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Volatile Pheromone Detection and Calling Behavior Exhibition: Secondary Mate-finding Strategy of the German Cockroach, *Blattella germanica* (L.)

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Chi-Wei Tsai and How-Jing Lee (1997) Volatile pheromone detection and calling behavior exhibition: secondary mate-finding strategy of the German cockroach, *Blattella germanica* (L.). *Zoological Studies* **36**(4): 325-332. The German cockroach is a gregarious species, and the male courtship behavior is mediated by the female's contact sex pheromone. The sexes usually congregate around food, shelter, or at a deposition site of aggregation pheromone, so no long distance searching is necessary for contact. In this study, we demonstrate that sexually receptive males not only detect the heterosexual odor, but also prefer the odors of virgin females over that of mated females. Sexually receptive females can also detect the heterosexual odor, but show no preference between the odors of either sex, nor do females exhibit a differential response to mated and virgin males. Sexually receptive virgin females not only increase locomotion to find mates, but also exhibit a calling behavior which releases a volatile sex pheromone. The longer a female does not sense the conspecific odor, the more frequent calling behavior is displayed. We suggest that German cockroach females increase locomotion and calling frequency as a secondary strategy when sexually receptive virgin females do not encounter males.

Key words: Calling behavior, Odor preference, Secondary strategy.

The German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae), is an important domiciliary pest which has been the subject of intensive investigations on various aspects of its biology and population control (Schal and Hamilton 1990, Rust et al. 1995). The courtship behavior in this cockroach has been well studied and thought to be mediated by a non-volatile contact sex pheromone from the female (Roth and Willis 1952, Nishida et al. 1974). The pheromone has 4 components, each of which alone can elicit the complete courtship wing-raising response in males (Nishida and Fukami 1983, Schal et al. 1990b). However, the mate-finding behavior in the German cockroach is not well understood. In general, resource-based aggregation can facilitate mate-finding of this cockroach (Schal et al. 1984). This "resource" for the cockroach in domiciliary habitats is possibly shelter, food, or the aggregation pheromone (Ishii and Kuwahara 1968, Schal et al. 1984, Wendler and Vlatten 1993).

Calling behaviors have been shown to be associated with volatile sex pheromone emission in several cockroach species (Willis 1970, Hales and Breed 1983, Smith and Schal 1990). Recently, Liang and Schal (1993b) reported that sexually receptive virgin German cockroach females exhibit a characteristic calling behavior during which a volatile sex pheromone is released. Female cockroaches initiate continuous calling during the sexually receptive stage, from the time their basal oocytes reach a length of 1.6 mm until mating or 24 h before ovulation (Liang and Schal 1993b). These findings created a need to investigate the roles volatile sex pheromone and calling behavior play in the mate-finding behavior of the German cockroach.

In this paper, we have outlined the sexual strategies that the female German cockroach may employ to achieve mate-finding, and suggest that

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increases of locomotion and calling frequency may serve as a secondary strategy. When sexually receptive virgin females do not encounter males by emitting contact sex pheromone or the aggregation pheromone, they will increase locomotion to meet potential mates and switch to calling behavior with release of volatile sex pheromone to attract potential mates.

MATERIALS AND METHODS

Insects

German cockroaches, *Blattella germanica*, were collected from houses in Taipei City, Taiwan, and reared for several generations in the laboratory. Cockroaches were kept in transparent plastic jars (4 l) with screen lids for ventilation. Food (dog chow) and water were provided ad libitum. Several pieces of styrofoam were added for shelter. Last-instar nymphs were removed and reared en masse in transparent plastic cups (5.5 cm × 9.5 cm dia.). Upon reaching adulthood, the sexes were separated and kept under the same conditions. All rearing was conducted at 28 °C and LD 16:8 h conditions.

Odor preference choice

T-shaped glass tubes, each with arms of 10 cm length and 1 cm in diameter, were used to test the odor preference of adult German cockroaches. Before the test, cockroaches were individually confined in a plastic tube (6 cm × 1.3 cm dia.) for 30 min to adapt to the conditions. After 30 min, 2 plastic tubes were connected to the upper ends of the T-shaped tube as the 2 choice stations. The cockroaches to be tested were individually confined in a glass tube (15 cm × 1.3 cm dia.) which was, in turn, connected to the lower stem of the T-shaped tube after 30 min of settlement. The perforated end panels of the 2 choice stations allowed airflow toward the tested cockroach. The airflow (1 m/sec) was created by suction from a vacuum pump connected to the base of the lower glass tube. A tested cockroach was released from the lower glass tube to make a choice. If it did not make a choice within 5 min, the cockroach was discarded. The choice was recorded as a turn toward one or the other upper arm of the T-shaped tube. All experiments were performed under dim red light at 28 °C.

The experiment was performed with the following 4 scenarios to detect whether sexually receptive German cockroaches could distinguish between the odors of conspecific individuals.

(1) Choice of sexually receptive adults between heterosexual individuals

Tested cockroach	Pair-choice stations	
14-d-old male	0-d-old female	7-d-old female
	none	0-d-old female
	none	7-d-old female
7-d-old female	0-d-old male	14-d-old male
	none	0-d-old male
	none	14-d-old male

(2) Choice of sexually receptive adults between hetero- and homo-sexually receptive individuals

Tested cockroach	Pair-choice stations	
7-d-old female	14-d-old male	7-d-old female
14-d-old male	14-d-old male	7-d-old female

(3) Choice of sexually receptive adults between virgin and mated heterosexual individuals

Tested cockroach	Pair-choice stations	
14-d-old virgin male	7-d-old mated female	7-d-old virgin female
7-d-old virgin female	14-d-old mated male	14-d-old virgin male

Mated adults were obtained by allowing them to mate once successfully 24 h before the experiment.

(4) Choice of sexually receptive adults between n-hexane extract of heterosexual's body surface

Tested cockroach	Pair-choice stations	
14-d-old male	0-d-old female	4-d-old female
14-d-old male	0-d-old female	7-d-old female
7-d-old female	0-d-old male	14-d-old male

This test aimed to determine if volatile sex pheromone alone can elicit expected response from the German cockroach. In order to obtain the volatile sex pheromone without the contamination of aggregation pheromone of male and female cockroaches, n-hexane was used to extract volatile sex pheromone from the body surface (Sakuma and Fukami 1990). The development of volatile sex pheromone production was also investigated by comparing behavioral attraction of n-hexane extract of sexually immature (0-d-old), newly sexually mature (4-d-old), or fully sexually mature (7-d-old) females.

The n-hexane extract from the body surface was obtained by immersing 5 equally conditioned cockroaches into 10 ml of n-hexane for 5 min. The extract was then absorbed by cotton which was used as a choice station.

The results, expressed as frequency of choice, were analyzed by the χ^2-test for goodness of fit (Steel and Torrie 1980) against random choice. The correction for continuity of the test criterion by F. Yates is:

$$\chi^2 = \Sigma\ (|\text{observed - expected}| - 0.5)^2/\text{expected}$$

Effects of conspecific odor on the calling frequency of females

Sexually receptive (6-d-old) females were singly confined in a transparent acrylic box (18 × 2.5 × 3 cm^3). Food (dog chow) and water were provided ad libitum. The box was connected through a piece of silicone tube (5 cm × 0.3 cm dia.) to other boxes where a 0-d-old male, 13-d-old male, or 6-d-old female was housed. An empty box was used as a control. The connective silicone tube allowed only air to flow between the boxes. The calling behavior of the females was recorded with an infrared video camera for 24 h at 28 °C in total darkness. The calling frequency was counted as the number of callings observed during the 1st min out of every 10 min during a 24-h period. Calling frequency of females in different treatments was analyzed by Kruskal-Wallis and Dunn tests (Daniel 1990).

To further accelerate the airflow between boxes, a vacuum pump was used to create 4 equal airflows (1 m/sec) for 20 min in each 4-h period. The same experimental setup was followed as previously described. Four boxes of sexually receptive females (6-d-old) were individually connected to boxes containing a 0-d-old male, a 13-d-old male, a 6-d-old female, or nothing. The calling behavior of the females was recorded with an infrared video camera for 24 h at 28 °C in total darkness.

Another similar experiment was set up to understand the effects of long-term exposure to conspecific odors for 6 d right after emergence. Tested females were exposed to conspecific odors when they were newly emerged (0-d-old). Only the calling frequency on the 7th day after emergence was counted.

After each test, the T-shaped tube or the acrylic boxes were wiped clean with n-hexane and aerated by a vacuum pump for 10 min. Then, they were washed again with 95% alcohol and aerated for another 30 min to eliminate any odor residue.

RESULTS

Odor preference choice

Sexually receptive 14-d-old male cockroaches preferred to approach the odors of females regardless of the females' sexual receptivity when the choice was between female's odor and no odor ($p < 0.05$, χ^2-test) (Fig. 1B, C). However, they showed equal preference for either the odor of sexual unreceptive (0-d-old) or receptive (7-d-old) females (Fig. 1A). These results demonstrate that sexually receptive males can detect and do prefer a female's odor even though it comes from females who are not capable of mating. Similar results were obtained with the preference choice of sexually receptive females (7-d-old) to the odors of males (Fig. 2). Sex-

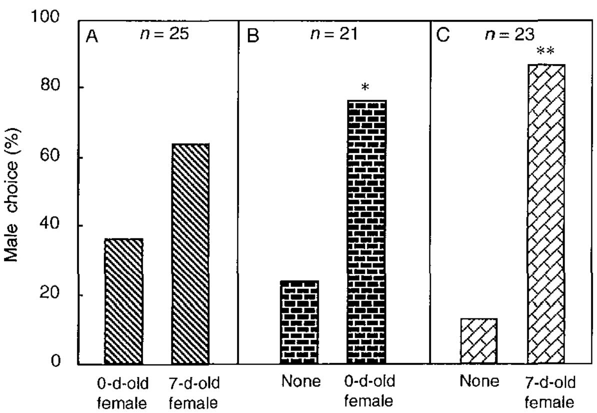

Fig. 1. Preference choice of sexually receptive (14-d-old) male *Blattella germanica*, between the odors of (A) 0-d-old and 7-d-old females; (B) none and 0-d-old female; (C) none and 7-d-old female in full darkness.
*significant difference ($p < 0.05$, χ^2-test). **significant difference ($p < 0.01$, χ^2-test).

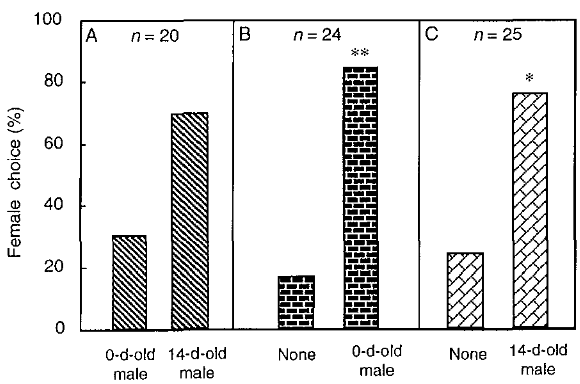

Fig. 2. Preference choice of sexually receptive (7-d-old) female *Blattella germanica*, between the odors of (A) 0-d-old and 14-d-old males; (B) none and 0-d-old male; (C) none and 14-d-old male in full darkness.
*significant difference ($p < 0.05$, χ^2-test). **significant difference ($p < 0.01$, χ^2-test).

ually receptive females could detect and did prefer either sexually receptive or unreceptive (0-d-old) male's odor ($p < 0.05$, χ^2-test) (Fig. 2B, C) over an empty control, but showed equal preference between the odors of sexually unreceptive and receptive males (Fig. 2A).

Sexually receptive males (14-d-old) preferred the odors of sexually receptive females over males ($p < 0.05$, χ^2-test) (Fig. 3A). However, sexually receptive females (7-d-old) did not discriminate between odors of sexually receptive males and females (Fig. 3B). These results indicate that while males express a significant discrimination ($p < 0.05$, χ^2-test) between male and female odors, females do not show the same level of preference.

Sexually receptive males (14-d-old) and females (7-d-old) showed different degrees of preference between heterosexual odors of mated and virgin individuals (Fig. 4). Sexually receptive males could distinguish and did prefer the odors of virgin over mated females ($p < 0.05$, χ^2-test) (Fig. 4A). However, sexually receptive females had no significant preference between odors of mated and virgin males (Fig. 4B). This finding matches the reproductive behavior of the German cockroach, because the female can only mate once in a reproductive cycle (Lee and Wu 1994), while the male, which has no such restriction, can mate repeatedly.

Sexually receptive adults were attracted to the n-hexane extracts from the heterosexual body surface of sexually receptive males and females (Fig. 5). Although 4-d-old females have barely reached a sexually receptive stage (Lee and Wu 1994), sexually receptive males did not express selective approach to their body surface extracts (Fig. 5A). From the results of significant preference ($p < 0.01$, χ^2-test) of males to sexually receptive female body surface extracts (Fig. 5B), the chemical signal of sexual receptivity could be detected and was preferred by sexually receptive males. Sexually receptive females also showed a significant preference ($p < 0.01$, χ^2-test) for the n-hexane extract of 14-d-old male's body surface over that of 0-d-old males (Fig. 5C). This preference choice demonstrates that females can also detect sexually attractive chemicals on the male's body surface.

Effects of conspecific odor on the calling frequency of females

The calling frequency of sexually receptive (6-d-old) females was not significantly affected by the presence of conspecific odor at 28 °C, in constant darkness (Table 1). Furthermore, the calling frequency of sexually receptive females was not influenced even when an artificial airflow (1 m/sec) was created to accelerate the transmission of odor (Table 1). Although the expression of female's calling behavior showed considerable variation among individuals, it was not affected by either heterosexual or homosexual odor. From these results, the calling behavior of the female is considered to be autonomous. When females were not exposed to conspecific odor for 6 d, their calling frequency was significantly higher ($p < 0.05$, Dunn test) in comparison with ones exposed to conspecific odor for 6 d (Table

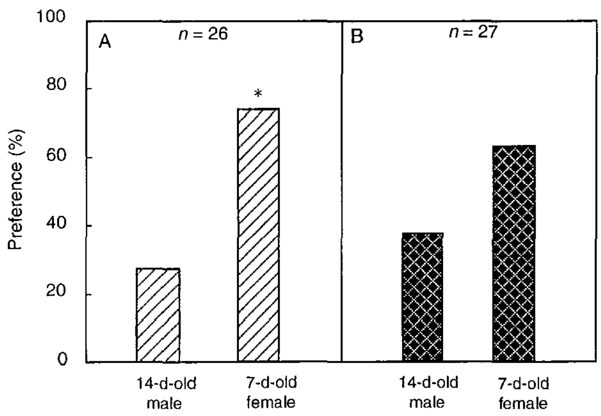

Fig. 3. Preference choice of sexually receptive 14-d-old males (A) or 7-d-old females (B) of *Blattella germanica*, between the odors of 14-d-old male and 7-d-old female in full darkness. *significant difference ($p < 0.05$, χ^2-test).

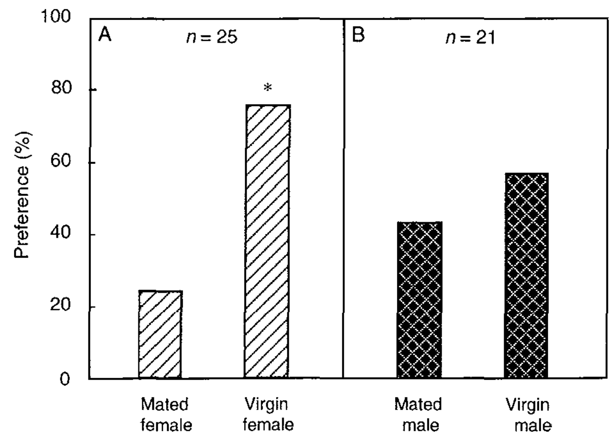

Fig. 4. Preference of sexually receptive individuals of *Blattella germanica* to the odor of mated or virgin heterosexuals in full darkness. (A) Choice of 14-d-old males between the odors of mated and virgin 7-d-old females; (B) Choice of 7-d-old females between the odors of mated and virgin 14-d-old males. *significant difference ($p < 0.05$, χ^2-test).

1). However, there was no significant difference in the other females' calling frequency when they were exposed to conspecific odor for 6 d. The sexually receptive females used in the 1-d exposure treatment were kept in a group before the video recording, but ones in the 6-d exposure treatment were kept individually before the recording. The results show that the longer sexually receptive females are isolated from conspecific odor, regardless of whether it is hetero- or homo-sexual odor, the higher the calling frequency. The calling behavior of sexually receptive females was not affected by the chemical signal from conspecific individuals as long as they were previously exposed to the conspecific odor.

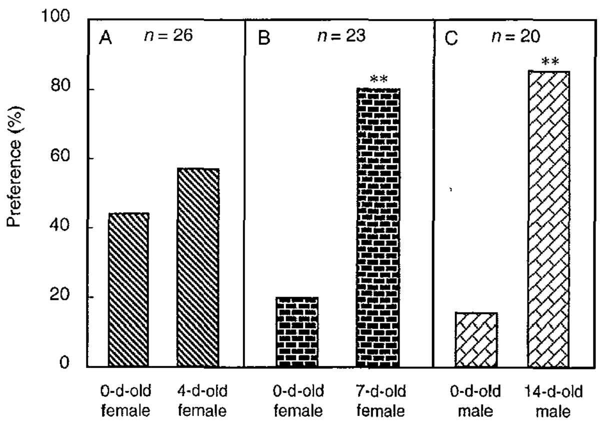

Fig. 5. Preference of sexually receptive individuals of *Blattella germanica* to the n-hexane extract of heterosexual's body surface in full darkness. (A) Choice of 14-d-old males between the extract of 0-d-old and 4-d-old females; (B) Choice of 14-d-old males between the extract of 0-d-old and 7-d-old females; (C) Choice of 7-d-old females between the extract of 0-d-old and 14-d-old males. **significant difference ($p < 0.01$, χ^2-test).

DISCUSSION

Odor involvement in mate-finding

Sexually receptive German cockroaches could detect and did prefer the existence of heterosexual odor when no odor or heterosexual odor were presented. However, they did not show preference for the odors of sexually receptive individuals when sexually receptive individuals didn't exhibit calling behavior or wing-raising pose (Figs. 1, 2). Since during rest, the opening of a female's volatile sex pheromone gland is concealed by the 9th tergite, the pheromone is released only when a female calls (Liang and Schal 1993a,c). In addition, the amount of the volatile sex pheromone found in the gland increases with age, which coincides with increasing calling frequency (Liang and Schal 1993b,c). Although it has been demonstrated that the amount of contact sex pheromone increases with age (Schal et al. 1990a,b 1991), the contact sex pheromone cannot be released into the air because its molecular size appears to be one of the largest ever found among insect pheromones (Nishida and Fukami 1983). During the odor preference experiments, none of the sexually receptive females exhibited calling behavior. Therefore, the male approach to the choice station was solely dependent on the volatile components of the aggregation pheromone. Similarly, a male must contact a female before releasing volatile components of tergal secretion by raising its wings (Brossut et al. 1975, Nishida and Fukami 1983). The only odor the female detected during the preference choice experiments was the volatile components of the aggregation pheromone, since both sexes can synthesize and release that pheromone (Ishii and Kuwahara 1978).

Table 1. Effect of conspecific odor on calling frequency of 6-d-old female German cockroaches at 28 °C, in constant darkness

		Female calling (no./day) (Mean ± S.D.[b])				
Treatment	n	none	0-d-old male	13-d-old male	6-d-old female	p
One-day exposure	40	21.3 ± 28.1	15.7 ± 16.9	15.0 ± 16.1	12.4 ± 12.8	> 0.05
One-day exposure with artificial airflow (20 min/4 h)	40	14.4 ± 15.1	16.2 ± 14.4	11.2 ± 12.3	3.3 ± 3.2	> 0.05
Six-day exposure[a]	40	57.1 ± 26.4*	19.4 ± 26.1	30.7 ± 24.8	18.1 ± 17.7	< 0.05

[a]The 6-d-old female was exposed to odor of a 0-d-old male, 7-d-old male, 0-d-old female, or to no odor for 6 d at 28 °C, LD 16:8 h conditions. The test was performed on the 7th day after the connection.
[b]Mean calling frequencies of different treated females were analyzed by Kruskal-Wallis and Dunn tests.
*Significant difference within the same column ($p < 0.05$, Dunn test).

Roth and Willis (1952) pointed out that an adult male German cockroach can use contact chemoreception to discriminate between females and males. Although sexually receptive males had a significant preference for sexually receptive female odor over that of male, sexually receptive females did not show preference for the odor of the opposite sex (Fig. 3). This raises the question of how males are able to distinguish between males and females when both of them fail to release volatile sex pheromones. In order to answer this question, we need to analyze the difference of aggregation pheromones between sexes. A female's calling behavior is completely suppressed by a successful mating (Liang and Schal 1993b). However, sexually receptive males preferred the odors of virgin females over mated females even though the virgin female did not perform calling behavior during the experiment (Fig. 4A). The male German cockroach secretes a chalk-white substance from the accessory glands to cover or partly cover the spermatophore in a recently mated female. This substance fits the descriptions of the sphragidal fluid (Roth and Willis 1952). We think this substance may be used to deter other approaching males. All these findings may provide a clue as to how females can avoid sexual harassment from males and divert energy and time, and thus increase feeding before forming an ootheca (Lee and Wu 1994). However, female adults showed no odor preference between mated or virgin males (Fig. 4B). Since a female German cockroach can only mate once in a reproductive cycle, whereas males can mate repeatedly, a female's indifferent response to mated or virgin males will not impede her reproductive success.

A female's contact and volatile sex pheromones as well as tergal secretion from males can be extracted with n-hexane (Brossut et al. 1975, Nishida and Fukami 1983, Liang and Schal 1993a). However, the volatile components of the aggregation pheromone are highly soluble in water, and little is extracted with n-hexane (Sakuma and Fukami 1990). When a female becomes sexually receptive at the age of 4 d, she is ready to mate (Lee and Wu 1994), although her volatile sex pheromone is insufficient to attract males (Fig. 5). The amount of volatile sex pheromone found in the pheromone gland is low on the 1st day after emergence but increases with age, and peaks on the 6th day (Liang and Schal 1993c). Our findings confirm the attractive function of the female's volatile sex pheromone, and the occurrence of female's release of sufficient sex pheromone later in adulthood than her sexual receptivity.

The volatile sex pheromone is released only when a female German cockroach performs the characteristic calling behavior (Liang and Schal 1993a). However, this behavior is considerably autonomous and it is not affected by the presence of conspecific odor (Table 1). The calling frequency of virgin females is significantly increased when a female does not sense any other conspecific odor for a long time (Table 1).

Mate-finding strategy

Since the German cockroach is a gregarious species, it usually does not need to travel far to find mates (Schal et al. 1983). Both females and males increase their locomotion when they are alone and sexually receptive (Lin and Lee 1996, Lin and Lee unpubl. data). This behavioral change allows sexually receptive individuals to meet potential mates. With their abilities to contact and recognize the opposite sex in groups by contact sex pheromone (Roth and Willis 1952), this behavior serves a reproductive function. Therefore, German cockroach can find mates and reproduce successfully without involving any volatile sex pheromone under normal environmental conditions. Since their living conditions are closely related to human shelters, this mate-finding strategy will increase the fitness of the species in a relatively stable environment. However, the risks of heavy inbreeding can be reduced by the dispersal stage of 3rd nymphal instars (Rivault 1989). This dispersal behavior will reduce the relatedness of individuals in groups when they are sexually receptive.

Although living groups of German cockroaches are usually congregated around resources such as food or shelter (Schal et al. 1984), some of them may live in isolation due to human disruption or may hide from a harsh environment. These individuals will preferentially approach the source of aggregation pheromone where they can join the group and mate with sexually receptive individuals. A female will increase its locomotion so much that it may even come up to walk during photophase against its nature of light avoidance (Lin and Lee 1996). It is energy costly to produce an ootheca (Mullins and Cochran 1986) which is equal to about 30% of the female's body weight, and each ootheca is converted from 90% of the nutrient acquired in this reproductive cycle (Kunkel 1966). Since females will produce an ootheca regardless of mating status, the penalty for failure to mate is severe (Lee and Wu 1994). Sexually receptive virgin females not only increase locomotion to search for mates, but they also exhibit calling behavior during which volatile sex pheromone is released. The calling frequency increases with age in a virgin female population (Liang and Schal 1993b), but the age-dependent frequency is not affected by the presence of conspecific odor (Table 1). The age-dependent calling frequency only increases when the female does not sense conspecific odor for a long time (Table 1). In addition, the onset of calling in adulthood occurs after a female has reached sexual receptivity, and its termination is achieved with a successful mating (Liang and Schal 1993b). These findings provide strong evidence that German cockroach females increase locomotion and calling frequency as a secondary strategy when the female does not initially find a mate by contact sex pheromone.

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揮發性性費洛蒙之偵測與呼喚行為之表現：德國蜚蠊 (*Blattella germanica* (L.)) 之次要配偶找尋策略

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德國蜚蠊是一種群聚性的昆蟲，通常雄蟲是利用接觸性性費洛蒙來引導其舉翅求偶的行為。雌蟲與雄蟲通常聚集在食物、棲所或聚集費洛蒙附近，因此兩性之間的接觸並不需要長距離的搜尋。然而在本研究中，我們證明了性接受雄蟲不僅可以偵測到雌蟲的氣味，而且偏好處女雌蟲的氣味甚於交尾過雌蟲。性接受雌蟲也可以偵測到雄蟲的氣味，但是對雄蟲和雌蟲的氣味則沒有顯著偏好，而且不能依氣味分辨出雄蟲是否曾經交尾。性接受雌蟲不僅增加活動量以找尋配偶，而且表現出呼喚行為，伴隨著揮發性性費洛蒙的釋放，以誘引雄蟲前來交尾。當處女雌蟲沒有接觸同種個體氣味的時間愈久，雌蟲呼喚的頻率愈高。所以，我們認為德國蜚蠊雌蟲利用增加活動量及呼喚頻率當作一種次要的配偶找尋策略。

關鍵詞：呼喚行為，氣味偏好，次要策略。

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