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EFFECTS OF SEX PHEROMONE ON LOCOMOTION IN THE MALE AMERICAN COCKROACH, *Periplaneta americana*

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Abstract—The locomotory activities of individual males of *Periplaneta americana* in a circular arena 2.5 m in diameter were investigated during the portion of the photocycle in which the cockroaches are most active. Control animals ran at an average speed of 10.86 cm/sec but remained immobile 68% of the time. Pauses in locomotion occurred frequently and at fairly regular intervals ($\bar{x} = 0.88$ sec). Males showed a strong tendency to remain near the sides of the arena. Sex pheromone presented in the center of the arena produced a reduction in immobility time and a slight increase in running speed. The frequency of pauses decreased, and the time between pauses became less regular. The proportion of time spent near the sides of the arena was greatly reduced also.

Key Words—Locomotion, sex pheromone, cockroach, *Periplaneta americana*, behavior.

INTRODUCTION

Periplaneta americana adults are not strong fliers. Although they may occasionally glide from a vertical surface to the ground, the vast majority of their movement from place to place is accomplished by walking or running. Many studies have been published which relate to locomotion in cockroaches: Hughes (1952) described locomotion in *Periplaneta americana* and *Blatta orientalis*. Studies by Delcomyn (1969, 1971a,b) on the coordination of leg movements have shown that *P. americana* uses an alternating tripod or alter-

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nating triangle gait at all speeds above 5 cm/sec. McConnell and Richards (1955) utilized photocells to measure running speeds over distances of 25 and 50 cm and found that *P. americana* was capable of speeds up to 130 cm/sec.

While the studies by Hughes and Delcomyn dealt primarily with the coordination of limb movements during locomotion, those of Darchen (1952, 1955, 1957) and Darchen and Richard (1960) described the search behavior of *Blattella germanica.*

To date, no information has been available concerning the search behavior of cockroaches in large open areas. Nothing is known about the paths that they follow, the distances they cover, their speed of movement, or even what proportion of their time is spent moving about. This study was conducted to provide information about the normal locomotory activities of cockroaches and the ways in which these activities are affected by the presence of sex pheromone.

METHODS AND MATERIALS

A group of 10 *P. americana* males was selected from laboratory colonies. The adult males selected were predominantly young because it was necessary that they have their antennae and all three pairs of legs intact. Some of these appendages are frequently lost during aggressive encounters rather early in life. Paper disks 9 mm in diameter coated with yellow luminescent paint (Dura tempera colors) were glued to the males' pronota. Clear plastic containers ($29 \times 18.5 \times 12.5$ cm) furnished with food and water served as housing cages for groups of five males. The animals were maintained on a 12:12-hr black light–white light cycle at $25 \pm 2°C$ in a room devoid of other cockroaches. They were kept under these conditions for two weeks before testing was initiated.

The locomotor activities of male cockroaches were examined in an 8-ft (2.5 m) circular arena. The floor of the arena consisted of two 4×8-ft sheets of $\frac{1}{4}$ in Masonite ($1.22 \text{ m} \times 2.44 \text{ m} \times 0.6$ cm) painted with flat black paint to reduce reflectance. The ends of a strip of galvanized sheet metal 20 cm high and 7.66 m long were joined together to form the sides. Petroleum jelly was applied to the metal to keep the test animals on the floor.

A motor-driven 35-mm single-lens-reflex camera was suspended from a wooden beam above the center of the arena. A 60 rpm synchronous motor was mounted on an adjacent beam in such a way that a slotted disk could be rotated in front of the camera lens. When photographing a cockroach in the arena, the disk rotating in front of the lens produced a stroboscopic effect, resulting in six exposures of 0.083-sec duration for each second the shutter remained open.

An Olympus OM-1 camera with a Zuiko 28-mm F3.5 lens was used for filming the cockroaches' movements. Kodak Tri-X film was rated at ASA 1600 and developed in Acufine for 6.5 min at 20°C and then fixed and washed normally. This technique produced dark sharp images in most cases and never gave unsatisfactory results.

During photographing, the arena was illuminated by low intensity black light (~365 nm). As a result, only the luminescent disks on the backs of the cockroaches reproduced on film. Using this technique, the light reflected from the disk on a moving cockroach produces a series of short streaks on the film, each of which represents the distance travelled in 0.083 sec. Although the cockroach can presumably see ultraviolet light, preliminary experiments with a 12:12-hr white light and black light photocycle revealed no significant differences in activity rhythms or mating behavior between the experimental animals and a group of controls maintained on a synchronized 12:12-hr light–total darkness cycle. It is likely that low-intensity ultraviolet illumination closely approximates the twilight conditions cockroaches often encounter at night.

Individual males were introduced into the arena, and after a 30-min adjustment period, their movements were photographed. One 20-sec exposure was taken each minute for 20 min. At the end of the 20-min test period, an inverted glass jar was placed over the male to restrict its movement (the inside of the jar was coated with petroleum jelly to prevent the male from climbing the sides). Thus confined, the male was moved to the perimeter of the arena, and a 5.5-cm disk of Whatman No. 1 filter paper treated with 10 μl of sex pheromone extract was introduced. After 5 min to allow for diffusion of the pheromone, the male was released and his activity sampled each minute for another 20 min. The extract was prepared from feces and filter papers taken from cages containing several hundred virgin females. The extraction technique used was that of Rust (1976) and used petroleum ether (Skelly F) as the solvent. Each of the 10 males was tested twice in this manner, with a minimum recovery time of 72 hr between tests. All observations were made during hours 3 and 4 of the black light (dark) cycle.

Laboratory-prepared sex pheromone extract was used in these experiments in order to ensure equal stimulus intensity for each of the males tested. Hawkins and Rust (1977) found that considerable variation in sex pheromone emission occurred between females and from day to day for individual females of *P. americana*. Bioassays similar to those of Block and Bell (1974) were conducted to determine approximately one female equivalent. It was determined that the level of male activity elicited by 10 μl of sex pheromone extract closely approximated the activity elicited by 24-hr filter papers from 250-ml beakers housing individual virgin females, i.e., one female equivalent.

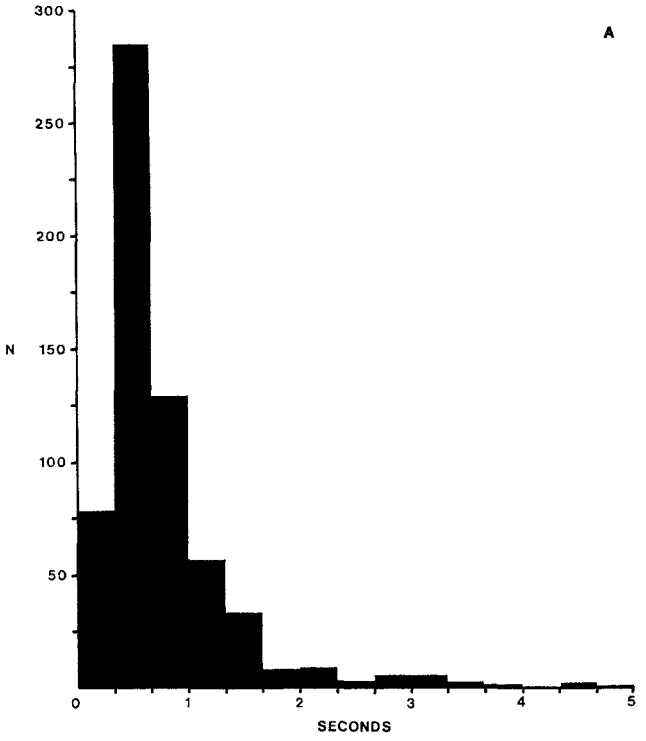
RESULTS AND DISCUSSION

When a cockroach is initially introduced into the arena, an escape response is elicited. The animal runs very rapidly in a nearly straight line until it reaches the wall. It then turns left or right and continues running rapidly along the perimeter of the arena for several seconds. It is not unusual for a cockroach to make several complete circuits around the arena before its running speed is noticeably reduced; it then begins to explore its new surroundings. After 30 min in the arena, the level of activity is considerably reduced. The male continues to walk about, but at a slower pace, and it may stop and remain stationary for minutes at a time. Locomotor activity during this period is presumably related to the circadian rhythm of activity rather than a continuation of the escape response.

P. americana males rarely maintain a steady pace for very long in this state. Instead, they walk a few centimeters, pause, walk a little farther, and pause again. A similar locomotor rhythm has been described for *Tenebrio* by Erber (1975). During test periods in which no prolonged inactivity occurred, the males paused an average of 8.6 times in each 20-sec sample or 25.8 times per min in the controls. In the presence of sex pheromone, the frequency of pauses declined to 6.2 per sample or 18.7 times per minute ($P < 0.001$; Wilcoxon's signed ranks test). These pauses show up on film as dark dots irregularly spaced, along the path. Because the dots are distinctly round and much darker than the streaks produced by a moving animal, they clearly denote where the cockroach has stopped. The distance traveled between pauses varies with the individual and is largely dependent on running speed, but the duration of locomotor activity is much more consistent, at least in the controls. In five randomly selected pairs of 20-min tests, the pauses in the controls were separated by 0.2–8.8 sec ($\bar{x} = 0.877$ sec) with 46% separated by only 0.5–0.67 sec of running time (Figure 1A). When pheromone was present, the duration of locomotor activity between pauses was less regular. Commonly, two or three pauses occurred in rapid succession followed by several widely separated ones. The time between pauses ranged from 0.2–7.7 sec with a mean of 1.27 sec (Figure 1B).

Although it is not possible to determine the duration of the individual pauses using this photographic technique, one can calculate the amount of time that the cockroach was immobile during a given 20-sec sample. Since the system provides six exposures per second during each sample, 120 streaks

FIG. 1. Frequency distribution of the duration of running activity between pauses in locomotion of *Periplaneta americana* males. Data from five randomly selected pairs of 20-min tests. (A) Control ($N = 699$; $\bar{x} = 0.88$ sec); (B) Sex pheromone present ($N = 407$; $\bar{x} = 1.27$ sec).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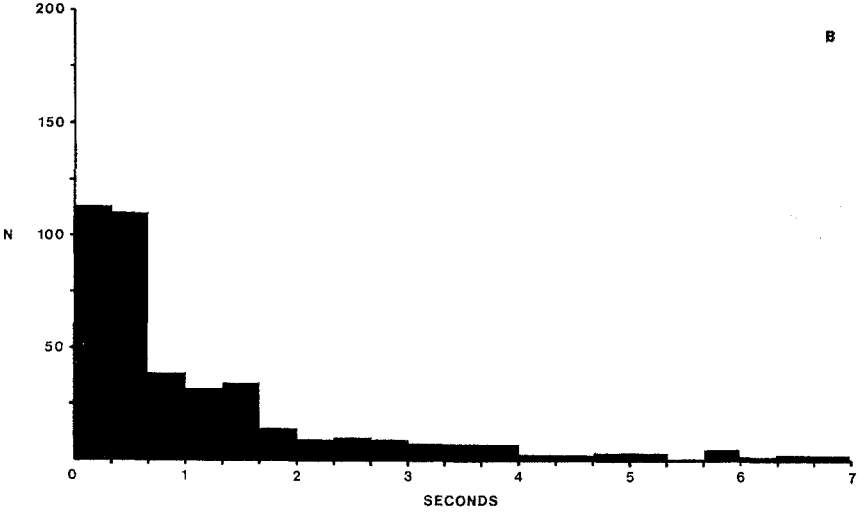
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would result if the animal remained in constant motion. By subtracting the total number of streaks and dark dots from 120 and dividing the remainder by 6 (the number of exposures per second), the total immobility time is obtained. Immobility time per minute is calculated by multiplying this number by three.

Using this technique, immobility time was calculated for each trial. Figure 2 shows the mean immobility times for each minute of the 20-min test period. The mean level of activity was 14% greater in the presence of pheromone. The peak of sex-pheromone-induced locomotor activity occurred 10 min after initial exposure. This peak was followed by a gradual and irregular decline in activity, i.e., increasing immobility time. In the controls, no marked trends were evident except for a decline in immobility time toward the end of the 20 min. This insignificant increase in activity may have been due to the cockroaches' increased familiarity with the arena or simply due to sampling error.

The response of males to sex pheromone at the relatively low concentrations utilized in these experiments is thus greatly different from their response to very high concentrations. At high concentrations, the greatest activity occurs in the first minute after exposure and then declines steadily (Hawkins and Rust, 1977). While there is no way to correlate the data presented here

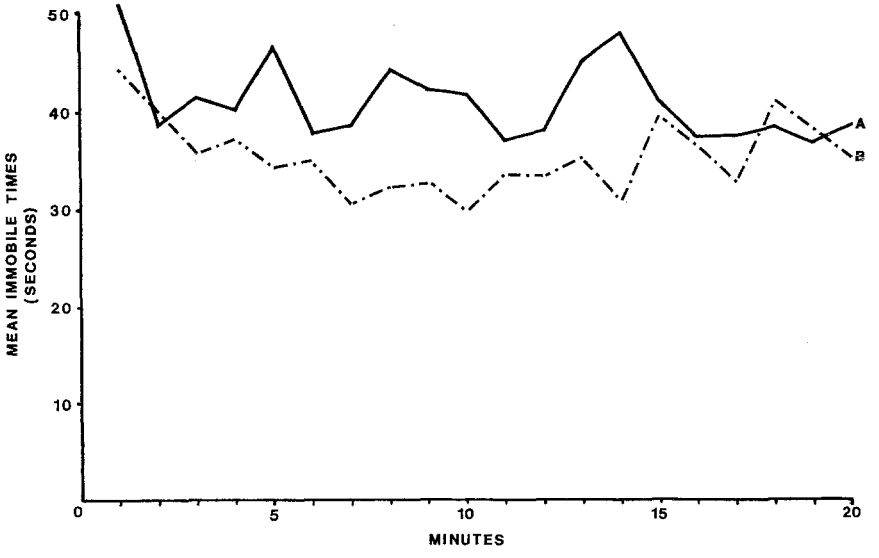

FIG. 2. Mean immobile times for males of *Periplaneta americana* during each minute of the 20-min testing period. (A = control; B = sex pheromone present.)

with the bioassays of Hawkins and Rust, it is evident that the maximum activity response does not necessarily occur at the moment of initial stimulation.

The controls remained immobile 68% of the time, i.e., 40.8 sec out of each minute, on the average. The variances were quite high from minute to minute for specific individuals as well as between individuals. Mean immobility time for individual animals ranged from 27.78 to 54.45 sec/min. Immobility times for the 20-sec samples ranged from 1.83 to 20 sec. As previously noted, it was not uncommon for a male to remain immobile throughout one or more of the 20-sec sampling periods. In fact, periods of prolonged immobility which produce just one very dark dot on the film occurred 1–10 times ($\bar{x} = 3.53$) per 20 exposures in the controls.

When sex pheromone was present, males still remained immobile for an average of 35 sec/min (58.4% of the time). Mean immobility times for individual animals ranged from 17.76 to 52.38 sec/min. As in the controls, immobility time ranged from 0 to 20 sec/20 sec sampling period in the pre-

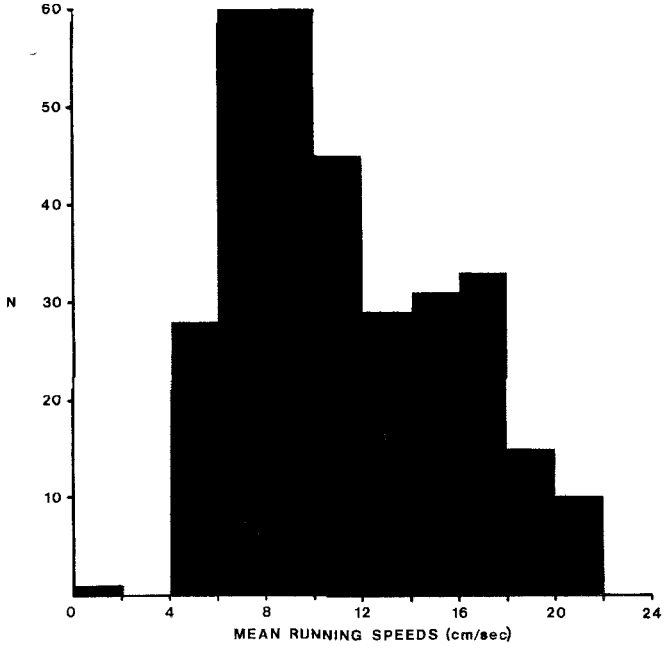

FIG. 3. Frequency distribution of the mean running speeds of the 312 control samples in which the cockroach did not remain stationary for the entire 20 sec. The distribution was not changed significantly by the addition of sex pheromone.

sence of pheromone. The decrease in immobility time due to pheromone is highly significant ($P < 0.01$; Wilcoxon's signed ranks test).

When they are not standing still, *P. americana* males move about at widely varying speeds. The over-all mean running speed in the controls was 10.86 cm/sec with the means of the 20-sec samples ranging from 5.22 to 17.32 cm/sec (Figure 3). Speeds in excess of 20 cm/sec were not uncommon, and the highest speed recorded was 38.8 cm/sec. Sex pheromone increases the speed of male locomotion but not to the extent that might be expected. The average running speed for the 20 trials was 11.42 cm/sec (range: 5.89–19.88). Maximum running speed within 20-sec sampling periods was generally higher than in controls, and the highest value recorded was 52.4 cm/sec, only 13.6 cm/sec faster than the peak without pheromone. Even this value is considerably below the highest speed measured by McConnell and Richards (1955), but they were measuring speeds generated by the cockroach's escape response.

Running speed may be influenced to some degree by whether the cockroach is turning or going straight, and whether it is following the side of the arena or crossing the center. However, the majority of drastic changes in direction are accomplished by positional changes during pauses, as in *Tenebrio* (Erber, 1975). Thus, many broad loops consist of a series of short, relatively straight runs with frequent pauses for directional changes. Lengthy pauses also occur frequently during long straight runs. Running speeds vary greatly in all portions of the arena, but the highest speeds recorded in the controls occurred during straight runs across the center. Males are able to change speed rapidly, and increases or reductions in speed of 10–15 cm/sec within a 0.167-sec interval frequently occur.

An interesting phenomenon occurs in the presence of sex pheromone. As the male orients toward the pheromone source in the center of the arena, and enters areas of progressively higher pheromone concentration, mean running speeds first increase and then decline close to the source (Table 1). The highest speeds occur in a broad band 30–90 cm away from the source. Speeds outside this band, either less than 30 cm or more than 90 cm from the source, were significantly slower with the slowest speeds occurring close to the source. No such trend was evident in the controls. The increase in locomotor speed that occurs at intermediate distances might be expected as a result of higher pheromone concentrations, but the slower speeds in the area of highest concentration are somewhat surprising. Presumably, the slower running speeds facilitate chemotactic orientation which occurs close to the source (Hawkins, 1978).

Darchen (1957) found that *Blattella* spent 94% of a 75-min test period in the outer 3 cm of a circular arena 28 cm in diameter. Although it was not possible to determine the exact amount of time spent by *Periplaneta* males

TABLE 1. MEAN RUNNING SPEEDS (CM/SEC) OF 14 *P. americana* MALES STIMULATED BY SEX PHEROMONE

Sample	Distance from source (cm)			
	0–30	31–60	61–90	91–120
1	16.53	19.70	20.79	19.72
2	4.93	5.83	6.95	6.51
3	13.18	17.93	18.48	12.91
4	13.68	16.94	15.12	9.28
5	13.04	22.12	21.44	19.34
6	10.81	16.99	16.10	14.73
7	13.61	17.60	17.18	19.67
8	14.41	18.39	13.43	13.31
9	11.71	18.34	19.88	19.00
10	9.42	15.77	14.68	12.20
11	12.62	12.89	14.89	15.40
12	5.19	5.57	7.64	5.43
13	11.56	17.26	20.12	18.24
14	11.66	14.00	15.71	14.98

	Wilcoxon's Signed Ranks Test		
	Groups		
	1–2	2–3	3–4
T_s	0[a]	37.5	15[b]
P	0.01	N.S.	0.05
N	14	14	14

[a] $P<0.01$.
[b] $P<0.05$.

in the outer portion of the arena, fairly accurate estimates were possible. By estimating to the nearest 25% what portion of an animal's path was restricted to the outer 30 cm of the 2.5-m arena, it was determined that control animals spent more than 70% of the time in that region. Of the 400 individual paths examined, 62% (248) lay entirely within the outer 30 cm while less than 10% (38) were completely outside it. Thirty-four percent of the time was spent within 2.5 cm of the sides. These data suggest a strong wall-seeking tendency which is presumably related to predator avoidance. Cracks and crevices in which cockroaches can hide from predators are likely to be more abundant along walls and the edges of other vertical structures such as rocks and tree

trunks. When pheromone was present, the wall-seeking tendency was considerably reduced. Males spent 63% of the time in the outer 30 cm. Forty-five percent of the paths were entirely within the outer 30 cm, and only 10% of the time was spent within 2.5 cm of the sides.

From an ecological point of view, perhaps the most interesting parameter is the distance that cockroaches travel. If an animal moves forward at a given speed at a more or less constant rate, it must necessarily traverse a certain amount of territory, i.e., speed and distance are interrelated. In attempting to control cockroach populations, it is important to have some knowledge of how far they are likely to wander during periods of activity. Dispersal studies of sewer populations of *P. americana* in Arizona by Jackson

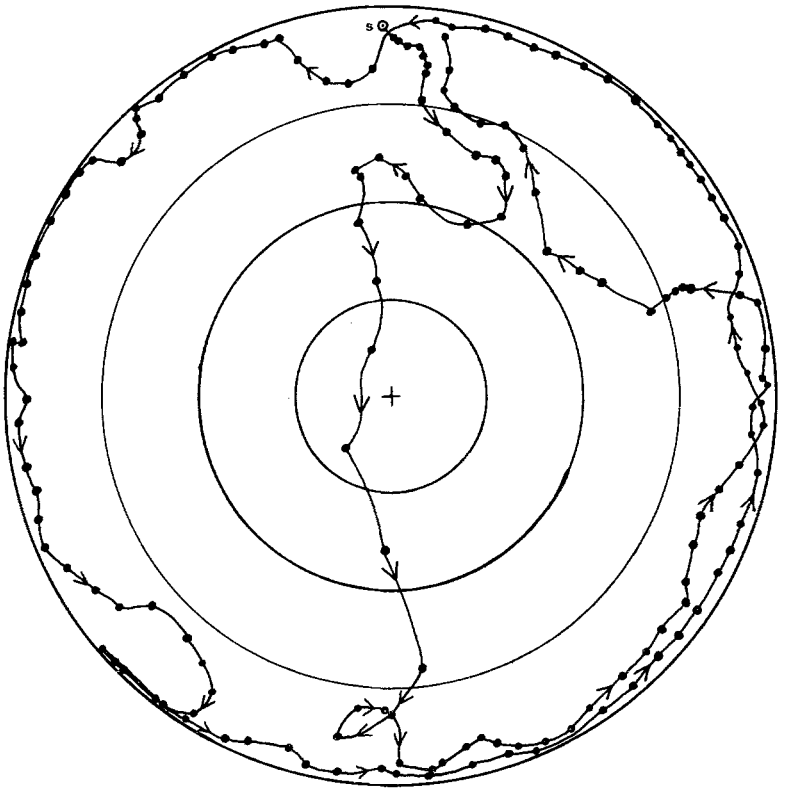

FIG. 4. A typical path traveled by an adult male of *Periplaneta americana* during 7 min of continuous filming with no sex pheromone present. Dots mark the locations of pauses of varying duration; arrows indicate the direction of movement (s = starting point).

and Maier (1955) and studies of the home-range behavior of populations in a deserted building by Wetherell and Breed (unpublished data) have suggested that individuals rarely travel very far during a given 24-hr period. This may be the case, but the results of these studies were far from conclusive.

In the 2.5-m circular arena, control animals moved about with an over-all average speed of 3.65 cm/sec for 20 min of testing during the portion of the dark cycle when Hawkins and Rust (1977) found them to be most active. (This figure includes numerous periods of prolonged inactivity as well as active periods.) This translates to a distance of 131.4 m/hr and suggests that males of *P. americana* are easily capable of traveling several hundred meters during a single night. However, since their paths are usually quite convoluted, total distance may not be correlated with linear distance. In fact, cockroaches rarely maintained the same directional heading for more than 1–2 sec at a time when they were not following the sides of the arena. A typical path across the open central portion of the arena can best be described as meandering—not a zigzag or a series of loops—but a path with frequent irregular changes of direction (Figure 4).

CONCLUSIONS

The locomotion of *P. americana* males in the 2.5-m circular arena is characterized by a generally low level of activity. They remain immobile approximately 68% of the time, and when they move, it is only at speeds averaging 5–14 cm/sec over 20 sec ($\bar{x}$ = 10.86 cm/sec). Pauses occur frequently, often being associated with marked changes of direction. Males exhibit a marked tendency to remain close to the sides of the arena and might be expected to follow walls and stay near corners under natural conditions. Even at such low levels of activity, cockroaches are easily capable of traveling several hundred meters in a single night, but their paths are apt to be so greatly convoluted that the linear distance from start to finish might be 30 m or less.

When a source of sex pheromone is placed in the center of an arena, immobility time decreases, running speed and distance traveled increase, the frequency of pauses decreases, and the time between pauses becomes less consistent. The proportion of time spent near the sides of the arena also decreases considerably. Thus the principal changes are a general increase in the over-all level of activity and reduction of the wall-following tendency.

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