Biology of *Symploce pallens* (Dictyoptera: Blattellidae)

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ABSTRACT Here, we describe the biology of a relatively new pest cockroach species in Southeast Asia, *Symploce pallens* (Stephens) (Dictyoptera: Blattellidae). *S. pallens* collected from Penang Island, Malaysia, were used for the biological parameter studies and were observed for molting and reproduction events. Nymphal development took 118.2 ± 1.7 d, with a mean of 9.5 ± 0.1 molts. The oothecal incubation period was 36.1 ± 0.2 d. Females produced a mean of 16.0 ± 10.2 oothecae, with mean 17.6 ± 0.1 nymphs per ootheca. Nymphal survivorship per ootheca was 90.4%, and 90.7% of nymphs achieved adulthood. The sex ratio did not deviate from 1:1. The mean longevity of adult males and females was 309.3 ± 7.6 and 322.6 ± 14.8 d, respectively. In general, *S. pallens* exhibited higher oothecal production and longer nymphal development and longevity compared with the German cockroach, *Blattella germanica* (L.).

KEY WORDS *Symploce pallens*, nymphal development, fecundity, longevity

The association between important urban pests such as the German cockroach, *Blattella germanica* (L.), and the brownbanded cockroach, *Supella longipalpa* (F.), and humans dates far back into history. A relatively new urban pest cockroach species known to infest domiciles in Malaysia and Singapore is *Symploce pallens* (Stephens) (Jeffrey et al. 1997, Lee and Lee 2000). Lee (2007) reported that ≈0.8–2% of the trapped cockroaches in residential premises in Penang, Malaysia, were *S. pallens*, and this species was present in 10–12% of cockroach-infested residential premises (n = 341). Jeffrey et al. (1997) trapped 583 specimens (443 nymphs, 81 females, and 59 males) of *S. pallens* from restaurants in several locations in Kuala Lumpur, Malaysia; sundry shops in Klang, Malaysia; and in a house in Pasir Mas, Kelantan, Malaysia. According to Lee and Ng (2009), *S. pallens* also is a prevalent pest in food preparation areas in Singapore.

S. pallens is circumtropical in distribution. It was believed to have originated from Africa. It is widely distributed in Africa (e.g., Cape Verdi Island, Kenya, Madagascar, Pemba Island, Senegal, and Zaire) and also has been found in Seychelles Island, Canton Island, Galapagos, Hawaiian Islands, Mexico, Tonga, and West Indies (Roth 1984). In the United States, it has been recorded in Key West, FL (Atkinson et al. 1991). It was first described as *Ectobius pallens* (Stephens 1835). Other names described earlier that ceased to be used include *Blatta capitata* (Saussure 1862), *Symploce hospes* (Perkins 1899), *Blatta deprivata* (Walker 1868), and *Symploce lita* (Hebard 1916). Roth (1984) clarified that the name *S. pallens* is the accurate name for *S. lita* that was found as a synonym of *S. hospes* (Perkins, 1899) by Hebard (1943).

S. pallens is a small cockroach, and the male is more robust (13.5–14.5 mm in length) than the female (Jeffrey et al. 1997). Females are smaller (≈12.5–13.5 mm in length from the tip of the head to the tip of the abdomen) (Jeffrey et al. 1997). Male cockroaches are excellent fliers, but the females are brachypterous, making them unable to fly. Their color is rather striking: The exposed head, pronotum, and tegmina are yellowish brown and lack any distinct pattern, and these areas are a lighter shade compared with the abdomen. The whip-like antennae are somewhat thick and blackish with a yellowish brown base. Nymphs are shiny dark brown or black with no distinct pattern on the pronotum, making it look smooth; this characteristic gives the species the common name of "smooth cockroach."

The eggs are carried externally after formation and later are deposited. Unlike the unrotated ootheca of *S. longipalpa* (Plecopterinae), the ootheca of *S. pallens* undergoes advanced rotation. This trait places *S. pallens* in the subfamily Blattellinae together with *B. germanica.* Although *B. germanica* carries its ootheca externally throughout embryogenesis, *S. pallens* drops its ootheca early. Little is known about the biology of *S. pallens.* Thus, the goal of this study was to describe selected biological parameters of *S. pallens*, its pest status, and potential integrated pest management strategies.

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Materials and Methods

Cockroach Culture. *S. pallens* used in this study were obtained from laboratory cultures established previously from wild cockroaches collected from Kampung Melayu and Sungai Batu on Penang Island (05°30′ N, 100°28′ E) from June through December 1998. They were reared in polyethylene aquaria measuring 35 by 19 by 28 cm (Guppy Plastic Ind., Sdn. Bhd., Malaysia) at 27.5 ± 2.0°C, 60 ± 5% RH, and a photoperiod of 12:12 (L:D) h. Water and mouse pellets (Gold Coin, Butterworth, Malaysia) were provided ad libitum. Gravid females were collected using a glass vial and reared separately in 5.4-cm-diameter by 8.5-cm-high polyethylene cups (ZFC-225, model 24PP, ZPI Guppy). The upper interior surface was coated with petroleum jelly to prevent escape. Water and mouse pellets were provided ad libitum, and a 5- by 10-cm sheet of folded paper served as a harborage.

Observation of Biological Parameters. Newly emerged nymphs that hatched on the same day were selected randomly, and four individuals were placed into new cups and subjected to the same treatment. The date of emergence was recorded on numbered cups and 20 replicates were used. Every morning and late evening, the nymphs were observed for evidence of molting. The numbers of days required for nymphal development, the lengths of stadia, and the total number of molts were documented.

Upon reaching adulthood, both male and female cockroaches were removed and placed separately in polyethylene cups to allow them to reach full maturity and to prevent mating. After 2 d of isolation, one male and one female were paired. Twenty replicates were used and monitored daily for reproduction events. The number of days of required for preoviposition, preincubation, and incubation were recorded. The preoviposition period is defined as the period between the release of an ootheca and the emergence of the next ootheca. The preincubation period is the interval between the emergence and the release of an ootheca, and the incubation period is the time between release and the hatching of an ootheca.

Every ootheca produced was removed and kept in a separate polyethylene cup until it hatched, and each was reared until adulthood was reached. The number of nymphs that emerged successfully into adults was counted. The number of offspring per ootheca, the total number of oothecae per female, the number of hatched oothecae per female, nymphal survivorship, the number of nymphs attaining adulthood, and the nymphal sex ratio were recorded. If both the adult male and female died, the mean longevity for both sexes was documented. No replacement was made for any cockroach that died during the study.

Body Size Regulation Study. To study body size regulation during nymphal development, gravid females were collected using a glass vial and reared separately in polyethylene cups under the same conditions described above. After the egg capsules were dropped, the females were returned to the culture, but the egg cases remained isolated until they hatched. Newly emerged nymphs that hatched on the same day were selected randomly and four individuals were placed into new polyethylene cups. Molting events were monitored daily.

Three days after the nymphs or adults had undergone molting, they were immobilized by leaving them in the freezer for 5 min. They then were laid horizontally with the legs stretched out on a petri dish filled with facial cotton to make mounting easier. The maximum width of the head capsule, the maximum width of the pronotum, the maximum length of the mesonotum along the axis of the wing bud, and the maximum length of the hind tibia from each larval instar and adult stage, as well as maximum oothecae dimensions, were measured using a stereoscope (SZ-PT, Olympus Optical Co., Ltd., Tokyo, Japan). Measurements were recorded using an NFK 1.67xLD lens (Olympus Optical Co., Ltd.) and Image Analyzer software (Soft Imaging System GmbH, Munster, Germany). Instars 1–3, instars 4–7, and instars 8–10 were categorized as early, intermediate, and late nymph age groups, respectively.

Statistical Analysis. Regression analysis (SPSS version 11.0.1, SPSS Inc. 2001) was used to determine whether there was any relationship between the nymphal stage and the period between molts. Relationships between oothecal number and the preoviposition period, preincubation period, incubation period, the number of offspring produced per female, nymphal survivorship, and the number of nymphs attaining adulthood were ascertained with regression analysis. The nymphal sex ratio of each strain was tested with a chi-square test for deviation from a 1:1 ratio.

Results and Discussion

Study Results. The time required for *S. pallens* to complete its nymphal development was 118.2 ± 1.7 d (range, 88–136 d) (Table 1). Male and female *S. pallens* molted nine times (108.3 ± 2.1 d) and 10 times (117.6 ± 2.6 d), respectively. The duration of each stadium was 13.9 ± 0.1 d (range, 7–27 d). The period

Table 1. Biological parameters of *S. pallens* observed in this study

Biological parameter	*n*	Mean ± SE
Nymphal development (d)	80	118.2 ± 1.7
Period between molts (d)	80	13.9 ± 0.1
Total no. molts	80	9.5 ± 0.1
Preoviposition period (d)	20	5.9 ± 0.2
Preincubation period (d)	20	2.1 ± 0.1
Incubation period (d)	20	36.1 ± 0.2
No. nymphs/ootheca	20	17.6 ± 0.1
No. oothecae/female	20	16.0 ± 10.2
No. hatched oothecae/female	20	15.8 ± 8.1
No. nonviable oothecae	4	1.1 ± 0.9
Total no. nymphs/female ± SE	20	485.4 ± 8.2
Nymphal survivorship (%)/ootheca	555	90.4
Nymphs attaining adulthood (%)	8,763	90.7
Nymphal sex ratio (male:female)	555	1.00:1.05
Male longevity (d ± SE)	20	309.3 ± 7.6
Female longevity (d ± SE)	20	322.6 ± 14.8

between molts increased with each succeeding molt ($r^2 = 0.88$), thus supporting the findings of Ross and Mullins (1995) for the German cockroach. The smooth cockroach has a longer nymphal development period compared with other prevalent cockroach pests such as *B. germanica* (Tanaka and Hasegawa 1979) and *S. longipalpa* (Koehler et al. 1990).

Preoviposition for *S. pallens* took 5.9 ± 0.2 d (range, 1–36 d) and significantly increased linearly with increasing oothecal number and female age ($r^2 = 0.63$, $P < 0.01$). The mean preincubation period was 2.1 ± 0.1 d (range, 1–7 d) and significantly increased linearly with increasing oothecal number and female age ($r^2 = 0.73$; $P < 0.01$). The incubation period of *S. pallens* oothecae was 36.1 ± 0.2 d (range, 24–48 d), which is slightly higher than that reported by Lee et al. (2000). However, it did not increase significantly with increasing oothecal number and female age ($r^2 = 0.003$, $P > 0.01$). The smooth cockroach had a longer incubation period than other common urban cockroach pests, such as the American and German cockroaches (Gould and Deay 1938, 1940) and the brownbanded cockroach (Gould and Deay 1940, Willis et al. 1958).

The number of nymphs produced by a female *S. pallens* per ootheca decreased linearly with increasing oothecal number and age ($r^2 = 0.72$, $P < 0.01$). The number of offspring produced per ootheca was 17.6 ± 0.1 nymphs (range, 6–22 nymphs). *S. pallens* females produced 16.0 ± 10.2 oothecae per female (range, 6–41). These values are significantly higher than those of *B. germanica*, which produce fewer oothecae because the oocytes do not mature in the ovaries while the ootheca is being carried (Roth and Stay 1962). The ovaries of *B. germanica* contain a number of oocytes, each in a different stage of development (Roth 1970). The number of oothecae produced was influenced by the maximum number of oocytes containing yolk in zone V per ovariole at the time of oviposition (Bonhag 1959). Based on data obtained by Illingworth (1915), Roth (1970) stated that oviparous Blattellidae such as *S. hospes* (Blattellinae) (=*S. pallens*) and *S. longipalpa* (Plectopterinae) differ in oothecal production because *S. hospes* had more than two oocytes in zone V, compared with only one in *S. longipalpa.* This is because new basal oocytes already contain yolk at the time the ootheca is completed and they mature faster than oocytes lacking yolk.

The mean number of hatched oothecae and the mean number of nonviable oothecae were 15.8 ± 8.1 and 1.1 ± 0.9, respectively, for *S. pallens.* The percentage of viable eggs declined with female age ($r^2 = 0.65$, $P < 0.05$). Roth and Willis (1952) reported that on the occasions in which the copulation period was long, a spermatophore was passed, resulting in 90% of females producing an ootheca, of which 85% were fertile.

The oothecal hatchability in *S. pallens* was 97.3%. The nymphal survivorship per ootheca was 90.4%, and the nymphs attaining adulthood was 90.7%. These values did not increase with increasing oothecal number and female age. The chi-square test revealed that the male:female ratio did not deviate far from 1:1, which is in agreement with the findings of Lee (1995) and Ross (1991) on *B. germanica.*

The longevity of adult male and female *S. pallens* was 309.3 ± 7.6 and 322.6 ± 14.8 d, respectively. These findings are in marked contrast with earlier studies by Lee et al. (2000), who reported longevity for male and female *S. pallens* of 148.8 ± 2.5 d and 146.1 ± 11.5 d, respectively. The longevity of adult males in the current study varied between 254 and 373 d, whereas the longevity for females ranged from 147 to 361 d. Females with greater longevity tended to produce more oothecae compared with those with lower longevity.

Smooth cockroach nymphs can easily be misidentified as small early instars of *Periplaneta americana* (L.) or *Periplaneta brunnea* (Burmeister). Table 2 shows the measurements of *S. pallens* in different stages of development. Wigglesworth (1972) stated that insects have a regulatory mechanism to determine the number of instars that will be produced based on the environmental conditions. There also might be a threshold size that must be attained to become adults (Blakley and Goodner 1978, Keil 1981, Tanaka 1981), although Bell (1990) reported that the mean size of

Table 2. Nymphal developmental period and body size measurements for *S. pallens*

Stage	Nymphal development (d ± SE)	*n*	Max. width of head capsule (μm ± SE)	Max. width of pronotum (μm) ± SE	Max. length of mesonotum along the axis of wing bud (μm ± SE)	Max. length of hind tibia (μm ± SE)	Max. length of ootheca (μm ± SE)	Max. width of ootheca (μm ± SE)	Max. ht of ootheca (μm ± SE)
Instar 1	n/a	80	705.1 ± 5.6	940.6 ± 11.4	1,767.9 ± 17.7	634.6 ± 12.0	n/a	n/a	n/a
Instar 2	11.2 ± 0.2	80	800.3 ± 7.7	1116.3 ± 17.0	2,031.8 ± 24.7	812.7 ± 14.0	n/a	n/a	n/a
Instar 3	12.2 ± 0.3	80	941.2 ± 16.0	1,385.9 ± 24.3	2,622.7 ± 37.3	979.8 ± 14.3	n/a	n/a	n/a
Instar 4	13.8 ± 0.2	80	1,178.1 ± 17.0	1,816.7 ± 35.7	3,571.2 ± 53.3	1,328.9 ± 22.6	n/a	n/a	n/a
Instar 5	14.5 ± 0.4	80	1,363.7 ± 23.5	2,178.3 ± 44.2	4,456.4 ± 61.6	1,672.8 ± 23.5	n/a	n/a	n/a
Instar 6	13.5 ± 0.2	80	1,461.6 ± 49.2	2484.3 ± 48.5	4,854.6 ± 64.0	1,890.2 ± 36.6	n/a	n/a	n/a
Instar 7	14.5 ± 0.2	80	1,619.6 ± 54.4	2,778.8 ± 52.8	5,655.7 ± 67.8	2,114.4 ± 48.9	n/a	n/a	n/a
Instar 8	14.0 ± 0.3	80	1,843.5 ± 57.1	3011.8 ± 53.3	6,025.2 ± 71.6	2,353.7 ± 53.9	n/a	n/a	n/a
Instar 9	13.7 ± 0.4	80	2,052.9 ± 41.3	3,601.0 ± 44.0	7,346.8 ± 63.5	2,830.4 ± 42.5	n/a	n/a	n/a
Instar 10	15.5 ± 0.4	80	2,072.6 ± 12.2	3641.9 ± 16.1	7,410.4 ± 24.0	2,909.0 ± 19.5	n/a	n/a	n/a
Male	17.0 ± 0.4	80	2,211.4 ± 14.8	3685.6 ± 36.9	1,0856.4 ± 76.9	4,304.3 ± 46.9	n/a	n/a	n/a
Female	17.0 ± 0.4	80	2,250.5 ± 20.8	4116.0 ± 50.7	9,430.0 ± 68.3	3,863.6 ± 27.3	n/a	n/a	n/a
Ootheca	n/a	100	n/a	n/a	n/a	n/a	5,522.0 ± 200.0	2,728.1 ± 34.1	1,897.3 ± 39.1

n/a, not appliciable.

individuals decreased in overcrowded conditions, allowing more individuals to be packed into a small area. Tanaka (1981) reported that by the late third instar, *B. germanica* had already determined the number of succeeding molts to reach a normal adult body size.

Although the results obtained in this study did not take the sexes of nymphs into account, the variation in measurements increased with each consecutive molt until it reached a certain instar at which the size variation was maximal. The differences in size between sexes accounted for this large discrepancy in variance. This certain instar was the eighth instar in *S. pallens.* The large difference in sizes occurred because some large nymphs would emerge as adults after the next molt, whereas others might have to undergo one or two more molts to reach adulthood. However, the difference in sizes was smaller between the final three instars for *S. pallens.* The maximum length of the mesonotum along the axis of the wing bud was significantly different between sexes in all adults, indicating large dissimilarities in body size.

Management of *S. pallens*. Management of *S. pallens* in residential premises and food preparation outlets should use the least toxic strategies possible. When looking for harborage sites, inspection should be targeted at warm and humid areas, such as tight corners, cracks and crevices, and areas around the kitchen sink, oven, and garbage bins. These areas not only serve as refugia for *S. pallens* adults and nymphs but also provide food and water for the cockroaches. Because *S. pallens* has a higher tolerance for lower water resources compared with other pest species such as B. *germanica* (our unpublished data), drier areas such as bedrooms and living rooms must also be inspected. Our trapping efforts revealed that most *S. pallens* were found inside dry kitchen cabinets, inside corrugated cardboard boxes in the kitchen, and in between stacks of unused plates and other utensils. Maintaining sanitation not only eliminates food and water resources for the cockroaches but also increases encounters with sprayed surfaces or bait stations for this otherwise cryptic species. Monitoring can be achieved using sticky traps, but traps should be placed near harborage sites.

Baits are useful in managing both adult *S. pallens* and nymphs. Baits containing slow-acting active ingredients such as hydramethylnon, fipronil, indoxacarb, and emamectin allow cockroaches to return to their harborages and thereby horizontally transfer the toxicants through coprophagy, necrophagy, and emetophagy. Because of the long incubation and nymphal development periods of *S. pallens*, the baits used should also be long lasting. The smooth cockroach produces a high number of ootheca per female and a high number of offspring per female, and it also exhibits a high percentage of nymphal survivorship. Thus, *S. pallens* has great potential to establish an infestation in a short period of time. When infestation is heavy and requires fast control, other possible population management approaches include ultra low volume spraying and misting of low toxicity pyrethroids.

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References Cited

Atkinson, T. H., P. G. Koehler, and R. S. Patterson. 1991. Catalog and atlas of the cockroaches (Dictyoptera) of North America North of Mexico. Misc. Publ. Entomol. Soc. Am. 78: 1–86.

Bell, W. J. 1990. Biology of the Cockroach, pp. 1–12. *In* I. Huber, E. P. Masler, and B. R. Rao [eds.], Cockroaches as models for neurobiology: applications in biomedical research, CRC, Boca Raton, FL.

Blakley, N., and S. R. Goodner. 1978. Size-dependent timing of metamorphosis in milkweed bugs (*Oncopeltus*) and its life history implications. Biol. Bull. Mar. Biol. Lab., Woods Hole Mass. 155: 499–510.

Bonhag, P. F. 1959. Histological and histochemical studies on the ovary of the American cockroach, *Periplaneta americana* (L.). Univ. Calif. Publ. Entomol. 16: 81–124.

Gould, G. E., and H. O. Deay. 1938. The biology of the American cockroach. Ann. Entomol. Soc. Am. 31: 489–498.

Gould, G. E., and H. O. Deay. 1940. The biology of six species of cockroach which inhabit buildings. Purdue Univ. Agric. Exp. Stn. Bull. 451: 1–31.

Hebard, M. 1916. Studies in the Group Ischnopterites (Orthoptera, Blattidae, Pseudomopinae). Trans. Am. Entomol. Soc. 42: 337–383.

Hebard, M. 1943. The Dermaptera and orthopterous families Blattidae, Mantidae and Phasmidae of Texas. Trans. Am. Entomol. Soc. 68: 239–310.

Illingworth, J. F. 1915. Notes on Hawaiian roaches. Proc. Hawaii. Entomol. 3: 136–140.

Jeffrey, J., M. Zahedi, P. Oothuman, S. Salehuddin, I. Vythilingam, and A. Sulaiman. 1997. *Symploce pallens* (Stephens) (Dictyoptera: Blattellidae)—a new pest cockroach from Peninsular Malaysia. Trop. Biomed. 14: 137–139.

Keil, C. B. 1981. Structure and estimation of shipboard German cockroach (*Blattella germanica*) populations. Environ. Entomol. 10: 534–542.

Koehler, P. G., R. S. Patterson, and R. J. Brenner. 1990. Cockroaches. pp. 101–105. *In* A. Mallis [ed.], Handbook of pest control, 7th ed. Franzak & Foster Co., Cleveland, OH.

Lee, C. Y. 1995. Toxicity, resistance and sublethal effects of selected insecticides on German cockroaches, *Blattella germanica* (L.) (Dictyoptera: Blattellidae) in Malaysia. Ph.D. dissertation, Universiti Sains Malaysia, Penang, Malaysia.

Lee, C. Y. 2007. Perspective in urban insect pest management in Malaysia. Vector Control Research Unit, Universiti Sains Malaysia, Penang, Malaysia.

Lee, C. Y., and L. C. Lee. 2000. Diversity of cockroach species and effect of sanitation on level of cockroach infestation in residential premises. Trop. Biomed. 17: 39–43.

Lee, C. Y., and L.-C. Ng. 2009. Pest cockroaches in Singapore: a scientific guide for pest management professionals. Singapore Pest Management Association, Singapore.

Lee, C. Y., M. S. Khalid, L. C. Lee, and N. L. Chong. 2000. Notes on the biological parameters of a new domiciliary

pest, the smooth cockroach *Symploce pallens* (Stephens) (Dictyoptera: Blattellidae). Trop. Biomed. 17: 49–52.

Perkins, R.C.L. 1899. Orthoptera. pp. 1–30. *In* D. Sharp [ed.], Fauna Hawaiiensis, vol. 2, part 1. Cambridge University Press, Cambridge, United Kingdom.

Ross, M. H. 1991. A comparison of reproduction and longevity in pyrethroid-resistant and susceptible German cockroach (Blattodea: Blattellidae) field-collected strains. J. Entomol. Sci. 26: 408–418.

Ross, M. H., and D. E. Mullins. 1995. Biology, pp. 21–47. In M. K. Rust, J. M. Owens, and D. A. Reierson [eds.], Understanding and controlling the German cockroach. Oxford Press, New York.

Roth, L. M. 1970. Evolution and taxonomic significance of reproduction in Blattaria. Annu. Rev. Entomol. 15: 75–96.

Roth, L. M. 1984. The genus *Symploce* Hebard. 1. Species from the West Indies. (Dictyoptera: Blattaria, Blattellidae). Entomol. Scand. 15: 25–63.

Roth, L. M., and B. Stay. 1962. Oocyte development in *Blattella germanica* and *Blattella vaga* (Blattaria). Ann. Entomol. Soc. Am. 55: 633–642.

Roth, L. M., and E. R. Willis. 1952. A study of cockroach behavior. Am. Mid. Nat. 47: 65–129.

Saussure, H. 1862. Orthoptera nova Americana (Diagnoses praeliminares) III. Rev. Mag. Zool. 14: 163–171, 227–234.

SPSS Inc. 2001. SPSS, version 11.0.1. SPSS Inc., Chicago, IL.

Stephens, J. F. 1835. Illustrations of British entomology. Mandibulata 6: 60, 64.

Tanaka, A. 1981. Regulation of body size during larval development in the German cockroach, *Blattella germanica.* J. Insect Physiol. 2: 587–592.

Tanaka, A., and A. Hasegawa. 1979. Nymphal development of the German cockroach, *Blattella germanica* L. (Blattaria: Blattellidae), with special reference to instar determination and intra-instar staging. Kontyu 47: 225–238.

Walker, F. 1868. Catalogue of the specimens of Blattariae in the collection of the British Museum. British Museum of Natural History, London, United Kingdom.

Wigglesworth, V. B. 1972. The principles of insect physiology, 7th ed. Chapman & Hall, London, United Kingdom.

Willis, E. R., G. R. Riser, and L. M. Roth. 1958. Observations on reproduction and development in cockroaches. Ann. Entomol. Soc. Am. 51: 53–69.

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