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The influence of nymphal and adult dietary protein on food intake and reproduction in female brown-banded cockroaches

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Abstract

Female brown-banded cockroaches, *Supella longipalpa* (F.) (Dictyoptera : Blattellidae), failed to elevate consumption rates when fed a 5% protein diet compared with females fed either 25% protein or commercial rat food. Adult performance was directly influenced by dietary protein level: Females fed 65% protein died rapidly, while in females fed 5% protein feeding and reproductive rates were reduced after production of three oothecae. In females fed a low protein diet as both late instar nymphs and as adults, mating was delayed and they required more time to form oothecae than females switched to 25% protein as adults. The role of nymphal reserves in adult reproduction is discussed.

Introduction

Studies with the German cockroach, *Blattella germanica* (L.), have revealed an intimate association between the availability of food and water and reproductive success (Roth & Stay, 1962; Kunkel, 1966; Mueller, 1978; Durbin & Cochran, 1985; Hamilton & Schal, 1988). Unlike the larger American cockroach, *Periplaneta americana* (L.), which may produce up to 5 oothecae without feeding between successive ovipositions, female German cockroaches incorporate 90% of the reserves accumulated during the pre-ovipositional interval into each ootheca (Kunkel, 1966). Food and water consumption are cyclical and closely related to the reproductive cycle in both species: Females feed intensely prior to oothecal production but only sparingly during oviposition and gestation (Bell, 1969; Cochran, 1983; Rollo, 1984; Durbin & Cochran, 1985; Hamilton & Schal, 1988). Mating in female German cockroaches is inhibited during starvation (Roth & Stay, 1962) and delayed when they are fed a stressfully high protein diet (Hamilton & Schal, 1988). In the absence of an adequate food supply, females either delay reproduction (Kunkel, 1966; Durbin & Cochran, 1985), or produce fewer and smaller oothecae (Mueller, 1978), with reduced percentage hatch of individual oothecae (Durbin & Cochran, 1985). Hamilton & Schal (1988) showed that during the first ovarian cycle, German cockroach females are able to compensate for low protein levels by elevating consumption and they produce oothecae of normal size and percentage hatch.

Dietary self-selection in nymphs of the brown-banded cockroach, *Supella longipalpa* (F.), has been investigated (Cohen *et al.*, 1987), but no studies of the feeding behavior of adults have been conducted to date. The brown-banded cockroach is an important pest species with virtually nothing known of the interactions between feeding, diet composition, and reproduction. Like the German cockroach, the brown-banded cockroach is small and must feed prior to oothecal production. However, unlike *B. germanica* females which carry the ootheca for a protracted period, *S. longipalpa* females oviposit a new ootheca every several days. Therefore, the effects of nutrient limitation should become evident much sooner in this species than in *B. germanica*. The present study on *S. longipalpa* is part of a comparison of feeding and nutrient procurement throughout the reproductive cycle of these two related species.

Table 1. Composition by weight (grams) of experimental diets

	5% protein	25% protein	65% protein
Yeast[1]	10	10	10
Salt[2]	4	4	4
Dextrin	85	61	13
Cellulose	20	20	20
Casein	1	25	73
Cholesterol	0.1	0.1	0.1

[1] Yeast contains approximately 50% protein

[2] Wesson's Modified Salt Mixture.

Material and methods

Insects were reared on commercial rat food pellets (Purina #5012) and water *ad libitum*. Approximately 500 late instar nymphs were maintained on rat food and water at 27 °C, 50% humidity, and an LD, 12:12 h photoperiod regime. A second group of 500 nymphs was maintained under identical conditions but received a 5% protein diet for 15 days prior to adult emergence in an effort to deplete nymphal protein reserves.

Females that emerged daily from each of the two groups of nymphs were equally divided among four experimental treatments until each group contained 20 insects. A total of eight treatments resulted which included nymphal history (low protein vs. rat food) and adult diet (5% protein, 25% protein, 65% protein, and ground rat food [23% crude protein]). The diet formulations are presented in Table 1 and are slightly modified from Cochran *et al.* (1979). Ground rat food was included in these experiments as a control and was used to demonstrate the adequacy of our 25% protein experimental diet for supporting adult reproduction.

Adult females were housed individually in 11 x 11 x 2 cm. plastic cages with experimental diet, water, and harborage continuously available. The diets were packed into size 3 'Beem' embedding capsules and presented to females from the day of adult eclosion (Day 0). Daily consumption was measured gravimetrically by weighing individual food vials at the conclusion of the dark cycle to the nearest 0.1 mg using a Mettler HK 160 balance. With humidity controlled at 50%, correction for daily fluctuations in water content of the diets proved unnecessary. For final analysis, daily consumption was converted to dry weight based on a conversion factor (0.95) obtained by drying twenty samples of each diet to constant weight at 60 °C. Consumption was monitored through the production of six oothecae in the females fed rat food as nymphs and through 2 oothecae in the female fed low protein as nymphs.

Beginning on the second day after emergence, females were presented daily (for 2 h in the middle of the dark cycle) with two males each until mating was observed. Once mated, females were denied access to males. Females that failed to mate by day 15 were excluded from the analysis. Individual females were examined twice daily (beginning and end of the scotophase) for reproductive events (i.e. formation, drop, or hatch of oothecae). All data were analyzed using an Analysis of Variance procedure and Duncan's Multiple Range Test. Because reproductive events were asynchronous among individuals, feeding data were re-aligned to each reproductive landmark (Cochran, 1983) in order to show the relationship between feeding and reproduction.

Table 2. Effects of dietary protein on longevity and lifetime fecundity of *Supella longipalpa* females reared on rat food as nymphs

Event	5% protein	25% protein	65% protein	Rat food
Longevity (days)	132.2^{a}	118.7^{ab}	26.6^{c}	110.3^{b}
Percent mating	90	80	5	95
Oothecae/female	6.8^{c}	13.0^{a}	–	9.2^{b}
Eggs/ootheca	15.0^{b}	16.2^{a}	–	15.7^{ab}
Percent hatch	84.9	95.6	–	88.9
Viable Oot/female	5.4^{b}	8.8^{a}	–	8.5^{a}
Nymphs/female	66.0^{b}	126.4^{a}	–	119.8^{a}
Nymphal weight (mg)	1.1^{a}	1.1^{a}	–	1.1^{a}

Means in the same row followed by the same letter are not significantly different (ANOVA, DNMRT $P > 0.05$).

Results

Females fed rat food as nymphs. Based upon comparisons of longevity, numbers and size of oothecae, total fecundity, and nymphal weight, our 25% protein diet equals or exceeds rat food in supporting the nutritional needs of reproducing female *S. longipalpa* (Table 2).

Sixty-five percent dietary protein appeared to be toxic to female *S. longipalpa*. Females fed this diet lived an average of 26.6 ± 2.2 days (se., N = 20) and only one female mated, but died before depositing an ootheca, at an age of 17 days (Table 2). Longevity was similar in females fed 5% and 25% protein. However, females that were fed 5% protein and mated, produced 48% fewer oothecae, 7% fewer eggs per ootheca, and had an 11% reduction in percentage hatch from individual oothecae, compared with females fed a 25% protein diet (Table 2). This resulted in a lower lifetime fecundity for females fed the 5% protein diet than for females fed 25% protein

Table 3. Time (days) between reproductive events of *Supella longipalpa* females fed rat food or a low protein diet as nymphs

Adult diet	5% protein		25% protein		Rat food	
Nymphal diet	5% protein	Rat food	5% protein	Rat food	5% protein	Rat food
A-M	9.4^{a}	9.2 A	8.9^{ab}	8.1 A	7.8^{b}	8.3 A
M-EC1	9.3^{a*}	6.1 A	6.0^{b}	5.1 B	5.2^{b}	4.9 B
A-EC1	18.7^{a*}	15.2 A	14.9^{b}	13.2 B	13.0^{b}	13.2 B
EC1-EC2	16.9^{a*}	7.9 A	10.2^{b*}	7.5 A	8.5^{b}	8.0 A
EC2-EC3	–	9.1 A	–	8.1 A	–	7.5 A
EC3-EC4	–	12.3 A	–	7.0 B	–	7.9 B
EC4-EC5	–	17.4 A	–	7.4 B	–	8.9 B
EC5-EC6	–	19.0 A	–	6.9 B	–	8.4 B
EC6-EC7	–	17.5 A	–	6.9 B	–	8.7 B
EC7-EC8	–	18.4 A	–	6.7 C	–	9.2 B
EC8-EC9	–	19.0 A	–	6.9 C	–	9.9 B

A = day of adult emergence, M = mating, EC1 = oviposition of first ootheca, EC2 = second ootheca, EC3 = third ootheca... The influence of adult diet is compared within each of the two nymphal diets: means in the same row followed by the same letter are not significantly different (ANOVA, DNMRT $P > 0.05$) Comparisons of adults raised on low protein diets as nymphs are denoted by lower case letters, and females raised on rat food as nymphs are denoted with upper case letters.

An * between 2 means indicates that the two nymphal treatments are significantly different (Student's T test, $P < 0.05$). Females reared on low protein food as nymphs were only examined through the production of two oothecae.

(Table 2). Weight of emergent nymphs was not affected by the level of dietary protein. Females fed the low protein diet had significantly longer first pre-ovipositional periods than females fed 25% protein (Table 3). The pre-mating interval of females fed the 5% diet was one day longer, but not significantly different from females fed 25% protein. Thus, females fed the 5% diet required significantly longer time to form the first ootheca after mating had occurred (Table 3). With the exception of this two day delay, females on both diets had similar timing of reproductive events over the first three oothecae. While females fed 25% protein maintained a constant rate of oothecal production with a period of approximately 7 days, the length of each successive ovipositional cycle increased in females fed the 5% protein diet (Table 3). Thus, the increased fecundity of females fed 25% protein was mainly due to a consistently short gonotrophic cycle, permitting production of more oothecae during their lifespan (Table 2).

Females fed the 25% protein diet also produced more oothecae than females fed rat chow (Table 2). Here too, the difference was due to gonotrophic cycles of shorter duration and a slightly longer lifespan (Table 3). However, females fed rat food and those fed 25% protein produced similar numbers of viable oothecae (oothecae that hatched, regardless of number of

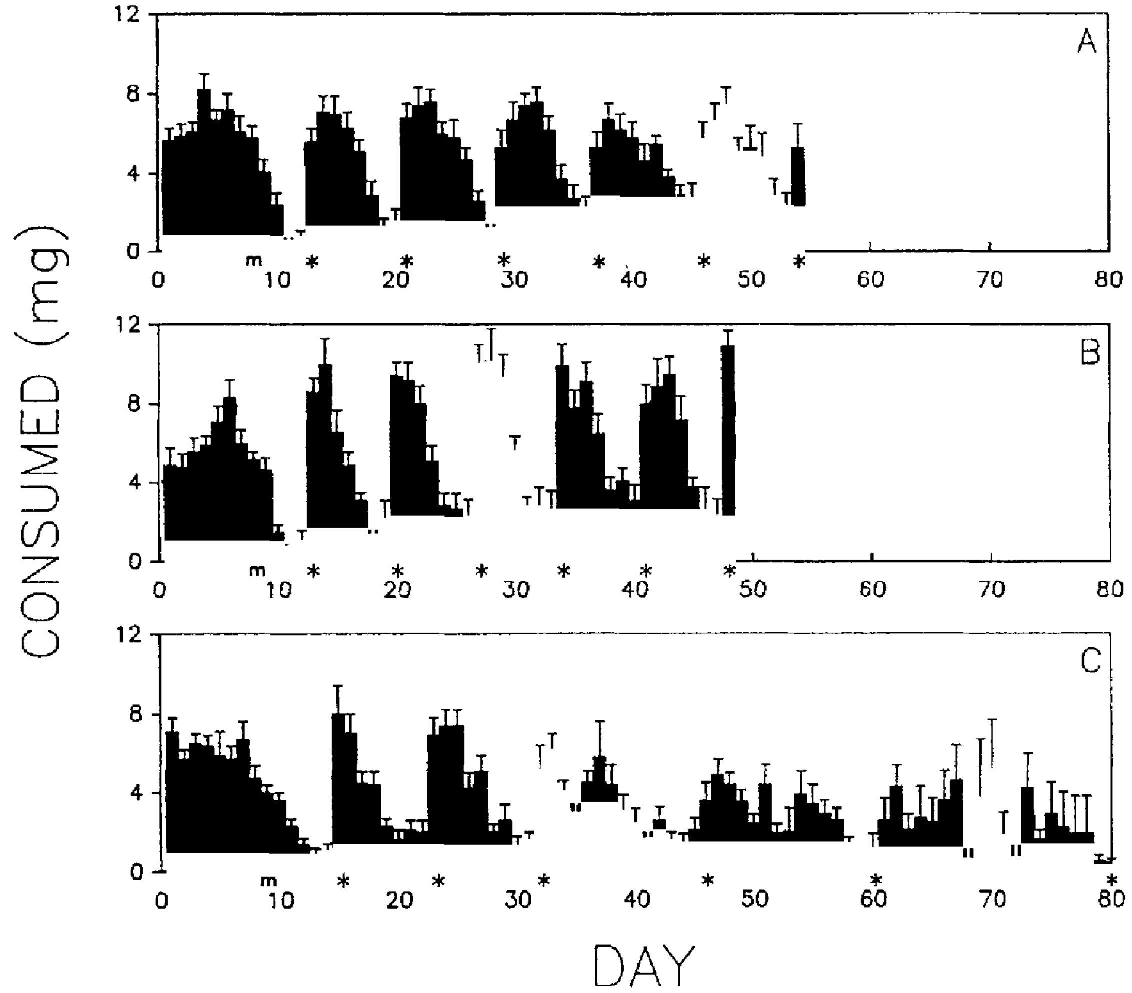

Fig. 1. Average daily consumption of female *Supella longipalpa* during successive reproductive cycles. (A) rat food fed females; (B) females fed a 25% protein diet; (C) 5% protein fed females. m = mating, * indicates oothecal deposition.

nymphs), which resulted in similar lifetime fecundity (Table 2). Females were allowed to mate only once and had males been continuously available, the realized fecundity might have been higher in 25% protein fed females.

Females fed low protein as nymphs. Females fed rat food as nymphs and only carbohydrates (dextrin) from adult emergence produced up to 2 oothecae (unpublished observation), suggesting that nymphal reserves might affect adult reproduction. Moreover, the gradual decrease in reproductive performance, and longer gonotrophic cycles (17.4–19 days) after the fourth ootheca in females fed the 5% protein diet (Table 3) suggested that females used a combination of nymphal stores and dietary intake to produce oothecae. Preliminary experiments showed that nymphal development was poor on the 5% protein diet. Therefore, to examine the effects of nymphal nutrition upon adult performance through 2 gonotrophic cycles, late instar nymphs were fed low protein diet for 15 days before adult emergence.

Females that fed on a low protein diet as nymphs and on 65% protein as adults died rapidly (18.5 ± 1.0 days) without mating or producing any oothecae. Adult longevity was not monitored in the other treatments. Time to mating was not significantly different in females fed 5% and 25% protein as adults, but the period from mating to deposition of the first ootheca was significantly longer in females maintained on low protein than in females switched to 25% protein (Table 3). This period was also 50% longer than in females switched from a rat food nymphal diet to a low protein diet as adults.

The effects of nutrient limitation became more pronounced after the first ootheca. Only 41% (7/17) of adult females fed 5% protein produced a second ootheca compared with 94% of the females fed 25% protein (17/18). Females in the low protein treatment required 60% longer to produce a second ootheca than females fed the 25% protein diet and they required more than twice as long as low protein fed females that were maintained on rat food as nymphs (Table 3).

Food intake. With all diets, females exhibited cyclical feeding patterns: They fed intensively prior to mating and the production of an ootheca, and only minimally during ovulation and oviposition. After depositing an egg case, females resumed feeding until the production of the next ootheca (Fig. 1).

After depositing the first egg case, daily food

Table 4. Milligrams of food consumed between reproductive events of *Supella longipalpa* females

Adult diet	5% protein		25% protein		Rat food	
Nymphal diet	5% protein	Rat food	5% protein	Rat food	5% protein	Rat food
A-M	46.0^{b}	55.9 A	42.2^{b}	52.0 A	54.4^{a}	56.1 A
M-EC1	24.3^{a}	18.5 A	19.1^{a}	19.1 A	16.3^{b}	13.7 B
A-EC1	69.9^{a}	74.5 A	61.3^{b}	71.1 A	70.8^{a}	69.8 A
EC1-EC2	49.5^{a}	33.2 B	41.5^{a}	43.2 A	32.6^{b}	39.9 A
EC2-EC3	–	38.1 B	–	48.3 A	–	40.8 AB
EC3-EC4	–	40.2 A	–	45.1 A	–	43.3 A
EC4-EC5	–	51.6 A	–	43.9 A	–	46.6 A
EC5-EC6	–	36.7 A	–	38.6 A	–	39.2 A

A = day of adult emergence, M = mating, EC1 = oviposition of first ootheca, EC2 = second ootheca, EC3 = third ootheca...
The influence of adult diet is compared within each of the two nymphal diets: means in the same row followed by the same letter are not significantly different (ANOVA, DNMRT $P > 0.05$). Comparisons of adults raised on low protein diets as nymphs are denoted by lower case letters, and females raised on rat food as nymphs are denoted with upper case letters.
Females reared on low protein food as nymphs were only examined through the production of two oothecae.

Table 5. Average daily consumption (mg) between reproductive events in *Supella longipalpa* females fed rat food or a low protein diet as nymphs

Adult diet	5% protein		25% protein		Rat food	
Nymphal diet	5% protein	Rat food	5% protein	Rat food	5% protein	Rat food
A-M	5.0^b	5.9 A	4.8^b	6.1 A	7.0^a	6.5 A
M-EC1	2.7^b	2.9 AB	3.2^a	3.5 A	3.1^{ab}	2.6 B
A-EC1	3.9^b	4.7 A	4.1^b	5.1 A	5.5^a	5.0 A
EC1-EC2	3.0^b	4.0 B	4.2^a	5.6 A	4.2^a	5.0 A
EC2-EC3	–	4.2 B	–	5.9 A	–	5.3 A
EC3-EC4	–	3.3 B	–	6.1 A	–	5.5 A
EC4-EC5	–	2.9 B	–	5.9 A	–	5.4 A
EC5-EC6	–	2.6 C	–	6.6 A	–	4.9 B

Sympbols and statistical treatment as in Table 4.

intake was significantly less for females fed a 5% protein diet than for females fed a 25% protein diet (Table 5). In general, females on both diets consumed similar amounts of food between successive oothecae (Table 4), but females fed low protein diets had longer gonotrophic cycles (Table 3).

The consumption data of females fed 5% protein as nymphs (Tables 4, 5) support the finding that, at the protein concentrations tested, adult females fed low protein do not elevate daily or total consumption to compensate for poor food quality. Daily feeding rates were generally lower in 5% protein fed females than in females fed 25% protein (Table 5). However, females on low protein required 42% more time to deposit the second ootheca, and total consumption between reproductive events was similar in both treatments.

Discussion

Supella longipalpa females exhibit cyclical feeding patterns (Fig. 1) similar to those documented for *B. germanica* (Cochran, 1983; Hamilton & Schal, 1988) and other oviparous and ovoviviparous cockroaches (Englemann & Rau, 1965; Bell, 1969; Rollo, 1984; Cochran, 1986). *S. longipalpa* is an excellent oviparous cockroach model for studies of the interactions of feeding, the endocrine system, and reproduction because it has a short gestation period without overlapping cycles of basal oocyte maturation, and the present data on feeding are closely related to endocrine events (Smith *et al.*, 1989).

Our data suggest an inverse relationship between adult dietary protein content and longevity in *S. longipalpa*. Females fed 65% protein died rapidly, regardless of nymphal diet. Feeding the same diet formulations to the related species *B. germanica*, Hamilton & Schal (1988) found that male longevity was greatest on the 5% protein diet, and least on the 65% protein diet. These data are in agreement with Haydak (1953) who, using similar diets, also showed an inverse relationship between dietary protein levels and longevity in three cockroach species (German, American and oriental). Mullins & Cochran (1973) implicate tryptophan metabolites as causing gut tumors which contribute to the excessive mortality of American cockroaches fed a high protein diet and they suggest that 'preferential storage' of urates at the expense of 'non-nitrogenous metabolism' may also contribute to mortality (Mullins & Cochran, 1975).

Egg production is costly both in terms of nutrient demands and longevity. Longevity in *Drosophila* females increases when the rate of egg production is reduced by either feeding low quality food or reducing oviposition sites (Partridge *et al.*, 1987). Partridge *et al.* (1987) hypothesize that the reduced longevity associated with egg production may be due to altered hormonal balances, metabolic rates or a preferential allocation of trace nutrients to developing eggs. However, female *S. longipalpa* fed the 25% protein diet produce almost twice as many oothecae (13 vs. 6.8), yet longevity is not significantly different (119 vs. 132 days) from females fed 5% protein (Table 2). Therefore, high reproductive rates in female cockroaches may not necessarily predispose them to reduced lifespans, but experiments with non-reproducing females and/or other diets are needed to resolve this issue.

When reared on rat food as nymphs, the reproductive rates of females on either of the diets are similar through the production of three oothecae (Table 3). Later reproduction is slower in females fed a low protein diet. We postulate that nutrient reserves, procured during the nymphal stage, may be significant for adult females feeding on low protein foods and allow 'normal' reproductive rates for a limited number of oothecae. In light of Gordon's (1959) discussion on the role of egg provisions in nymphal development of *B. germanica* and Durbin & Cochran's (1985) report that female German cockroaches utilize nutritional reserves to ensure oothecal hatch during periods of food and water deprivation, the concept of reserves affecting adult reproduction seems plausible. After the production of three oothecae, stored reserves may be reduced and females must acquire the necessary nitrogen from the diet; this takes progressively longer with each successive ootheca until the reserves are depleted.

Many insects compensate for low food quality by increasing consumption (House, 1965; McGinnis & Kasting, 1967; Simpson & Absigold, 1985; Absigold & Simpson, 1987; Simpson *et al.*, 1989). However, most studies with caterpillars and flies have diluted the whole diet with either indigestible substances or with water, rather than manipulate the protein-to-carbohydrate ratio. *B. germanica* females fed a 5% protein diet *ad libitum* elevate consumption during the first gonotrophic cycle and reproduce normally (Hamilton & Schal, 1988). *S. longipalpa* females, on the other hand, do not appear to compensate for low dietary protein and reproduction suffers, particularly after extended periods on low protein/high carbohydrate diets. It is important to note that locusts compensated for dilution of the protein component of their diet from 28% to 14% (Simpson & Absigold, 1985), but not to 7% (Simpson, personal communication). It is therefore possible that 5% protein in an otherwise nutritious diet may elevate consumption in *B. germanica*, but is beyond the compensatory capacity of *S. longipalpa*.

When faced with calorically dense diets, rats increase their levels of basal metabolism and activity in an effort to defend body weight (Keesey & Powley, 1986; Collier & Squibb, 1967). Female cockroaches fed low protein/high carbohydrate foods undoubtedly consume excess energy in the diet, but the question of how cockroaches deal with excess energy remains largely unanswered. When fed an unnutritious, high energy diet for two weeks, American cockroaches do not increase activity levels (Rollo, 1984). Hamilton & Schal (unpublished) found that, after the production of two oothecae, dry body weights of female *S. longipalpa* fed high carbohydrate diets were significantly greater than rat food fed females. Thus, cockroaches may simply store excess dietary carbohydrate. However, more research is needed before any conclusions about energy budgets in *S. longipalpa* can be drawn.

Females fed a low protein diet as both nymphs and adults consume less and delay both mating and egg case production compared with females switched to either 25% protein or rat food (Table 3). Apparently, feeding for 15 days on a low protein diet reduces nymphal reserves which would otherwise be mobilized for reproduction. Since the adult female does not elevate feeding in response to either low dietary protein or low nymphal reserves, the reproductive output is significantly reduced. When females fed low dietary protein as nymphs are switched to rat food as adults, consumption and reproductive intervals are almost identical to females fed rat food as both nymphs and adults. Therefore, it appears that nymphal diet is important in adult performance when the adult diet is of poor quality, but failure to accumulate nymphal reserves can be rectified by adult feeding.

An important question that remains unanswered is whether feeding last instar nymphs a low protein diet merely reduces stored reserves or alters other aspects of adult reproductive physiology which are manifested when adults feed on poor quality foods. Larval specific proteins reach high titers in the hemolymph of immature cockroaches prior to molting and disappear rapidly from adult hemolymph (Kunkel & Lawler, 1974). These proteins are presumably used in cuticular development, but they many also be used in growth and maturation of reproductive tissues. Reproduction could be impaired in adults which failed to accumulate this reserve from suboptimal diets. It is interesting that females raised on rat food as nymphs and switched to the 25% protein diet significantly out-performed adult females fed rat food (Tables 2, 3). The results suggest that diets that maximize reproduction may be different from diets that best support nymphal development.

These data argue for the importance of protein, carbohydrate, and nymphal nutritional history in regulating meal dynamics of *S. longipalpa*. Cohen *et al.* (1987) showed that *S. longipalpa* nymphs self-select specific protein and carbohydrate levels during each instar. Protein intake remains consistently low, whereas carbohydrate intake is initially high and decreases throughout the instar. It would be interesting to determine whether such self-selecting nymphs optimize procurement of nutrients for adult reproduction in addition to maximizing nymphal developmental rate. A similar self-selection experiment with adult females may yield valuable information on protein and carbohydrate demands during the reproductive cycle in this species. Because of the potential for inducing relatively large changes in food consumption in some insects by manipulating diet composition, and because of the increasing utility of toxic baits in cockroach population management (Schal & Hamilton, 1990), more research is needed in this area.

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Résumé

Influence des protéines contenues dans l'alimentation larvaire et imaginale sur la prise d'aliments et la reproduction de Supella longipalpa

La consommation et la reproduction de *S. longipalpa* ont été examinées lors de la consommation d'aliment standard pour rat et de régimes artificiels contenant 5, 25 et 65% de protéines. Les femelles élevées sur régime à 5% de protéines ne consomment pas plus et leur reproduction est significativement inférieure à celle de femelles élevées sur aliment standard ou à 25% de protéines; après la production de 3 oothèques, la reproduction de ces femelles se ralentit, leur consommation diminue et les oothèques deviennent plus petites que celles des femelles élevées sur un régime à 25% de protéines. Nous supposons que les premiers cycles reproductifs de ces femelles ont été assurés avec les réserves accumulées pendant la vie larvaire. Les femelles alimentées sur régime à 5% de protéines à la fois pendant le dernier stade larvaire et pendant la vie imaginale ont besoin de beaucoup plus de temps pour s'accoupler et pour produire des oothèques que les femelles alimentées sur régime à 5% pendant le dernier stade larvaire et transférées adultes sur un régime à 25% de protéines. Ainsi, les réserves larvaires sont une ressource importante améliorant la reproduction des adultes ayant un régime pauvre en protéines. Cependant, le passé alimentaire larvaire a peu d'effet sur la reproduction des adultes alimentés convenablement.

References

Absigold, J. D. & S. J. Simpson, 1987. The physiology of compensation by locusts for changes in dietary protein. J. exp. Biol. 129: 329–346.

Bell, W. J., 1969. Continuous and rhythmic reproductive cycle observed in *Periplaneta americana* (L). Biol. Bul., Woods Hole 137: 239–249.

Cochran, D. G., 1983. Food and water consumption during the reproductive cycle of female German cockroaches. Ent. exp. & appl. 34: 51–57.

Cochran, D. G., 1986. Biological parameters of reproduction in *Parcoblatta* cockroaches (Dictyoptera : Blattellidae). Ann. Entomol. Soc. Am. 79: 861–864.

Cochran, D. G., D. E. Mullins & K. J. Mullins, 1979. Cytological changes in the fat body of the American cockroach, *Periplaneta americana* in relation to dietary nitrogen levels. Ann. Entomol. Soc. Am. 72: 197–205.

Cohen, R. W., S. L. Heydon, G. P. Waldbauer & S. Friedman, 1987. Nutrient self-selection by the omnivorous cockroach *Supella longipalpa*. J. Insect Physiol. 33: 77–82.

Collier, G. & R. L. Squibb, 1967. Diet and activity. J. Comp. Physiol. Psychol. 64: 409–413.

Durbin, E. J. & D. G. Cochran, 1985. Food and water deprivation effects on reproduction in female *Blattella germanica*. Ent. exp. & appl. 37: 77–82.

Engelmann, F. & I. Rau, 1965. A correlation between feeding and the sexual cycle in *Leucophaea maderae* (Blattaria). J. Insect Physiol. 11: 53–64.

Gordon, H. T., 1959. Minimal nutritional requirements of the German roach, *Blattella germica* (L.). Ann. N.Y. Acad. Sci. 77: 290–351.

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.

House, H. L., 1965. Effects of low levels of the nutrient content of a food and of nutrient imbalance on the feeding and nutrition of a phytophagous larva, *Clerio euphorbiae* (Linnaeus) (Lepidoptera : Sphingidae). Can. Ent. 97: 62–68.

Keesey, R. E. & T. L. Powley, 1986. The regulation of body weight. Ann. Rev. Psychol. 37: 109–133.

Kunkel, J. G., 1966. Development and the availability of food in the German cockroach, *Blattella germanica* (L). J. Insect Physiol. 12: 227–235.

Kunkel, J. G. & D. M. Lawler, 1974. Larval-specific serum protein in the order Dictyoptera-I. Immunologic characterization in larval *Blattella germanica* and cross-reaction throughout the order. Comp. Biochem. Physiol. 47B: 697–710.

McGinnis, A. J. & R. Kasting, 1967. Dietary cellulose: effect on food consumption and growth of a grasshopper. Can. J. Zool. 45: 365–367.

Mueller, P., 1978. The effect of temporary food and water deprivation on the development of laboratory colonies of the German cockroach. Z. gest. Hyg. Gren. 24: 122–126.

Mullins, D. E. & D. G. Cochran, 1973. Tryptophan metabolite excretion by the American cockroach. Comp. Biochem. Physiol. 44B: 549–555.

Mullins, D. E. & D. G. Cochran, 1975. Nitrogen metabolism in the American cockroach-I. An examination of positive nitrogen balance with respect to uric acid stores. Comp. Biochem. Physiol. 50A: 489–500.

Partridge, L., A. Green & K. Fowler, 1987. Effects of egg-production and of exposure to males on female survival in *Drosophila melanogaster*. J. Insect Physiol. 33: 745–749.

Rollo, C. D., 1984. Resource allocation and time budgeting in adults of the cockroach, *Periplaneta americana*: the interaction of behaviour and metabolic reserves. Res. Popul. Ecol. 26: 150–187.

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

Schal, C. & R. H. Hamilton, 1990. Integrated suppression of synanthropic cockroaches. Annu. Rev. Entomol. 35: 521–551.

Simpson, S. J., L. Barton Browne & A. C. M. van Gerwen, 1989. The patterning of compensatory sugar feeding in the Australian sheep blowfly. Physiol. Ent. 14: 91–105.

Simpson, S. J. & J. D. Absigold, 1985. Compensation by locusts for changes in dietary nutrients: behavioral mechanisms. Physiol. Ent. 10: 443–452.

Smith, A. F., K. Yagi, S. S. Tobe & C. Schal, 1989. *In vitro* juvenile hormone biosynthesis in adult virgin and mated female brown-banded cockroaches *Supella longipalpa* J. Insect Physiol. 35: 781–785.