Reproduction and Development of *Blattella asahinai* (Dictyoptera: Blattellidae)

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ABSTRACT The development of the Asian cockroach, *Blattella asahinai* Mizukubo, was studied under laboratory conditions. Immature development and adult longevity were 67.8 and 103.5 d for females and 65.7 and 48.5 d for males. Females produced an average of 3.7 oothecae, 64.6% of which were viable. Viable oothecae contained an average of 37.5 eggs with an 88% rate of hatch. Females required 13 d after eclosion to produce the first ootheca and 7.9 d between dropping one ootheca and producing the next. Viable oothecae were incubated an average of 19.2 d. Nonviable oothecae were either dropped within 4 d or carried for a period similar to the incubation period of viable oothecae. The estimated lifetime reproductive potential of female Asian cockroaches was 79.6 hatched eggs. This estimate is similar to that of another outdoor species, *Blattella vaga* Hebard, but approximately one half that of the closely related German cockroach, *B. germanica* (L.), under similar conditions. Tests in the field and laboratory indicated that chemical control is feasible with application of residual pesticides to lawns and low vegetation where Asian cockroaches are found.

KEY WORDS Insecta, *Blattella asahinai*, Asian cockroach, reproductive biology

THE ASIAN COCKROACH, *Blattella asahinai* Mizukubo, is the most recently reported addition to the exotic cockroach fauna of the United States (Roth 1986, Atkinson et al. 1990). This species was introduced into central Florida and is spreading throughout the state (Koehler & Patterson 1987, Brenner et al. 1988, Brenner 1990). Based on its distribution in the Old World (Roth 1985 [treated as *B. beybienkoi* Roth], Brenner 1990), its eventual distribution will probably extend over a wide area in the southern United States.

Blattella asahinai is the closest known relative of the German cockroach, *B. germanica* (L.) (Roth 1985), the major household pest species in the United States and most of the world (Cornwell 1968, Ebeling 1975). Unlike the German cockroach, *B. asahinai* appears to be primarily an outdoor species, although it is attracted to light and enters structures (Brenner et al. 1988, Brenner 1990). Nothing is known of the biology of this species in its native range, and the species was not even recognized as distinct until 1981 (Mizukubo 1981). Recent work in the U.S. has focused on ecology, pest status, and control (Brenner 1988, 1990; Brenner et al. 1988), genetics (Ross 1988, 1989), and comparisons of immature stages with the German cockroach (Ross & Mullins 1988). Our study was initiated to obtain information on basic parameters of development, longevity, and reproductive biology. An additional objective was to evaluate residual pesticide treatments of infested lawns or low vegetation for outdoor control of this species.

Materials and Methods

Thirty-three newly eclosed adult females were placed individually in 0.95-liter glass jars. A newly eclosed adult male was placed with each female. Males were replaced after death, so that there was never a period longer than 1 d during which a living male was not present in each jar. Jars were capped with a disk of window screen inside the screw-on rim to prevent escape because both sexes are capable of flight. Cockroaches were taken from a colony maintained at the Insects Affecting Man and Animals Research Laboratory, USDA–ARS, in Gainesville, Fla., established in 1986 from adults collected near Tampa, Fla.

Laboratory rat chow pellets were used for food (the same food source used in colony maintenance); water in a cotton-stoppered 20-ml plastic vial was provided ad libitum. Jars were held at in a room 25°C at 50% RH with a 12:12 (L:D) photoperiod. Actual humidity within the jars was probably higher because of the water vial. Survival, oothecal production and status, and egg hatch were monitored daily after each female died. After eggs hatched, live nymphs, and eggs per ootheca (determined from egg chambers in the empty ootheca) were counted. Longevity data were collected for the original males introduced with females and for replacement males.

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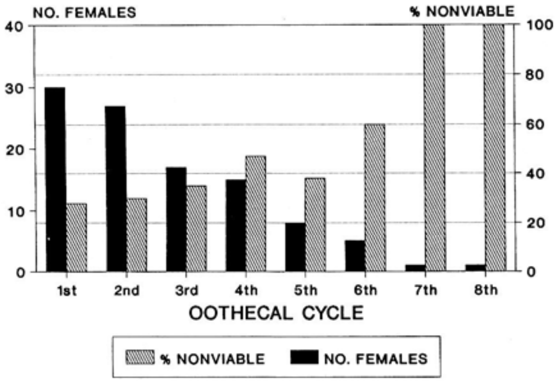

Fig. 1. Number of female *Blattella asahinai* that produced oothecae and percent of these that were nonviable by oothecal cycle (n = 30 of 33 females that produced oothecae).

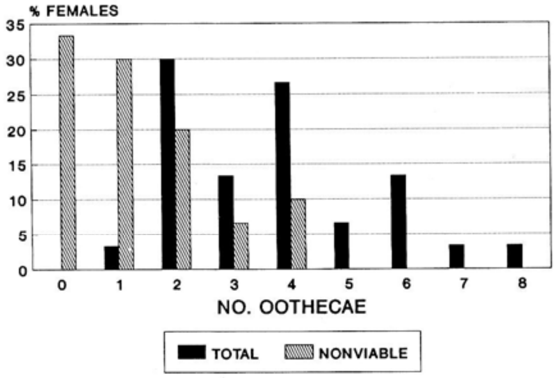

Fig. 2. Frequency distribution of total and nonviable oothecae produced per female *Blattella asahinai* (n = 30 females that produced oothecae).

Thirty-five newly hatched nymphs, each from a different ootheca from a total of 13 different females, were held individually in Petri dishes with food pellets and water and checked daily until adulthood to determine the duration of immature development. Thirty-two individuals (13 females and 19 males) survived to adulthood.

Number of eggs and nymphs per ootheca, preoviposition period (time between drop of an ootheca and appearance of subsequent one), incubation period (time a viable ootheca was carried), and time to abortion (time that nonviable ootheca was carried) were compared for all females by oothecal cycle by analysis of variance (ANOVA) with the general linear models (GLM) procedure. Means were separated with Tukey's method because this test controls the experimentwise error rate (P = 0.05; SAS Institute [1988]). Summary statistics were derived with the MEANS and UNIVARIATE procedures.

Pesticide tests were done in a bahia grass lawn in full sunlight in Gainesville. Treatments were applied in three blocks in a complete randomized block design. Treated plots were 1-m squares separated within blocks by 1 m. Blocks were separated from each other by 1 m. Pesticides were applied on 3 April 1990. Granular formulations were washed into the soil with 5.5 liters of water from a garden hose. Emulsions and suspensions were prepared in 200 ml water and applied in 1-liter plastic hand sprayers. A different sprayer was used for each formulation. No additional water was added to sprayed plots. Pesticides applied were ethoprop (mocap, Rhone-Poulenc, Research Triangle, N.C.) applied at the rate of 2.8 kg (AI)/ha, carbaryl (sevimol 40% flowable, Rhone-Poulenc) at 2.24 kg (AI)/ha, diazinon 2% granular (Ciba-Geigy, Greensboro, NC) at 4.8 kg (AI)/ha, and isazophos (triumph 47.92% emulsifiable concentrate, Ciba-Geigy) at 4.6 kg (AI)/ha. Heavy rainfall (3.8 cm) fell the night after treatment beginning ≈5 h after application.

Treated sod was tested for activity by cutting rectangles with a sharp spade to a thickness of 2.5–5 cm. The undisturbed turf, litter, and upper layers of soil were placed into clear plastic boxes (15 by 25 by 13 cm), completely filling the bottoms. Adult male cockroaches were anesthesized with CO_2 and released into the boxes, which were then covered with plastic lids. Mortality was evaluated after 24 h. Bioassays were performed at 24 h, 1 wk, and 2 wk after treatment. Percentage mortality data were normalized with the arcsine square root transformation and compared among treatments by ANOVA. Means were separated with Tukey's method (P = 0.05; ANOVA procedure, SAS Institute [1985]).

Results

Asian cockroach females carry their oothecae until eggs hatch. This behavior also occurs in *Blattella germanica* and *B. vaga* (Cornwell 1968, Ebeling 1975). Thirty of 33 females produced at least one ootheca (Fig. 1, 2), averaging 3.7 oothecae per female (Table 1). One female produced eight oothecae, the last two of which were not viable (ootheca dropped, no eggs hatched). Abortion rates averaged 35.4% (number of nonviable oothecae as percentage of total oothecae) but increased with oothecal cycle from 28% for the first cycle to 100% for the seventh and eighth cycles (Fig. 1). The higher oothecal abortion rate in older females may be related to their poor physiological condition. The number of females producing oothecae appeared to be normally distributed (Fig. 2), but the number of females producing nonviable oothecae was strongly skewed to the right (Table 1, Fig. 2). A small number of females accounted for a disproportionate share of the nonviable oothecae.

Females required an average of 13 d after eclosion to produce the first ootheca (Table 1, Fig. 3) and 7.9 d for subsequent oothecae (from time the previous ootheca dropped). The initial preoviposition period was significantly greater than that of

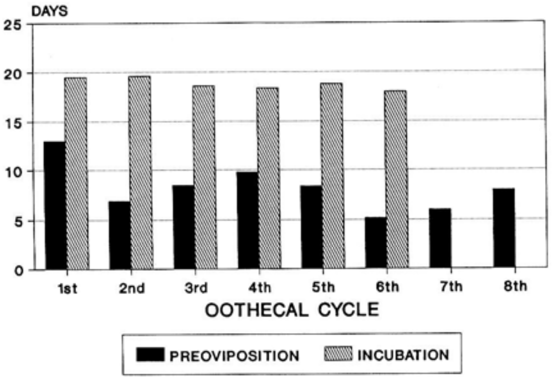

Fig. 3. Preoviposition and incubation periods (ds) of *Blattella asahinai* by oothecal cycle (see Fig. 1 for sample sizes).

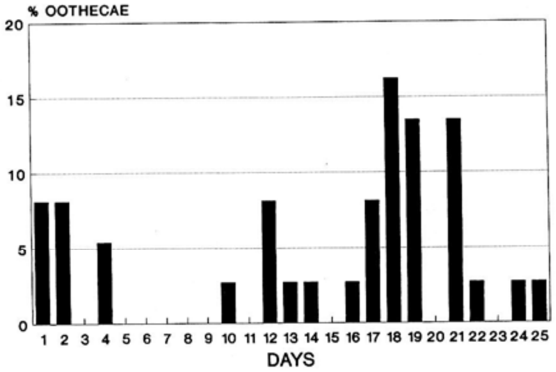

Fig. 4. Frequency distribution of periods nonviable oothecae carried before dropping by *Blattella asahinai* females ($n = 37$).

the subsequent periods ($t = 3.42$; df = 106; $P > .01$). Most cockroach species require a longer period to produce the first ootheca (Willis et al. 1958). Differences between subsequent preoviposition periods were not significant ($F = 1.94$; df = 5, 102; $P > 0.01$). Preoviposition times after an ootheca was aborted did not differ significantly from those following production of viable oothecae (8.96 ± 1.16 d ($\bar{x}$ ± SE) for 23 oothecae and 7.47 ± 0.97 d for 57 oothecae). Incubation periods (days fertile oothecae carried before egg hatch) (Table 1, Fig. 3) averaged 19.2 d for all oothecae (range, 16–26 d). Differences between mean development times for different oothecal cycles ($F = 2.81$; df = 5, 59; $P > 0.02$) were observed, but these did not follow any obvious pattern.

Females carried nonviable oothecae for an average of 14.5 d before abortion (Table 1). Eight oothecae were dropped within 4 d; the remainder were carried 10 d or longer (Fig. 4). Nonviable oothecae carried for 10 d or longer were held an average of 17.9 ± 0.66 d, $n = 29$) before being dropped; this period was nearly the same as the incubation period for viable oothecae. These data suggest that two distinct mechanisms are involved in abortion. When oothecae are aborted after a few days, females may be in poor physiological condition. In fact, 50% (four of eight cases in which oothecae were aborted in ≤4 d) of these females died shortly afterward. The frequency distribution of preoviposition periods (Fig. 5) was strongly skewed to the right. Very long preoviposition times appeared to be related to the probability that a subsequently produced ootheca would be nonviable. A greater proportion (four of nine cases) of oothecae produced after an initial preoviposition period of longer than 2 wk were not viable compared with the proportion (5 of 21) of those produced within a preoviposition period of 2 wk ($\chi^2 = 1.3$, df = 1, n.s.). The same was true for subsequent oothecal cycles (6 nonviable of 10 total oothecae and 22 of 70, respectively ($\chi^2 = 3.14$; df = 1; n.s.). Although these differences in proportions of nonviable oothecae were not significant statistically,

Table 1. Summary statistics for reproductive parameters, immature development, and adult longevity for *B. asahinai*

Parameter	n[a]	$\bar{x}$	Median	Min	Max	SE
Oothecae/♀	30	3.7	4	1	8	0.30
Nonviable oothecae/♀	30	1.2	0.5	0	4	0.25
Preoviposition period, first ootheca, d	30	13.0	7	5	29	1.35
Preoviposition period, subsequent oothecae, d	79	7.9	6	2	37	0.77
Incubation period, d	65	19.2	19	16	26	0.15
Period nonviable oothecae carried, d	37	14.5	18	1	25	1.2
Eggs/ootheca	66	37.5	38	20	44	0.53
Nymphs/ootheca	66	33.3	35	5	44	1.0
Females						
Immature development, d	13	67.8	67	60	80	1.5
Adult longevity, d	33	103.5	108	31	161	6.9
Males						
Immature development, d	19	65.7	65.5	52	81	1.48
Adult longevity, d	36	48.5	46.5	3	151	5.11

[a] Sample size is based on number of individuals (i.e., females, males, or oothecae) for which parameter was exhibited or relevant.

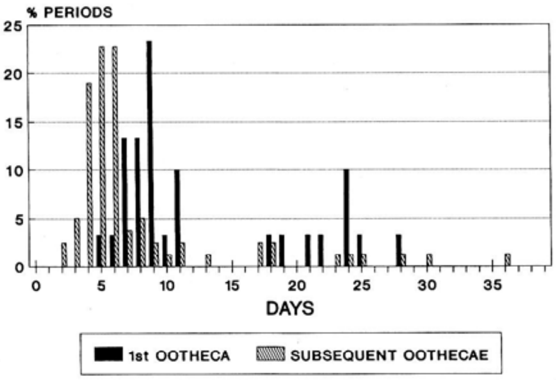

Fig. 5. Frequency distributions of preoviposition times for the first ($n = 30$) and subsequent oothecae ($n = 79$) of *Blattella asahinai*.

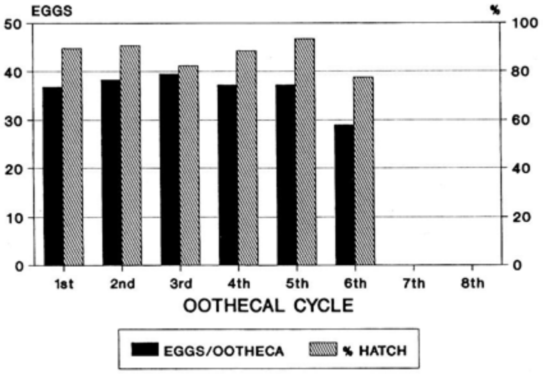

Fig. 6. Eggs per ootheca and percent hatch by oothecal cycle of *Blattella asahinai* (see Fig. 1 for sample sizes).

the relationship between preoviposition period and viability warrants further study. Nonviable oothecae carried for the normal incubation period may contain unfertilized eggs. Willis et al. (1958) showed that virgin *B. vaga* females produced normal-sized oothecae and carried them the same length of time as fertile oothecae, even though no hatch was observed. Cochran (1979) showed that most female *B. germanica* females produced a normal complement of viable oothecae from a single mating, although some did mate again. Although we replaced males after death so that females were always accompanied by a male, successful matings may not have occurred.

Viable oothecae contained an average of 37.5 eggs, from which an average of 33.3 nymphs (88%) hatched (Table 1). Number of eggs and nymphs per ootheca ($F_{\text{eggs}} = 2.53$; df= 5,60; $P > 0.01$; F_{nymphs}

Table 2. Comparison of reproductive rates, immature development, and adult longevity of *B. asahinai*, *B. germanica*, and *B. vaga*

Observation	Species[a]		
	B. asahinai	*B. germanica*	*B. vaga*
Oothecae/♀	3.7 ± 0.30 (30)	6.6 ± 0.5 (9)	5.5 ± 0.4 (25)
Initial preoviposition period, d[b]	13.0 ± 1.35 (30)	7.8 ± 0.2 (9)	7.9 ± 0.2 (25)
Successive preoviposition periods, d[c]	7.9 ± 0.77 (79)	4.8	4.4
Incubation period, d[d]	19.2 ± 0.15 (65)	17.2 ± 0.1 (48)	19.8 ± 0.1 (84)
Time females carry oothecae from which eggs did not hatch, d[e]	15.7 ± 1.08 (34)	16.9 ± 1.5 (8)	20.0 ± 0.3 (38)
Abortion rate (% oothecae from which eggs did not hatch)[f]	35.4 (110)	12.7 (63)	26.1 (165)
Eggs/ootheca	37.5 ± 0.53 (66)	36.7 ± 0.9 (56)	27.7 ± 0.7 (122)
% Hatch[g]	88.8	75.7	69.0
Lifetime fecundity (eggs)[h]	79.6	141.7	77.7
Females			
Immature development, d	67.8 ± 1.5 (13)	46.2[i] (56)	53.7[i] (50)
Adult longevity, d	103.5 ± 6.9 (33)	153.0 ± 9 (9)	150.0 ± 12 (22)
Males			
Immature development, d	65.7 ± 1.48 (19)	46.2[i] (47)	60.1[i] (48)
Adult longevity, d	48.5 ± 5.11 (33)	128.0 ± 8 (10)	101.0 ± 6 (25)

[a] Data for *B. vaga* and *B. germanica* from Tables IX–XII of Willis et al. (1958); Willis et al. held cockroaches at 30°C, so direct comparisons are not possible. Mean ± standard error of mean (sample size of adults or oothecae).

[b] Time from eclosion to first ootheca.

[c] Time from hatch or drop of previous ootheca to appearance of subsequent one after the first. Tabulated values for *B. germanica* and *B. vaga* were calculated by subtracting incubation period from time between subsequent oothecae from data in Table IX of Willis et al. (1958).

[d] Period from appearance of ootheca until egg hatch.

[e] Willis et al. (1958) excluded all oothecae which were carried ≤1 d; we have done likewise here. Including those data would change the tabulated values to: 14.5 ± 1.1 (37). See text for discussion.

[f] Percent nonviable (aborted) oothecae of total oothecae produced.

[g] (Avg nymphs per ootheca/avg eggs per ootheca) × 100.

[h] Lifetime fecundity = (avg oothecae/female) × (1 − abortion rate) × (avg eggs/ootheca) × (% hatch).

[i] Recalculated from Willis et al. (1958: 63, Tables XI, XII, individuals reared in isolation). Because means and standard errors were calculated separately according to the number of instars, it is not possible to estimate the standard error for all individuals.

= 0.91; df = 5, 60; n.s.) did not differ significantly between successive oothecae (Fig. 6) for the first five oothecae produced (range 20–44). Numbers of eggs and nymphs were significantly lower for the sixth ootheca (29 ± 1.0, n = 2) than for other oothecae. Ross & Mullins (1988) noted that some oothecae produced in a laboratory colony of Asian cockroaches (also from central Florida) were smaller than usual. They contained 26–28 eggs compared with an average of 43.0 eggs in normal oothecae. These authors suggested that such oothecae might be produced by older females. Willis et al. (1958) showed a reduction in eggs per ootheca for German cockroaches after the fourth ootheca and a consistent decline for the field cockroach after the first ootheca.

Females required 67.8 d (Table 1) to reach adulthood after hatching, slightly longer than the 65.7 d required by males. Adult females lived an average of 103.5 d. Adult male longevity was much lower, averaging 48.5 d. Similar data for other *Blattella* species are given by Willis et al. (1958). However, cockroaches in their study were held at 30 rather than 25°C as in our study. Females require slightly longer to develop as immatures and live slightly longer as adults than males of other *Blattella* species. Duration of immature development for both sexes is shortest for the German cockroach, intermediate for the field cockroach, and longest for the Asian cockroach (Table 2). Conversely, adult longevity is shortest for Asian and longest for German cockroaches. The markedly lower longevity of adult male versus female Asian cockroaches is much more pronounced than in the species studied by Willis et al. (1958).

The only pesticide treatment that produced 100% mortality 24 h after application was isazophos (Table 3), which continued to kill all Asian cockroaches exposed 1 wk after application. After 2 wk, isazophos failed to kill appreciable numbers of cockroaches. Other treatments produced some mortality but had no residual effect under the conditions of this study. Performance was undoubtedly compromised by the heavy rainfall that occurred the evening after treatment.

Table 3. Percentage mortality ($\bar{x}$ ± SE) of adult male Asian cockroaches on treated sod after 24 h of exposure

Treatment	Interval after application		
	24 h	1 wk	2 wk
Mocap[a]	47 ± 6.7b	—	—
Sevimol	27 ± 8.8b,c	0b	0b
Triumph	100a	100a	7 ± 3.7a
Diazinon	50 ± 16.7b	0b	0b
Check	3 ± 3.3c	0b	0b

SE cannot be calculated for means of 0 or 100% because all values are equal. Means not followed by the same letter are not significantly different at the 0.05 level.

[a] Samples not taken for mocap after 24 h.

Discussion

A recent revision of the genus *Blattella* by Roth (1985) suggests that *B. asahinai* is the closest known relative of *B. germanica*. Neither species is closely related to *B. vaga*, the field cockroach, another introduced species found in the southwestern United States. *B. vaga* (Cornwell 1968, Ebeling 1975) and *B. asahinai* (Roth 1986, Brenner et al. 1988) breed outdoors and are more similar to each other ecologically than either species is to the German cockroach.

Compared with the German cockroach (Table 2), Asian cockroaches produce fewer oothecae (with approximately the same number of eggs), have longer initial and subsequent preoviposition periods, and their eggs require slightly longer to hatch. Field cockroaches (Table 2) produce more oothecae than Asian cockroaches, but these oothecae contain fewer eggs. Both Asian cockroaches (this study) and field cockroaches (Willis et al. 1958) had much higher abortion rates than German cockroaches kept under similar conditions. A crude estimate of potential lifetime fecundity can be calculated for each species by multiplying oothecae per female, proportion of viable oothecae (1 − proportion aborted), number of eggs per ootheca, and percentage hatch. Despite differences in almost all reproductive parameters, estimates of lifetime fecundity for Asian and field cockroaches are similar (79.6 and 77.7 viable eggs per female, respectively) (Table 2). The estimated lifetime fecundity of German cockroaches (141.7 viable eggs per female) is nearly double that of either of the outdoor species. When the shorter immature development time of German cockroaches is considered, this difference becomes even more pronounced.

These estimates must be viewed with a certain amount of skepticism because holding isolated male–female pairs in Mason jars under laboratory conditions probably does not reflect conditions under which any of these species is commonly found. The formula used to estimate lifetime female fecundity does not consider survival, development rates, and other important factors that affect reproductive potential of populations. Experimental conditions were probably more favorable for German cockroaches, with their proven ability to breed indoors as a domiciliary pest, than for the outdoor Asian or field cockroaches. The higher abortion rates, lower fecundity estimates, and longer development times for Asian and field cockroaches compared with those of German cockroaches may reflect not only innate differences in reproductive potential but also the effect of laboratory conditions unfavorable for the outdoor species. Nonetheless, our results suggest that German cockroaches have a considerable advantage in biotic potential under indoor conditions compared with the other two species.

Recent data on seasonal differences in population structure of Asian cockroach populations in central

Florida show that adults are virtually absent in December and January and again in June and July (Brenner 1990), suggesting that there may be two broad generations annually. Minimum generation time (female immature development time + initial preoviposition period + oothecal incubation period) under laboratory conditions is ≈100 d. Total life span for females from this study, including oothecal incubation, nymphal development, and female longevity is 188.5 d, almost exactly 6 mo. Although Asian cockroaches breed continuously in colony indoors, seasonal changes in temperature and possibly humidity may prevent this from occurring in the field; this would certainly be the case if the Asian cockroach spreads northwards to any appreciable degree.

Our preliminary data on control of the Asian cockroach by application of pesticides to infested turf indicate that chemical control is feasible. Such treatments should also be effective in areas with low vegetation and leaf litter. Asian cockroaches are not known to burrow, and pesticide residues on foliage or in the upper layers of the litter would be most effective. Because Asian cockroaches are primarily perceived as pests when adults are flying, timing outdoor pesticide applications to seasonal peaks in adult abundance might reduce local populations to acceptable levels with a minimal number of applications.

Fecundity, development, longevity, and seasonal changes in population should be studied for Asian cockroaches under conditions more similar to those encountered outdoors. Asian cockroaches of both sexes fly actively in the field and have been observed feeding on homopteran honeydew and fruits (Brenner et al. 1988, Brenner 1990). Development times of nymphs held in groups should be studied because German and field cockroach nymphs develop faster in groups than when held in isolation (Willis et al. 1958). Larger rearing containers and alternative food sources with a high sugar content might significantly increase Asian longevity and fecundity, providing more realistic estimates of biological parameters.

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