

Repellent scent-marking behaviour of the sweat bee *Halictus (Seladonia) aerarius* during flower foraging*

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Abstract – Several social bee species of the family Apidae use scent marks on flowers left by previous visitors to improve foraging efficiency, but scent marking has not been demonstrated in other social bees. Experiments were conducted to confirm the ability of the eusocial sweat bee *Halictus (Seladonia) aerarius* (Hymenoptera: Halictidae) to use scent marks to detect flowers within 3 min of foraging by the same individuals or by conspecifics. Rejection responses were evident on two plant species, *Erigeron annuus* and *Justicia procumbens*. The proportion of hovering rejection responses to visited flowers differed among plant species. Repellent responses to visited flowers of *J. procumbens* decreased without replenishment of nectar. We suggest that the duration of scent marks used by *H. aerarius* is not adjusted to nectar replenishment and that this bee uses different rejection responses depending on the resources expected when revisiting flowers. This strategy may be considered a basal trait in the bee's evolution.

social bee / Halictidae / foraging behaviour / repellent effect / scent marks / floral resources

1. INTRODUCTION

The spatial distribution of floral resources is complex and difficult to predict. To forage efficiently for acquisition of floral rewards, bees attempt to use spatial foraging patterns for patchy resources (e.g., Thomson, 1996; Williams and Thomson, 1998; Makino and Sakai, 2004) or adjust the proportion of visiting flowers per patch (e.g., Dreisig, 1995; Ohashi and Yahara, 1998, 2002; Goulson, 2000). Although these foraging strategies may reduce the probability of revisiting non-rewarding flowers, it is difficult for a bee to discriminate between non-rewarding flowers and rewarding flowers each time it visits a patch. However, it is clear that the quantity of resources available in flowers rejected by bumblebees is less than that in unvisited flowers (Corbet et al., 1984; Marden, 1984; Wetherwax, 1986; Kato, 1988).

To visit rewarding flowers selectively, bees assess floral resources directly. For example, pollen content (Dobson and Bergström, 2000) and nectar content (Heinrich, 1979) are assessed by pollen or nectar scents. In addition, bees distinguish between rewarding and non-rewarding flowers through olfactory cues such as scent marks on flowers (e.g., Cameron, 1981; Schmitt and Bertsch, 1990; Goulson et al., 1998). The effects of scent marks left by previous visitors have two interpretations, i.e., attraction or rejection. Although attractant responses to scent marks on natural flowers have not been examined (Williams, 1998; Goulson et al., 2000), many studies have shown attraction to artificial resources in honeybees (Free, 1970; Ferguson and Free, 1979; Free and Williams, 1979, 1983; Williams and Poppy, 1997), bumblebees (Cameron, 1981; Schmitt and Bertsch, 1990; Schmitt et al., 1991) and stingless bees (e.g., Aguilar and Sommeijer, 2001; Nieh et al., 2003; Schmidt et al., 2005). Repellent effects on floral resources have been observed in honeybees (Giurfa and Núñez, 1992, 1993a, b; Giurfa, 1993; Giurfa et al.,

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1994) and bumblebees (Goulson et al., 1998; Stout et al., 1998; Williams, 1998; Stout and Goulson, 2001, 2002). The repellent effects decrease with the replenishment of nectar volume, and the duration of the effect differs among flower species (Stout and Goulson, 2001). Regarding the different roles of scent marks, several studies have shown that different responses to the scent marks could result from different interpretation of the same chemicals according to the abundance of resources and the context in which they are presented (Saleh and Chittka, 2006; Witjes and Eltz, 2007).

Scent marking by social bees in the family Apidae is well documented, and several studies have found evidence for the use of scent marks by solitary bees, including carpenter bees *Xylocopa virginica texana* (Frankie and Vinson, 1977), flower bees *Anthophora plumipes* Pallas (Gilbert et al., 2001) and wool-carder bees *Anthidium manicatum*; (Gawleta et al., 2005). Reader et al. (2005) reported that hoverflies avoided flowers visited by bumblebees and honeybees. However, little is known about the ability of social bees belonging to other bee families to use scent marks. Here we focused on bees of the family Halictidae because only *Agapostemon nasutus* is known to visually assess floral resources (Goulson et al., 2001). Also, several bees have a sociality similar to that of honeybees and bumblebees. We therefore tested the following three points. We asked whether *Halictus (Seladonia) aerarius* Smith (Hymenoptera: Halictidae) uses scent marks to detect flowers visited by themselves or conspecifics, whether the revisitation rate is related to nectar renewal, and whether they show the same response to the scent marks when visiting different flower species.

2. MATERIALS AND METHODS

2.1. Flowers and bee species

The experiments were conducted on a rice field levee (120 m²) in Nagaokakyo, Kyoto, Japan (34°55'N, 135°40'E). Observations took place between 0900 and 1600 h on clear and sunny days

from July to September 2003, 2004, and 2005. Weather conditions were hot and humid during the study. A large observation area was used to reduce the possibility of observing the same individuals. The eusocial sweat bee *Halictus (Seladonia) aerarius* Smith (Halictidae: Halictinae) is a generalist, visiting many plant species within its life cycle (Sasaki, 1985). It usually collects both pollen and nectar at the same time. We used individuals that visited flowers naturally. Eastern daisy fleabane *Erigeron annuus* (L.) (Asteraceae) and trailing water willow *Justicia procumbens* L. (Acanthaceae) were common plant species in the coppice and were the main floral resources used by *H. aerarius* in the field. The maximum nectar volume of *J. procumbens* was 0.3 µL (Yokoi, unpubl. data). *Erigeron annuus* flowers from May to July. Its inflorescence is a capitulum with numerous individual florets, and it attracts pollinators for long periods. Nectar is not visible to the human eye from the outside because each inflorescence is too small. Although *J. procumbens* flowers from July to September, each inflorescence remains open for only a single day. The anthers can be seen from outside while the nectar is not visible to humans.

2.2. Responses to foraged flowers

The experimental design used to test whether the sweat bees use scent marks was based on Goulson et al. (1998, 2001). After foraging by a bee, we cut the flower along with the pedicel, and using forceps, we offered the flower within 3 min to the next visitor, which was a conspecific or the same individual. We identified original forager by chasing each individual until offering the foraged flower again. To eliminate the possibility that bees remember flower positions, the cut flower was moved to a location distant from its original one. We prepared unvisited flowers by netting the flowers until they opened and offered the flowers to visitor as described above. To investigate responses to scent marks, we classified the behaviour into three patterns following Corbet et al. (1984) and Schmitt and Bertsch (1990): hovering, a bee approached the flower within 1 cm but did not land; landing, a bee landed on the flower and departed quickly without foraging; and probing, a bee landed on the flower and extended its proboscis to forage on nectar or pollen. We defined both hovering and landing as rejection responses, because bees collected neither nectar nor pollen during these behaviours. Flowers were used only once and were discarded after each test.

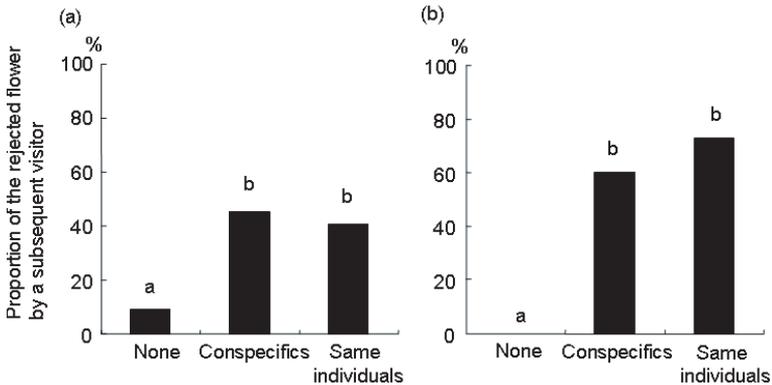


Figure 1. The rate of rejection of *Halictus aerarius* to the flowers previously foraged either by conspecifics or by same individuals before 3 min in two flower species, *Erigeron annuus* (a) and *Justicia procumbens* (b). Different letters indicate significant differences among bars.

2.3. Comparison of rejection responses between flower species

To test for differences in the rejection responses of *H. aerarius* to scent marks when visiting different flower species, we compared the hovering and landing response to visited flowers within 3 minutes either by conspecifics or by the same individuals on each plant.

2.4. Duration of scent marking

After foraging by a bee, we covered the visited flower with a net and recorded the time of the visit. After a specific amount of time (3, 10, 20, 40, and 60 min) passed, we cut the flower with the pedicel and offered it to conspecifics. We used the same behaviour classification as described above. Flowers were used only once and were then discarded.

2.5. Nectar renewal rates

Forty-seven flowers of *J. procumbens* were randomly selected and covered using a net until they opened. We removed all of the nectar using micro-capillary tubes and then measured nectar volume after 3, 10, 20, 40, and 60 min. The nectar renewal rate of *E. annuus* was not investigated because the flowers were too small to measure the nectar volume.

2.6. Statistical analyses

JMP statistical software (third edition, SAS Institute Inc., Cary, NC, USA) was used for statistical analyses. Fisher's exact probability test was used for a comparison between unvisited flowers (control) and flowers visited by conspecifics or by the same individuals in both flower species. Because of the comparison of rejection responses between flower species, the proportions of bees rejecting these foraged flowers were examined using the same test. Relationships between the time from initial to subsequent visitor foraging and the rejection rate were compared using logistic regression. To investigate the nectar renewal rate, we compared the initial nectar volumes of flowers to those at each time interval using Mann-Whitney *U*-tests because the data were not normally distributed.

3. RESULTS

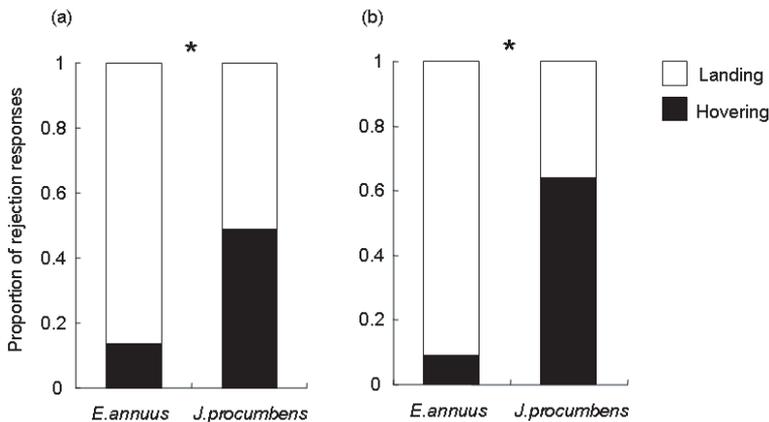
3.1. Responses to foraged flowers

Halictus aerarius rejected *E. annuus* flowers within the first 3 min after they were foraged on by the same individual or by conspecifics (Fig. 1a). The rejection rate differed significantly from that of the control flowers (i.e., those not previously foraged on); individuals of *H. aerarius* significantly rejected flowers on which they had previously foraged (41%, $n = 27$) and flowers foraged on by conspecifics (45%, $n = 64$; Tab. I). Bees also

Table I. Results of Fisher's exact probability test for the comparison of the proportion of flowers rejected between plant species.

Previous visitor	Flower species			
	<i>E. annuus</i>	<i>J. procumbens</i>	<i>E. annuus</i>	<i>J. procumbens</i>
	<i>P</i>	<i>P_{adj}</i>	<i>P</i>	<i>P_{adj}</i>
Same individuals vs. none	0.0003	*	0.0024	*
Conspecific vs. none	< 0.0001	*	0.0002	*
Same individuals vs. conspecific	0.8179	NS	0.1099	NS

P_{adj} = adjusted probabilities following sequential Bonferroni correction with a significance level of *P* = 0.05; * *P* < 0.05.

**Figure 2.** Comparison of rejection responses of *Halictus aerarius* between flowers foraged by (a) conspecifics or (b) same individuals within 3 min. Fisher's exact probability test; * *P* < 0.05.

significantly rejected *J. procumbens* flowers within the first 3 min after they were foraged on by the same individual or by conspecifics (Fig. 1b). Individuals of *H. aerarius* rejected 73% (*n* = 88) of flowers that they had previously foraged on and 60% (*n* = 88) of flowers foraged on by conspecifics (Tab. I).

3.2. Comparison of rejection patterns between flower species

The proportion of hovering and landing responses to foraged flowers by the previous visitor differed significantly between plant species (Fig. 2). Moreover, the proportion of hovering responses in *J. procumbens* was larger than in *E. annuus* foraged on by conspecifics (Fisher's exact probability test: *P* = 0.0017) and by the same individual (Fisher's exact probability test: *P* = 0.0008).

3.3. Duration of scent marking

In both plant species, the rejection rate of flowers decreased 60 min after the last visitor foraged (Fig. 3). The time since the last bee visited was inversely related to the proportion of flowers rejected by conspecifics (*E. annuus*: likelihood ratio $\chi^2_1 = 37.2853$, *P* < 0.0001; *J. procumbens*: likelihood ratio $\chi^2_1 = 4.4682$, *P* = 0.0345). There was a significant difference between control flowers and flowers within 40–60 min of the last visit (Tab. II). The rejection rate of *E. annuus* flowers did not differ significantly between control flowers and those that were foraged on again within 40–60 min.

3.4. Nectar renewal rates

After the artificial removal of nectar, there was no replenishment of nectar in *J. procumbens* at each time interval (Fig. 4). There was a

Table II. Difference in rejection rate with regards to duration of scent marks left by conspecifics in comparison with control flowers.

Plant species	Bee species	Time since previous bee visit (min)				
		3	10	20	40	60
<i>E. annuus</i>	<i>H. aerarius</i>	0.0008*	0.0009*	0.0217	> 0.9999	0.6971
<i>J. procumbens</i>	<i>H. aerarius</i>	< 0.0001*	< 0.0001*	< 0.0001*	< 0.0001*	0.0014*

P_{adj} = adjusted probabilities following sequential Bonferroni correction with a significance level of $P = 0.05$:
* $P < 0.05$.

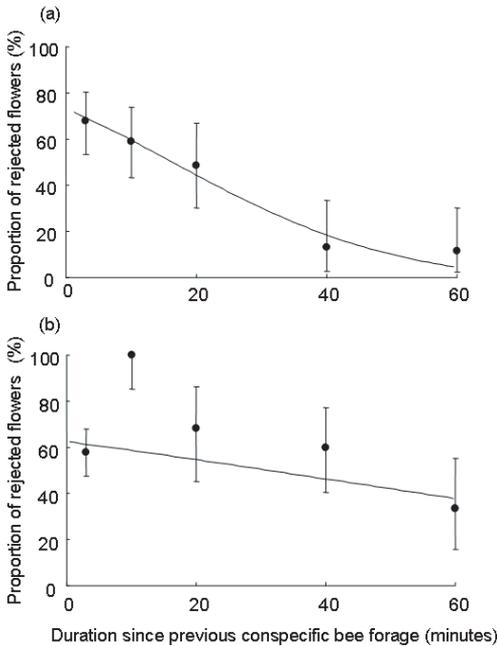


Figure 3. Results of relationship between duration and rejection rate of flower *Erigeron annuus* (a) and *Justicia procumbens* (b) since last bee visited. Bold lines show the confidence limits. Error bars represent \pm SE.

significant difference between the initial nectar volume and the volume at all subsequent time intervals (Fig. 4). The volume of nectar was still not completely replenished 60 min after removal (Mann-Whitney U -test: $P < 0.0001$).

4. DISCUSSION

Our results indicate that *H. aerarius* is able to use scent marks to avoid visiting previously foraged flowers (Fig. 1). Honeybees and bumblebees show a high rejection rate within short

time intervals for certain plant species (Corbet et al., 1984; Goulson et al., 1998; Stout et al., 1998; Stout and Goulson, 2002). Scent marks have a repellent effect for the same individuals and for conspecifics. In *H. aerarius*, the hovering rejection rate differed between plant species. The hovering rejection rate was higher for *J. procumbens* than for *E. annuus* (Fig. 2). It is likely that the difference in rejection responses is related to the floral resources expected when revisiting. The nectar volume of *J. procumbens* was not replenished (Fig. 4), whereas in flowers of *E. annuus*, constant rewards would be expected because most visitors used only a few florets in each inflorescence. Avoiding visited flowers would be more advantageous in foraging on *J. procumbens* than on *E. annuus*. Scent marks optimize foraging efficiency by reducing the time spent visiting unrewarding flowers (Giurfa and Núñez, 1992; Williams, 1998). We thus suggest that *H. aerarius* also selects an advantageous strategy to reduce the energetic cost of searching flowers it has already visited.

The rejection rate tended to decrease after 60 min in both plant species (Fig. 3a, b). The rejection rate in *E. annuus* decreased significantly after 20–40 min compared to the control, whereas that in *J. procumbens* remained high (Tab. II). Interestingly, the nectar volume of *J. procumbens* was not replenished despite the decreased rejection rate. Several studies have shown that the duration of rejection corresponds to the period required for nectar replenishment in some flower species (Stout et al., 1998; Stout and Goulson, 2001, 2002). Because resource levels are highly variable among plant species and are subject to change over time (Heinrich, 1979), generalist bee species may learn to evaluate the quality

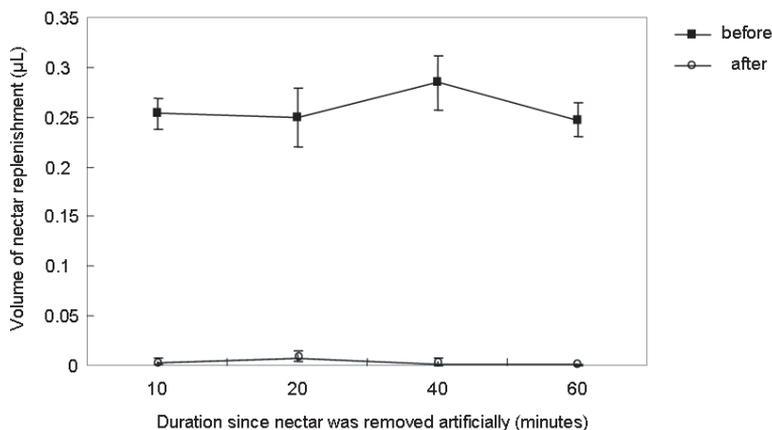


Figure 4. Initial nectar volume of *Justicia procumbens* and that replenished after each time interval. Errors bars represent \pm SE.

of resources according to the plant species. However, our results showed that duration of repellent marks left by sweat bees is not related to nectar replenishment of the plant species. We suggest that the adjustment of scent mark duration is not always possible in social bee species. It would be interesting to know whether other bees such as solitary bees or other social bees adjust the effect of scent marks in relation to nectar replenishment of the flowers they visit.

The chemical compounds in scent marks differ among bee species. Repellent scent marks of honeybees are 2-heptanones secreted from the mandibular glands (Giurfa, 1993). Carpenter bees secrete repellent chemicals from the Dufour gland (Frankie and Vinson, 1977). Bumblebees use blends of hydrocarbons secreted from the tarsi; these compounds have a similar composition among bumblebee cuticles (Schmitt et al., 1991; Goulson et al., 2000; Eltz, 2006). It is likely that sweat bees use chemical compounds commonly found in other bee species, although this has not been investigated. The possible use of physical cues left by scarring the flower could be ruled out because such marks are effective for a long time and the associated rejection rates should be constant; however, by expanding our data we can support or refute this suggestion.

The floral scent can be different between two plant species because the chemical com-

position of floral scent varies widely from species to species in terms of both the number and identity of volatiles (Dobson, 1994). We can not rule out the possibility that the two flowers have different chemical compounds that either mask or promote the use of those chemical cues. This would require further investigation by other techniques.

Our study represents the first evidence of scent marks by social bees not belonging to the Apidae to detect unrewarding flowers. To further our understanding of the mechanisms and evolutionary origins of scent-marking strategies, it is necessary to compare foraging behaviours among different bee groups. Given that repellent odour-marking of floral resources is found in honey bees and bumble bees, our results suggest that this strategy may be a basal trait in the evolution of bees.

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Marquage olfactif répulsif par l'abeille *Halictus (Seladonia) aerarius* lors du butinage des fleurs.

Abeille sociale / Halictidae / comportement de butinage / effet répulsif / marquage olfactif / ressources florale

Zusammenfassung – Repellentmarkierung von Blüten bei der Furchenbiene *Halictus (Seladonia) aerarius* beim Besammeln der Blüten. Die räumliche Verteilung der Blütenressourcen ist komplex und schwierig vorhersagbar. Um Blüten effizient zu besammeln, nutzen die Bienen mehrere auf Blütensignalen wie Pollen und Nektar beruhende Strategien, mit denen sie die Blütenressourcen abschätzen. Zusätzlich zu diesen Signalen können soziale Bienen der Familie Apidae geruchliche Anzeiger wie die von früheren Blütenbesuchern zurückgelassenen Duftmarken wahrnehmen, um hierdurch ihre Sammeleffizienz zu steigern (z.B. Giurfa et al., 1994; Stout und Goulson, 2001; Schmidt et al., 2005). Einige Solitärbiene nutzen ebenfalls Duftmarken (Frankie und Vinson, 1977; Gilbert et al., 2001; Gawleta et al., 2005). Während Duftmarkierung bei sozialen Bienen der Apidae gut dokumentiert sind, sind diese bei den sozialen Halictidae nur wenig untersucht. Wir führten Untersuchungen über die Fähigkeit der sozialen Furchenbiene *Halictus (Seladonia) aerarius* durch, anhand von Duftmarken zuvor besuchte Blüten zu erkennen. Hierzu schnitten wir kürzlich besuchte Blüten zusammen mit dem Blütenstiel ab und boten sie innerhalb von 3 Minuten den gleichen Individuen oder Artgenossen an. Hierbei wurden Ablehnungsreaktionen bei zwei Pflanzenarten, dem einjährigen Feinstrahl *Eriogon annuus* und dem Acanthusgewächs *Justicia procumbens* festgestellt (Abb. 1). Die Ablehnungsrate für Blüten von *J. procumbens* war größer als die bei Blüten von *E. annuus* (Abb. 2). Die Dauer der Ablehnung nahm bei beiden Pflanzen nach 60 Minuten ab (Abb. 3). Dies ist der erste Hinweis auf die Nutzung von Duftmarkierungen bei den sozialen Halictidae zur Erkennung bereits genutzter Blüten. Obwohl der Nektar bei *J. procumbens* nicht wieder aufgefüllt wurde (Abb. 4), nahm der Repellenteffekt besuchter Blüten mit der Zeit ab. Die Dauer der Nutzung von Duftmarkierungen durch *H. aerarius* war daher nicht auf die Nektarergänzung abgestimmt, und die Furchenbienen schienen unterschiedliche Ablehnungsreaktionen in Abhängigkeit ihrer Ressourcenerwartung beim Wiederbesuch der Blüten zu haben. Wir nehmen daher an, dass *H. aerarius* ihr Ablehnungsverhalten modifiziert um hierdurch die Sammeleffizienz zu steigern. Da Duftmarkierung von Blütenressourcen sowohl bei Honigbienen als auch bei Hummeln vorkommt, weisen unsere Ergebnisse darauf hin, dass dies eine in der Evolution der Bienen ursprüngliche Strategie darstellt.

Soziale Bienen / Halictidae / Sammelverhalten / Repellenteffekt / Duftmarken / Blütenressourcen

REFERENCES

- Aguilar I., Sommeijer M. (2001) The deposition of anal excretions by *Melipona favosa* foragers (Apidae: Meliponinae): behavioural observations concerning the location of food sources, *Apidologie* 32, 37–48.
- Cameron S.A. (1981) Chemical signals in bumblebee foraging, *Behav. Ecol. Sociobiol.* 9, 257–260.
- Corbet S.A., Kerslake C.J., Brown C., Morland N.E. (1984) Can bees select nectar-rich flowers in a patch? *J. Apic. Res.* 23, 234–242.
- Dobson H.E.M. (1994) Floral volatiles in insect biology, in: Bernays E.A. (Ed.), *Insect-Plant Interactions Vol. V.*, CRC Press, Florida, pp. 48–71.
- Dobson H.E.M., Bergström G. (2000) The ecology and evolution of pollen odors, in: Dafni A., Hesse M., Pacini E. (Eds.), *Pollen and Pollination*, Springer Wien, New York, pp. 63–88.
- Dreisig H. (1995) Ideal free distributions of nectar foraging bumblebees, *Oikos* 72, 161–172.
- Eltz T. (2006) Tracing pollinator footprints on natural flowers, *J. Chem. Ecol.* 32, 907–915.
- Ferguson A.W., Free J.B. (1979) Production of a forage-marking pheromone by the honeybee, *J. Apic. Res.* 18, 128–135.
- Frankie G.W., Vinson S.B. (1977) Scent marking of passion flowers in Texas by females of *Xylocopa virginica texana* (Hymenoptera: Anthophoridae), *J. Kans. Entomol. Soc.* 50, 613–625.
- Free J.B. (1970) Effect of flower shapes and nectar guides on the behaviour of foraging honeybees, *Behaviour* 37, 269–285.
- Free J.B., Williams I.H. (1979) Communication by pheromones and other means in *Apis florae* colonies, *J. Apic. Res.* 18, 16–25.
- Free, J.B., Williams I.H. (1983) Scent-marking of flowers by honeybees, *J. Apic. Res.* 22, 86–90.
- Gawleta N., Zimmermann Y., Eltz T. (2005) Repellent foraging recognition across bee families, *Apidologie* 36, 325–330.
- Gilbert F., Azmeh S., Barnard C., Behnke J., Collins S.A., Hurst J., Shuker D. (2001) The Behavioural Ecology Field Course. Individually recognizable scent marks on flowers made by a solitary bee, *Anim. Behav.* 61, 217–229.
- Giurfa M. (1993) The repellent scent-mark of the honeybee *Apis mellifera ligustica* and its role as a communication cue during foraging, *Insectes Soc.* 40, 59–67.

- Giurfa M., Núñez J.A. (1992) Honeybees mark with scent and reject recently visited flowers, *Oecologia* 89, 113–117.
- Giurfa M., Núñez J.A. (1993a) Efficient floret inspection by honeybees in capitula of *Carduus acanthoides*, *Ecol. Entomol.* 18, 116–122.
- Giurfa M., Núñez J.A. (1993b) Visual modulation of a scent-marking activity in the honeybee, *Apis mellifera* L., *Naturwissenschaften* 80, 376–379.
- Giurfa N.M., Núñez J.A., Backhaus W. (1994) Odour and colour information in the honeybee, *Apis mellifera* L., *J. Comp. Physiol. A* 175, 773–779.
- Goulson D. (2000) Why do pollinators visit proportionally fewer flowers in large patches? *Oikos* 91, 485–492.
- Goulson D., Hawson S.A., Stout J.C. (1998) Foraging bumblebees avoid flowers already visited by conspecifics or by other bumblebee species, *Anim. Behav.* 55, 199–206.
- Goulson D., Stout J.C., Langley J., Hughes W.O.H. (2000) Identity and function of scent marks deposited by foraging bumblebees, *J. Chem. Ecol.* 26, 2897–2911.
- Goulson D., Chapman J.W., Hughes W.O.H. (2001) Discrimination of unrewarding flowers by bees: direct detection of rewards and use of repellent scent marks, *J. Insect Behav.* 14, 5, 669–677.
- Heinrich B. (1979) Resource heterogeneity and patterns of movement in foraging bumblebees, *Oecologia* 40, 235–245.
- Kato M. (1988) Bumblebee visits to *Inpatiens* spp.: pattern and efficiency, *Oecologia* 76, 364–370.
- Makino T.T., Sakai S. (2004) Findings on spatial foraging patterns of bumblebees (*Bombus ignites*) from a bee-tracking experiment in a net cage, *Behav. Ecol. Sociobiol.* 56, 155–163.
- Marden J.M. (1984) Remote perception of floral nectar by bumblebees, *Oecologia* 64, 232–240.
- Nieh J.C., Ramírez S., Nogueira-Neto P. (2003) Multi-source odor-marking of food by a stingless bee, *Melipona mandacaia*, *Behav. Ecol. Sociobiol.* 54, 578–586.
- Ohashi K., Yahara T. (1998) Effects of variation in flower number on pollinator visits in *Cirsium purpuratum* (Asteraceae), *Am. J. Bot.* 85, 219–224.
- Ohashi K., Yahara T. (2002) Visit larger displays but probe proportionally fewer flowers: counterintuitive behaviour of nectar-collecting bumble bees achieves an ideal free distribution, *Funct. Ecol.* 16, 492–503.
- Reader T., MacLeod I., Elliott P.T., Robinson O.J., Manica A. (2005) Inter-order interactions between flower-visiting insects: Foraging bees avoid flowers previously visited by hoverflies, *J. Insect Behav.* 18, 51–57.
- Saleh N., Chittka L. (2006) The importance of experience in the interpretation of conspecific chemical signals, *Behav. Ecol. Sociobiol.* 61, 215–220.
- Sasaki Y. (1985) Studies on the social structure of *Halictus (Seladonia) aerarius* (Smith) (Hymenoptera, Apidae), Dissertation, Tokyo University of Agriculture, Tokyo, Japan.
- Schmidt V.M., Zucchi R., Barth F.G. (2005) Scent marks left by *Nannotrigona testaceicornis* at the feeding site: cues rather than signals, *Apidologie* 36, 285–291.
- Schmitt U., Bertsch A. (1990) Do foraging bumblebees scent-mark food sources and does it matter? *Oecologia* 82, 137–144.
- Schmitt U., Lübke G., Francke W. (1991) Tarsal secretion marks food sources in bumblebees (Hymenoptera: Apidae), *Chemoecology* 2, 35–40.
- Stout J.C., Goulson D. (2001) The use of conspecific and interspecific scent marks by foraging bumblebees and honeybees, *Anim. Behav.* 62, 183–189.
- Stout J.C., Goulson D. (2002) The influence of nectar secretion rates on the responses of bumblebees (*Bombus* spp.) to previously visited flowers, *Behav. Ecol. Sociobiol.* 52, 239–246.
- Stout J.C., Goulson D., Allen J.A. (1998) Repellent scent-marking of flowers by a guild of foraging bumblebees (*Bombus* spp.), *Behav. Ecol. Sociobiol.* 43, 317–326.
- Thomson J.D. (1996) Trapline foraging by bumblebees: I. Persistence of flight-path geometry, *Behav. Ecol.* 12, 158–164.
- Wetherwax P.B. (1986) Why do honeybees reject certain flowers? *Oecologia* 69, 567–570.
- Williams C.S. (1998) The identity of the previous visitor influences flower rejection by nectar-collecting bees, *Anim. Behav.* 56, 673–681.
- Williams C.S., Poppy G.M. (1997) Responses of individual honey bees to artificial feeders visited by themselves and to feeders visited by hive mates, *J. Apic. Res.* 36, 105–108.
- Williams N.M., Thomson J.D. (1998) Trapline foraging by bumble bees: III. Temporal patterns of visitation and foraging success at single plants, *Behav. Ecol.* 9, 612–621.
- Witjes S., Eltz T. (2007) Influence of scent deposits on flower choice: experiments in an artificial flower array with bumblebees, *Apidologie* 38, 12–18.