Effects of Dietary Protein Levels on Reproduction and Food Consumption in the German Cockroach (Dictyoptera: Blattellidae)

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Ann. Entomol. Soc. Am. 81(6): 969-976 (1988)

ABSTRACT. The effects of four diets (commercial rat food, 5, 25, and 65% protein) on reproduction and daily food consumption of male and female German cockroaches were investigated. Females compensate for low dietary protein levels by elevating consumption rates and reproduce normally. Conversely, a high-protein diet significantly delayed mating in females and resulted in smaller oöthecae. Percentage hatch of oöthecae and male sexual maturation were unaffected by dietary protein content. Males that were allowed to copulate twice a week, ate more, and died sooner than males allowed to mate only once. The role of diet composition in regulating feeding behavior is discussed.

KEY WORDS. Insecta, *Blattella germanica*, feeding, compensation

NITROGEN, particularly as proteins, is often implicated as a limiting factor in insect reproduction (McCaffery 1975, Barton Browne et al. 1980). The interaction between protein feeding and egg production has been studied most extensively in Diptera (Dethier 1961, Roberts & Kitching 1974, Belzer 1978, Barton Browne et al. 1979, Barton Browne & Kerr 1986). For example, Barton Browne et al. (1976) documented that females of the Australian sheep blowfly, *Lucilia cuprina* Wiedemann, become sexually receptive only after ingesting a protein meal. Representatives from other orders also have been examined and tend to show similar relationships between feeding and reproduction. Slansky (1980) demonstrated that egg production was delayed in female milkweed bugs on reduced food rations. Oöcyte development in the migratory locust, *Locusta migratoria migratorioides* R. and F., is arrested when food quality is poor (McCaffery 1975). When female locusts that previously have been fed adequate food are placed on a low-protein food source, the rate of egg pod production falls and oöcyte resorption increases. Although starvation is known to delay or inhibit mating and increase oöcyte resorption in cockroaches (Roth & Stay 1962, Bell 1971, Bell & Bohm 1975, Sams 1975), the effects of diet quality on sexual receptivity and oöcyte maturation have not been investigated in cockroaches.

Early studies on cockroach feeding have centered on developing adequate diets by varying levels and ratios of essential nutrients (House 1949a,b; Noland et al. 1949a,b; Noland & Baumann 1951; Haydak 1953; Gordon 1959). In this early literature, the optimum level of dietary protein for *Blattella germanica* (L.) was reported to range from 11% (Haydak 1953) to 40% (Noland & Baumann 1951). Haydak (1953) reported that longevity of three species of cockroaches (German, oriental, and American) decreases as dietary nitrogen increases. He noted that insects fed a high-protein diet died with distended abdomens, presumably because of the accumulation of excess urate crystals between the intersegmental membranes. In later studies with American cockroaches, Mullins & Cochran (1973, 1975a) documented the toxic effects of high-protein diets and urate accumulation.

Because of its low toxicity and low solubility in water, uric acid (as urates) is the most common nitrogenous excretory product of terrestrial insects. However, few cockroaches void detectable levels of uric acid in their feces (Mullins & Cochran 1972, Cochran 1981). Excess dietary nitrogen is converted to urates and stored in urate cells (urocytes) of the fat body (Cochran et al. 1979, Mullins 1979, review: Cochran 1985). Urocytes are surrounded by mycetocytes that contain symbiotic microbes. It is believed that these intracellular bacteria are capable of metabolizing stored urates (Cochran 1985). Curiously, even when fed extremely high levels of dietary nitrogen, American and German cockroaches continue to produce and store uric acid in the fat body and other tissues, which may ultimately lead to their death (Haydak 1953, Mullins & Cochran 1975a). However, when dietary nitrogen becomes limited, internal urate stores are mobilized, presumably with the help of mycetocyte bacteria (Mullins & Cochran 1975b). Thus, uric acid appears to act as a nitrogen store for use when dietary nitrogen is limited.

Several patterns of uric acid excretion have been reported in cockroaches (see Cochran 1985 for a

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full account). Although most cockroaches do not void uric acid in the feces, within the Blattellidae a few genera void discrete urate pellets when levels of dietary nitrogen are high. German cockroaches do not void urates in the feces, but males release uric acid along with the spermatophore during copulation (Roth & Dateo 1964). Roth & Dateo (1964) state that "mating appears to be an important means of excreting uric acid in males of *B. germanica.*"

However, Cochran (1975) speculated that uric acid released during copulation does not serve an excretory function, but rather, acts as a nutrient source for reproducing females. Mullins & Keil (1980) documented that females of *B. germanica* mobilize male-derived ^{14}C-labeled uric acid as a nitrogen source for öothecal production.

Several studies have examined the relationship between feeding and reproduction in the German cockroach (Roth & Stay 1962, Kunkel 1966, Cochran 1983, Durbin & Cochran 1985), but they all have used commercial dog food diets. Our study was undertaken to examine the interaction between dietary protein levels, daily consumption, and reproduction in German cockroaches.

Materials and Methods

Insects. Approximately 500 late-instar nymphs of the VPI-normal strain of German cockroaches (voucher specimens located at Rutgers University Entomology Museum) were held in an emergence cage in a Percival incubator (Percival Manufacturing Company, Boone, Iowa) at 27°C, 50% RH, and a 12:12 (L:D) photoperiod. Nymphs were fed on a standard diet of Purina #5012 Rat Chow pellets (Ralston Purina Company, St. Louis, Mo.) and water until adult eclosion. Newly emerged adults were collected hourly during the light cycle. Food was removed when collection of emergent adults was not possible. Insects that emerged while the food was removed were also included in the treatment groups (i.e., <12 h old and unfed). This procedure assured that insects fed exclusively upon the experimental diets following adult emergence. Males and females were placed into separate experiments as described below.

Females. All females that emerged on a given day were divided equally among four treatments until each group contained 20 insects. Treatments consisted of a low-protein diet (5%), a medium-protein diet (25%), a high-protein diet (65%), and ground Rat Chow (approximately 23% protein). The diet formulations that were used are shown in Table 1 and are slightly modified from Cochran et al. (1979). Rat food was included as an experimental treatment and served as a reference with which our data can be compared to those of previous workers. The diets were finely ground, mixed extensively with glass beads to ensure homogeneity and packed into small embedding capsules (Beem Capsules size 3, Better Equipment for Electron Microscopy, Bronx, N.Y.). These food vials were presented to females from the first day of adult life and were continuously available thereafter. Females were provided water ad lib. and housed individually in clear plastic cages (11 by 11 by 2 cm), which allowed gravimetric quantitation of food consumption. Daily consumption by individual females was measured during the first 2 h of each light period using a Mettler HK 160 balance (Mettler Balances and Instruments, Hightstown, N.J.). Because the incubator controlled humidity precisely (50 ± 5%), it was unnecessary to correct for fluctuations in water content of food. Consumption data were converted to dry weight based upon a conversion factor (0.95) obtained by drying 20 samples of each diet to constant weight in a 60°C oven.

Table 1. Composition (grams) of experimental diets

	Diets		
	5% protein	25% protein	65% protein
Yeast[a]	10	10	10
Salt mixture[b]	4	4	4
Dextrin	85	61	13
Cellulose	20	20	20
Casein	1	25	73
Cholesterol	0.1	0.1	0.1

[a] Yeast contains approximately 50% protein.
[b] Wesson's Modified Salt Mixture, Bio-Serv, Frenchtown, N.J.

Four days after adult emergence, each female was presented daily with two males (2 h in the middle of the dark period) until she mated. During the 2-h interval, females were examined every 15 min until observed copulating. The age when mating occurred was recorded along with the ages of formation and hatch of öothecae. Daily food consumption and timing between these events were analyzed using SAS Institute (1982) Analysis of Variance (ANOVA) and Duncan's (1955) Multiple Range procedures.

Males. Males were treated in a similar manner (i.e., 20 insects per treatment; 5, 25, 65%, and rat food diets), but only daily consumption, age at first mating, and longevity were recorded. Two additional treatments were included: 5% protein diet and access to receptive females twice per week, 65% protein diet and access to females twice per week. From the day of emergence (day 0), all males were presented with 8-d-old virgin females for 2 h in the middle of the dark cycle until they were observed copulating. From that point, only males in the frequent copulation groups were allowed to mate twice per week. The rationale for these treatments was based on the data of Haydak (1953), which reported that high protein levels increase mortality in *B. germanica* and Roth & Dateo (1964), which reported that mating is a means of uric acid release. Therefore, frequent matings should increase longevity in males fed a high-protein diet. Males on a low-protein diet with frequent copulations were included to investigate the effects of copulation on meal size. Daily consumption for all groups of males was monitored for 60 d.

Table 2. Days between landmark events in reproductive cycle of *B. germanica* females at 27°C

Diet	Interval[a]		
	A–M	M–EC	EC–H
5% protein	7.2 ± 1.1b	2.8 ± 0.2b	18.7 ± 0.5b
25% protein	7.9 ± 1.1b	2.8 ± 0.2b	18.1 ± 0.9c
65% protein	11.5 ± 1.2a	4.1 ± 0.2a	18.3 ± 0.5bc
Rat food	7.7 ± 1.4b	3.1 ± 0.2b	19.8 ± 0.4a

Means (±SD) in the same column with the same letter are not significantly different ($P < 0.05$; ANOVA; Duncan's [1955] multiple range test).

[a] A, day of imaginal molt; M, mating; EC, formation of oötheca; H, hatch.

Table 3. Percentage mating, number of eggs, and hatch per oötheca of *B. germanica* females

Diet	% mating	E[a]	% hatch
5% protein	90	40.8 ± 4.9a	87.9 ± 11.4
25% protein	80	40.3 ± 3.7a	91.3 ± 4.9
65% protein	40	25.0 ± 1.0b	91.7 ± 7.5
Rat food	85	43.2 ± 3.8a	87.5 ± 10.7

Means (±SD) in the same column with same letter are not significantly different ($P < 0.05$; ANOVA; Duncan's [1955] multiple range test).

[a] E, no. eggs per oötheca.

Results and Discussion

Rat Food. Females fed standard rat food (approximately 23% protein) mated on average 7.7 d after the imaginal molt (Table 2). Oöthecae appeared 3.1 d after mating, were incubated for 19.8 d (Table 2), and contained 43.2 eggs, 87.5% of which hatched (Table 3). These results are similar to those of Cochran's (1983) work that used the same strain of *B. germanica*. We observed somewhat shorter reproductive intervals than those reported by Cochran (1983). However, differences in rearing temperatures between the two experiments (21–25°C compared with 27°C) are sufficient to explain the slight inconsistencies between the studies.

Females. With all diets, females had cyclical feeding patterns as documented for *B. germanica* (Cochran 1983) and other oviparous and ovoviviparous cockroaches (Engelmann & Rau 1965, Bell 1969, Rollo 1984, Cochran 1986). Before mating and the production of an oötheca, females have a period of intense feeding. While carrying an oötheca, feeding is sporadic and consumption is low (Fig. 1).

Females fed 5% protein, 25% protein, and rat food showed no significant differences (ANOVA; Duncan's Multiple Range Test, $P > 0.05$) in their premating interval (7.2–7.9 d; Table 2), percentage of females that mated successfully (80–90%; Table 3), number of eggs per öotheca (40.3–43.2; Table 3), and percentage of embryos that hatched (87.5–91.3%; Table 3). Insects that fed on the 25% experimental diet and ground rat food consumed similar amounts of food throughout each respective interval in the reproductive cycle (Table 4). This indicates that the diet containing 25% protein may be as adequate as the standard rat food diet for supporting the prereproductive nutritional requirements of an adult female *B. germanica*.

Based upon previous work with locusts (McCaffery 1975) and blowflies (Barton Browne et al. 1979), low levels of dietary protein would be expected to arrest or delay oöcyte maturation until sufficient nitrogen stores became available. Neither of these alternatives occurred. Thus, either a 5% protein diet is sufficient to support at least one reproductive cycle, or females can alter feeding patterns, meal sizes, or both, to compensate for the low levels of dietary protein.

Females that fed on a low-protein diet ate significantly more food before mating compared with other treatments (Table 4). These results suggest that *Blattella* females compensate for low protein–high carbohydrate levels in the diet by consuming at higher rates. Apparently to some extent, *Blattella* females regulate the quality of food by modulating the quantity consumed depending upon the protein–carbohydrate levels. Whether individual meals were larger or more frequent cannot be answered from these data. In a study that specifically addressed compensatory mechanisms in locusts, Simpson & Absigold (1985) found that meal frequency, not meal size, increased when food quality was low. However, when recovering from a period of starvation, American cockroaches increase meal size, not frequency of meals (Rollo 1984). A study of this type would be appropriate for *Blattella*.

Although before mating, females on a low-protein diet ate more than females on other diets, they consumed less in the 2.8-d period between mating and oviposition (Table 4). This may indicate that if excess food is consumed during one interval, less is needed subsequently. Another, more plausible explanation, may be that females will remain unreceptive to courting males until sufficient nitrogen stores for oöthecal production have been accumulated. After this requirement has been met, high levels of carbohydrate may be necessary for production of oöthecae and possibly for use during the subsequent gestation period. This would explain the high rate of consumption of the low-protein–high-carbohydrate diet before mating (in order to accumulate proteins), and the low intake during oöthecal production (high carbohydrate levels).

Conversely, females on the high protein–low carbohydrate diet ate less before mating and significantly more than either of the experimental diets during oöthecal production (Table 4). Moreover, though not statistically significant, females on a high-protein diet appear to consume more during gestation than females in other treatments; this suggests that carbohydrates may be limiting during this stage.

When female American cockroaches are switched from an adequate diet (i.e., dog food or equivalent) to a protein-free diet, their reproductive cycles con-

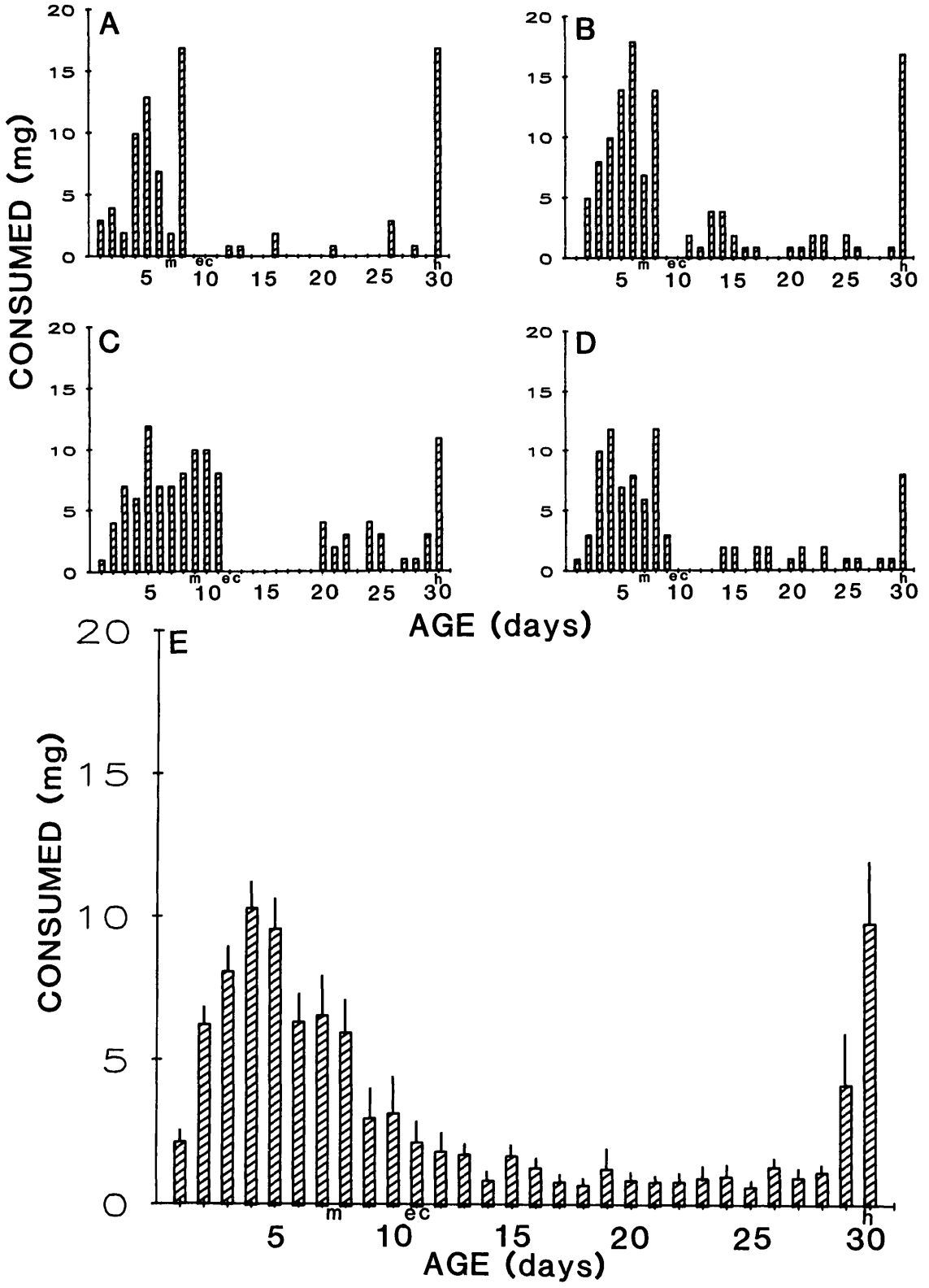

Fig. 1. Feeding patterns of *B. germanica* females fed rat food. A–D are representative graphs for individual females. E is a plot of average daily consumption (±SE) over time for the 17 females that mated and produced in oötheca. Letters above days refer to reproductive events (m, mating; ec, egg case formation; h, egg case hatch).

Table 4. Total food consumed (mg) per female between landmark events in the reproductive cycle of *Blattella*

Diet	Interval[a]			
	A–M	M–EC	EC–H	A–H
5% protein	75.3 ± 8.1a	4.9 ± 4.3c	22.3 ± 7.0a	103.7 ± 5.9a
25% protein	52.6 ± 8.8b	12.2 ± 5.5b	25.5 ± 8.2a	93.5 ± 8.3b
65% protein	37.2 ± 10.0c	22.8 ± 16.4a	35.4 ± 11.3a	104.5 ± 4.8a
Rat food	58.1 ± 11.8b	15.8 ± 7.7ab	23.3 ± 12.2a	101.3 ± 11.0a

Means (±SD) in the same column with same letter are not significantly different ($P < 0.05$; ANOVA; Duncan's [1955] multiple range test).

[a] A, day of imaginal molt; M, mating; EC, formation of oötheca; H, hatch.

tinue at a near normal (Rollo 1984) or slightly elevated rate (Mullins & Cochran 1975b). The effects of nutrient limitation should be more pronounced in *Blattella* than *Periplaneta* because *Blattella* females use 90% of accumulated reserves for the production of each oötheca, whereas *Periplaneta* females can produce up to 5 egg cases without refeeding (Kunkel 1966). Apparently, during different stages of the reproductive cycle, females have different nutritional demands, and they may select foods to meet these demands. A self-selection experiment throughout the reproductive cycle of *Blattella* may be needed to test this hypothesis. Interestingly, there are no differences among rat food, high-protein, and low-protein diets in the total amount consumed from the imaginal molt to hatch of oöthecae (Table 4).

A high-protein content in the diet was detrimental to survival and reproduction of female *Blattella*. Twenty-five percent of the 20 females died before mating and only 40% (6) of the survivors copulated. Mating was delayed by about 4 d, oöthecae were formed more slowly after copulation (4.1 d; Table 2) and contained significantly fewer eggs (Table 3). However, females on a high-protein diet that successfully mated and oviposited did not differ from females in other treatments in incubation time (Table 2) and percentage of hatch (Table 3) of oöthecae. Therefore, it appears that females that survive a stressful pre-ovipositional period are as successful as other females. This implicates dose-dependent toxic effects by the high-protein diet. Haydak (1953) attributed the toxicity of high-protein diets to a "choking" of the fat body by uric acid. Mullins & Cochran (1975a) suggested that the toxic effects of a high-protein diet in *P. americana* may be due to the accumulation of ammonia or tryptophan metabolites. They implicate the quinoline compounds xanthurenic and 8-hydroxyquinaldic acids as contributing to gut lesions (Mullins & Cochran 1973).

Females fed a low-protein diet are able to elevate consumption to support normal growth and reproduction. Conversely, females fed a high-protein diet have increased mortality, and decreases in consumption and reproduction. Thus, it appears that females can compensate for low levels of dietary protein more easily than they can for high-protein diets. However, feeding exclusively upon high-protein foods is relatively rare in the natural habitat, and regulation and detoxification can be accomplished less readily.

Although not specifically examined in these investigations, it was observed that all females, regardless of diet, elicited male courtship starting on day 4 (days 0–3 were not tested). Females fed 65% protein were courted starting on day 4, but mated on day 11.5, approximately 4 d after the other treatments (Table 2). Apparently, female receptivity, not attractiveness to males, is altered by fluctuations in dietary protein.

Males. Unlike females, males did not have feeding cycles (Fig. 2). Males among all treatments had the same pattern of small daily meals (1–2 mg).

The effect of dietary protein level on males' daily consumption, sexual maturation, and longevity is shown in Table 5. Unlike females, male sexual maturation (A–M) was unaffected by dietary protein content. However, daily consumption and longevity appear to be closely related to diet composition. Males fed 5% dietary protein ate the smallest daily meals (1.2 mg) and lived the longest (214 d), whereas males fed 65% dietary protein had the shortest lifespan (67.4 d) and largest daily consumption (2.1 mg). If males were optimizing nitrogen intake, then the daily consumption data would be reversed (i.e., lowest intake of highest protein diet). Therefore, it appears that dietary carbohydrate levels are more important for males. Because the low-protein diet has a high carbohydrate content and the high-protein diet has low carbohydrate levels (Table 1), males may be regulating intake to consume more of the low-carbohydrate diet and less of the high-carbohydrate diet. Further experiments are needed to elucidate whether this relationship is maintained over a wide range of diet compositions.

Because their reproductive costs are low, males of most insect species require considerably less protein than do females. Mullins & Cochran (1975b) found that male American cockroaches are in a positive nitrogen balance when fed 5% dietary protein; females, however, fluctuate between positive and negative, but end up in a negative nitrogen balance after 17 wk on this diet. Therefore, the thesis that males are not optimizing nitrogen intake has some empirical basis. Of particular interest is whether a bimodal relationship exists between daily consumption and dietary protein level. As protein content in the diet decreases further, males would be expected to increase consumption to sup-

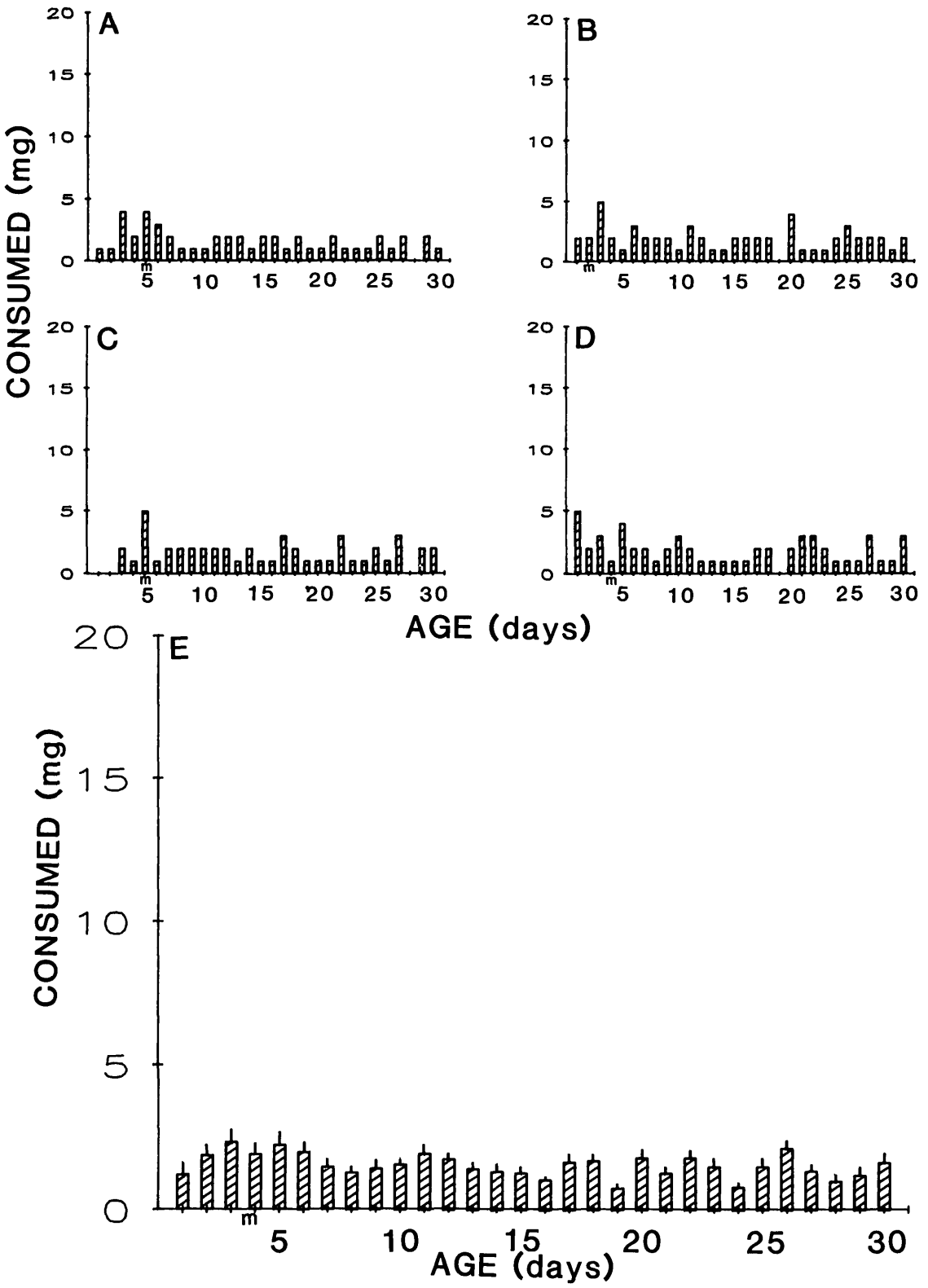

Fig. 2. Feeding patterns of *B. germanica* males fed rat food. A–D are representative graphs for individual males. E is a plot of average daily consumption (±SE) over time for all 20 males in the experiment. Letter m above day refers to day of mating.

Table 5. Daily consumption, longevity, and premating interval of male *B. germanica*

Diet	Daily consumption (mg)	Interval[a]	
		A–M (d)	A–D (d)
5% protein	1.2 ± 0.4d	4.0 ± 1.8a	214.1 ± 45.1a
25% protein	1.4 ± 0.3c	4.0 ± 1.6a	129.7 ± 34.0c
65% protein	2.1 ± 0.5a	3.8 ± 1.5a	67.4 ± 10.4d
Rat food	1.6 ± 0.4b	3.8 ± 1.8a	151.1 ± 23.4b

Means (±SD) in the same column with the same letter are not significantly different ($P < 0.05$; ANOVA; Duncan's [1955] multiple range test).

[a] A, day of imaginal molt; D, death; M, mating.

port reproductive tissues, particularly if they copulate frequently.

The effects of frequent copulation on daily consumption and longevity of males on two diets are presented in Table 6. Our hypothesis was that frequent copulation (twice per week) would increase longevity in males fed a high-protein diet by providing an opportunity to dispose of uric acid. However, males fed a 65% protein diet and allowed frequent copulation also consumed significantly more ($t = 7.7$, df = 128, $P = 0.05$; Student's t test) and died earlier ($t = 3.33$, df = 38) than once-mated controls. In males fed 5% protein and allowed frequent copulation, daily consumption was also significantly elevated ($t = 4.44$, df = 122, $P = 0.05$ Student's t test) and longevity was shortened ($t = 3.09$, df = 26). The time to sexual maturation was the same between treatments (Table 6).

Thus, on high- and low-protein diets, males that are allowed frequent copulation consume at higher rates, presumably to meet the demands of high spermatophore and uric acid production. However, the elevated consumption rates seen in both groups may reflect different metabolic demands. Males on a 5% protein diet may consume at high rates in order to accrue sufficient nitrogen for spermatophore and uric acid production; the males on 65% protein diet may consume and process large amounts of food to secure carbohydrates. Concurrent with this increased consumption rate in both groups is an increased demand to metabolize and process large quantities of food. This added cost of frequent copulation may manifest itself in a shorter total lifespan. Unfortunately, this experiment did not include a treatment of intermediate protein and carbohydrate levels (i.e., 25% diet) with frequent copulation. According to our hypothesis, males under these conditions would not be expected to have elevated consumption rates when compared with controls that have mated once, because adequate levels of protein and carbohydrate levels would be available in the diet.

Our results suggest some interesting interactions between diet composition, feeding, the reproduction in the German cockroach, *Blattella germanica*. In females, specific "hungers" throughout various stages in the ovarian cycle are suggested, but these require further study. The effects of very low levels of dietary protein (i.e., less than 5%) on feeding and reproduction would provide useful information on nitrogen budgeting in this species. The physiological basis for decreased longevity in frequently copulating males awaits further documentation. Finally, the role of diet composition in regulating cockroach meal dynamics would add valuable information to our understanding of feeding behavior.

Table 6. Effect of frequent copulation on daily food consumption and longevity of male *B. germanica* fed low- and high-protein diets

Diet	Daily consumption (mg)	Interval[a]	
		A–M (d)	A–D (d)
5% protein	1.2 ± 0.4a	4.0 ± 1.8a	214.1 ± 45.1a
5% protein (+ mating)	1.6 ± 0.6b	3.7 ± 1.8a	153.6 ± 56.6b
65% protein	2.1 ± 0.5a	3.8 ± 1.5a	67.4 ± 10.4a
65% protein (+ mating)	2.9 ± 0.8b	3.7 ± 1.7a	54.1 ± 5.9b

Means (±SD) for daily consumption and lifespan are significantly different (Student's t test $P < 0.05$) between groups allowed to mate and their respective control group.

[a] A, day of imaginal molt; D, death; M, mating.

Acknowledgment

We thank M. May, T. Shapas, and D. Sutherland for comments on the manuscript. Supported in part by grants to C.S. from U.S. Public Health Service (NIH Grant HD-21891), the Rutgers University Research Council, and by a New Jersey Pest Control Association Scholarship to R.L.H. This is New Jersey Agricultural Experiment Station Publication No. D-08170-16-87 supported by State funds and by U.S. Hatch Act.

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Received for publication 23 November 1987; accepted 28 June 1988.