

# The role of learning in the mating biology of a sweat bee *Lasioglossum zephyrum* (Hymenoptera: Halictidae)

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**Summary.** Results from experiments on the role of learning in the mating biology of a sweat bee, *Lasioglossum zephyrum* (Hymenoptera: Halictidae), are described in this paper. Male learning of individual female odors is important in natural populations (Table 1), as has been shown in the laboratory. Four other hypotheses are unlikely to account for the observed behavior: (1) Female odors dissipate rapidly; (2) Males learn and then avoid the study area; (3) Males or females produce repellents which are effective against other males; or (4) Males recognize their own odor on previously-contacted females, which they subsequently avoid. Regarding questions of “male preference” and “optimal outbreeding,” Tables 2 and 3 show there are no consistent preferences for more novel or less novel female odors.

## Introduction

Many animals are able to recognize familiar or genetically related individuals (Fletcher and Michener 1987; Hepper 1986). A primitively eusocial sweat bee, *Lasioglossum (Dialictus) zephyrum* (Halictidae), is a species whose kin-recognizing ability has been particularly well studied (e.g., Greenberg 1979; Hölldobler and Michener 1980; Michener and Smith 1987). Females distinguish between nestmates and non-nestmates in nature, probably enabling them to prevent inter- and intra-specific parasitism, and at least in the laboratory they are able to discriminate degrees of genealogical relatedness. Laboratory studies show that males possess similar sensory abilities, and that they too can discriminate among females according to degrees of familiarity (Smith 1983).

On the basis of laboratory studies demonstrating learning, Smith (1984) hypothesized that males might use their discriminating ability in nature in a context of “optimal outbreeding;” that is, natural selection favors those males having a preference for females (mates) of a certain degree of genetic relatedness (see Bateson 1983). An alternative hypothesis is that males approach and attempt copulation with any female and, if that female is not receptive (true for most workers), then during subsequent encounters the previously unreceptive female is “ignored,” as are other females that have similar odors, e.g., close relatives (Smith and Wenzel, in press; Barrows 1975a; Michener and Smith 1987). According to this hypothesis, males learn odors to avoid “wasting time” with unreceptive females under conditions of presumably intense male-male competition. Kukuk (1985) suggested that males of *L. zephyrum* deposit an “antiaphrodisiac” on females prior to copulation (see Discussion). This paper reports experiments on the possible role of male learning in the mating biology of these bees in natural populations.

## Methods

### *Natural history*

*Lasioglossum zephyrum* is a small bee (range of ♀ forewing length  $\cong$  4.2–4.7 mm). Females usually nest in vertical banks along streams and rivers, from May to September in Kansas, USA (Batra 1966). There are several broods per season, and the sex ratio becomes progressively less female-biased toward the end of the summer, when fewer workers are produced. In late July and August female reproductives (overwintering gynés) are produced, and at this time a populous nesting aggregation will have hundreds to many thousands of males patrolling the site. Males fly up to 20 cm over and in front of the banks where females are nesting, and are commonly observed pouncing on standing, walking, or flying females. They also

briefly pounce on stationary males, small black sphecoid wasps, ants, etc. Most of the females that a male encounters are not receptive and refuse the male's attempts; they are probably workers which typically do not mate (Batra 1966; Michener 1974). Females and males copulate briefly (10–42 s), often near the entrance of a nest (see Barrows 1975b).

#### Male learning

An experiment on the role of learning was made during July and August 1985, at a large nesting aggregation of *L. zephyrum* in a south-facing bank on an island (Farm Island) in the Kansas River approximately 6 km east of Lawrence, Douglas Co., Kansas, USA. This aggregation is continuous along a bank for about 40 m, and three sites (*A*, *C*, *B*) at intervals of about 10 m were selected *within* the aggregation; *A* and *B* were 20 m distant. Large numbers of males were patrolling at each of the three sites, and subjectively the densities were similar.

For each replicate two or three female bees were collected from each of 6–9 nests (2–3 nests from *A*, 2–3 from *B*, etc.) with an aspirator. Females were individually placed in clean labeled vials, and then transported to the laboratory where they were killed by freezing. These females were probably workers, with one from each nest being a guard bee; when a nest is disturbed, typical queen behavior is to run quickly to the bottom of the burrow and away from the source of the disturbance (Michener 1974), so queens were probably not collected. Vials containing females were kept in a freezer or, for the return trip to the aggregation, in a container with ice. Prior to each replicate, the vials with bees were recoded and randomized by another person (see *Acknowledgements*), so that during tests I did not know the source of any bee.

Each series of bees was tested the day after it was collected. A test involved taking a frozen female from a vial, sticking an insect pin through the thorax, and then placing the pinned bee in the aggregation about 1.5 cm above the ground surface. For a period of 2 min the number of males *approaching* the pinned female and those *contacting* her were counted using hand counters. Males were not marked, and it was not possible to distinguish between counting the same male twice and counting two males once each. "Contact" varied from a momentary landing on the female to more extended attempts to copulate, in which males sometimes everted their genitalia. "Approach" is a more subjective measure and, as used here (after Cane and Tengö 1981), indicates that a male oriented toward the female and flew within 5 cm of her, hovering nearby and zig-zagging along a serpentine flight path. Females were tested at sites *A* and *B*, and then a second time at both *A* and *B*, and then at a third site, *C* (e.g., *A1*, *B1*, *A2*, *B2*, *C*; note the order of testing was not blind). Whether the testing began at *A* or *B* was determined by a coin toss for each female. The total duration for a complete test of a female was about 15 min. Six replicates were made, involving a total of 135 female bees and 631 presentations.

To determine if female odors dissipate appreciably during the time of testing, 15 females were individually presented four times to males as described above. Presentations at 0, 15, 30, and 60 min following exposure to air were at a different location for each time interval; these locations were chosen to have approximately the same densities of males as sites *A–C*. In between tests the females were left exposed to the air, away from the aggregation.

#### Male preference

An experiment on male preference was made during August, 1984, at three nesting aggregations in Douglas Co., Kansas:

(1) Farm Island (FI) – see above; (2) River Front Park (RFP) – bees nested in a southwest-facing bank along the Kansas River, about 2 km north of Lawrence; and (3) County Line (CL) – bees nested in a west-facing bank of Tuey Creek (in the Marais des Cygnes River drainage, a different drainage system from sites 1 and 2), about 30 km south of Lawrence along the Douglas-Franklin County line. This site had fewer nests and patrolling males than did sites (1) and (2).

For all replicates ( $n=13$ , total of 423 tests), one female bee was removed from each of 5 nests at each of the 3 aggregations. Each group of 15 bees (plus 5 control bees, see below) was prepared and presented as described for the first experiment. Some females were tested only at CL (4 replicates); others at both CL and FI (3 replicates); and for 6 replicates each bee was tested at all 3 sites. Additionally, a set of 5 bees was collected, washed in three changes of hexane, and baked at 75° C for 72 h. Presumably these females lacked any odors that males might use as cues, and they were presented individually during 4 replicates as controls.

The experiment described above on the relative attractiveness of females to males at *different* aggregations was repeated *within* one aggregation using data collected during first presentations of bees in the first experiment ( $n=135$  bees), as well as 8 additional replicates ( $n=187$  bees, total  $n=322$ ) in which bees were presented only once at sites *A*, *B* and *C*.

#### Statistical considerations

The density of males at various sites was not quantified. In order to correct for differences in male density, the number of contacts per female was divided by the number of approaches to that female. This measure of "attractiveness" (contacts/approach =  $C/A$ ) is a ratio and the statistical distribution of this proportion is not known. An arcsine transformation of the data seems biologically inappropriate because "approach" and "contact" are not independent. The data resulting from these experiments should be viewed in this light. Also, preliminary laboratory observations suggest that social facilitation (*sensu* Clayton 1978) may influence the rate of male pouncing; if substantiated, interpretation of data given in Tables 2 and 3 becomes more difficult (see Kullenberg 1956). Means are given with their standard errors.

## Results

Consistent with laboratory and other field studies, males were attracted to odor cues produced by the females. The number of males contacting frozen untreated females (mean  $C/A=0.29$ ,  $n=423$ ) was significantly greater than the number contacting extracted and presumably odorless females (mean  $C/A=0.06$ ,  $n=120$  females) ( $P<0.001$ , Mann Whitney *U*-test).

### 1. The role of learning

When tested twice at the same location (i.e., *A* or *B*) the number of *contacts per female* was significantly greater for the first presentation ( $\bar{x}=9.5 \pm 0.4$ ,  $n=270$ ) than for the second ( $\bar{x}=4.8 \pm 0.22$ ) ( $P<0.0001$ , Wilcoxon sign rank test, pooled for sites *A* and *B*). Five hypotheses could explain this finding: (1) males mark females with an antiaphrodisiac prior to intromission (Kukuk 1985); (2)

**Table 1.** Mean number of approaches, contacts, and contacts/approach for females presented to patrolling males at a nesting aggregation (Farm Island). Females were presented twice at sites *A* and *B*, and once at site *C* ( $n=91$  bees), and twice at *A* and *B* for  $n=44$  bees (total presentations = 631)

Site & Trial	Approaches	Contacts <sup>a</sup>	Contacts/approach <sup>b</sup>
<i>A1</i>	19.3±0.8	9.6±0.6	0.50±0.017
<i>A2</i>	14.9±0.6	4.8±0.3	0.32±0.014
<i>B1</i>	17.9±0.7	9.1±0.5	0.49±0.016
<i>B2</i>	13.6±0.6	4.6±0.3	0.34±0.014
<i>C1</i>	20.9±0.7	12.3±0.6	0.57±0.012

<sup>a</sup> Significant values are given in the text, with data pooled over sites

<sup>b</sup> For all pairwise comparisons,  $P>0.05$ ; Student-Newman-Keuls test

males learn that these females are not receptive and tend not to respond to their learned odors during subsequent presentations (Barrows 1975a; Smith 1983); (3) female odors dissipate rapidly, and they have less odor during subsequent presentations; (4) males learn to avoid the places at which females are presented; or (5) males deposit individually distinctive marks enabling them to recognize their own odor, and so ignore a previously courted female (males do not respond to marks of other males) (Assem et al. 1980).

For presentations of the *same* females at a third site *C*, the number of *contacts* increased to levels comparable to those from *A1* or *B1*, and significantly greater than for second presentations, *A2* or *B2*, ( $P<0.0001$ , Wilcoxon sign rank test; Table 1). This result eliminates hypotheses (1) and (3) above; if either of these were tenable, then presentations at *C* would yield results similar to or less than those obtained for *A2* and *B2*; that is, female attractiveness to males would decline as a function of the order of presentation (e.g.,  $A1 \geq B1 > A2 \geq B2 > C$ ). Additional evidence against the rapid dissipation of odors (hypothesis 3) comes from repeatedly testing the same females over 60 min time. For 15 females the mean number of *contacts* by males following 0, 15, 30, and 60 min exposure to air is  $9.8 \pm 0.59$ ;  $10.1 \pm 0.56$ ;  $9.9 \pm 0.48$ ; and  $9.2 \pm 0.44$ , respectively. If site learning is important (hypothesis 4), then sites should become progressively unattractive over the course of an experiment. There were many cases in which females presented at the end of a replicate were contacted more frequently than those presented at the beginning, unless the females were nestmates (see below). Males were not individually marked, so it is impossible to assess the relevance of hypothesis 5 based on the data collect-

**Table 2.** Mean number of contacts/approach for females collected from three source aggregations and presented to males at each of these aggregations. For a given male population, pairwise differences among females are not significantly different ( $P>0.1$ ). Sample sizes are given in parentheses. Comparisons are made within rows

Male population tested	Sources of frozen females		
	County line	River front park	Farm island
County line	0.28±0.02 (50)	0.24±0.04 (54)	0.31±0.03 (45)
River front park	0.34±0.03 (27)	0.40±0.03 (49)	0.32±0.04 (50)
Farm island	0.22±0.03 (35)	0.28±0.03 (58)	0.29±0.05 (55)

ed; laboratory studies suggest that this hypothesis is untenable (see Discussion).

A Student-Newman-Keuls test (Sokal and Rohlf 1981) for differences among contact per approach (C/A) between sites or trials showed that none of the pairwise comparisons were significantly different at the 5% level. As noted above, "contact" and "approach" are probably not independent, which helps account for this result, and points to imprecision in this bioassay (see discussions in Kullenberg 1956; Silverstein 1984).

Support for a learning hypothesis (No. 2) comes from the decreasing attractiveness of nestmates (probably closely related) tested at the same place. Comparing the trios or duos of nestmate females used, the number of *contacts* per female decreased as a function of the sequence of presentations at sites *A*, *B*, or *C*. The mean number of contacts (pooled over sites & trials) for first nestmates ( $\bar{x}=9.5 \pm 0.47$ ,  $n=230$ ) was significantly greater than that for second nestmates ( $\bar{x}=7.2 \pm 0.33$ ,  $n=230$ ) ( $P<0.0001$ ), which was slightly greater than that for third nestmates ( $\bar{x}=6.2 \pm 0.43$ ,  $n=143$ ) ( $0.1 > P > 0.05$ ). In short, nestmates tested at the same place in an aggregation are progressively less attractive, yet are, on the average, similarly attractive when tested at different sites within an aggregation (cf. Smith 1984).

## 2. The role of male preference

Tables 2 and 3 give results from the second experiment. For a given aggregation the mean C/A was largest in 2 of 3 cases for those females collected at the same aggregation where tests occurred. The differences are small, and it is difficult to interpret the data statistically because of the problems mentioned above. When rank scores for individuals

**Table 3.** Mean number of contacts/approach for females collected at three sites within one aggregation at Farm Island, and presented to males at each of these sites. Each site is separated by about 10 m, and A and B are 20 m distant. For a given male "population" pairwise differences among females are not significant ( $P > 0.1$ ). Sample sizes are given in parentheses. Comparisons are made within rows

Males tested	Sources of frozen females		
	A	C	B
A	0.47 ± 0.03 (40)	0.45 ± 0.03 (35)	0.43 ± 0.03 (39)
C	0.59 ± 0.02 (31)	0.57 ± 0.02 (31)	0.58 ± 0.03 (31)
B	0.48 ± 0.03 (40)	0.47 ± 0.03 (35)	0.48 ± 0.03 (40)

were pooled, pairwise differences between aggregations were not significant ( $P > 0.1$ , Wilcoxon sign rank test). Given the acuity of this bioassay, these data show no male "preference" at the population level (Table 2). Within one aggregation there was no indication that males prefer females from more distant areas of the aggregation (Table 3).

## Discussion

### 1. Learning and mating behavior of *Lasioglossum zephyrum*

The following conclusions emerge from this study: (1) learning plays an important role in the mating biology of *Lasioglossum zephyrum* in natural populations, as is well-known from laboratory studies (Barrows 1975a, b; Barrows et al. 1975; Greenberg 1982; Smith 1983; reviews by Hölldobler and Michener 1980; Michener and Smith 1987); (2) for the population studied in Kansas there is no evidence for an antiaphrodisiac (but see Kukuk 1985); and (3) there is no evidence that males react differently to females from more distant sites (probably lower relatedness) relative to females from nearby.

Darwin (1871, vol. I: 364ff.) described observations on aculeate Hymenoptera, and suggested that their ability to learn and recognize individuals is probably important under sexual selection (also Robson and Richards 1936; Lloyd 1980). Ways in which learning may enhance evolutionary divergence of social and sexual signals are described by West-Eberhard (1983, 1984). Results from the first experiment demonstrate that males learn odors of individual females, and that male- or female-produced repellents do not account for the

observed behavior. These conclusions are similar to those drawn from laboratory studies. Barrows (1975a, b; Barrows et al. 1975) presented filter papers impregnated with the odors of individual females to caged males of *L. zephyrum*, and recorded the number of times males contacted small black discs placed on the floor of the cage. When a filter paper with the odor of a female A was presented, followed by the presentation of a second paper with the odor of the same female, the number of contacts was greater for the first presentation than for the second. If a series of different female odors were presented between the two presentations of A's odor, then the number of contacts was, on average, the same for all first presentations, and again decreased when the second paper of A was presented. This decrease in response to the same odor presented on a different filter paper precludes the possibility that males deposit an antiaphrodisiac because they did not previously contact the second paper. For the same reasons, these data cannot be explained by assuming males deposit their own odors during contact and later avoid the smell of themselves (hypothesis 5, Results).

Male learning in *L. zephyrum* was further studied in the laboratory by Smith (1983) who showed that males, like females, are able to learn the odors of individual females and then generalize this information to recognize close relatives of the learned females (see Mostofsky 1965). Under controlled conditions males can discriminate degrees of relatedness among females and, based on experience with an unreceptive female, modify their behavior so that later they are less likely to be attracted to that female or to her close relatives (Smith 1983). In the study reported here, the number of males contacting a series of females (each a nest-mate of the others) declined as a function of the order in which they were presented. In nature, therefore, males also generalize from the odors of females to those of their presumed relatives, confirming Smith's findings. If non-receptive and receptive female siblings have similar odors, then it is unusual that males generalize, because eventually they would ignore receptive females. One possibility is that the odors produced by receptive females differ qualitatively or quantitatively from those produced by non-receptive females.

### 2. The significance of recognition of unreceptive females

At an aggregation of *L. zephyrum* there are typically hundreds to thousands of males flying about,

and they are not obviously aggressive to one another (personal observation; Batra 1966; Michener 1974). Males probably compete for receptive females (see Alcock et al. 1978; Thornhill and Alcock 1983). Preliminary mark-recapture studies suggest each male stays in a limited subsection of the aggregation (one marked male was recaptured in the same 1 m<sup>2</sup> area 13 days after marking; and see Greenberg 1982; also Kukuk et al. 1985 for another halictid bee). Males of a Colombian halictid, *Caenohalictus eberhardorum*, also apparently do not fly over an entire aggregation, but restrict their activity to a limited portion of it (Michener et al. 1979). This site-fidelity implies that a male will repeatedly encounter the same worker females which usually do not mate, and which frequently go in and out of the nests on foraging trips. A possible explanation for the behavior of *L. zephyrum* males is that they learn females' odors and subsequently "know" that a given female will not mate because, based on previous experience, that female was not receptive. This is an important consideration because, relative to the total female population, only very few females are receptive, and usually there are numerous other males.

A second, perhaps complementary, hypothesis for male learning was given by Smith (1984) incorporating Bateson's (1973, 1983) ideas on "optimal outbreeding". Data from natural populations neither support nor reject it; more novel or less novel females are not more attractive to males (Smith 1984; present study). This interpretation requires that *L. zephyrum* males be the more discriminating sex, which Knoppin (1985: 103) asserts is true. In general, however, males are less discriminating than females (for reasons why, see e.g., Darwin 1871; Fisher 1958; Trivers 1972; Alexander and Borgia 1979; West-Eberhard 1983). For *L. zephyrum*, as noted above, (1) most females are *never* sexually receptive, and (2) the peak of gyne (=receptive female) production coincides with the peak of male production (Batra 1966). In theory, opportunities for males to be especially discriminating are probably infrequent because of presumed competition for access to receptive females. To the extent that this is true, whether a female is receptive or not is probably more important than is relatedness per se.

If there are selective pressures to optimally outbreed, then learning, within relatively viscous populations (Michener 1974; Kukuk and Decelles, 1986) could produce mating patterns similar to those expected from an optimal outbreeding hypothesis (Bateson 1983), without requiring that males choose mates on the basis of their degree

of relatedness. Males may learn the odors of female nestmates while in the natal nest, and they later are less attracted to the odors of nestmate females (Greenberg 1982). These data suggest reasons why the frequency of matings between close relatives is probably low. The frequency of matings between completely unrelated individuals is probably also low because philopatry to the natal area implies that such foreign individuals will be encountered rarely. Most matings then, are likely to be between individuals having intermediate degrees of relatedness. The role of female choice has not yet been examined for any halictid bees.

On the basis of a study at a nesting aggregation of *L. zephyrum* in New York, USA, Kukuk (1985) suggested that males deposit a pheromone on females which other males perceive and so avoid that marked female. For reasons given below, the evidence presented in support of that conclusion is weak, as it is for some other species with putative "antiaphrodisiacs" (see Eberhard 1985). In the population of bees which Kukuk studied multiple mating may be common (Kukuk 1985, footnote 11), which suggests such an antiaphrodisiac, if present, is not particularly effective.

Kukuk used black nylon models impregnated with female odors at various concentrations, as well as models with female odors on which live males walked and so deposited "male odors" (= antiaphrodisiac). Using such methods any "male odors" collected were acquired from non-copulating males, implying an antiaphrodisiac is deposited prior to copulation. The highest concentration of female odor tested by Kukuk (1985) elicited significantly more "hover" responses than the other cues. Her Table 2 shows there are no significant differences among any of the lesser concentrations or the high concentration of female odor plus "male odor" (the odor concentrations listed in her Table 2 are different from those of her Table 1 because of typographical errors, P. Kukuk, *in litt.*). Kukuk supposed that the unique character of the models with the highest concentration of female odor is due to the high concentration combined with lack of the "male odor", and therefore males deposit an antiaphrodisiac.

In her study Kukuk did not address data showing that males learn females' odors (references above; present study). This consideration is relevant because males were exposed repeatedly to the *same* compounds (at different concentrations), and so prior experience probably influenced male response. During these experiments males contacted models, with or without "male odor", only twice (Kukuk 1985, footnote 16). No explanation is giv-

en for why males rarely contacted any of the models. Using Dufour's gland extracts, as well as synthetic macrocyclic lactones, Smith et al. (1985) report that males commonly contacted treated black nylon models in nature; caged males in the laboratory frequently pounce on small black discs (e.g., Barrows 1975a; Barrows et al. 1975; Greenberg 1982; personal observation), and this behavior is enhanced in the presence of female odor.

One of the more interesting and unresolved questions is why the same frozen female often evokes very different responses ("attractiveness") when presented to different populations (aggregations) of males. In some cases a female was rarely or never contacted at one site, and at another aggregation was so attractive that at the end of the test the pinned female had to be shaken vigorously to disperse the crowd of males crawling over her. This variation shows in part the bioassay used is insufficiently precise to discriminate effects due to social facilitation, learned preferences, or stochastic and idiosyncratic differences.

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