

Differential Development and Reproduction of the German Cockroach (*Dictyoptera: Blattellidae*) on Three Laboratory Diets

RICHARD A. COOPER AND COBY SCHAL

Department of Entomology, Cook College, Rutgers University,
New Brunswick, New Jersey 08903

J. Econ. Entomol. 85(3): 838-844. (1992)

ABSTRACT Development of nymphs and oocyte maturation in adults were examined in *Blattella germanica* (L.) reared on three commercial diets. Nymphs fed rat food developed significantly faster than nymphs fed two commercial dog foods. Similarly, oocytes matured more quickly in adult females that were raised on rat food than in females raised on dog food. Nymphal development and oocyte maturation were slower in insects that were fed whole dog food pellets than in insects fed ground dog food, suggesting that grinding the diet diminishes a mechanical barrier in whole dog food pellets. Comparisons of processed canine food and unprocessed canine food indicated that diets were significantly inferior after the steam extrusion process. Rat food is normally not subjected to such conditions and both processed and unprocessed rat food are equally suitable for *B. germanica*. The significance and implications for comparative studies with cockroaches are discussed.

KEY WORDS Insecta, *Blattella germanica*, nutrition, reproduction

NUTRITIONALFACTORS can exert profound short- and long-term effects on the development and reproduction of insects (see reviews by Bernays 1985, Dadd 1985, Reinecke 1985, Waldbauer & Friedman 1991). Although the general nutritional requirements of most insects are similar, the optimal sources, types, and proportions of nutrients vary widely among species and among different developmental and reproductive stages (Dadd 1985).

Research on the nutritional requirements and the regulation of feeding in cockroaches has generally included minimally defined diets that allow for the addition, deletion, substitution, or alteration of the proportions of nutrients (e.g., Gordon 1959). However, most work on cockroaches does not examine nutritional factors directly; commonly, more crudely defined diets, including various laboratory foods, are used for maintenance of colonies. The sources and proportions of component nutrients vary widely in these diets, and constituents other than the essential nutrients may act as growth factors or affect the texture, palatability, and digestibility of the diet, changing its utility to the insect (Vanderzant 1974, Bernays 1985, Dadd 1985, Slansky 1982, Slansky & Scriber 1985). Despite the fact that different investigators use different commercial or specially formulated diets, the tacit assumption is made that use of different diets does not preclude comparisons of results from different laboratories. Dog food and rat food are nutritionally complex, relatively adequate for

maintaining colonies of cockroaches, and routinely used in many research laboratories. Herein we examine differences between these diets to test this assumption.

Some insects can effectively withstand short periods of starvation or nutrient limitation, but most exhibit altered rates of development and reproduction under such conditions (see Engelmann 1970). The German cockroach, *Blattella germanica* (L.), is highly sensitive to both food deprivation and specific nutrient limitation, particularly proteins (Noland & Baumann 1951; Haydak 1953; Kunkel 1966, 1981; Roth & Stay 1962; Hamilton & Schal 1988). We therefore hypothesized that if various laboratory diets differ nutritionally they might result in differential development and reproduction in this cockroach. Furthermore, our preliminary observations indicated that nymphal development in *B. germanica* was slower on whole pellets of laboratory food compared with ground food, suggesting a mechanical barrier to feeding.

In this report we document that several life history parameters of the German cockroach are sensitive to changes in the diet and result in delayed adult emergence and reproduction on some diets. We also elucidate a mechanism for the deficiency of some commercial diets. Finally, we discuss the implications of these findings for physiological and biochemical studies that use these diets interchangeably with the German cockroach and other species of cockroaches.

Materials and Methods

Insects. German cockroaches were obtained from a stock colony raised on whole Purina Rat Chow (number 5012, Purina Mills, St. Louis, Mo.) and water at 27 ± 0.5°C and a photoperiod of 12:12 (L:D). Cockroaches were collected from the stock colony at various developmental stages and placed on one of several diets on which nymphal development and oocyte maturation were examined. All experiments were conducted at 27 ± 1.0°C, 50% RH, and a photoperiod of 12:12 (L:D).

Diets. We suspected, based on preliminary results, that the rate of nymphal development would be affected by the size of the food items. To test this hypothesis, dog chow (number 1780, Ralston Purina, St. Louis, Mo.) and rat chow were ground with a mortar and pestle and sieved sequentially to obtain the following three ranges of particle sizes: 0.7-1.0 mm, 1.7-2.6 mm, and 2.6-4.0 mm.

Results of the nymphal development study suggested that differential growth might be related to the differing degrees of compression and extrusion experienced by different diets during production. Rat and dog foods in the form of meal before processing are relatively dry, with a similar fat content of 4.5 and 4% respectively (D. Hopkins, personal communication). Rat chow meal is pressed into a cylindrical shape with two cut ends and a dry smooth surface. However, dog chow meal is steam extruded under high pressure and temperature; during this process, an additional layer of 5% animal fat is sprayed onto the outer surface. The end product is a hard round pellet with a "baked" lipid surface and a total fat content that is twice that of rat food (D. Hopkins, personal communication).

The hard, greasy outer surface of dog food might act as a mechanical barrier, especially to young nymphs. Because we were unable to obtain unprocessed Purina Dog Chow, we used Purina Canine Chow (number 5006, Purina Mills), which is similar in nutritional composition and processing to Purina Dog Chow. To control for the different fat contents of the processed diets, the fat contents of canine and rat meals were raised to 9.0% in some experiments by first dissolving animal fat (Purina Mills) in methanol and petroleum ether (1:3 by vol) and then impregnating it into the meal.

Nymphal Development and Oocyte Maturation. Groups of 20 newly hatched nymphs were weighed, placed together in petri dishes (15 by 2 cm), and provided with water and either whole or ground dog or rat food. On a weekly basis, nymphs were counted and weighed, food and water were replaced, and debris was removed. The time until eclosion and imaginal weights were also recorded.

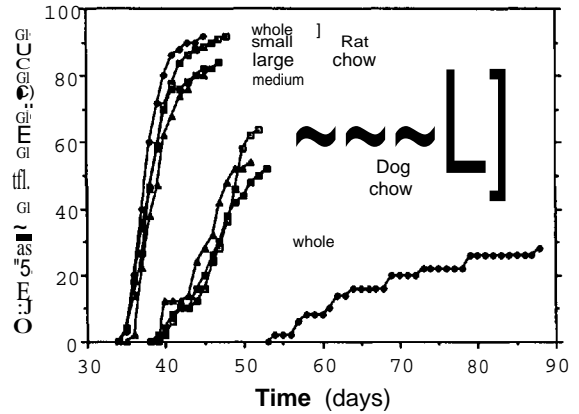


Fig. 1. Cumulative percentage emergence of adult females raised on either rat or dog food ground to various extents. Neonate nymphs were fed either rat or dog food. Small, medium, and large food sizes refer to 0.7-1.0, 1.7-2.6, and 2.6-4.0 mm respectively, as described in the Materials and Methods. Five groups of 20 nymphs each were used for each treatment.

To avoid deleterious effects of isolation (Gadot et al. 1989), newly emerged adult females from various experimental treatments were placed in 15 by 2 cm petri dishes in groups of two to five. On day 7, the basal oocytes of each female were measured with an ocular micrometer in a dissecting microscope.

Nymphal development and oocyte maturation were also compared in cockroaches fed either unprocessed canine or rat chow or the processed form of each diet including dog chow, which was ground to 0.7-1.0 mm.

Statistical Analyses. All results were analyzed either with analysis of variance and Games-Howell multiple comparison of means with unequal variances (P ≤ 0.05 [Super ANOVA 1989]) or with Student's t test (P ≤ 0.05).

Results and Discussion

Nymphal Development. Almost twice as many female nymphs that were fed rat food reached adulthood, compared with nymphs fed dog food (Fig. 1). Nymphs that were raised on rat food also eclosed significantly earlier than those fed dog food (Fig. 1, Table 1). However, newly emerged adult females attained similar mean body mass on both diets (Table 1), suggesting that delays in eclosion in females fed dog food were from a slower increase in body mass. In all dietary treatments, neonates that were fed rat food gained significantly more mass during the first 5 wk of development than nymphs that were fed dog food (Fig. 2). These differences were apparent within 1 wk and continued to increase throughout the remainder of nymphal development.

Grinding the food pellets significantly improved the usefulness of dog food, but not rat

Table 1. Day of eclosion and adult weight ($i \pm \text{SEM}$) of *B. germanica* females raised on either Purina Dog Chow or Rat Chow ground to various mesh sizes

Mesh size, mm	Dog chow			Rat chow		
	n	Day of eclosion	Mean weight, mg	n	Day of eclosion	Mean weight, mg
0.7-1.0	26	47.3 \pm 0.6a	63.8 \pm 0.8a	73	39.1 \pm 0.3a	63.6 \pm 0.8a
1.7-2.6	29	45.9 \pm 0.7a	63.3 \pm 0.9a	42	39.4 \pm 0.4a	65.9 \pm 1.1a
2.6-4.0	26	46.5 \pm 0.7a	64.5 \pm 0.8a	42	38.7 \pm 0.8a	64.0 \pm 0.8a
Whole pellets	14	66.4 \pm 2.7b	63.5 \pm 1.2a	46	38.2 \pm 0.2a	63.9 \pm 0.9a

Within columns, means followed by the same letters are not significantly different ($P > 0.05$, ANOVA and Games-Howell multiple comparison of means [Super ANOVA 1989]). All comparisons of the mean day of eclosion for respective mesh sizes of dog food and rat food are significantly different ($P < 0.05$, Student's *t* test). All comparisons of the mean weight for respective mesh sizes of dog food and rat food are not significantly different ($P > 0.05$, Student's *t* test).

food, for *B. germanica* female nymphs. The size of the rat food diet had no significant effect on mean body mass of 5-wk-old nymphs (Fig. 2), the percentage of females eclosing successfully, or their mean day of eclosion (Fig. 1, Table 1). Differences in the mean day of eclosion were <1.2 d ($=3\%$ of the mean), and had no consistent relation to the size of the food. In contrast, nymphs that were provided whole dog food pellets gained significantly less mass after 5 wk of development than nymphs that were fed ground dog food (Fig. 2). Whole dog food pellets also retarded nymphal development by $\approx 43\%$ compared with the developmental period exhibited by insects that were fed ground dog food (Fig. 1, Table 1); whole dog food also reduced the percentage of eclosing females by $\approx 50\%$. However, there were no significant differences in all three parameters among nymphs fed dog food ground to various mesh sizes (Table 1). Although developmental rates were improved by grinding the dog food diet, significant differences in the mean day of eclosion persisted between equally ground dog food and rat food diets (Table 1). This supports our conclusions that a mechanical barrier in whole dog food pellets is responsible for the slower growth and development of

nymphs, and that rat food supports nymphal development significantly better than does dog food, regardless of the mesh size of the diet.

Reproduction. At eclosion, females attained similar mean body masses on all dietary treatments, including whole dog food pellets (Table 1). However, these females exhibited different reproductive rates, as indicated by their basal oocyte lengths. Basal oocytes were significantly larger in 7-d-old adults that were reared on rat food than in females reared on dog food (Fig. 3A). These differences persisted on all mesh sizes of the two diets, but were greatest on whole pellets. Within either diet, the size of food particles did not affect oocyte maturation except in females raised on whole dog food. In the latter, the basal oocytes were significantly smaller than in all other treatments (Fig. 3A).

Differences in oocyte maturation between females diminished when they were fed rat food until the last instar or until adult emergence (Fig. 3B and C). Significant differences persisted only when last instar or adult females were switched from rat food to whole dog food. These results suggest that reserves acquired during earlier instars may be mobilized during the first gonotrophic cycle in *B. germanica* females that are switched to deficient diets.

Comparison of Processed and Unprocessed Diets. Differences between whole and ground dog food suggest that physical attributes such as texture, hardness, and homogeneity might be involved. However, because the inferiority of dog food compared with rat food can be ameliorated only in part by grinding, the processed dog food may also be nutritionally deficient.

To test this hypothesis, we obtained unprocessed meals of these diets. Because we were unable to obtain unprocessed Purina Dog Chow, we used Purina Canine Chow, which is similar in nutritional composition and processing to Purina Dog Chow. During the commercial extrusion (dog chow and canine chow), the quality of these diets for *B. germanica* might be altered. Nymphs that were fed extruded ground canine or dog foods weighed less, reached the adult stage later, and experienced higher mortality than

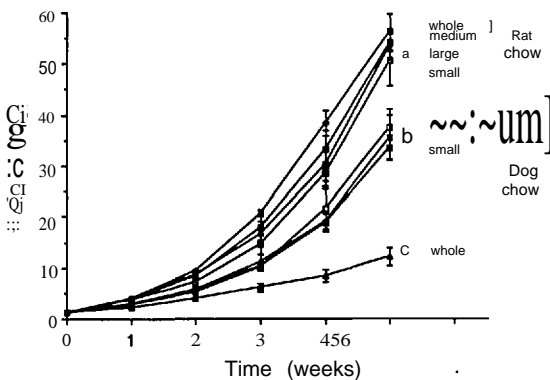


Fig. 2. Mean wet weight (\pm SEM) of nymphs on the 5th wk of development. Insects were treated as in Fig. 1. Different letters indicate significant differences among treatments ($P < 0.05$; ANOVA and Games-Howell multiple comparison of means [Super ANOVA 1989]).

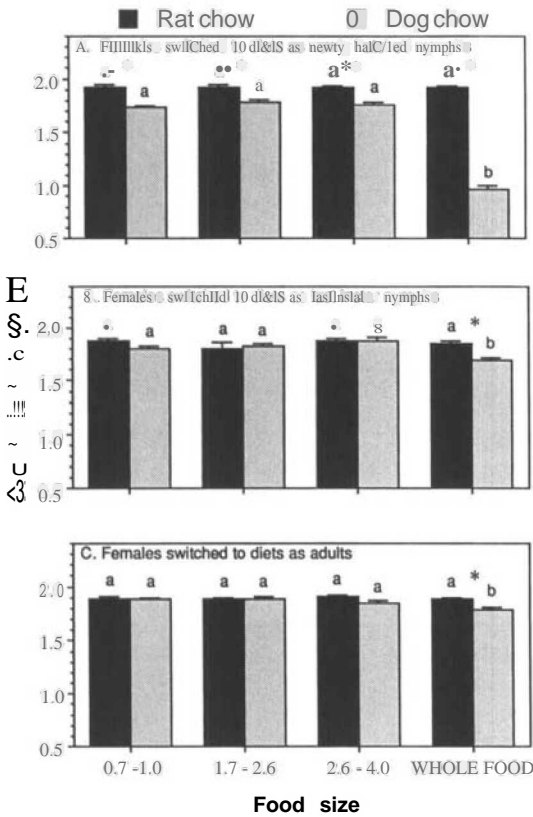


Fig. 3. Oocyte size in 7-d-old adult females that were fed rat food or dog food (whole pellets or ground to smaller mesh sizes). Nymphs and adults were either maintained on rat food or switched to dog food as (A) newly hatched nymphs, (B) as last instars, or (C) as newly emerged adults. Bars indicate SEM. Different letters within the same food indicate significant differences among food sizes ($P < 0.05$, ANOVA and Games-Howell multiple comparison of means [Super ANOVA 1989]); *, Significant differences between diets of a particular mesh size ($P < 0.05$, Student's t test).

nymphs fed processed (pressed) rat food (Fig. 4 and 5, Table 2). Although *B. germanica* females performed significantly better on extruded canine food than on extruded dog food, nymphs that were fed unprocessed forms of these diets attained similar weights (Fig. 4) and exhibited similar adult emergence patterns (Table 2). Conversely, nymphs that were fed either processed or unprocessed rat food exhibited identical developmental and mortality patterns. The addition of animal fat to unprocessed diets, which resulted in diets of similar compositions to the processed diets, did not alter nymphal developmental rates or the number of adult females that emerged (Fig. 4 and 5; Table 2). These results indicate that the commercial extrusion process in production of canine diet diminishes its suitability for *B. germanica*. Although this could not be investigated with dog chow, a similar phenom-

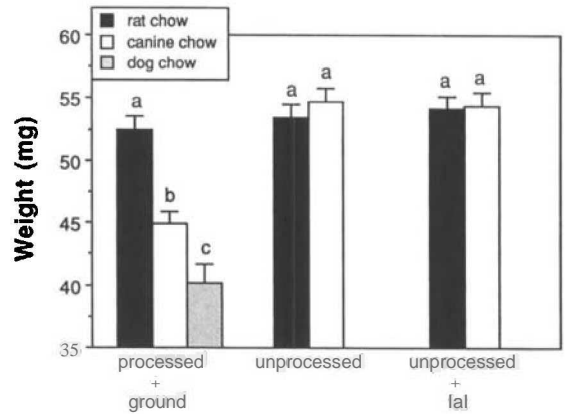


Fig. 4. Mean wet weight (\pm SEM) of nymphs in the 5th wk of development. Newly hatched nymphs were fed rat or canine meal (unprocessed) with or without fat added (see *Materials and Methods*); or rat, canine, or dog food (processed) that was ground to 0.7-1.0 mm. Different letters indicate significant differences among treatments ($P < 0.05$; ANOVA and Games-Howell multiple comparison of means [Super ANOVA 1989]).

non might explain the reduced growth and reproduction of cockroaches on this diet.

Steam extrusion may affect diets in at least two ways. First, by producing a "baked" lipid exterior, this process may introduce a mechanical barrier that reduces food intake and retards development and reproduction. This hypothesis was supported by the accelerated development of nymphs that were fed extruded ground dog food compared with extruded whole pellets. Similar effects of texture and hardness of diets have been reported in other insects (Vanderzant 1969). Second, steam extrusion may alter the composition or digestibility of the diet. Nymphs that were fed unextruded canine diet exhibited significantly faster growth than nymphs fed extruded ground canine diet. Extrusion subjects the diet to high temperatures and pressures, which may have adverse effects on dietary constituents including vitamins, starches, and amino acids.

Relationship to Other Studies. These results have important implications to numerous studies on the life history, physiology, toxicology, behavior, and biochemistry of cockroaches and possibly other insects. For example, in *Spodoptera frugiperda* (J. E. Smith), changes in glutathione S-transferase activity as a result of dietary changes can affect tolerance of organophosphate insecticides (Clark 1989). Whether different laboratory diets have similar effects on the German cockroach remains to be determined.

Different results from different laboratories on the same cockroach species have generally been attributed to different environmental conditions (particularly temperature), different experimental protocols (such as anesthetics), and different

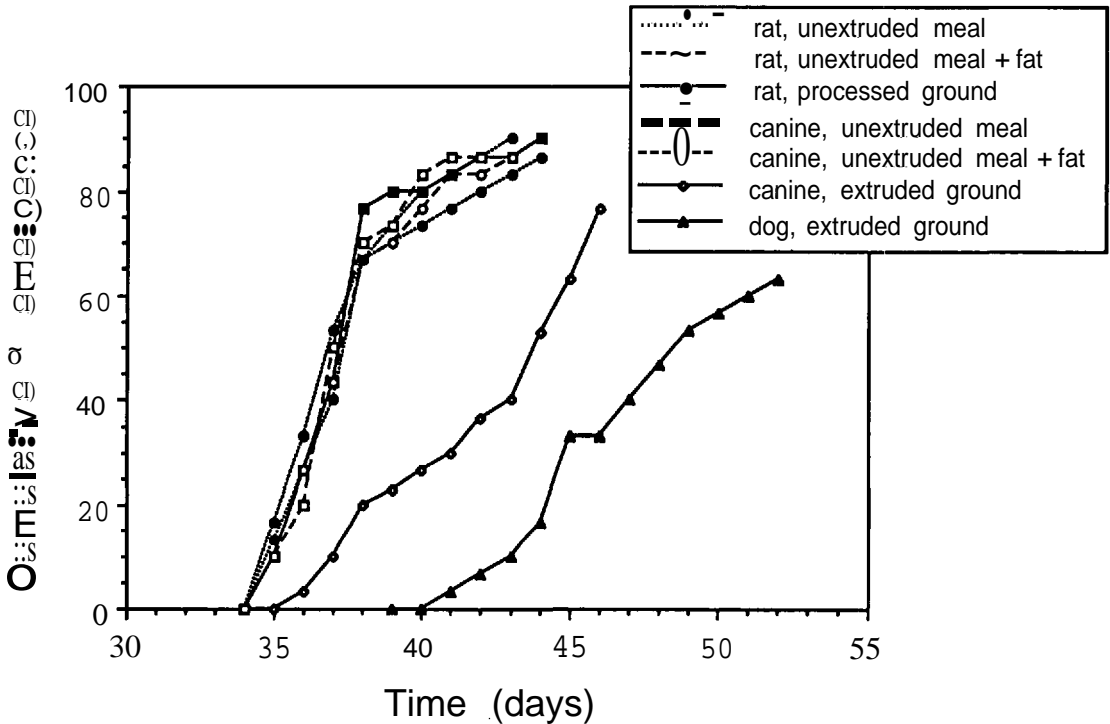


Fig. 5. Cumulative percentage emergence of adult females raised on either rat or canine meal (unprocessed); or processed rat, canine, or dog food that was ground to 0.7-1.0 mm.

strains that may be differentially responsive to the experimental manipulation. However, dietary differences are rarely considered. Despite the fact that different diets are used in various laboratories, the diets are presumed to be equally adequate for growth and reproduction of cockroaches. Based on the present work, we suggest that some discrepancies in the literature might be explained in part by the nutritional state of the insects. Regulation of the cockroach corpus allatum (CA) may be taken as an example.

In all cockroaches studied to date, the CA, which synthesizes juvenile hormone (JH), is restrained to varying degrees by signals from the brain (for reviews, see Feyereisen [1985] and Tobe & Stay [1985]). Specific cues such as those from mating, feeding, and various social stimuli can, together or independently, lift the brain inhibition on the CA (e.g., Cadot et al. 1989).

Therefore, denervation of the CA has generally been considered to mimic these species-specific stimuli. In all cockroach species that have been examined, CA-denervation potentiates JH synthesis and oocyte maturation beyond the normal levels exhibited by females that experience all the appropriate cues. Our data suggest that certain commercial diets may be deficient for some cockroach species, possibly resulting in varying degrees of CA inhibition in normally grown females, as shown by suppressed oocyte maturation.

This hypothesis pertains to a current dispute in the literature. Weaver (1984) showed that CA-denervation of mated American cockroaches, *Periplaneta americana* (L.), reduced both JH synthesis and oocyte growth. These results contradicted Pipa's (1982) conclusions that CA-denervation potentiates oocyte maturation in

Table 2. Day of eclosion and emergence weights (% ± SEM) of *B. germanica* females raised on processed and unprocessed laboratory diets

Form of diet	Rat chow		Canine chow		Dog chow	
	n	Day of eclosion	n	Day of eclosion	n	Day of eclosion
Processed (0.7-1.0 mm)	25	37.6 ± 0.4Aa	23	42.0 ± 0.7Bb	19	45.9 ± 0.6C
Unprocessed	26	37.9 ± 0.4Aa	27	37.5 ± 0.4Aa		NA
Unprocessed + fat	26	37.7 ± 0.4Aa	26	37.7 ± 0.4Aa		NA

Within columns, means followed by different letters are significantly different (P < 0.05, ANOVA and Games-Howell multiple comparison of means [Super ANOVA 1989]). Within rows, means followed by different capital letters are significantly different (P < 0.05, ANOVA and Games-Howell multiple comparison of means). NA, not available.

starved virgin females. In addition to the differences in experimental conditions between the two research laboratories (outlined in Pipa [1986]), our data with *B. germanica* suggest that differences in diets may have contributed significantly to this discrepancy. In Pipa's laboratory, cockroaches were fed dog food, whereas Weaver provided them with a ground mixture of oatmeal, dog food, peanuts, and yeast powder (17:10:4:1, respectively). If the latter dietary mixture is more adequate for *P. americana*, the CA of fed mated females in Weaver's experiments would be more disinhibited than those in Pipa's studies, explaining their conflicting results. Indeed, our preliminary results indicate that JH release rates are greater in the CA of *B. germanica* females that were fed rat food than in females fed dog food, and that the degree of disinhibition by nerve transection is inversely related to the absolute (control) rate of JH synthesis (C.S., unpublished data).

A second example is related to our observations that in the first gonotrophic cycle, the female German cockroach mobilizes nutrient reserves from earlier instars as well as those acquired during the intensive preovulatory feeding period, and that superior nymphal diets may buffer the effects of inferior adult diets (Fig. 3). The effect of starvation on subsequent oocyte development in *P. americana* was investigated in four different laboratories (Kunkel 1966, Bell 1971, Weaver & Pratt 1981, Pipa 1982). In three of the studies, females were fed ad libitum before oviposition of the first ootheca, after which they were starved. In each study, however, the diet was different as were the results. Kunkel (1966) reported that starved females produced four to five oothecae; in studies by Bell (1971) and Weaver & Pratt (1981), starved females produced no more than three oothecae. The percentages of females ovulating a second, third, and fourth time also varied by as much as 59% among the three studies. Kunkel (1966) used Ken-L Ration and Purina Rat Chow; Weaver & Pratt (1981) used a mix of dog food, oatmeal, peanuts, and yeast; and Bell (1971) used an unspecified laboratory diet. The possibility that nutrition may have affected these results was considered by Weaver & Pratt (1981), who suggested that both the quantity and the quality of food consumed before starvation may have affected the amount of stored metabolites available to females. This notion appears to be supported by Pipa's (1982) results demonstrating that <1% of *P. americana* females fed Purina Dog Chow ovulate when starved upon eclosion.

Finally, several works report widely disparate life history parameters in *P. americana* (see Roth 1981). Some of these differences can probably be explained by the diversity of the diets, which include potato cubes, raw meat, apples, and bananas, as well as various dog foods and lab diets

(Gould & Deay 1938, Rau 1940, Geir 1947, Willis et al. 1958, Kunkel 1966).

Our results with *B. germanica*, together with inferences from *Periplaneta* and other species, suggest that the quality of laboratory diets may directly or indirectly profoundly affect the interpretation of endocrinological, biochemical, and toxicological studies. We strongly suggest that detailed descriptions of dietary regimes be given in such reports.

Acknowledgment

We thank D. Hopkins (Purina Mills) for providing Purina rat and canine meals, Purina Canine Chow, animal fat, and technical information on their commercial processing. Supported in part by grants from USDA-CSRS (90-34103-5413) and the Charles and Johanna Busch Memorial Fund to C. Schal and the Thomas J. Headlee Fellowship to R. A. Cooper. This article is New Jersey Agricultural Experiment Station publication D-08928-08-91, supported by State Funds and by the U.S. Hatch Act.

References Cited

- Bell, W. J. 1971. Starvation-induced oocyte resorption and yolk protein salvage in *Periplaneta americana*. *J. Insect Physiol.* 17: 1099-1111.
- Bemays, E. A. 1985. Regulation of feeding behaviour, pp. 1-32. In G. A. Kerkut & L. I. Gilbert [eds.], *Comprehensive insect physiology, biochemistry and pharmacology* vol. 4, 1st ed. Pergamon, Oxford.
- Clark, A. G. 1989. The comparative enzymology of the glutathione S-transferase from non-vertebrate organisms. *Compo Biochem. Physiol.* 92B: 419-466.
- Dadd, R. H. 1985. Nutrition: Organisms, pp. 313-390. In G. A. Kerkut & L. I. Gilbert [eds.], *Comprehensive insect physiology, biochemistry and pharmacology* vol. 4, 1st ed. Pergamon, Oxford.
- Engelmann, F. 1970. *The physiology of insect reproduction*. Pergamon, Oxford.
- Feyereisen, R. 1985. Regulation of juvenile hormone titer synthesis, pp. 391-429. In G. A. Kerkut & L. I. Gilbert [eds.], *Comprehensive insect physiology, biochemistry and pharmacology* vol. 7, 1st ed. Pergamon, Oxford.
- Gadot, M., E. Bums & C. Schal. 1989. Juvenile hormone biosynthesis and oocyte development in adult female *Blattella germanica*: Effects of grouping and mating. *Arch. Insect Biochem. Physiol.* 11: 189-200.
- Gier, H. T. 1947. Growth rate in the cockroach *Periplaneta americana* (Linn.). *Ann. Entomol. Soc. Am.* 40: 303-317.
- Gordon, H. T. 1959. Minimal nutritional requirements of the German cockroach, *Blattella germanica*. *Ann. N.Y. Acad. Sci.* 77: 290-351.
- Gould, G. E. & H. O. Deay. 1938. The biology of the American cockroach. *Ann. Entomol. Soc. Am.* 31: 489-498.
- Hamilton, R. L. & C. Schal. 1988. Effects of dietary protein levels on reproduction and food consumption in the German cockroach (Dictyoptera: Blattellidae). *Ann. Entomol. Soc. Am.* 81: 969-976.
- Haydak, M. H. 1953. Influence of the protein level

- of the diet on the longevity of cockroaches. *Ann. Entomol. Soc. Am.* 46: 547-560.
- Kunkel, J. G. 1966. Development and the availability of food in the German cockroach, *Blattella germanica* (L.). *J. Insect Physiol.* 12: 227-235.
1981. A minimal model of metamorphosis: Fat body competence to respond to juvenile hormone. pp. 107-129. *In* B. Ghovindan, S. Friedman & J. G. Rodriguez [eds.], *Current topics in insect endocrinology and nutrition*. Plenum, New York.
- Noland, J. L. & C. A. Baumann. 1951. Protein requirements of the cockroach *Blattella germanica* (L.). *Ann. Entomol. Soc. Am.* 44: 184-188.
- Pipa, R. L. 1982. Neural influence on corpus allatum activity and egg maturation in starved virgin *Periplaneta americana*. *Physiol. Entomol.* 7: 449-455.
1986. Disinhibition of oocyte growth in adult virgin *Periplaneta americana* by corpus allatum denervation: Age dependency and relatedness to mating. *Arch. Insect Biochem Physiol.* 3: 471-483.
- Rau, P. 1940. The life history of the American cockroach *Periplaneta americana* Linn. (Orthop.: Blattellidae). *Entomol. News* 51: 121-124, 151-155, 186-189, 223-227, 273-278.
- Reinecke, J. P. 1985. Nutrition: Artificial diets. pp. 391-419. *In* G. A. Kerkut & L. I. Gilbert [eds.], *Comprehensive insect physiology, biochemistry and pharmacology*, vol. 4, 1st ed. Pergamon, Oxford.
- Roth, L. M. 1981. Introduction. pp. 1-14. *In* J. Bell & K. G. Adiyodi [eds.], *The American cockroach*. Chapman & Hall, New York.
- Roth, L. M. & B. Stay. 1962. Oocyte development in *Blattella germanica* and *Blattella vaga* (Blattaria). *Ann. Entomol. Soc. Am.* 55: 633-642.
- Slansky, F. Jr. 1982. Toward a nutritional ecology of insects. *Proc. 5th Int. Symp. Insect-Plant Relationships*, Wageningen.
- Slansky, F., Jr., & J. M. Scriber. 1985. Food consumption and utilization. pp. 87-163. *In* G. A. Kerkut & L. I. Gilbert [eds.], *Comprehensive insect physiology, biochemistry and pharmacology* vol. 4, 1st ed. Pergamon, Oxford.
- Super ANOVA. 1989. Abacus Concepts, Inc., Berkeley, Calif.
- Tobe, S. S. & B. Stay. 1985. Structure and regulation of the corpus allatum. *Adv. Insect Physiol.* 18: 305-432.
- Vanderzant, E. S. 1969. Physical aspects of artificial diets. *Ent. Exp. Appl.* 12: 642-650.
1974. Development, significance, and application of artificial diets for insects, *Annu. Rev. Entomol.* 19: 139-160.
- Waldbauer, G. P. & S. Friedman. 1991. Self-selection of optimal diets by insects. *Annu. Rev. Entomol.* 36: 43-64.
- Weaver, R. J. 1984. Effects of food and water availability, and of NCA-1 section, upon juvenile hormone biosynthesis and oocyte development in adult female *Periplaneta americana*. *J. Insect Physiol.* 30: 831-838.
- Weaver, R. J. & G. E. Pratt. 1981. Effects of starvation and feeding upon corpus allatum activity and oocyte growth in adult female *Periplaneta americana*. *J. Insect Physiol.* 27: 75-83.
- Willis, E. R., R. R. Riser & L. M. Roth. 1958. Observations on reproduction and development in cockroaches. *Ann. Entomol. Soc. Am.* 51: 53-69.

Received for publication 27 March 1991; accepted 5 December 1991.