysis was performed using the Duncan program (Duncan, 1991) and the results obtained were transformed following the function $L(t) = (K(t)/\pi)^{1/2} - t$, where t is the spatial step (scale; in this study 25 cm) with which the test was performed (Haase, 1995). If the observed $L(t)$ curve stays above the upper envelope of the expected curve for randomness for a given distance (step), the distribution is clumped (nests are in clusters), while if it stays below the lower envelope, the distribution is regular (nests are dispersed).

The behavioural data were analysed using non-parametric statistics because conditions for parametric tests were not met. The difference in male activity (number of records for feeding or perching) between the four observed plants was tested using the χ^2 -test. Differences in the hourly distribution of the frequency of female nectar feeding, female pollen foraging, male nectar feeding and male perching were tested using Kruskal–Wallis followed by multiple pairwise comparisons using Dunn's procedure. We used the

The Spearman test was used to verify the linear correlation between the number of perching records and the number of perched plants across marked males.

Results

Nest density in the aggregation was 1.5 nests/m², and nests were randomly distributed within the area, as the $L(t)$ function fell within the confidence envelope at all steps (fig. 2A–2B). Females were frequently seen at nest entrance (fig. 2C) or returning to the nests after a foraging trip, but no males were observed on the nesting site.

Bryonia dioica plants observed in this study contained from 17 to 59.6 flowers each (average of the first and last counts) and were visited frequently by males and females of *A. florea* (119–429 contacts in total during the study, 19.8–71.2 contacts per day). The most commonly observed behaviour was male feeding ($n = 429$), followed by male perching ($n = 188$) and female foraging ($n = 119$), particularly nectar-only feeding ($n = 98$). The distributions of these activities across the hours of the day were roughly similar, starting at 10:00, peaking at mid-day, and stopping after 17:00 (fig. 3). A closer inspection revealed, however, that female pollen foraging peaked between 11:00 and 12:00 and female nectar foraging peaked between 13:00 and 15:00 (fig. 3). On the other hand, male perching activity spanned the largest temporal window during the day (12:00–16:00), while males fed more frequently between 13:00 and 15:00 (fig. 3). Median values for periods of activity were invariably 14:00 for all groups with the exception of female pollen foraging, which had a median of 12:00 (fig. 3), and a Kruskal–Wallis test revealed that overall activity of females and males largely overlapped during the day, but female pollen foraging occurred significantly earlier ($K = 31.3$, $21 < n > 429$, $df = 3$, $P < 0.0001$; multiple pairwise comparisons using Dunn's procedure: $P < 0.0001$ between pollen foraging and all the others categories, and $0.33 < P > 0.81$ between all the other pairs of categories).

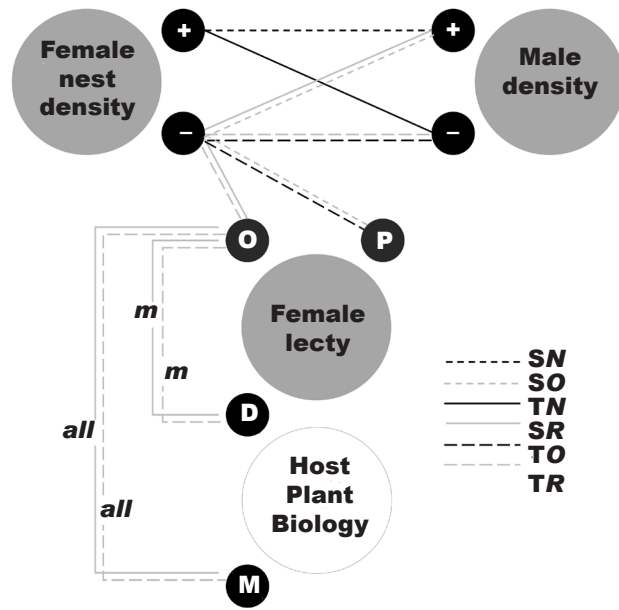


Fig. 1. Schematic representation of the expected relationships between female nest density, male density, male behaviour (S, scramble competition; T, territoriality), female lecty (O, oligolectic; P, polylectic) and plant reproductive biology (M, monoecious; D, dioecious). Rendez-vous can occur at the female nesting site (N), at resource-based sites (R), or in other sites (O). In case of R-sites, rendez-vous can occur mostly on male plants (m) or plants of both sexes (all). See text for details.

Fig. 1. Representación esquemática de las relaciones esperadas entre la densidad de nidos de las hembras, la densidad de los machos, el comportamiento de los machos (S, competencia por acaparamiento; T, territorialidad), la especialización en el uso de las plantas por parte de las hembras (O, oligoléctica; P, poliléctica) y la biología reproductiva de la planta (M, monoica; D, dioica). Los encuentros entre machos y hembras pueden ocurrir en el sitio de anidación de las hembras (N), en sitios donde se encuentran los recursos para las hembras (R) o en otros lugares (O). En el caso de sitios R, los encuentros pueden ocurrir principalmente sobre plantas masculinas (m) o sobre plantas de ambos sexos (all). Véase el texto para obtener información detallada.

We recorded a total of 103 and 16 female visits, respectively, on male plants and female plants, and a total of 472 and 145 male visits, respectively, on male plants and female plants. Male feeding and male perching (fig. 4A) both seemed to be most abundant on the male plant with the greatest number of flowers (about 59) (fig. 4B). The χ^2 -test showed that the numbers of both perching and feeding were significantly higher on that male plant ($\chi^2 = 22.02$ and $\chi^2 = 35.07$, respectively ($df = 3$)). The other three plants had a similar number of flowers (about 17–21) and were visited by males with similar frequency (fig. 4B). Males may prefer male plants over female plants because they are the only sex providing pollen for female bees, or because they simply aggregate on plants with more flowers to feed on. Although our sample size was too small to test for either possibility, males still seemed to perch more on male plants once having taken into account the number of flowers *per* plant; the number of perching records on male plants (*per* flower) was almost four times

higher than that on female plants (4.21 vs. 1.24). On the contrary, males seemed to feed more equally on both male (8.14) and female (5.82) plants.

Some of the 20 marked males seemed to have a clear preference for one of the two male plants observed during the study (fig. 5). In particular, six males were recorded on a single plant (or almost on a single plant, > 90 % of records) for at least three days (up to four days) (fig. 5). Ten additional males were only recorded on one or two days, and always on a single plant, while the remaining four males were observed shifting plants, even in a single day (fig.4). Even in these cases males seemed to spend more time on one of the two plants (66 %–88 % of records) (fig.5). The number of visited plants by a marked male may also depend on the number of visits recorded for that male during the study, so that males that only visited one plant may be those with a low number of observations. However, this seems unlikely since the number of visited plants did not

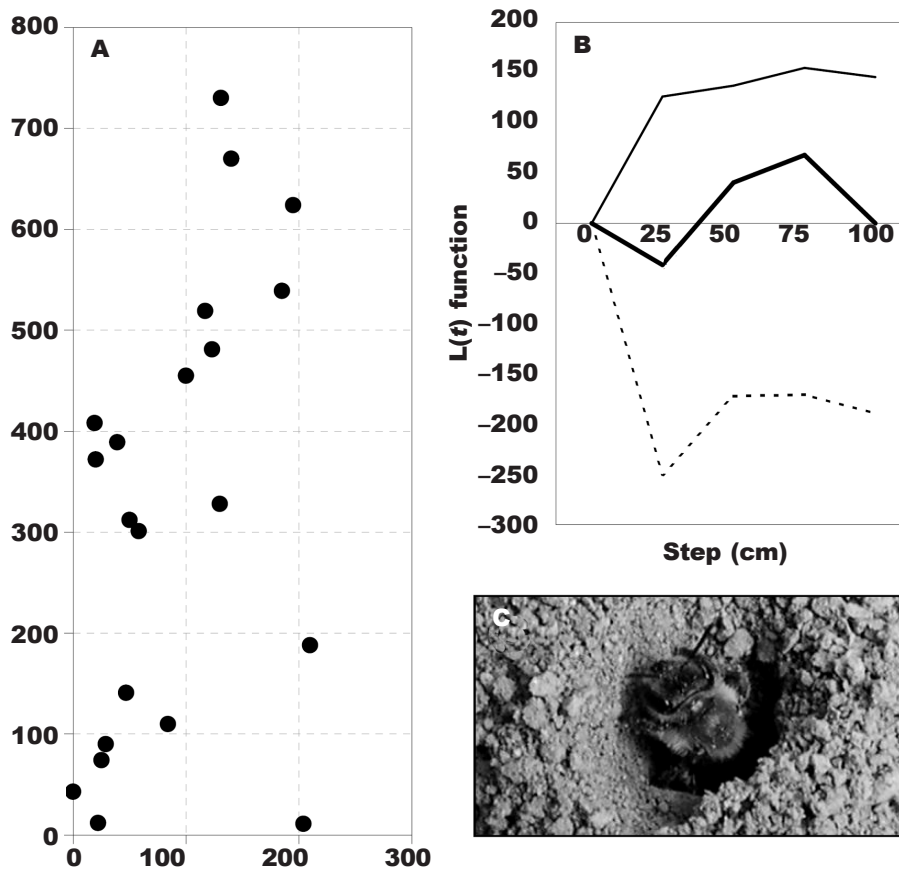


Fig. 2. A, map of nests in the studied aggregation of *A. florea*; B, Ripley's $L(t)$ function for the *A. florea* nest aggregation (bold line: transformed Ripley's K function ($L(t) = (K(t)/n)^{1/2} - t$), calculated from observed data and for given spatial steps (scale); thin line: upper 95% confidence envelope; dashed line: lower 95% confidence envelope; step used was 25 cm); C, *A. florea* female protruding from its nest.

Fig. 2. A, mapa de nidos en la agregación estudiada de *A. florea*; B, función $L(t)$ de Ripley para la agregación de nidos de *A. florea* (línea en negrita: función K transformada de Ripley ($L(t) = (K(t)/n)^{1/2} - t$), calculada a partir de datos observados y para determinados pasos espaciales (escala); línea delgada: límite superior del intervalo de confianza del 95%; línea discontinua: límite inferior del intervalo de confianza del 95%; el paso espacial utilizado fue de 25 cm); C, *A. florea* hembra que se asoma desde su nido.

increase with the number of records across marked males (Spearman correlation test, $\rho = 0.21$, $n = 13$, $P = 0.49$) (we excluded the seven males with only one record).

Discussion

The relationship of *A. florea* and plants of the genus *Bryonia* is probably as old as the long history of *Bryonia* in Eurasia (L. Larkin, personal communication quoted in Volz and Renner, 2008) and there is great overlap between ranges of these bees and their host plants (Westrich, 1989; Schröder and Lunau, 2001). This strict relationship is thus likely to have influenced the behaviour of the bees, not only in terms of foraging

behaviour by females (e.g. pollen collection), but also in terms of male mating tactics. With this study, we provide quantitative data on the behaviour of males and females of *A. florea* in a first attempt to understand the relationship between male density, female density, and pollen specialization by females. These are, however, provisional results that can be biased due to the small sample size, so that it is necessary to obtain additional data to perform a formal test of the predictions on mating strategy based on these variables. In any case, our results at least suggest that the hypothesis that the evolution of reproductive systems and strategies is driven by the distribution in space and time of receptive females and by female reproductive life-history (Shuster and Wade, 2003) may also be valid for *A. florea*.

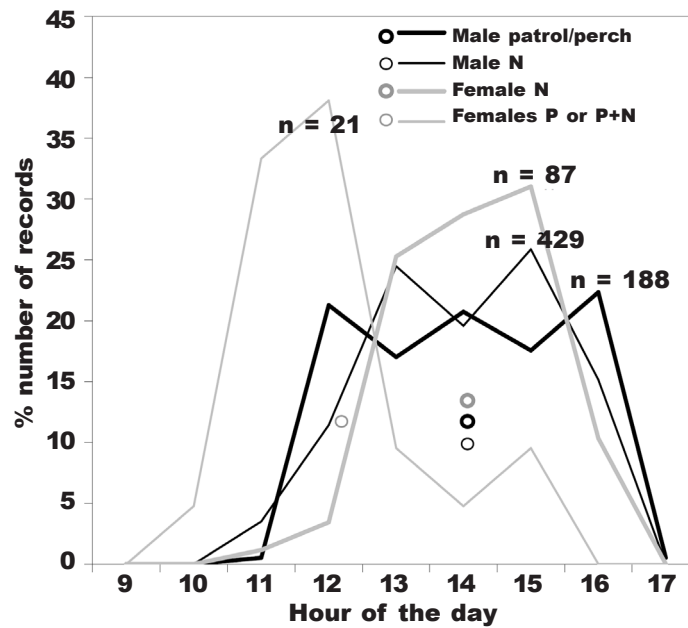


Fig. 3. Daily patterns of *A. florea* female foraging (N, nectar; P, pollen; P+N, pollen and nectar), male foraging (N, nectar) and mate-searching behaviour (patrol, patrolling the plant; perch, perching on plant leaves).

Fig. 3. Patrones diarios de recolección de las hembras de *A. florea* (N, néctar; P, polen; P+N, polen y néctar), de recolección de los machos (N, néctar) y de comportamiento de búsqueda de pareja (patrol, patrullando las plantas; perch, posándose en las hojas de la planta).

In our studied population of *A. florea*, females nested in a low-density, randomly arranged aggregation, and males did not mate at the nesting site. This agrees with the prediction that if females nest in low-density, males would search for a mate at flowers (resources) or non-resource sites rather than at nesting sites (Alcock et al., 1978; Ayasse et al., 2001; Paxton, 2005; see fig. 1). The small observed nest aggregation departed from the more common trend of a clumped arrangement of nests observed in fossorial bees and wasps (Potts and Willmer, 1998; Polidori, 2017; Polidori et al., 2008; Asís et al., 2014). However, at least a couple of *Andrena* species (*A. wilkella* (Kirby, 1802) and *A. nigroaenea* (Kirby, 1802)) were also observed nesting in a random pattern in loose aggregations (Tengö et al., 1990; Schiestl and Ayasse, 2000). The studied nest aggregation was found close to *B. dioica* plants, in accordance with the fact that foraging ranges of *Andrena* bees of comparable body size to *A. florea* (11–12 mm of body length) does not generally exceed 1000 m radius from nests (Zurbuchen et al., 2010). The distance between nests and host plants for another population of this species was indeed reported to be about 1 km (Edwards and Williams, 2004), though it is likely to be more common to find lower distances.

Males were only observed to search for females exclusively on *B. dioica* flowers, according to the prediction that, at low female (nest) density, ma-

les of oligolectic bees would use resource-based, rendez-vous sites (Paxton, 2005). Female pollen specialization in this species can be visible even in the adjustment of the female bee foraging behaviour at a daily scale: females collect pollen considerably earlier in the morning (peak at 11:00–12:00) than their collection of nectar (peak at 14:00–15:00), i.e. when pollen presentation by the staminate flowers is also peaking (Schröder and Lunau, 2001). Previous observation on foraging behaviour by females of this species reported similar daily curves, with pollen collection peaking even earlier, at 10:00–11:00 (Schröder and Lunau, 2001). Differences between populations in the time of pollen foraging may be related to temperature or other climatic or biotic factors which are as yet unknown.

Males of *A. florea* were abundant on plants and were not aggressive towards one another, with no evidence of territorial behaviour, likely reflecting the unpredictable distribution of females (Alcock et al., 1978). Theory predicts that male scramble competition would be favoured in case of high male density (Alcock et al., 1978; Ayasse et al., 2001; Paxton, 2005, see fig. 1). However, although a lack of territorial behaviour generally leads to no fixed home ranges in individual males (Paxton, 2005) it seems that a certain temporal constancy in the use of perched plants (up to several days) occurs in *A. florea* males. This would agree with findings in some

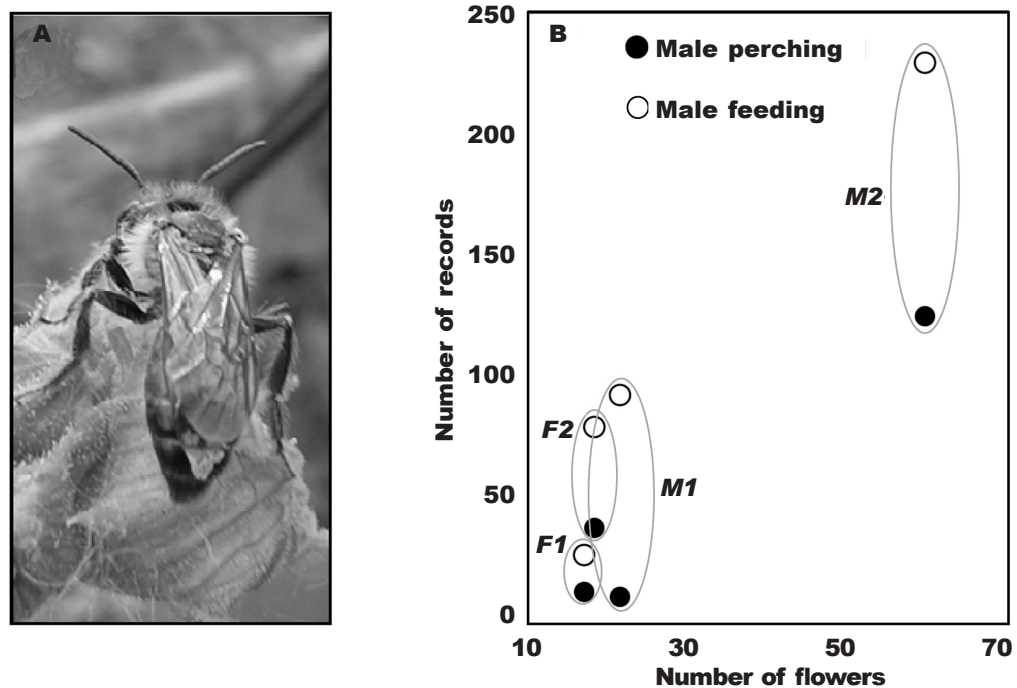


Fig. 4. A, *A. florea* male perching on a *B. dioica* leaf on a male plant; B, number of flowers on the four studied plants plotted against the number of male activity records (perching and feeding) on the plants. Median values calculated across plants are shown.

Fig. 4. A, macho de *A. florea* posado en una hoja de una planta masculina de *B. dioica*; B, número de flores en las cuatro plantas estudiadas y registros de actividad de los machos (posado y alimentación) en las plantas. Se muestran los valores medianos calculados por planta.

other bee species, where males may show temporally constant home ranges (at least within scales of some days) but do not defend them (thus they are not territorial) (Willmer et al., 1994).

The home ranges of marked males seemed to be on male plants only, in keeping with our hypothesis that males would mainly patrol/control the plants that reward the most limited resource for females (pollen). The fact that males most often use male plants for mating purposes is supported by their nectar-feeding distribution, which seemed to depend more on flower number on the plant. If this pattern is confirmed in a larger dataset, this would be the first case of an oligolectic bee species, as far as we know, showing this bias of male mate-searching on male plants. Variation in male home range size is common in bees. Males of some species confine their search to one or only a few plants, while those of other species can use a much larger area (Free and Butler, 1959; Stiles, 1976). For example, large home ranges (> 49 m²) of male *Andrena erigeniae* Robertson, 1891 are set on the females' strictly-associated host plant *Claytonia virginica*, with individually marked males overlapping their areas (Barrows, 1978). However, the much larger home ranges recorded for males of this species

(compared to those found here for *A. florea*) may be due to the different reproductive biology of this plant, where each flower acts as a male (pollen available to pollinators) for approximately one day and then acts as a female for one day or more (Motten et al., 1981). Thus, there would be no benefit for males of *A. erigeniae* to concentrate on single plants while seeking a partner, but it would be beneficial for *A. florea* males to focus on male plants (leading to smaller ranges).

As for *A. florea*, males of some other bee species spend most of their time perched or hovering, waiting for females (Alcock et al., 1978; Paxton, 2005). It is not known if *A. florea* males mark *B. dioica* leaves with female-attracting pheromones, as was observed in males of other bee species perching on plants waiting for females (Alcock et al., 1978; Paxton, 2005), or if they just increase the probability to intercept a receptive female by perching most often on male plants. Marking secretions from males have been reported from a few *Andrena* species (Priesner, 1973; Bergström et al., 1982; Tengö et al., 1990), opening the possibility that this behaviour also occurs in *A. florea*. It is also unknown whether virgin females possess a cuticular hydrocarbon profile that signals to (or is used as a cue by) males, thus guiding them

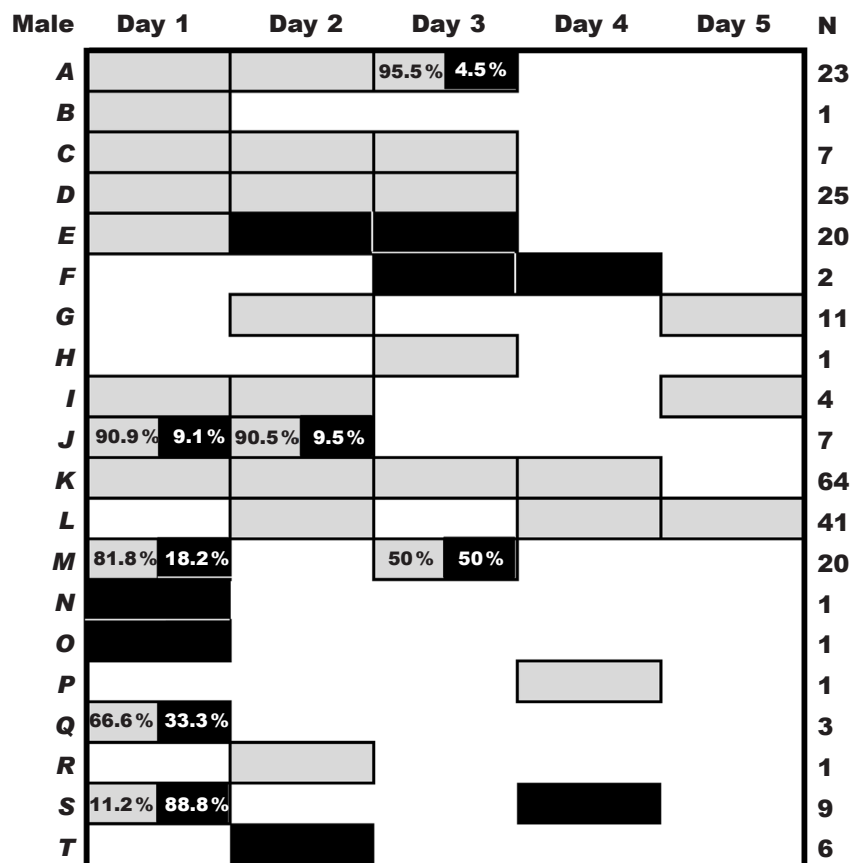


Fig. 5. Percent frequency of recaptures on the two male plants (grey or black) for each of the 20 marked males and for five subsequent days. If no percentage is given, the male stayed that day only on one of the two plants (100% of recaptures). Numbers on the right represent the sample size (number of observations) for each of the marked males.

Fig. 5. Frecuencia (%) de recapturas en las dos plantas masculinas (gris o negro) de cada uno de los 20 machos marcados y durante cinco días seguidos. El porcentaje no aparece si ese día el macho solo permaneció en una de las plantas (100 % de las recapturas). Los números a la derecha representan el tamaño de la muestra (número de observaciones) de cada uno de los machos marcados.

to copulate only with receptive females. Such a situation is known for *A. nigroaenea*, for which males were observed to search for females on the nesting site rather than on host plants (Schiesti and Ayasse, 2000). Other *Andrena* species show males searching for females on the nesting sites, such as *A. erythronii* Robertson, 1891 (Michener and Rettenmeyer, 1956), *A. flavipes* Panzer, 1799 (Butler, 1965) and *A. vaga* Panzer, 1799 (Rezkova et al., 2012). However, available, though often scattered, data seem to show that *Andrena* males patrol and mate on flowers more frequently than at other places (reviewed in Barrows, 1978; see also Paxton, 2005). Furthermore, territorial behaviour was observed in males of very few *Andrena* species (e.g. *A. foxii* Cockerell, 1898; Thorp, 1969; Linsley et al., 1973).

Our findings on *A. florea* share some observations with those on other oligolectic *Andrena* species. For

example, a population of *A. erigeniae* nesting in a low- to moderate-density aggregation (1–21 nests/m²) has occasionally been collected on a number of plant species, but females appear to be entirely restricted for pollen to *C. virginica*, and data from collecting records indicate that mating probably takes place on flowers of this exclusive pollen-rewarding host plant (Davis and LaBerge, 1975). *Andrena agilissima* (Scopoli, 1770) is also known to have a resource-based rendez-vous site (Paxton, 2005) (and even intra-nidal mating upon adult emergence, Paxton et al., 1999), but the studied nest aggregation of this species was very large and dense (Giovannetti et al., 2003; Polidori et al., 2005). On the other hand, Stephen (1966) reported that males of *Andrena perplexa* Smith, 1853 patrol the nesting site and most copulas occurred there. *Andrena nigrae* Robertson, 1905 and *A. mariae* Robertson, 1891 were observed

while mating on *Salix* spp., their only source of pollen (Miliczky, 1988). The association between lecty status and rendez-vous site does not seem, however, to be very clear, since cases of polylectic bee species using resource-based rendez-vous sites are also known (review in Paxton, 2005). An extreme example is *Andrena prunorum* Cockerell, 1896, whose males were observed patrolling cultivated cherry, peach, pear, and apple, according with the great polylecty (77 host plant genera in 32 families) shown by females (Miliczky, 2008). Classification of mating tactics in relation to bee biological traits itself is sometimes difficult, given that certain variation in mating tactics was reported even at an intra-specific level for several *Andrena* species (e.g. Paxton, 2005; Paxton et al., 1999, Paxton and Tengö, 1996).

In conclusion, in this paper we provide novel information on the behaviour of *A. florea*, a European species of oligolectic bee strictly associated with *Bryonia* plants. Our data can be used for further analysis of the mating strategy of this species, including a more formal and quantitative test of the predictions arising from the interaction between female and male densities and resource specialization in bees. Interestingly, we found certain home range constancy exclusively on male plants, and we suggest that the reproductive biology of the host plant should be taken into account in new studies on bees in order to see how widespread this phenomenon is. Detailed information on the behaviour of wild bees is fundamental as an element to take into consideration while making conservation plans that aim to protect pollinators.

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