EFFECTS OF FOOD QUALITY ON THE AMERICAN COCKROACH

THE EFFECTS OF FOOD QUALITY
ON THE LIFE HISTORY TACTICS
OF THE
AMERICAN COCKROACH,
Periplaneta americana

By

LOVAYE JOCELYN KAJIURA, B.Sc.

A Thesis
Submitted to the School of Graduate Studies
in Partial Fulfilment of the Requirements
for the Degree
Master of Science

McMaster University

MASTER OF SCIENCE (1990) MCMASTER UNIVERSITY
(Biology) Hamilton,Ontario

TITLE: The effects of food quality on the life history tactics of the American cockroach, *Periplaneta americana*.

AUTHOR: Lovaye Jocelyn Kajiura, B.Sc.
(McMaster University)

SUPERVISOR: Dr. C.D. Rollo

NUMBER OF PAGES: xi, 94.

ABSTRACT

The American cockroach, *Periplaneta americana*, is an abundant and globally distributed species. Much of its success is attributed to its remarkable ability to alter rates and utilization efficiencies of behavioural and physiological processes so as to maintain growth and reproduction within nutritionally variable environments. This study utilized artificial diets diluted with cellulose to investigate the impact of food quality on the life history tactics of this species and the compensatory mechanisms involved in offsetting these impacts.

To investigate the impact of diet quality on the life history tactics of the American cockroach, seven dietary regimes were implemented. The control condition consisted of an unaltered 100% quality diet. The remaining six treatments were diluted with cellulose resulting in diet qualities of 50%, 25%, 10%, 5%, 2.5%, and 0%.

The parameters examined included mortality, longevity, instar number, instar durations, growth, maturation dates, maturation sizes, dry mass budgets, and reproduction. The dry mass budgets involved observations of growth rate, feeding rate, assimilation rate, respiration rate, assimilation efficiency, efficiency of conversion of ingested food into biomass, and efficiency of conversion of digested food into biomass. Reproductive studies entailed observations of oothecal production, oviposition intervals, inter-oviposition intervals, mass of oothecae, oothecal dimensions, egg number, oothecal cannibalism, and hatching dates.

Strongly canalized development was achieved by resilient compensatory responses indicative of altered physiological and behavioural features. Cockroaches developed and reproduced adequately even when nutrient concentration was reduced to 25% of the controls. The declines in various key parameters were considerably less than expected from the degree of dietary dilution. In addition, elevated consumption and enhanced conversion efficiencies strongly suggest that cockroaches normally function at submaximal levels.

The applied relevance of this research entails possible ramifications into the regulation and control of cockroaches. Furthermore, such knowledge enhances our

understanding of not only diverse lifestyles but also the degree of variability to which insects may modify life history features in response to resource supply.

ACKNOWLEDGEMENTS

I wish to sincerely thank Dr. C. David Rollo for his guidance and constructive comments. By employing Dr. Rollo's creative approach to investigating ecological topics, this research experience has proven to be truly rewarding and enlightening.

Immense gratitude is extended to Nancy Ternyik ("The Super Tech"), Denise Dibbs, Michelle Senchyna, Richard Koson and Line Mongeau for their much needed technical assistance.

Special thanks is expressed to Marisa Venier and John Hannah. Their unparalleled humour and genuine enthusiasm were always cheerfully accepted as sources of motivation and encouragement as was their friendship. Thanks for the inspiration to "just get it done" !

I also wish to thank "just a few other friends" whose help has been unlimited throughout the duration of this endeavour : Elisa Mason, Vandy Thomas, Tracey Hinds, Brigitte Girard, Julie Weavin, Ana Albernaz, France Rouleau, Irene Bajkai, Helena Taivainen, Andrew Buffery, Ross Shepherd, Roger Eamer, Rick Jobin, Terry

Geissler, Marvin Gundermann, Shomy Shafai, Alex Macfarlane, Ed Malkin, Jim Mackrory, Charlotte Kobelka, Patrick Morash, Gary LeGresley, Joe Toth, Beverly Donick, Isabel Casey, Michelle Antonik, Warren DeForest, Ruth Orwig, Michael Floroff, Bill Henderson, George Morash, Carolyn Piva, Karen Proctor, Karen Veldboom, Dr. Jurek Kolasa, Dr. Douglas Davies, Dr. Tom Collier, Mrs. Pat Hayward, Sheela Veerabahdra, Janice Davies, Mike Pollard, Mr. Rob Gilles, Mr. Ray Procwat, George Timmins, Valerie Bryce, Analia, Paul and Karen, Cindy, Deb, Carol, Gabe, Dorothy, Nancy, Paula, Gerry, Kevin, George, Monica, Janet, and Joanne Field.

Lastly, I wish to thank my Mom, Dad, brother Jason, Grandma, and my dog Punkin for their avid and enduring support throughout the entire progress of this project.

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INTRODUCTION

Cockroaches are one of the most successful groups of organisms as reflected by their global distribution and local abundance. A dilemma commonly resolved by cockroaches entails their survival through periods of low food abundance and quality. In the laboratory, by the employment of artificial diets, we may qualitatively simulate the nutritionally variable conditions likely to be encountered by cockroaches.

Few studies have focused on the nutritional versatility of the American cockroach, Periplaneta americana. This may be attributed to its longer developmental period, as previous investigators have regarded the German cockroach, Blattella germanica, as a more convenient subject with its relatively short generation time. Thus current knowledge has been mainly extrapolated from studies of the German cockroach (Melampy and Maynard 1937; Seamans and Woodruff 1939; Gordon 1959; Kunkel 1966; van Herrewege 1974; Durbin and Cochran 1985; Hamilton and Schal 1988). Consequently, an assessment of the degree and variability to which Periplaneta americana can alter its physiological rates and behavioural processes in response to reduced diet quality would be highly informative.

Most studies have employed the optimality theory framework of maximization ,as reviewed by Gunderman (1989). The optimization theory assumes that cockroaches should exhibit behaviours and processes which are maximized to constant levels (Pyke 1984). Observed behaviours which occur suboptimally often result in the invalidation of the optimization theory.

An alternative perspective to the aforementioned theory entails that organisms are "safely tuned" to the levels of environmental resource supply (Case 1978; Calow and Townsend 1981; Rollo 1986; Shibata and Rollo 1988). An individual's rates and processes are thus geared to its surrounding ecological conditions. Rollo (1986) proposed that feeding is not maximized but adjusted to growth rate. Furthermore growth rate is not maximized but compromised by numerous internal and external constraints. Being intermittent feeders and scavengers, it may be more advantageous for cockroaches to possess rates and efficiencies which are adapted to average or poor ecological conditions rather than those tighly set to rare circumstances of abundant food supply. If early instar nymphs adjusted their physiological rates and behavioural processes with respect to food quality, this may generate divergence in their observed life history tactics. Hence this investigation tested the validity of each of the above alternative views.

Waddington (1966) proposed two types of developmental patterns: 1) canalized development as reflected by highly homeostatic growth trajectories with deviations resisted and corrected, and 2) plastic development as displayed by divergent pathways which not only may be internally canalized but also may lead in different directions. The relationship between homeostasis and plasticity is complex. Homeostasis may be achieved by the plasticity or the increased rates of various processes.

The present study addressed the effects of diet quality on the life history variables of the American cockroach. It was necessary to examine measurements of mortality, growth, maturation dates, maturation sizes, dry mass budgets, and reproduction. Differences between cockroaches reared on varying qualities of diet may have resulted from phenotypic plasticity or genotypic variation. The relative significance of the later factor was not investigated. However, the role of phenotypic flexibility with regards to variation was closely examined.

Phenotypic plasticity denotes any response which results from different environmental conditions which allows an organism to adopt different states or growth trajectories (Greene 1989). Compensatory responses allow organisms to achieve or maintain the homeostatic levels of their performance via alterations in their physiological and behavioural activities. Compensatory responses incur related costs and benefits. Hence research is essential to investigate not only the ability or inability of individuals to compensate for environmental perturbations but also the ultimate consequences of their actions with regards to fitness.

MATERIALS AND METHODS

I. General Rearing Conditions :

Seventy first instar nymphs, of similar live mass ($\sim$ 3.1 milligrams), were collected from laboratory colonies of Periplaneta americana. Colonies were maintained in glass terrariums at 25 °C with food (ground Purina Dog Chow® and granulated sucrose) and water provided ad libitum. All pre-weighed nymphs were reared individually in transparent plastic boxes, 10 cm X 10 cm X 7.5 cm deep (Fig. 1). Fine nylon mesh, secured over each container's opening, ensured ventilation and prevented escape. As the nymphs matured, the nylon mesh was replaced with a sturdy plastic lid covered with 2 mm aluminum mesh screen. A moist cotton pad was arranged on a platform over each container's lid to maintain high humidity.

Water was accessible via either a small test tube supported by a modified Tygon® tubing clamp or an 8 mm hole in the lid of a 4 cm diameter petri dish, which was bound around its circumference with Parafilm®. A tissue wick was inserted through each water vessel's opening. This feature provided a functional water reservoir and prevented cockroaches from entering and drowning. Water was supplied ad libitum.

All cockroaches were maintained in a photoperiod of light:dark 12:12 h at 28 ± 2 °C. The photoregime entrained the circadian rhythm of nocturnal activity and diurnal homing to dark shelters (cannisters, 5 cm long and 2.5 cm in diameter) (Sutherland, 1982; Rollo, 1984).

II. Preparation of Artificial Diets :

To investigate the life histories of cockroaches on diets of varying quality, first instar *Periplaneta americana* were reared on a series of artificial diets. The utilization of artificial diets was advantageous as it allowed precise control of the nutrient composition for each treatment. The high quality 100% diet was Shibata and Rollo's (1988) modification of the nutritionally complete caterpillar diet described by Horie and Watanabe (1983).

All ingredients listed under Mixture A (Appendix A) were combined thoroughly with 73.2 mL of distilled water. Agar was then dissolved into 208.5 mL of distilled water, which had been heated to 38 °C. This preparation (Mixture B) was subsequently blended with Mixture A and allowed to cool to 16 °C. The remaining heat-labile ingredients (Mixture C: ascorbic acid, vitamin B, and the fungicide Tegosept®) were then mixed into 18.3 mL of distilled water, and added to the above ingredients. The entire mixture was thoroughly mixed to ensure even consistency. The final mixture was then poured into pyrex crystallization dishes and allowed to congeal at the 2 °C storage temperature.

The other six treatments consisted of diets with the same nutrient balance and water content as the 100% diet but with the nutrient quality reduced to either 50%, 25%, 10%, 5%, 2.5%, or 0% of the 100% diet's composition by dilution with cellulose. Cellulose powder (Alphacel® non-nutritive bulk), which is neither a phagostimulant nor a feeding deterrent, served as the inert filler. Vitamin B was present in a relatively small quantity in the 100% diet, and its proportion was unaltered for the five lower quality diets. The 0% quality diet was composed entirely of agar and water.

Standard sized food pellets were produced by pressing a modified 10 cc syringe (Fig. 2) into the solidified diet and cutting 1 cm segments from the extruded core. Each food pellet was much larger than an individual cockroach could consume in twenty-four hours. All partially consumed pellets were collected and replaced with fresh food pellets daily.

III. Variables Investigated

Growth and Maturation, Experimental Protocol:

To determine the effects of diet quality on life history tactics, seventy newly emerged nymphs were randomly and equally divided among seven treatments: 100%, 50%, 25%, 10%, 5%, 2.5%, and 0% quality diets. Unfortunately, difficulties in sexing these insects led to unequal sex ratios among treatments. This problem will be discussed where appropriate in the results. All nymphs were examined three times daily to ensure that moulting or mortality was detected. The wet mass of each cockroach was measured at nine day intervals, at which time the rearing containers were cleaned. Continuous observations were maintained for a 515 d period.

Individual nymphs (first to third instar) were handled using an aspirator. Each nymph was transferred to a pre-weighed aluminum foil cup (Fig. 3), which possessed a closure that was easily manipulated to contain or release the cockroach without injury. The nymph's live mass was then measured to the nearest milligram by an electrobalance.

For larger cockroaches (fourth instar to adult), an inverted plastic petri dish bottom was first placed over the cockroach. A paper card was then inserted under the enclosed insect. The petri dish top was placed beneath the petri dish bottom while the card was removed (Fig. 4). The contained cockroach was then weighed and returned to its rearing container.

These techniques reduced handling and the possibility of accidentally excising an insect's antennae or injuring other appendages. Furthermore, these methods avoided the employment of an anaesthetic or cool temperatures to facilitate handling. Handling, injury, or anaesthetics are all likely to influence growth and maturation, particularly if employed at regular intervals.

Growth and Maturation, Analytical Methods:

For the period from 1st instar until the adult ecdysis, means (± standard errors) were calculated from the daily records in each treatment for the number of instars, instar durations, maturation dates, maturation sizes, and mortality rates. Female and male growth data were analysed separately for all variables except instar durations and mortality rates. To estimate growth rate, wet mass (Day 0 to Day 198) was transformed to logarithms (base e) and plotted against time. This yielded a straight line for each animal (Figs. 5 and 6). The slope of this line (first order regression) provided an accurate measure of the exponential rate of growth. Mean values were then determined for each treatment. Data obtained for instar duration, growth rates, maturation dates and maturation sizes were analysed by one-way analysis of variance.

Dry Mass Budgets :

Dry mass budgets for each nymph were performed over 36 consecutive days, beginning on Day 153 and terminating on Day 189 of the experiment. Ten pre-weighed food pellets of each diet quality were oven-dried at 60 °C to constant mass then re-weighed to obtain their water content. These hydration values were subsequently employed to estimate the initial dry mass of food pellets presented to the cockroaches from their known wet mass. All partially consumed food pellets were collected daily and oven-dried to constant mass at

60 °C. Consumption was thereby estimated by subtracting the actual oven-dried mass of each partially consumed pellet from its estimated original dry mass. Thus, the dry mass of food consumed was calculated by the following equation:

$$\text{Dry Mass of Food Consumed (mg)} = \text{Wet Mass of Original Food Pellet (mg)} - \text{Estimated Water Content of this pellet} - \text{Actual Dry Mass of Food Pellet Remaining after feeding (mg)}$$

Faeces were also collected and oven-dried to constant mass at 60 °C.

Growth was determined by the live mass of each nymph, measured at the beginning and end of the mass budget experiment. A sample of ten similarly sized cockroaches were killed by freezing and then oven-dried to constant mass at 60 °C to obtain a wet mass to dry mass conversion factor. The dry mass of each investigated insect was then determined using this conversion factor so that growth could also be represented in dry mass units.

Individual mass budgets were ascertained through the compilation of the following variables:

C = total dry mass of food consumed, (mg/36d)

F = total dry mass of faeces deposited, (mg/36d)

G = total dry mass gained by each nymph, (mg/36d)

A = total dry mass of food assimilated = C-F, (mg/36d)

R = total dry mass respired = C-(G + F), (mg/36d)

Food utilization and conversion efficiencies were calculated for each insect :

1. Assimilation Efficiency (%) = AE = (C - F)/C X 100%
2. Efficiency of Conversion of the Ingested Food into Growth (%) = ECI = G/C X 100 % = Gross Production Efficiency (GPE) of some studies
3. Efficiency of Conversion of the Digested (Assimilated) Food into Growth (%) = ECD = G/(C - F) X 100% = Net Production Efficiency (NPE) of some studies

<u>Mass Budget</u>, <u>Analytical Methods</u>:

The mass budget was performed early in the experiment before males and females had diverged in size. Consequently, the data for all sexes were pooled. Overall means (± standard errors) were calculated for each investigated variable. One-way analyses of variance (ANOVA) were performed to compare treatments using MINITAB , Version 7. Differences were further differentiated by Newman-Keuls multiple range tests.

Reproduction, Experimental Protocol:

Upon maturation, each adult _Periplaneta americana_ female was tranferred to a slightly larger ventilated breeding container (Fig. 7). Healthy adult _Periplaneta americana_ males were obtained from stock colonies and introduced into the female occupied containers.

After each pair had mated, observations were tabulated daily to assess the status of each female's reproductive cycle according to the critera: 1) no ootheca visible, 2) carrying an ootheca externally, or 3) ootheca deposited. Each female was observed for at least 13 reproductive cycles. A record of oothecal cannibalism was maintained. Each deposited ootheca was collected, weighed, and measured (length X width X breadth in mm). The number of eggs per ootheca was determined by examination of their demarcation on the ootheca's exterior. Collected oothecae were maintained under the same conditions as the experimental cockroaches.

Reproduction, Analytical Methods:

Means (± standard errors) for individual females and overall mean values for all females of each treatment were calculated for: 1) the number of days spent carrying oothecae, 2) the number of days between the deposition of oothecae, 3) the mass of oothecae, 4) the dimensions of oothecae, 5) the number of eggs in oothecae, and 6) the incubation period of oothecae. The proportions of oothecae cannibalized were computed for each individual, as were overall values for all members of each treatment. One-way analysis of variance (ANOVA) and Newman-Keuls multiple range tests were applied to variables for which sufficient data were obtained.

RESULTS

I. Mortality

Nymphs reared on diets with only 10%, 5%, and 2.5% of the 100% diet's composition suffered much earlier and higher mortality in comparison to those cockroaches nurtured on the high (100%), medium (50%), and low (25%) quality diets (Table 1). All cockroaches on the 10%, 5%, 2.5%, and 0% treatments failed to survive beyond the third instar (Tables 1 and 2). Surprisingly, nymphs on the 0% diet, which were fed exclusively indigestible agar, survived on average for 26.8 days and to the second instar of development.

Mortality was essentially zero for the 100%, 50%, and 25% diets (Table 1). Ninety-seven percent of the cockroaches on the 100%, 50% and 25% treatments matured into reproductively competent adults. The only death on these three treatments occurred accidentally early in the experiment and was not attributed to the effects of the experimental diet. The cockroach had fouled its body with the petroleum jelly barrier of the holding arena, which was used to prevent the escape of cockroaches during weighing. The petroleum jelly interfered with moulting. The cockroach failed to open along its mid-dorsal line, and consequently succumbed before escaping from its exuvium.

II. Instar Durations and Number of Nymphal Moults

The mean instar durations of the high, medium, and low quality diets were not significantly different as determined by a one-way analysis of variance,($p > 0.05$). Despite this, several general trends were observed as documented in Table 2. Firstly, nymphal instars gradually increased in duration with each succeeding moult. Furthermore, as diet quality was progressively reduced, the corresponding mean instar durations lengthened slightly. In addition, the standard error values show that much greater variation in instar durations occurred for cockroaches reared on the 50% and 25% quality diets compared to those fed the 100% diet.

The number of moults required to attain maturation ranged from 10 to 14. The overall mean values did not differ greatly between treatments (Table 3), but cockroaches reared on diluted diets generally required more moults to reach adulthood than those reared on the high quality diet.

II. Growth Rates

The measurements of mean wet mass for cockroaches belonging to the 100%, 50%, 25% treatments were obtained at nine day intervals. Despite enormous differences in diet quality, the growth curves of the three treatments were unexpectedly similar (Figs. 8, 9, and 10). Cockroaches reared on the high, medium, and low quality diets showed slight trends to grow at high, moderate, and low rates, respectively. However, the standard errors were large and increased with time (Appendix B, C, and D) so statistical significance could not be resolved with these sample sizes based on lifetime performance.

It should be noted that due to time constraints and the labour intensive demands of the experimental procedures performed, it was necessary in terms of practicality to limit each treatment's sample size to relatively small numbers. Hence it was anticipated that the variation within treatments may have been in some cases too high to permit the detection of significant differences due to limited statistical resolution.

Initially, the overall mean growth rates for each of the treatments were determined for the period from Day 0 to Day 81. A one-way ANOVA of these data obtained statistical significance ($p < 0.05$, Table 4). The 100% treatment's cockroaches possessed higher growth rates (0.0332 ± 0.0011 mg/d) whereas the 50% and 25% treatments had intermediate (0.0276 ± 0.0013 mg/d) and lower (0.0223 ± 0.0016 mg/d) growth rates respectively. When the same analysis was performed with data for the period Day 0 to Day 198, statistically significant differences between the three treatments were not observed (Table 5, 100%= 0.0218 ± 0.0008 mg/d, 50%= 0.0218 ± 0.0016 mg/d, 25%= 0.0207 ± 0.0011 mg/d).

When the growth rates of females and males were considered separately, females possessed slightly higher growth rates in comparison to the males within the same treatment. Unfortunately, general trends between treatments were less distinct due to the relatively small sample sizes of the groups and the limited statistical power of the analysis.

IV. Maturation Dates and Maturation Sizes

Maturation dates for the three investigated treatments were not significantly different (ANOVA $p > 0.05$, Table 6). Nonetheless, cockroaches tended to mature later when raised on diets diluted with cellulose. On average, members of the 100% treatment generally matured earlier (269.7 ± 9.4 days) whilst those of the 50% and 25% treatments matured successively later (304.3 ± 19.9 d and 315.7 ± 23.5 d respectively).

Significant differences in maturation sizes were not revealed when the data from the three experimental treatments were analysed by a one-way analysis of variance (Table 6). Despite this, examination of the overall mean maturation sizes revealed several basic trends. The 100% treatment cockroaches were generally smaller than the 50% treatment cockroaches (100% = 1000.6 ± 55.7 mg, 50% = 1068.0 ± 66.0 mg). The 25% treatment cockroaches matured not only at the slowest rate but also to the smallest size (952.8 ± 61.6 mg).

When the maturation dates and sizes of females and males were considered separately, basic developmental trends were again exhibited (Table 6). In general, females matured slightly earlier in comparison to the males of the same treatment. The 100%, 50%, and 25% females also achieved maturation sizes which were 1.2, 1.6, 1.3 times greater than the corresponding treatment's males. With both sexes, the time required to reach maturation increased with decreased diet quality (females: 100%= 243.3 ± 4.4 d, 50%= 303.3 ± 24.7 d, 25%= 314.4 ± 45.8 d, males: 100%= 290.8 ± 7.5 d, 50%= 308.5 ± 25.5 d, 25%= 317.0 ± 19.8 d). Unfortunately, distinct trends were less obvious with respect to maturation sizes.

V. Dry Mass Budgets

To investigate the behavioural adaptations and compensatory feeding responses of cockroaches reared on foods of varying nutrient composition, it was essential to examine the effects of food quality on the dry mass budgets for each treatment.

When fed diluted diets , *Periplaneta americana* nymphs generally attempted to maintain their intake of nutrients by consuming larger quantities of food (Table 7). However, those nymphs given diets with only 10%, 5%, 2.5%, and 0% of the 100% treatment's nutrient quality failed to compensate and offset the deleterious effects of the dietary dilution. Consequently, their growth was severely impaired and hence resulted in rapid mortality.

Growth was not significantly different between cockroaches of the 100%, 50%, and 25% quality treatments. The dry mass gain was only slightly impaired as nymphs reared on the 50% nutrient diet grew at 79% of the high quality treatment's rate. Similarly, growth did not significantly decline for nymphs reared on the 25% experimental diet. These insects grew at 78% of the controls.

A one-way analysis of variance did not indicate any significant differences in the amounts consumed by the cockroaches of the high, medium, and low quality treatments (100%= 295.82 ± 40.74 mg, 50%= 603.39 ± 187.16 mg, 25%= 627.03 ± 104.58 mg). A major problem was that the variation in the lower quality treatments was markedly greater than in the 100% treatment, evidently a treatment-induced effect. Bartlett's test for the homogeneity of variance showed the assumption of uniform variance to be strongly invalidated. Thus, an analysis of variance showed no significance, even though means differed and standard error bars did not overlap. This failure to obtain significance may be attributed to canalization of development. Given the magnitude of the treatments, the insignificance of such results is reflective of the formidable compensatory ability of the American cockroach.

When the diet was diluted to only 50% of the normal 100% diet's nutrient composition, nymphs ingested approximately 2.04 times as much food as the cockroaches of the 100% "control" treatment. Thus, the amount of 50% diet consumed by the nymphs was slightly more than expected based on the degree of dietary dilution, (actual = 603.39 mg = 204% increase in consumption, expected = 591.64 mg = 200% increase in consumption). Hence, the cockroaches of the 50% treatment clearly attempted to compensate for reduced food quality by appropriate increases in feeding.

Nymphs reared on diets which had been diluted to 25% of the 100% quality concentration, further increased their food consumption to nearly 2.12 times the 100%'s level. However, the amount of 25% diet consumed was much less than expected (actual = 627.03 mg, expected = 1183.28 mg),indicating that feeding could not be increased anymore.

The amount of faeces deposited between the three treatments were significantly different (ANOVA $p < 0.01$). Furthermore, Newman-Keuls multiple range testing determined that the 100% treatment's faecal production significantly differed from that of the 50% and 25% treatments. Whereas, the amount of faeces produced by the cockroaches of the 50% and 25% treatments did not differ significantly.

Analysis of variance did not reveal significant differences for the measurements of assimilation rates and respiration rates between the three treatments. Nevertheless,the results indicated a general progression of decreasing levels, 50%, 100%, and 25% respectively. (assimilation rates: 50% = 7.27 ± 2.18 mg/d, 100% = 5.98 ± 0.72 mg/d, 25% = 4.29 ± 0.55 mg/d, respiration rates: 50% = 6.36 ± 1.86 mg/d, 100% = 4.83 ± 0.50 mg/d, 25% = 3.40 ± 0.38 mg/d).

Assimilation efficiency declined with increased dietary dilution. Significant differences between all three treatments were resolved by Newman-Keuls multiple range analysis. The assimilation efficiences of the 50% and 25% treatments , when expressed as a percentage of the controls, were actually higher than their expected values (50% treatment: actual = 44.99%, expected =

37.18%, 25% treatment: actual = 26.98%, expected = 18.59%).

The efficiency of conversion of ingested food to body mass (ECI) declined with increased amounts of dietary diluent. The ECI values for the 25% and 50% treatments did not differ significantly, whereas the 100% treatment did significantly differ from these values as determined by Newman-Keuls multiple range testing. The 50% ECI value was much lower than expected based on the degree of dietary dilution , (actual = 4.41%, expected = 6.52%). Conversely, the 25% ECI exceeded its expected value (actual = 4.01%, expected = 3.32%).

The efficiency of conversion of digested food into body mass (ECD) did not differ significantly between treatments. Moreover, the ECD values for the 50% and 25% treatments were much higher than expected (50% treatment: actual = 10.04%, expected = 8.89%, 25% treatment: actual = 17.34%, expected = 4.44%).

VI. Reproduction

The mean number of oothecae produced per female decreased significantly with increased dietary dilution ($p < 0.01$, Table 8). Newman-Keuls testing identified that the mean number of oothecae produced by the 100% females was significantly greater than the other treatments ($p < 0.05$, 100% = 40, 50% = 25 and 25% = 19 oothecae). The oviposition intervals and inter-oviposition intervals, as characterized by the number of days the females spent carrying oothecae and the number of days between the oothecal deposition respectively, increased with reduced dietary concentration. Statistical differences were not resolved for values of the former reproductive index while those of the later differed significantly between treatments. In addition, Newman-Keuls testing revealed that the mean inter-oviposition interval for the 25% treatment was significantly greater compared to the other treatments, ($p < 0.05$,actual: 25% = 6.53d, 50% = 4.37d, and 100% = 3.78d ,expected: 25% = 15.12d, 50% = 7.56d, and 100% = 3.78d). Thus compensation is also evident in reproduction.

Oothecal mass generally increased with decreased nutrient quality, however, oothecal dimensions and egg numbers remained constant between the three experimental treatments. The proportion of cannibalized oothecae was relatively low for the high and medium quality diets, 6.3% and 6.6% respectively, and completely absent from the 25% treatment. Due to time constraints, hatching dates were recorded for only a small number of oothecae (100% n=6, 50% n=7 and 25% n=1) so statistical differences could not be resolved with such small sample sizes. The oothecae deposited by females reared on the medium and lower quality diets generally required shorter periods of time to hatch in comparison to those of the 100% treatment.

DISCUSSION

The present study investigated the effects of food quality on the life history tactics of the American cockroach, *Periplaneta americana*. The discussion is divided into five sections, each dealing with the treatments (100%, 50%, 25%, 10%, 5%, 2.5%, and 0% diets) and their variables (mortality, instar durations and instar numbers, maturation dates and maturation sizes, dry mass budgets, and reproduction). These sections relate and compare the results of this investigation to those of the cited literature.

I. Mortality

Periplaneta americana survived poorly on diluted artificial diets that contained more than seventy-five percent cellulose (Table 1). Diets reduced to less than 25% quality were severely inadequate and sustained cockroaches for only short periods (mean longevities: 10% = 66.1 d, 5% = 55.0 d, 2.5% = 32.4 d, 0% = 26.8 d).

Under conditions of poor food quality, cockroaches often utilize stored nutrients from their haemolymph and fat body reserves, as noted by Mullins and Cochran (1975b), Calow and Townsend (1981), and

Downer (1981). Early instar nymphs have relatively small storage reserves and high metabolic rates (Rollo 1986). Thus, the rapid demise of the 10%, 5%, 2.5% and 0% treatments was probably attributable to the depletion of storage reserves and the inability of reducing metabolisms. Consequently, these cockroaches failed to circumvent the impact of the ensuing dietary deficiences (Gier 1947; Slansky 1982a,b; Rollo 1986).

In natural settings, these cockroaches may have obtained adequate nutrition via cannibalism however this was avoided by individual rearing. Thus food quality can have an enormous effect on mortality. It is startling that nymphs reared on these low quality diets even survived for such lengths of time. Gordon (1968) revealed that the maternal carryover of reserves may strongly influence the growth and survival of offspring. Since all mothers had been reared on nutritionally complete diets (granulated sucrose, ground Purina Dog Chow®, and water), possibly the carryover of maternal reserves had initally helped the nymphs survive on the low quality diets.

II. Instar Durations and Instar Numbers

When reared on low quality diets, nymphal development was prolonged by either increased instar numbers or durations (Tables 2 and 3), as was previously observed by Seamans and Woodruff (1939), Griffiths and Tauber (1942a,b), Robertson (1960), Peters and Barbosa (1977), Scriber and Slansky (1981), and Pearson and Knisley (1985).

Cockroach development was discontinuous. Nymphs passed through 10 to 14 instars, during which exoskeletons were shed and replaced by larger ones. These results agree well with those of earlier studies which found that the number of nymphal moults of Periplaneta americana varied from 6 to 14 (Nigam 1933; Gould and Deay 1938; Griffiths and Tauber 1942b; Gier 1947; Willis et al. 1958). Although deficient diets generally delayed moulting (Table 2), Kunkel (1966) demonstrated that only a minimal period of adequate food availability was required for its initiation. Cockroaches are intermittent feeders and scavengers which forage for unpredictable supplies of food. Hence, the ability to postpone growth until food of adequate quality becomes available is a highly adaptive strategy.

III. Maturation Dates and Maturation Sizes

Statistical analysis revealed that no

significant differences existed between maturation dates and maturation sizes for the examined treatments. These findings were partially due to low sample sizes and high variation since distinct trends were identified. However, the compensatory ability of the species largely cancelled out these effects thus the results strongly indicate a remarkable canalization of development. These comparisons between treatments were somewhat confounded by variable sex ratios (e.g. the overall mean maturation size of the 50% treatment may have been biased by the greater number of females). Females generally achieved masses 1.2 to 1.6 times greater than males, which is indicative of their reproductive role as egg producers. A more detailed analysis was therefore carried out with sexes differentiated.

With varying nutritional conditions, there exists related maturation sizes which confer to a particular species best fitness. Fitness is defined as an organism's relative genetic contribution to succeeding generations. Cockroaches should therefore display strategies which ensure a growth, maturation and reproductive schedule that maximizes their contribution to subsequent generations. The size dependency of life history variables, such as developmental time and fecundity, act as selective forces which strongly influence the attained maturation size.

Large maturation size is generally associated with greater fecundity. To achieve larger body sizes, cockroaches must either grow for prolonged periods or grow more rapidly. Calow and Townsend (1981) revealed that the more quickly an organism develops the sooner it becomes reproductively competent and begins generating offspring. However, faster growth rates incur greater metabolic costs. Longer maturation time is associated with reduced fitness, if fitness partly depends on the time available for reproduction between maturation and death.

Conversely, the potential costs related to smaller maturation size include decreased abilities to disperse and mate successfully, reduced longevity and fecundity, as well as, a greater susceptibility to adverse environmental conditions, competition, and predation. Thus each cockroach must evaluate the potential costs and benefits of reduced developmental time associated with smaller maturation size, and increased fecundity acquired from prolonged development and larger maturation size (Cole 1954; Calow 1977b;

Gould 1982; Slansky 1982a,b; Rollo and Shibata unpublished).

Development was highly canalized. Variation in the observed parameters with differing diet quality was slight as cockroach morphology was very similar between treatments. Differences in mass were mainly attributed to storage and sex effects. Periplaneta americana exhibited a well marked ability to regulate maturation size by extending their duration of development. This situation occurred, provided that the artificial diet was not too deficient. Within such a dietary regime, as displayed by the 25% treatment group, development was further extended, however these animals achieved slightly smaller sizes compared to the other treatments. Despite this, maturation sizes were probably much larger than those that would have been attained had the 25% cockroaches not prolonged their development.

When reared on the low and medium quality diets, cockroaches chose to prolong development rather than produce a much smaller adult (Roth and Willis 1952; Tanaka 1981). In this way, cockroaches attempted to scale their sizes in response to environmental constraints and opportunities and thereby successfully matured into reproductively competent individuals.

A species' size dependent relationship with predators may strongly influence its maturation size (Gadgil and Bossert 1970; Cohen 1976; Schaffer 1974; Enders 1975; Calow 1984; Calver et al. 1989). Early instar nymphs are particularly vulnerable to predation. Hence the rapid development, characteristic of the 100% treatment group, would be highly advantageous as the time spent in the vulnerable small stages of their nympal periods would be sharply reduced.

In contrast, the prolonged development of the 25% and 50% treatments would result in increased exposure to predators and other mortality agents. Due to reduced food quality, the 25% and 50% treatment cockroaches devoted much of their time to compensatory feeding. These cockroaches ate not only nocturnally during scotophase but also during the normally inactive diurnal photophase period. In natural settings, this type of feeding behaviour would incur an enormous risk due to the increased threat of predation. For example, cockroaches released at midday in Barbados were immediately eaten by lizards (Rollo personal communication). Smaller lizards had trouble catching adult cockroaches whereas large lizards had no difficulty.

If predation is higher for smaller individuals, large body sizes may be favoured. Conversely, smaller sizes may be selected if predation is higher for larger individuals. Calver et al.(1989) revealed that the former situation is indicative of cockroaches, as their predators generally displayed declining capture efficiencies with increasing prey size.

Slansky and Scriber (1985) proposed that selection may favour larger maturation sizes, as they allow for greater accumulation of storage reserves. Increased reserves permit longer survival during periods of low or poor food availability. Perhaps for these reasons, the 25% and 50% treatment groups prolonged growth to reach larger maturation sizes.

It was anticipated that cockroaches reared on the 100% quality diet would notably reduce developmental time whilst still maintaining or further increasing maturation size. The 100% treatment group which matured earlier, surprisingly did so at slightly smaller masses than those that matured later to greater masses on the

50% quality diet (Table 6). Shibata and Rollo (1988) similarly observed that terrestrial slugs, Deroceras laeve, reared on high quality diets, matured earlier at smaller masses than those fed low quality diets which matured later at heavier masses.

In general, well-nourished cockroaches survived for longer periods than malnourished ones (Table 1). It is thus conceivable that within their lifetime, 100% treatment cockroaches would produce more overlapping generations than both the 25% and 50% treatments. According to Rollo and Shibata (unpublished), fitness could then be theoretically maximized by the population's intrinsic rate of increase rather than by greater individual fecundity associated with larger size. This would account for the observed trend of earlier reproduction at smaller body sizes of the high quality diet cockroaches. The potential benefits gained from the compounded contribution of parental and offspring reproduction would counteract those obtained from increased individual fecundity obtained by larger size. Earlier reproduction at slightly smaller maturation size would then be considered highly adaptive for the success of the species.

In nature, cockroaches frequently encounter conditions of low food quality and quantity. These environmental settings may select for rapid development to smaller sizes. Support for this assertion comes from the unexpected finding that some cockroaches continued to increase in mass even after adult ecdysis. Body mass may have increased, however, morphologically the animals remained fixed in size by the adult moult. Morphology is probably more crucial to predator risk. Mass increases may have been related to fecundity or storage reserves.

IV. Dry Mass Budgets

Under conditions of poor food quality, compensation may be achieved via three possible strategies. Insects may compensate for reduced food quality by: 1) greater consumption of the same food, 2) enhanced utilization and conversion efficiency of food, or 3) selection of alternative sources of nourishment (McNair 1982; Simpson and Abisgold 1985; Geissler and Rollo 1987). Although statistically significant differences between the treatments were only established for a few of the examined variables, very obvious trends were evident for most factors (Table 7).

Consumption

In this study, food was provided ad libitum which subsequently allowed cockroaches to compensate for reduced diet quality by increased food consumption(Table 7). Previous studies have similarly demonstrated that insects consume greater amounts of diluted diets (Dadd 1960; McGinnis and Kasting 1967; House 1965; Gordon 1972; Slansky and Feeny 1977; Bignell 1978; Slansky and Scriber 1985; Abisgold and Simpson 1987; Timmins et al. 1988; Slansky and Wheeler 1989). Cockroaches reared on the 50% and 25% quality diets compensated very effectively, although not completely, for the imposed reduction in food quality.

Despite the fact that low quality treatments consumed more than double the food of those fed 100% diets, and the standard errors among treatments did not overlap, ANOVA did not detect significant differences at the 0.5% level. A Bartlett's test demonstrated that the assumption of homogeneity of variance was not upheld. The lower quality treatments showed remarkably higher variation and this is undoubtedly one reason why an ANOVA failed.

The increased consumption of diluted diets may have been due to elevated rates of crop emptying (Bernays and Simpson 1982). Treherne (1957) observed that the rate of crop emptying increased with decreased osmotic pressure of the ingested food. This finding would account for the consumption of greater quantities of diluted diets. With the 25% and 50% quality diets, concentrations of utilizable nutrients were much lower thus resulting in increased crop emptying which subsequently permitted increased compensatory feeding. Conversely, the high nutrient concentration of the 100% quality diet resulted in reduced rates of crop emptying. The precise physiological basis of these mechanisms remains obscure. It is unclear whether the osmotic pressure of the haemolymph or crop contents determines the rate of crop emptying. However, Gordon (1968) suggested that pharyngeal osmoreceptors control the rate of valve opening between the insect's crop and gut.

Total compensation was not realized possibly due to the increased metabolic demands associated with increased feeding. These costs include not only the additional energy required for ingestion, utilization, and excretion of large quantities of food, but also the dilution of digestive enzymes and the reduction of assimilation efficiencies linked with increased feeding rates (Calow 1977a,b; Scriber and Slansky 1981; Slansky 1982a,b).

The benefits obtained through increased compensatory feeding must have exceeded the costs as increased consumption enabled the 50% and 25% treatments to attain dry mass gains which were 79% and 78% of the controls, respectively. The slightly reduced growth of the 25% treatment group may have resulted from increased food intake not being large enough to compensate for decreased food quality. Nonetheless, cockroaches displayed a remarkable ability to compensate for enormous differences in food quality.

The controls consumed less than the 50% and 25% treatments, which suggests that cockroaches normally function submaximally. Hence, the observed compensatory feeding negates the optimum foraging theory which assumes that intake rates occur maximally (Krebs et al. 1981; Slansky 1982a; Pyke 1984). The 0% treatment group consumed non-nutritious indigestible agar. This provided further evidence against the optimal foraging theory, which predicts that non-nutritious diets should be avoided. As previously noted by Geissler and Rollo (1987), malnourished cockroaches were more apt to sample the novel agar food pellets.

Faeces

Dietary dilution had a significant effect on faecal production. Faecal deposits increased with decreased food quality, with the 50% and 25% treatments producing four and five times more than the controls,respectively. Clearly if faecal output was significantly different, feeding must have been as well even if the variation in consumption was too high to detect statistically significant differences.

Growth

Although individual rearing is unnatural, it was necessary in order to control against the effects of cannibalization. As revealed by Wharton et al. (1968), faster growth may be achieved by group rearing. Although an analysis of variance revealed that significant differences between growth rates diminished with time (Day 0 to 198), decreased food quality initially (Day 0 to 81) reduced growth (Tables 4, 5, and 7). Due to compensatory responses, the observed growth rates differed less than expected from the degree of dietary dilution.

Bernays and Simpson (1982) documented that most species are adapted to acquire food effectively from the niche in which they have evolved. Moreover, an organism's rates and processes may be "safely tuned" to the levels of resources typically found in its milieu (Calow 1977b, Case 1978; Calow and Townsend 1981; Rollo 1986). Results suggest that Periplaneta americana is well-adapted for survival on medium and low quality food types which is characteristic of its natural habitats. Understandably, the slower growth rates which are adjusted for low quality food would be more advantageous than high growth rates. The results strongly refute the optimality theory as growth rates were not maximized or maintained at constant levels amongst the treatments.

There are two possible explanations for the observed results: 1) growth rate was lower than expected due to the constraint of some factor, or 2) growth rate was lower via adaptive adjustment. Results support the later explanation as the declines in key parameters were much less than expected. Because the results did not indicate reductions which were proportional to the degree of dietary dilution, evidence in favour of constraint is weak.

Assimilation and Respiration

Mean measures of assimilation rates were much higher than those predicted by the degree of dietary dilution. Although the medium quality diet was diluted 50% with cellulose, compensatory feeding maintained assimilation rates to 122% of controls. Rollo and Hawryluk (1988) similarly observed that aquatic snails (Stagnicola elodes), reared on medium quality diets, assimilated more than the controls. Rollo and Hawryluk (1988) revealed that if stressful conditions persist, organisms may intensify or enhance their activities. The 25% treatment assimilated at rates 72% of the controls. Perhaps the compensatory responses of these cockroaches were insufficient to offset the negative effects of the dietary dilution.

The efficiency of food uptake from the gut was estimated from values of assimilation efficiency (AE). Results confirmed the commonly observed inverse relationship between increased rates and decreased efficiencies (Waldbauer 1968; Calow 1977a,b; Slansky and Scriber 1985, Rollo and Hawryluk 1988). Increased consumption of diluted diets elevated the rates of food passage through the gut. Consequently, the retention times for digestion and assimilation were reduced thus resulting in lower assimilation efficiencies.

Mean values of assimilation efficiency significantly declined with increased dietary dilution ($p < 0.0005$). The 50% treatments achieved efficiencies which were 67% of the controls whereas the 25% treatments attained values which were 26% of the controls. However, the assimilation efficiencies particularly with the 50% diet were higher than expected. These enhanced efficiencies support previous findings by Schroeder (1975) and Slansky and Wheeler (1989) that organisms may alter their food utilization efficiencies in response to poor dietary conditions.

Increased consumption and enhanced assimilation efficiency did not completely offset the slower growth imposed by reduced diet quality. However,they did mitigate some of the negative effects caused by dietary dilution. The slower growth rates of the 50% and 25% treatments may have incurred greater maintenance costs thus resulting in increased respiration. The greater respiration of the 50% treatment (132% of controls) was probably due to higher feeding rates. The 25% treatment exhibited respiration rates which were 70% of the controls,indicating that allocation was shifted to other factors. Increased consumption of the 25% treatment did not fully offset the costs of reduced assimilation and respiration.

Food Conversion Efficiencies

The efficiency of conversion of ingested food into biomass (ECI) significantly declined with increased dietary dilution ($p < 0.0005$). Conversion efficiencies of the 50% and 25% treatments were 33% and 31% of the controls, respectively. Decreased efficiencies of the 50% treatment were attributed to the higher metabolic costs of increased consumption. Conversion efficiencies of the 25% treatment were slightly greater than expected. Results confirmed the negative relationship between ECI and feeding rate previously observed by Rollo and Gunderman (1984).

The efficiency with which absorbed nutrients were utilized for growth (ECD) for the 50% was slightly greater than the expected 50% reduction (56% of the controls). Conversion efficiencies of the 25% treatment were unexpectedly higher (98% of the controls). These results suggest that cockroaches attempted to offset the effects of dietary dilution by more efficient food utilization.

Cockroaches deal with the 25% and 50% quality diets in a remarkably different ways. Specifically, the 50% cockroaches increase respiration and attempt to compensate by increasing the rates of all parameters. The 25% cockroaches cannot increase many of the parameters (e.g. feeding) much more. Thus they alter their tactics and decrease their costs via lower respiration. This strategy allows the same growth as the 50% treatment but incurred a cost which was probably behaviourally via low activity.

V. Reproduction

Numerous studies have documented the effects of food quality on reproduction (Gier 1947; Willis et al. 1957; Gordon 1959,1967; Kunkel 1966; Bignell 1978; Rollo and Gunderman 1984; Durbin and Cochran 1985; Scriber and Slansky 1985; Hamilton and Schal 1988; Rollo and Hawryluk 1988; Shibata and Rollo 1988; Slansky and Wheeler 1989). Results of this study confirmed those of previous authors that reproduction is adjusted to the levels of available resources.

The mean number of oothecae produced by Day 486 significantly decreased with increased dietary dilution (Table 8, $p < 0.01$). Females reared on the high quality diet produced more oothecae than females of the 50% and 25% treatments. The mean number of oothecae produced by females reared on the medium quality diet was slightly higher than expected (62% of controls). Similarly, cockroaches of the 25% treatment unexpectedly maintained reproduction to 48% of the controls.

Females delayed the initiation of reproductive cycles under conditions of reduced food quality. Hence, the temporal dynamics of the system may have accounted for the slower frequencies of oothecal production of the 50% and 25% treatments. This reduction in oothecal production was reflected by progressively longer oviposition and inter-ovipostion intervals for the medium and lower quality diets.

Cockroaches of the medium and low quality diets devoted greater reproductive effort into oviposition behaviours. Females of the 50% and 25% treatments often hid and concealed their egg cases, whereas the 100% females deposited them indiscriminantly. By elevated consumption and reduced oothecal production, females reared on the medium and low quality diets appeared to emphasize egg quality.

Although statistical differences were not detected, the 50% and 25% treatments generally produced larger eggs which hatched earlier than those of the 100% treatment. This greater parental investment in offspring survival was evident in both oviposition behaviours and resource allocation to eggs. It is also possible that females adaptively adjust the growth trajectories of their progeny by such variations in egg size (Shibata and Rollo 1988). Certainly, the carryover of greater maternal reserves would help nymphs survive through the early developmental stages on the low quality diets.

Diet quality had no effect on the dimension of oothecae or the number of eggs, which suggests that these features are under intense selection pressure or evolutionary constraint.

The proportions of cannibalized oothecae were relatively small. The 100% and 50% females only cannibalized oothecae which were discoloured or malformed. This behaviour thereby recycled any nutrients used in the production of non-viable oothecae. Consequently the strategies displayed by female <u>Periplaneta americana</u> were highly adaptive as they avoided any wasteful reproductive efforts used to generate offspring with low probabilities of survival.

Strangely, cockroaches reared on the 25% quality diets produced heavier oothecae which indicates a greater parental investment. This is consistent with the fact that they did not cannibalize their oothecae. These results are somewhat surprising as previous studies have reported that starvation often causes oothecal reabsorption and egg cannibalism (Bell 1971). Thus, reproductive investment was evidently higher for the cockroaches of the low quality diet treatment.

CONCLUSIONS

Periplaneta americana greatly offset the effects of reduced food quality on growth and reproduction via compensatory responses in various physiological and behavioural parameters. With food of medium or low quality, cockroaches modified feeding behaviours and enhanced utilization. This allowed Periplaneta americana to prolong its development and achieve a much larger maturation size than would have been attained had it not responded in a resilient compensatory manner.

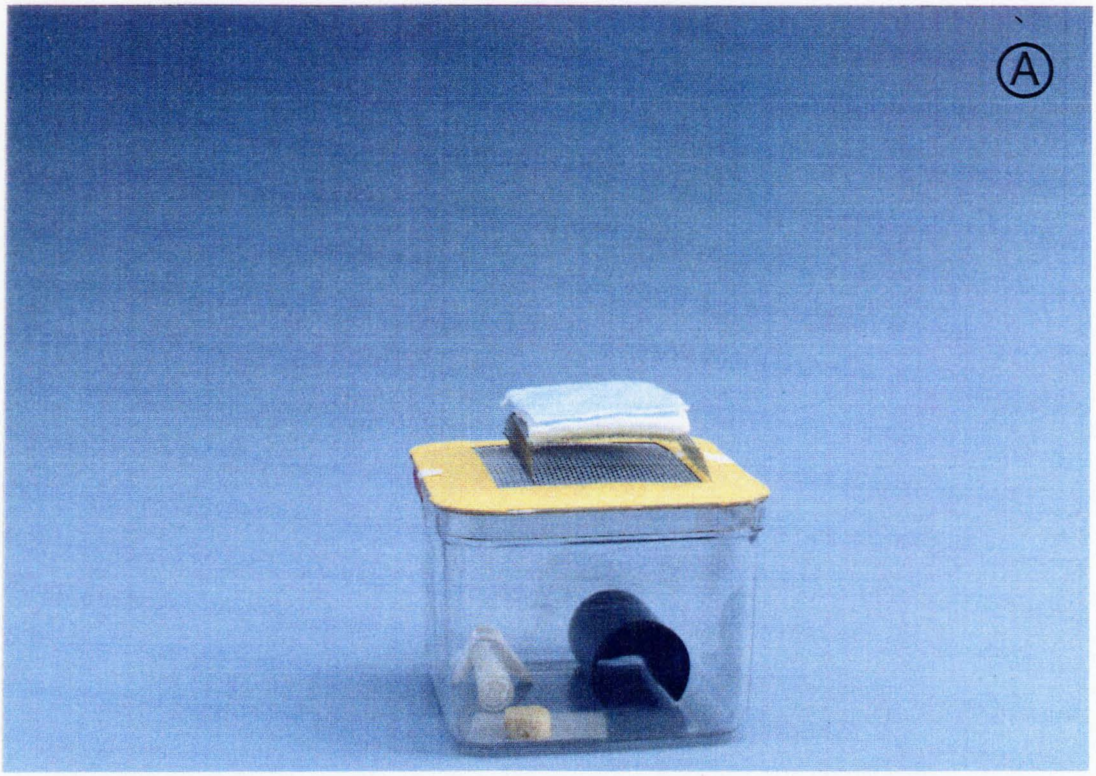
Results suggest that Periplaneta americana normally functions submaximally. The high plasticity of various life history features would ensure its survival through unfavourable conditions. Furthermore, the observed intraspecific variation is highly adaptive as Periplaneta americana may alter its growth, maturation, and reproduction to fit the surrounding ecological conditions.

The reproductive studies strongly suggest that further adjustments involved altered investment in allocation to eggs and maternal care. Thus, a broad behavioural and physiological constellation of adaptive features were realigned to achieve a different ecological focus as food quality was diminished.

Slansky and Wheeler (1989) noted that few studies have examined the ability of insects to modify food consumption and utilization in response to known variations in food quality. The results of this study will hopefully stimulate further research into the extrinsic factors affecting life history variables. Stimac (1982) emphasized that this basic information is essential, as understanding the factors which influence a species' feeding, growth, and reproduction will facilitate our attempt to synthesize an effective means of their regulation and control.

Figure 1. Cockroach rearing container
(10 cm X 10 cm X 7.5 cm)
A. Front view
B. Top view

m = moist cotton pad on platform
v = ventilated lid
s = shelter
w = water vessel
f = food pellet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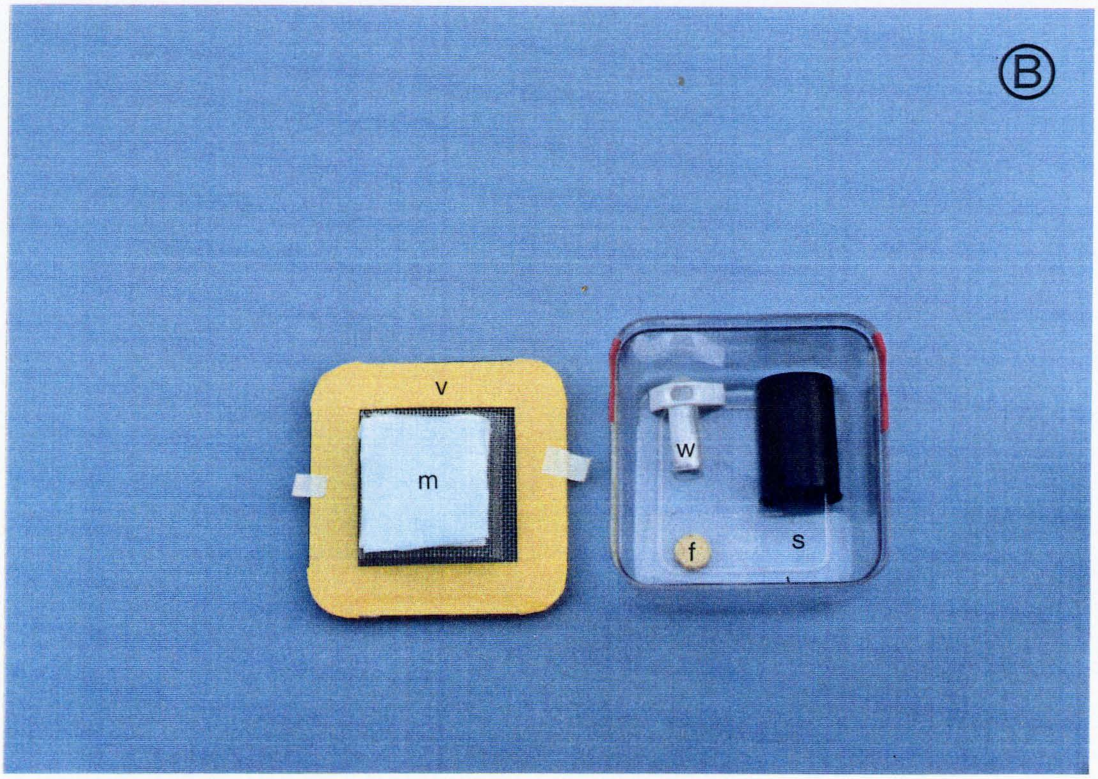

Ⓑ
v
m
w
f
s

Figure 2. Food pellet formation, using a modified 10 cc syringe.

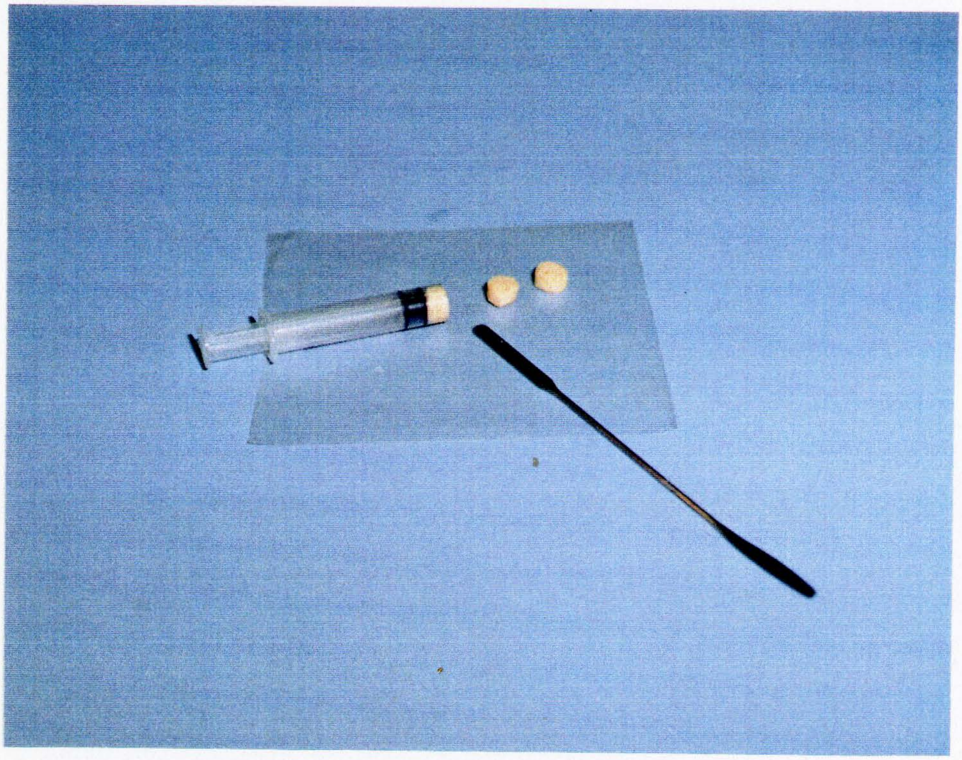
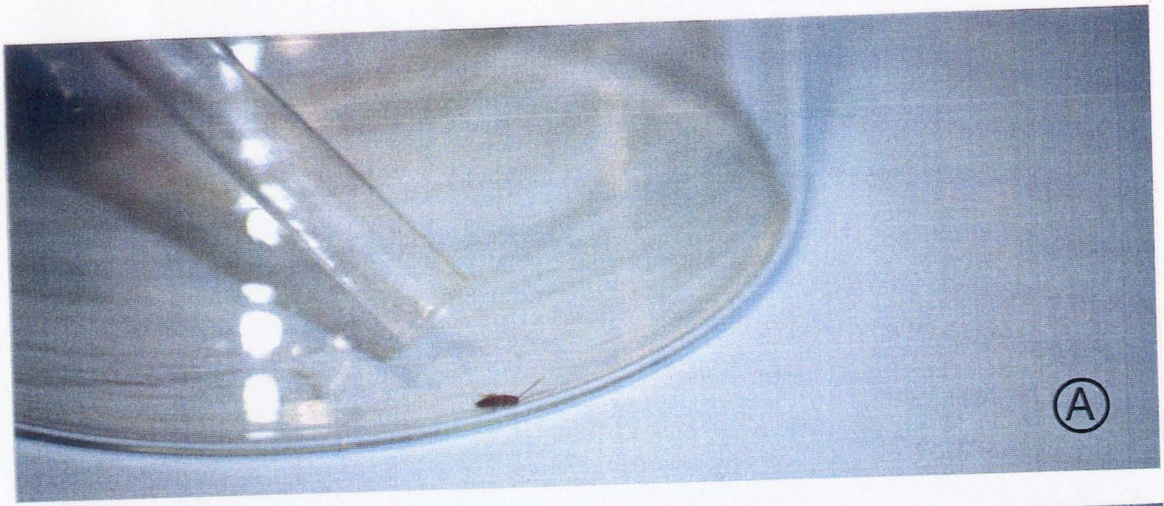


Figure 3. Cockroach weighing technique (first to third instar):

A. nymph handled using an aspirator,

B. nymph transferred to a pre-weighed aluminum foil cup,

C. live wet mass measured using an electrobalance.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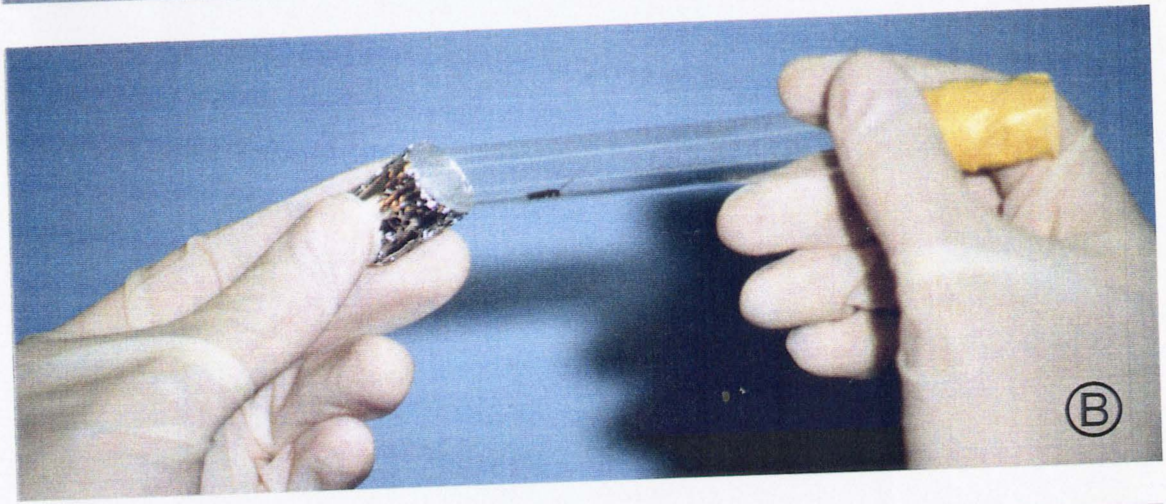
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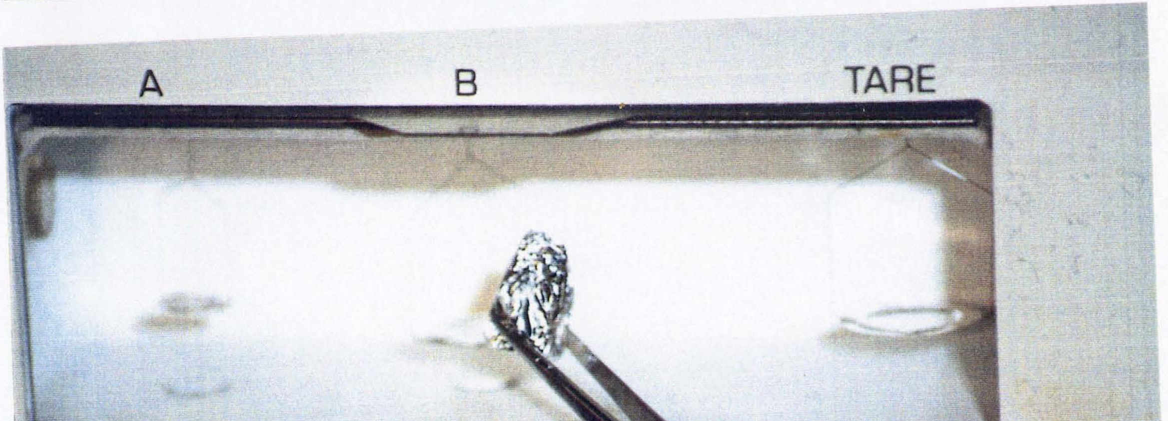
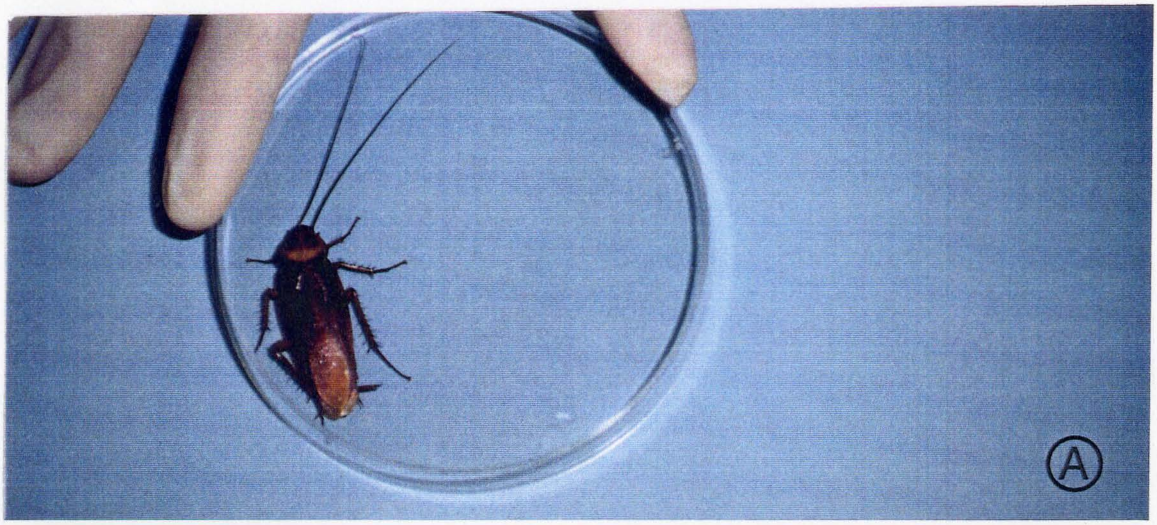

A
B
TARE
ZERO
COARSE
FINE
TARE
Ⓒ

Figure 4. Cockroach weighing technique (fourth instar to adult):

A. isolation of insect using a petri dish,

B. insertion of paper card under the enclosed insect,

C. removal of card and containment of cockroach.


A


B

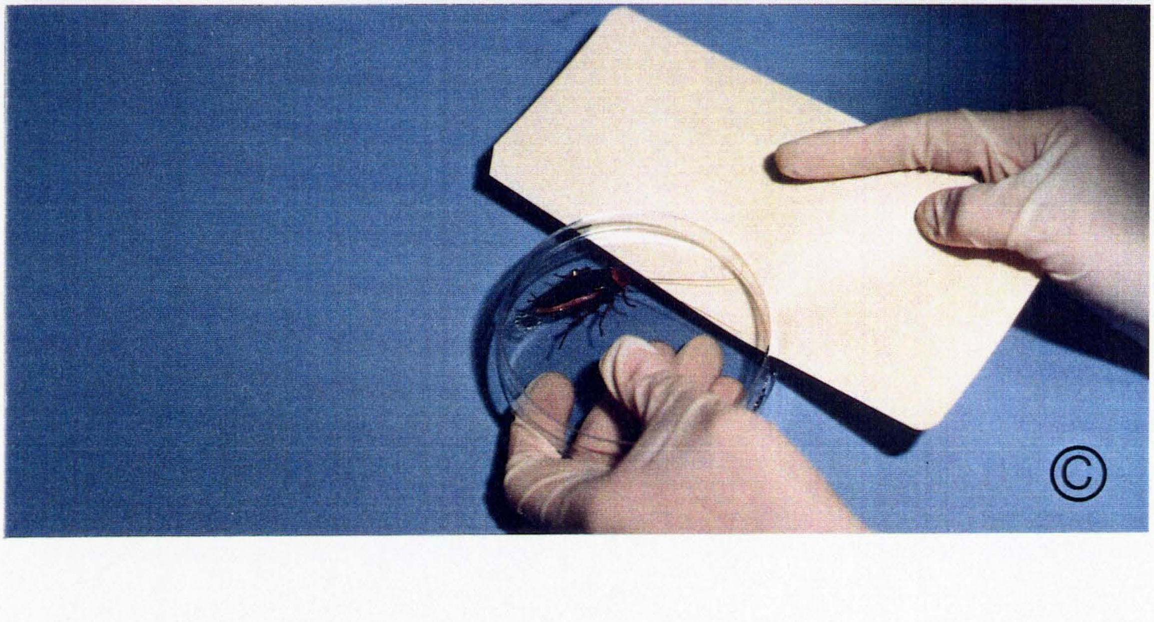

C

Figure 5. Growth of a typical Periplaneta americana nymph (Day 0 to 198) reared on a high quality artificial diet. The duration of the nymphal instars has been included to illustrate the corresponding effects of moulting on mass increases.

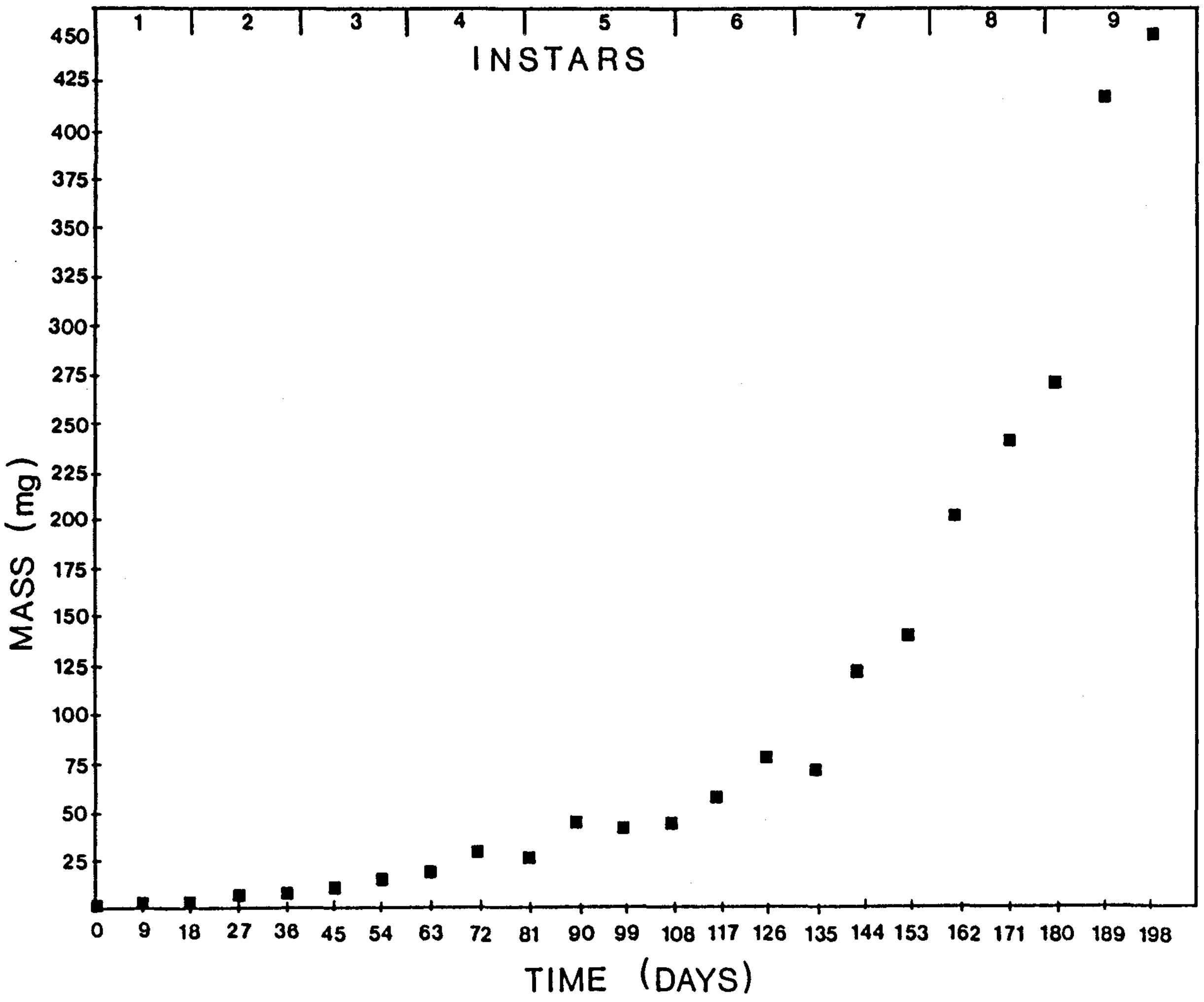

1
2
3
4
5
6
7
8
9
INSTARS
MASS (mg)
450
425
400
375
350
325
300
275
250
225
200
175
150
125
100
75
50
25
0
9
18
27
36
45
54
63
72
81
90
99
108
117
126
135
144
153
162
171
180
189
198
TIME (DAYS)

Figure 6. Regression analysis of the growth a typical *Periplaneta americana* nymph (Day 0 to 198) reared on a high quality artificial diet.

The equation of the fitted line was:

$\text{LOG MASS} = 1.7787 + 0.02519 * (\text{TIME})$

$r = 0.9938$, $p < 0.01$

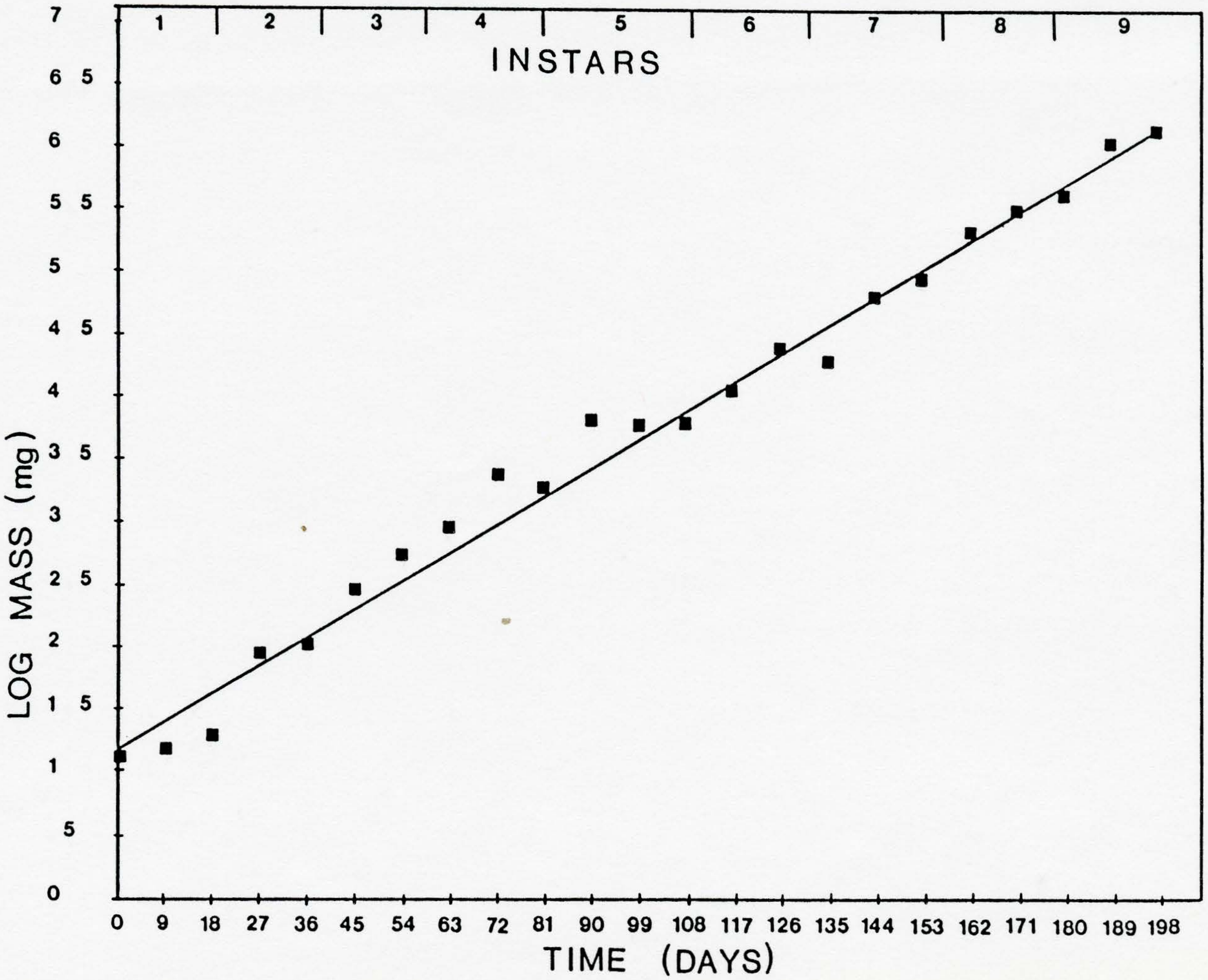

1
2
3
4
5
6
7
8
9
INSTARS
LOG MASS (mg)
7
6 5
6
5 5
5
4 5
4
3 5
3
2 5
2
1 5
1
5
0
0
9
18
27
36
45
54
63
72
81
90
99
108
117
126
135
144
153
162
171
180
189
198
TIME (DAYS)

Figure 7. Cockroach breeding containers:

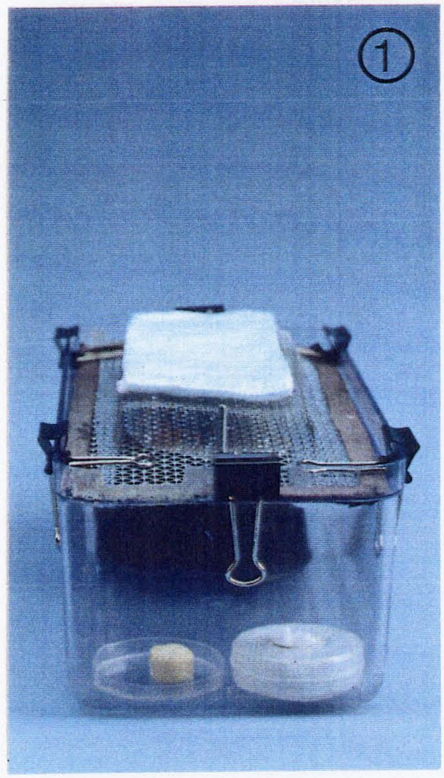
Type A (20 cm X 10 cm X 8 cm)

1. Front view, 2. Top view

Type B (17 cm X 12 cm X 10 cm)

3. Front view, 4. Top View

m = moist cotton pad on platform
v = ventilated lid
s = shelter
w = water dish
f = food pellet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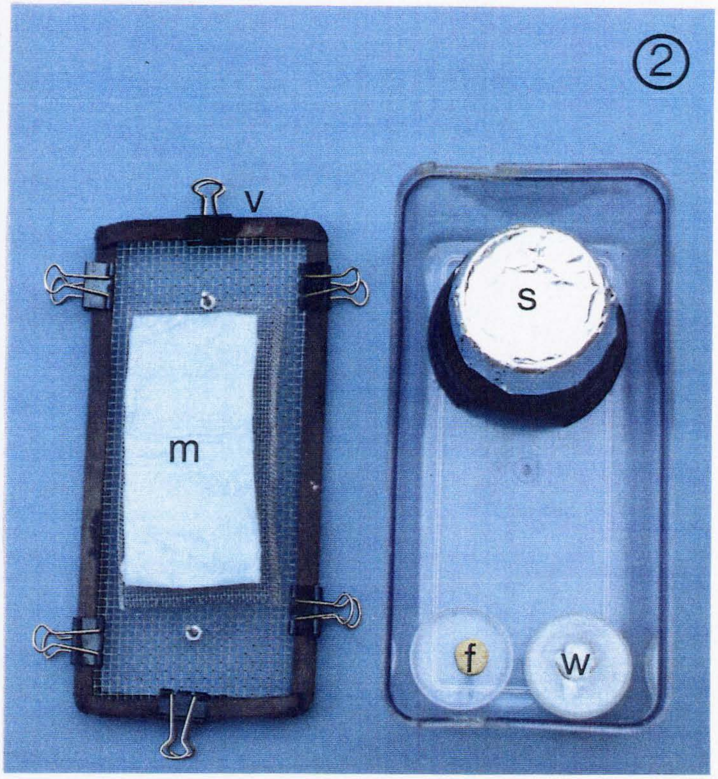
②
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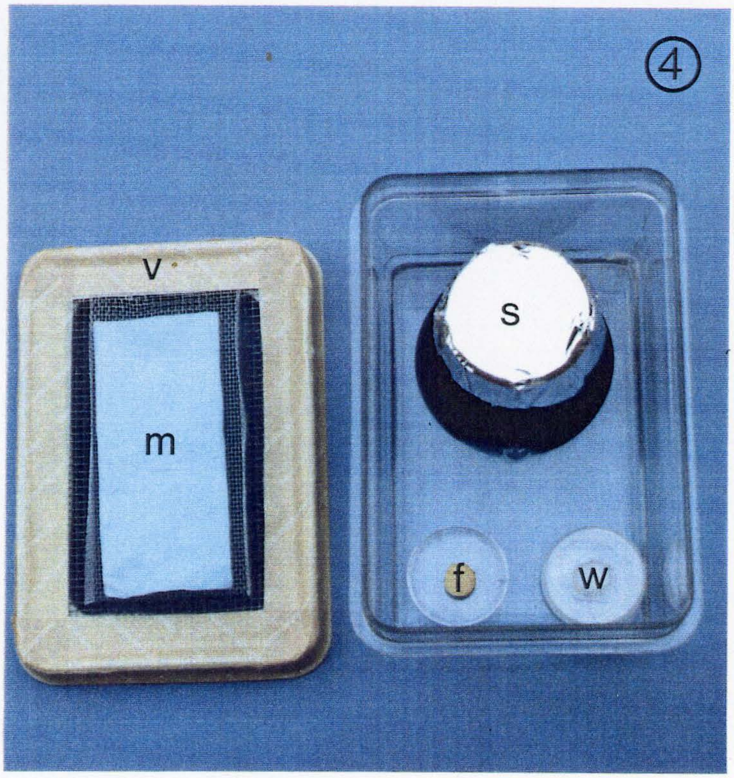
③


④
v
m
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w

Figure 8. Growth of male and female _Periplaneta_ _americana_ over 198 days (mean live mass ± SE) on artificial diets of varying composition.

■= high quality 100% diet, n=9

●= medium quality 50% diet, n=10

▲= low quality 25% diet, n=10

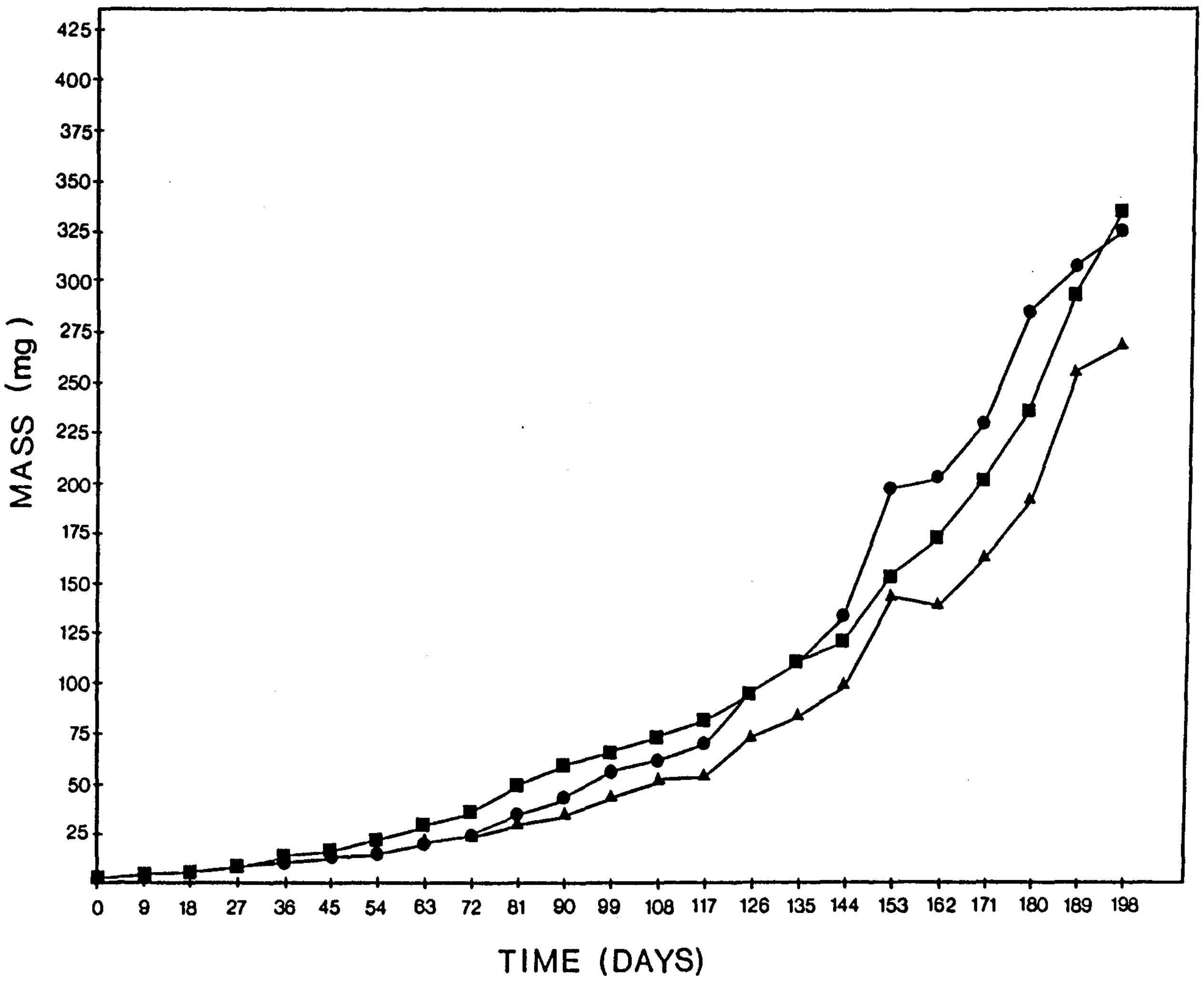
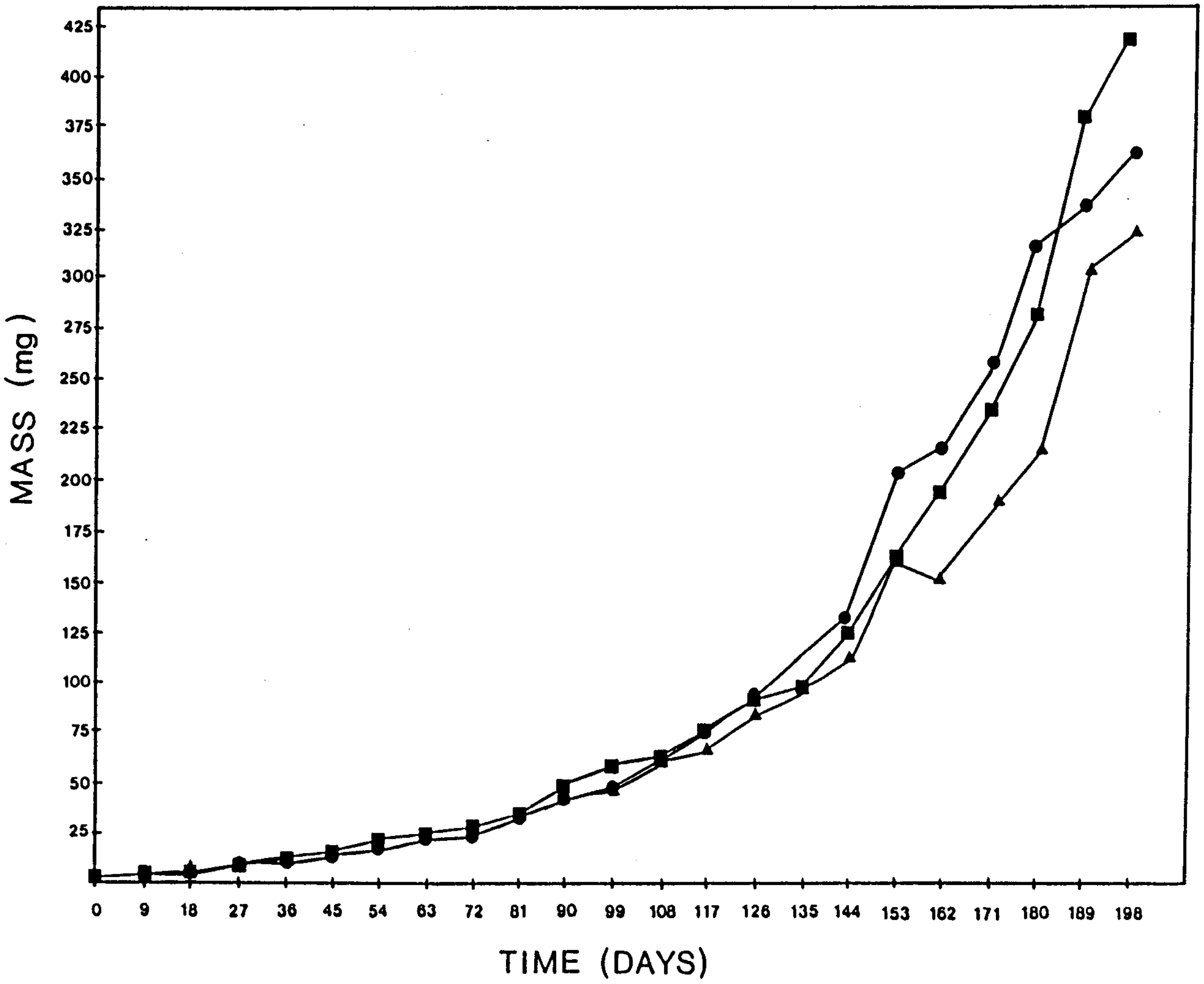

MASS (mg)
425
400
375
350
325
300
275
250
225
200
175
150
125
100
75
50
25
0
9
18
27
36
45
54
63
72
81
90
99
108
117
126
135
144
153
162
171
180
189
198
TIME (DAYS)

Figure 9. Growth of female <u>Periplaneta americana</u> over 198 days (mean wet mass ± SE) on artificial diets of varying composition.

■= 100% diet, n=4

●= 50% diet, n=8

▲= 25% diet, n=5


MASS (mg)
425
400
375
350
325
300
275
250
225
200
175
150
125
100
75
50
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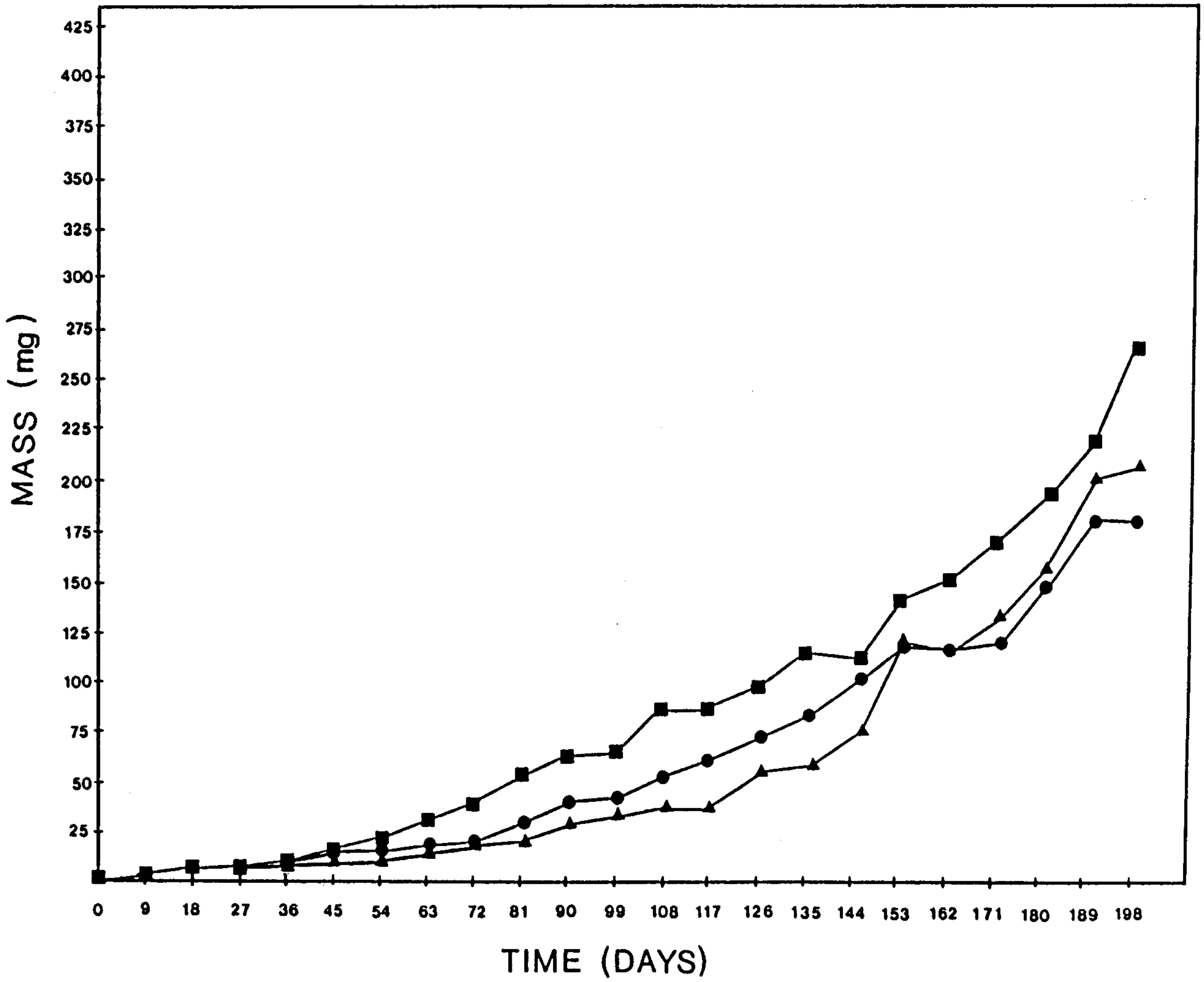
9
18
27
36
45
54
63
72
81
90
99
108
117
126
135
144
153
162
171
180
189
198
TIME (DAYS)

Figure 10. Growth of male *Periplaneta americana* over 198 days (mean wet mass ± SE) on artificial diets of varying composition.

■= 100% diet, n=5

●= 50% diet, n=2

▲= 25% diet, n=5


MASS (mg)
425
400
375
350
325
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275
250
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200
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18
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171
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189
198
TIME (DAYS)

Table 1. Longevity (means ± SE) of *Periplaneta americana* cockroaches fed artificial diets of varying composition.
Sex was not differentiated.

Diet Quality (%)	Mortality Before Maturation (%)	Longevity (days)			Maximum Longevity (days)
		Mean	SE	n	
100	10	-	-	10	> 519
50	0	-	-	10	> 519
25	0	-	-	10	> 519
10	100	66.1	2.36	10	81
5	100	55.0	7.46	10	99
2.5	100	32.4	2.26	10	45
0	100	26.8	1.43	10	36

Table 2. Comparison of instar durations (means ± SE) for *Periplaneta americana* reared on varying qualities of diet.

Diet Quality		INSTAR DURATIONS (days) 1	2	3	4	5	6	7	8	9	10	11	12	13
100%	$\bar{X}$	16.1	16.3	19.5	20.7	25.7	30.7	27.6	30.2	28.1	30.7	34.4	44.0	
	SE	0.8	1.1	0.7	0.6	1.7	2.0	2.2	2.3	2.1	1.9	1.7	0	
50%	$\bar{X}$	16.8	21.5	22.3	21.2	29.5	24.5	24.4	33.8	29.1	39.1	39.1	37.0	
	SE	0.8	1.6	1.6	0.7	5.1	1.6	1.5	3.7	2.2	4.0	3.5	3.5	
25%	$\bar{X}$	15.9	20.7	23.3	30.8	28.8	28.6	40.8	38.8	30.7	31.7	36.9	34.5	47.0
	SE	16.5	1.5	2.3	4.5	3.5	5.5	10.6	9.9	2.3	1.8	3.8	1.5	0
10%	$\bar{X}$	16.5	32.0											
	SE	0.9	1.9											
5%	$\bar{X}$	16.9	29.6											
	SE	0.6	1.0											
2.5%	$\bar{X}$	13.7												
	SE	0.6												
0%	$\bar{X}$	12.8												
	SE	1.0												

Table 3. Mean number of moults ± SE to adult maturation for *Periplaneta americana* reared on 100%, 50%, and 25% quality diets.

Diet Quality	MOULTS TO MATURATION								
	Overall			Females			Males		
	Mean	SE	n	Mean	SE	n	Mean	SE	n
100%	11.7	0.2	9	11.3	0.3	4	12.0	0.3	5
50%	12.1	0.3	10	12.0	0.3	8	12.5	0.5	2
25%	11.9	0.3	10	11.2	0.4	5	12.6	0.4	5

Table 4. Mean growth rates and standard errors for *Periplaneta americana* (Day 0 to 81) reared on artificial diets of varying nutrient quality.

GROWTH RATE (log mg/day)

Diet Quality	Overall			Females			Males		
	Mean	SE	n	Mean	SE	n	Mean	SE	n
100%	* 0.0332	0.0011	9	0.0325	0.0009	4	0.0331	0.0021	5
50%	* 0.0276	0.0013	10	0.0280	0.0016	8	0.0263	0.0002	2
25%	* 0.0223	0.0016	10	0.0230	0.0015	5	0.0217	0.0015	5
10%	0.0155	0.0009	10						
5%	0.0126	0.0030	10						
2.5%	0.0178	0.0015	10						
0%	0.0219	0.0045	10						

* Indicates significant differences between means (ANOVA, $p < 0.05$).

Only the three highest quality diets were subjected to ANOVA.

Sex was not differentiated for the four lowest quality diets.

Table 5. Comparison of mean growth rates and SE for *Periplaneta americana* nymphs reared on artificial diets of varying nutrient quality for 198 days from the first instar.

Diet Quality	GROWTH RATE (log mg./day)								
	Overall			Females			Males		
	Mean	SE	n	Mean	SE	n	Mean	SE	n
100%	0.0218	0.0008	9	0.0237	0.0012	4	0.0202	0.0006	5
50%	0.0218	0.0016	10	0.0224	0.0020	8	0.0196	0.0027	5
25%	0.0207	0.0011	10	0.0215	0.0019	5	0.0207	0.0014	5

Significant differences were not revealed by one-way ANOVA ($p > 0.05$).

Table 6. Mean maturation dates and sizes for *Periplaneta americana* cockroaches fed artificial diets of 100% 50%, and 25% quality.

MATURATION DATE (days)

Diet Quality	Overall			Females			Males		
	Mean	SE	n	Mean	SE	n	Mean	SE	n
100%	269.7	9.4	9	243.3	4.4	4	290.8	7.5	5
50%	304.3	19.9	10	303.3	24.7	8	308.5	25.5	2
25%	315.7	23.5	10	314.4	45.8	5	317.0	19.8	5

MATURATION SIZE (mg)

Diet Quality	Overall			Females			Males		
	Mean	SE	n	Mean	SE	n	Mean	SE	n
100%	1000.6	55.7	9	1112.3	82.5	4	911.2	50.8	5
50%	1068.0	66.0	10	1161.6	26.9	8	693.5	18.5	2
25%	952.8	61.1	10	1105.0	63.2	5	800.6	35.2	5

Significant differences were not revealed when data was analysed by one-way ANOVA at 5% level of significance.

Table 7. Comparison of means ± SE for various measures of the dry mass budget of _Periplaneta americana_ fed artificial diets of varying nutrient content. Sex was not differentiated. Values in parentheses within columns express results for the diluted diet as a percentage of the undiluted diet.

	Quality of Diet						
	100%		50%		25%		ANOVA
MEASUREMENT	Mean	SE	Mean	SE	Mean	SE	
Total dry mass gain (mg/36d)	41.36	8.30	32.64 (79)	12.43	32.13 (78)	9.08	NS
Total consumption (mg/36d)	295.82	40.74	603.39 (204)	187.16	627.03 (211)	104.58	NS
Total faeces (mg/36d)	80.43^{a}	14.99	341.54^{b} (425)	111.06	472.31^{b} (587)	87.75	$p < 0.01$
Total asssimilate (mg/36d)	215.39	25.99	261.85 (122)	78.77	154.72 (72)	20.06	NS
Total respiration (mg/36d)	174.03	18.31	229.20 (132)	67.16	122.58 (70)	13.79	NS
Growth rate (mg/d)	1.14	0.23	0.90 (79)	0.34	0.89 (78)	0.25	NS
Feeding rate (mg/d)	8.21	1.13	16.76 (204)	5.19	17.41 (211)	2.90	NS
Defecation rate (mg/d)	2.23^{a}	0.41	9.48^{b} (425)	3.08	13.11^{b} (587)	2.43	$p < 0.01$
Assimilation rate (mg/d)	5.98	0.72	7.27 (122)	2.18	4.29 (72)	0.55	NS
Respiration rate (mg/d)	4.83	0.50	6.36 (132)	1.86	3.40 (70)	0.38	NS
AE (%)	74.36^{a}	1.69	49.99^{b} (67)	3.99	26.98^{c} (36)	3.24	$p < 0.0005$
ECI (%)	13.04^{a}	1.21	4.41^{b} (33)	0.81	4.01^{b} (31)	1.04	$p < 0.0005$
ECD (%)	17.78	1.85	10.04 (56)	2.16	17.34 (98)	4.77	NS

Probabilities were determined by one-way ANOVA, tested at 5% level of significance. Significant differences within rows were differentiated by Newman-Keuls multiple range tests, and are indicated by different superscripts.

Table 8. Comparison of measures of reproduction for female *Periplaneta americana* reared on artificial diets of 100%, 50%, and 25% quality.

		Quality of Diet			
Measurement		100%	50%	25%	ANOVA
Mean number of oothecae produced/female by Day 486		40^{a}	25^{b}	19^{b}	$p < 0.01$
	n	158	196	76	
Number of Days spent carrying visible oothecae = oviposition interval (days)	Mean	1.94	2.36	2.54	NS
	SE	0.10	0.12	0.19	
	n	158	196	76	
Number of Days between deposition of oothecae = inter-oviposition interval (days)	Mean	3.78^{a}	4.37^{a}	6.53^{b}	$p < 0.01$
	SE	0.15	0.18	0.30	
	n	158	196	76	
Mass of ootheca (mg)	Mean	71.79	76.31	79.71	NS
	SE	1.19	0.88	1.34	
	n	158	196	76	
Dimensions of oothecae (l x w x b mm)	l	8	8	8	NS
	w	4	4	4	
	b	3	3	3	
Number of eggs		16	16	16	NS
Proportion of oothecae cannibalized (%)	(%)	6.3^{a}	6.6^{a}	0.0^{b}	$p < 0.05$
	n	158	196	76	
Hatching date (days)	Mean	54.83	49.28	48.0	
	SE	0.70	0.77	0.0	
	n	6	7	1	

Probabilities were determined by one-way ANOVA. tested at 5% level of significance. Significant differences between treatments were differentiated by Newman-Keuls multiple range tests and are indicated by different superscripts.

Appendix A. The composition of the seven artificial diets fed to *Periplaneta americana*.

	Quality of Diet						
	100%	50%	25%	10%	5%	2.5%	0%
INGREDIENTS	% Composition (by mass)						
MIXTURE A							
Starch	7.8	3.9	1.95	0.78	0.39	0.195	--
Sucrose	7.8	3.9	1.95	0.78	0.39	0.195	--
Soyabean oil	2.3	1.15	0.575	0.23	0.115	0.0575	--
Wesson salt mixture	3.5	1.75	0.875	0.35	0.175	0.0875	--
Citric acid	0.4	0.2	0.10	0.04	0.02	0.01	--
Soya flour	31.2	15.6	7.8	3.12	1.56	0.78	--
Sorbic acid	0.2	0.1	0.05	0.02	0.01	0.005	--
Wheat germ	20.96	10.48	5.24	2.096	1.048	0.524	--
Cellulose powder	12.5	50.0	75.0	90.0	95.0	97.5	--
Distilled water	73.2	73.2	73.2	73.2	73.2	73.2	73.2
MIXTURE B:							
Agar	11.7	12.08	6.02	2.414	1.172	0.2925	30
Distilled water	208.5	208.5	208.5	208.5	208.5	280.5	208.5
MIXTURE C:							
Ascorbic acid	1.6	0.80	0.4	0.16	0.08	0.04	--
Vitamin B	0.04	0.04	0.04	0.04	0.04	0.04	--
Tegosept	3 drops	3 drops	3 drops	3 drops	3 drops	3 drops	--
Distilled water	18.3	18.3	18.3	18.3	18.3	18.3	18.3

Appendix B: Growth of *Periplaneta americana* (Day 0 to 198), mean wet mass (± SE), fed artificial diets of varying quality.
100% n=9, 50% n=10, 25% n=10.

Quality of Diet

	100%		50%		25%	
	WET MASS (mg)					
Days	Mean	SE	Mean	SE	Mean	SE
0	3.2	0.05	3.1	0.08	3.06	0.11
9	4.8	0.44	4.83	0.21	4.67	0.32
18	5.75	0.60	5.11	0.43	6.04	0.41
27	8.63	0.49	7.91	0.28	8.48	0.56
36	13.96	1.56	9.59	1.01	10.35	1.00
45	16.19	1.27	12.41	1.09	12.45	1.57
54	21.44	2.27	14.1	1.03	13.91	1.69
63	28.82	2.98	20.2	2.03	19.03	3.42
72	35.24	3.16	24.49	2.78	22.2	3.43
81	48.22	4.75	34.22	3.61	28.13	7.12
90	58.1	5.91	42.4	5.57	32.89	8.88
99	64.62	6.12	55.62	8.18	40.98	9.72
108	92.16	7.09	60.7	7.75	49.50	11.83
117	80.56	8.27	69.0	12.44	51.5	14.27
126	93.78	8.18	94.5	16.52	70.8	14.26
135	109.78	11.0	108.2	21.78	81.6	17.32
144	120.11	10.24	132.5	28.72	96.6	20.86
153	151.33	11.36	196.1	48.76	140.5	18.10
162	170.44	13.83	201.8	55.61	135.2	19.55
171	199.89	24.54	228.6	61.17	160.1	23.22
180	234.78	25.24	283.9	85.11	189.9	26.30
189	291.33	34.17	306.6	88.79	253.1	40.74
198	332.89	44.01	324.6	86.40	266.3	47.99

Appendix C: Growth of female *Periplaneta* *americana* (Day 0 to 198), mean wet mass (± SE), fed artificial diets of varying quality. 100% n=4, 50% n=8, 25% n=5

Quality of Diet

	100%		50%		25%	
	WET MASS (mg)					
Days	Mean	SE	Mean	SE	Mean	SE
0	3.13	0.10	3.13	0.10	2.9	0.12
9	4.23	0.48	4.73	0.25	4.66	0.38
18	5.30	0.72	4.98	0.52	6.06	0.74
27	7.68	0.79	7.99	0.34	8.2	0.65
36	11.30	1.48	9.39	1.23	11.3	1.86
45	14.3	1.47	11.99	1.32	14.06	2.91
54	17.3	1.53	14.01	1.25	16.02	2.93
63	25.48	2.39	20.34	2.57	21.68	6.93
72	31.95	1.74	25.44	3.43	26.0	6.70
81	38.05	6.91	35.05	4.51	36.12	13.89
90	51.48	3.74	43.09	7.03	40.72	17.94
99	59.1	6.53	52.45	8.67	51.32	18.99
108	64.88	7.85	62.75	9.67	61.4	23.35
117	75.5	7.10	72.25	15.52	65.8	28.11
126	94.5	8.86	99.5	20.35	82.6	28.04
135	102.25	12.97	114.6	26.90	99.6	33.51
144	130.0	12.52	141.5	35.40	117.6	41.07
153	161.75	17.46	216.2	59.06	157.2	33.83
162	191.0	17.55	223.8	67.55	153.2	36.43
171	234.3	35.45	255.4	73.87	186.4	37.68
180	281.3	34.33	318.1	103.25	219.0	41.71
189	377.75	39.85	337.0	108.9	303.8	62.10
198	421.3	67.18	360.8	107.7	325.6	71.40

Appendix D: Growth of male Periplaneta americana (Day 0 to 198), mean wet mass (± SE), fed artificial diets of varying quality. 100% n=5, 50% n=2, 25% n=5

	Quality of Diet					
	100%		50%		25%	
	WET MASS (mg)					
Days	Mean	SE	Mean	SE	Mean	SE
0	3.3	0.03	3.0	0.1	3.22	0.16
9	5.26	0.65	5.25	0.25	4.68	0.56
18	6.12	0.95	5.65	0.65	6.02	0.43
27	9.4	0.40	7.6	0.1	8.76	0.97
36	15.64	2.30	10.4	1.6	9.4	0.76
45	17.7	1.81	14.1	1.2	10.84	1.13
54	24.74	3.32	14.45	1.23	11.8	1.40
63	31.5	4.95	19.63	1.15	16.38	1.11
72	37.88	5.50	20.7	0.2	18.4	0.98
81	52.02	7.23	30.9	1.5	20.14	1.78
90	63.4	10.08	39.65	1.05	25.06	1.66
99	69.04	9.92	43.3	1.5	28.64	3.25
108	78.0	11.17	52.5	1.5	37.6	3.75
117	84.6	14.39	56.0	3.0	37.2	4.94
126	93.2	13.93	74.5	14.5	59.0	7.70
135	115.8	17.72	82.5	16.5	63.6	8.06
144	112.2	15.77	96.5	20.5	75.6	7.09
153	143.0	15.57	115.5	34.5	123.8	13.82
162	154.0	18.76	114.0	42.0	117.2	15.18
171	172.4	31.43	121.5	36.5	133.8	25.69
180	197.6	28.43	147.0	64.0	160.8	30.80
189	222.2	23.72	185.0	70.0	202.4	48.23
198	262.2	38.11	180.0	54.0	207.0	59.23

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