

REGULATION OF FOOD INTAKE  
IN THE  
AMERICAN COCKROACH

LONG AND SHORT TERM  
REGULATION OF FOOD INTAKE  
IN THE  
AMERICAN COCKROACH, Periplaneta americana (L.)  
(ORTHOPTERA: BLATTIDAE)

By

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## Abstract

Cockroaches apparently select balanced diets using simple, but robust rules (Geissler & Rollo 1987). These rules are general enough to deal with a complex habitat yet sufficiently specific to contribute a balanced diet, thus leading to the successful maintenance of fitness. Both internal and external stimuli are integrated to elicit the appropriate responses. Feedback information concerning nutritional status may be short-term (e.g. immediate physiological state or sensory input) or long-term (e.g. storage reserves, hormones or learning) so that both coarse and fine-tuning mechanisms are involved in the choice of nutritious and non-toxic foods. The insects' ability to evaluate palatability (scent and taste cues) and nutritional value are essential aspects of the decision-making process.

This study investigated the general mechanisms governing changes in preferences with respect to tradeoffs between short and long-term stimuli. On a short-term scale, animals should prefer foods that present immediate positive stimuli according to their innate disposition. However, if a food does not meet long-term physiological needs, the animal should develop an aversion and learning may override a decision based upon a short-term stimulus, or alter innate preferences entirely.

The experimental protocol involved measuring amounts and time spent eating. Where appropriate, these values were related to female reproductive productivity to show the link between nutrition and reproductive capacity (fitness). Investigations demonstrated the ability of cockroaches to use coarse controls to compensate for long term general starvation as well as specifically depleted nutrients such as carbohydrates and protein. Cockroaches also showed discrimination between the quality of carbohydrate diets. The ranking of palatability among foods was not a fixed attribute but varied relative to the items available.

With large nutritional imbalances that required time to correct, dietary management was less discriminatory with respect to food quality and was largely concerned with increased quantity. Relatively well nourished animals showed much greater selectivity with regard to quality. Thus, the coarse and fine-tuned control systems stressed different strategic tactics. Reproductive success was linked to responses to malnourishment. Reproductive output was increased even over control levels when animals compensated for energy depletion by switching to alternate resources. This contradicted the prediction of maximization of reproductive output (fitness) by maximization of energy intake from optimality theory.

The results were interpreted with respect to optimal foraging theory, the currently accepted paradigm for ecological feeding relations. The results not only conflicted with the predictions of optimal foraging theory in most respects, they suggest a completely different paradigm that is incompatible with a hypothesis of maximization of net energy gain. Instead, cockroaches appear to regulate feeding with respect to evolutionarily determined set points related to innate growth and production rates. Moreover, the criteria for decisions are a multiplicity of nutritional requirements, not simply energy, as proposed by optimal foraging theory. Some of the decisions made with respect to nutritional balancing result from direct response to external or internal stimuli, and others are a learned association between long-term benefits and correlated sensory cues.

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## INTRODUCTION

The paradigm of nutritional ecology assumes that there is an ideal or best physiological potential leading to a life history that will maximize fitness (Slansky & Scriber 1985). Achieving and maintaining this ideal state would require an unconstrained environment where water and nutrition are complete and search and handling costs are minimal. Other factors such as competition, temperature, humidity, predators, parasites and disease must also be optimal or unconstraining. Given an uncertain environment, animals may rarely achieve the optimum, but their behaviour should be adapted to achieve the best possible compromise. Nutritional ecology is based on the idea that animals must achieve at least adequate nutrition and avoid poisons, but given high environmental uncertainty they must evolve a decision making apparatus for selecting a dietary balance that meets physiological demands (McFarland 1977, Townsend & Calow 1981). Survival and reproductive success (the two key components of fitness) can both be measured and compared for animals on different diets (House 1949). For example, individuals given a choice between diets can be compared to individuals that are forced to eat a particular regime. Such studies can reveal both how important decision-making is and

to what extent some choices are better than others. If there is adaptive value to giving some foods priority there should be mechanisms whereby preferences are ranked (McFarland 1977).

Adaptations related to nutritional ecology span physiological, behavioural and morphological attributes. The nutritional context involves types of food eaten, the extent of specialization, manner of feeding, degree of dispersal ability, energetics and how nutrients are converted, utilized and allocated within the body (Slansky 1982a,b, Townsend & Calow 1981, Futuyma 1983 a,b). The present study brings together the behavioural and physiological regulation of foraging in the American cockroach, Periplaneta americana (L.).

## LITERATURE REVIEW

This study involved behavioural and physiological aspects of the nutritional ecology of Periplaneta americana. The results were interpreted in terms of the empirical effects of nutrient manipulation on the animals and how their responses compared with predictions from the accepted paradigm of animal foraging regulation: optimal foraging theory. Thus, the literature review is comprised of sections regarding the assumption of maximization, feeding motivation, discrimination of food attributes and various physiological attributes. The relationship of these topics to existing foraging models is explored.

### I. Maximization theory

The cornerstone of optimality theory is the hypothesis that animals either maximize energy intake or minimize the amount of time expended feeding (Emlen 1966, Pulliam 1974, Pyke 1984). Adaptations that improve foraging rate or efficiency are assumed to increase fitness since feeding success is directly linked to mortality and reproduction. Fitness is not necessarily measured in terms of reproductive output (the most obvious variable) in maximization theory because it is difficult to directly correlate foraging and reproductive success (Schoener 1971,

Pulliam 1974, 1975). There are also various assumptions that are made when optimal foraging is tested (Krebs et al. 1981, Pyke 1984). These are: (1) There is a specific nutrient component of the diet that is optimized (usually energy). (2) Food items contain constant amounts of the component being optimized. (3) Handling times of foods are constant. (4) Foods are encountered at a constant rate while the animal is foraging. (5) Animals are omnipotently knowledgeable of food quality and distribution patterns. (6) Fitness is maximized by optimal choices and behaviour. These assumptions become more specific as particular examples are considered.

Foraging by bees has been extensively used to support the optimality perspective (Frisch 1967, Pyke 1978b, Waddington & Holden 1979, Hodges 1981, 1985) since they are small, high metabolism organisms that collect energy and have an open-ended hunger. The specific assumptions are as follows. The nutrient component that is optimized is nectar (energy) and pollen (protein) is ignored. Nectar consumption is easily measured in terms of volume and sugar concentrations. Flowers experiencing similar environmental conditions should contain similar nectar quantity and quality (not true). Intra-species handling times should be equal (not true). Many of the assumptions include the bee's

perception of the environment. The bee must be able to perceive distances, quantity and quality of nectar intake and flower types in order to make foraging decisions (Waddington & Holden 1979).

Thus, the three basic predictions of optimality theory are: (1) animals should maximize intake of a chosen nutrient and/or minimize foraging time (Emlen 1966), (2) there will be a constant preference for foods with the highest benefit/cost ratio even when other foods become more abundant (Vickery 1984), (3) a food should be eaten or completely ignored (Pulliam 1974, Charnov 1976). All of these predictions were tested in the present study. The first prediction has been supported by energetics studies performed with bees (Heinrich 1975, 1976a, 1976b, 1979). The second prediction was not tested in the conventional sense since abundance was kept constant and equal for all foods in the experimental protocol. However, some experiments where different foods were provided and then ranked do shed some light on this idea. This prediction has been supported by foraging in rodents (Vickery 1984) and invertebrates (Elner & Hughes 1978). The third prediction has had conflicting support. Foragers that are relatively specialized commonly follow the "all-or-nothing" prediction (Heinrich 1979, Marden 1984). However, omnivores commonly sample new foods



(Rozin 1976, Rozin & Kalat 1971, Geissler & Rollo 1987). Given the current theory, P. americana should prefer and maximize intake of that food containing the most energy. Moreover, this preference should be fixed, and increased consumption over normal (already maximized) levels should not be possible.

## II. Sensitivity to food cues

If food types other than energy (e.g. protein) are also considered important nutrients, then an alternative method of selecting foods would be controlled mixing of food types. However, any kind of control requires certain capabilities of the animal. These include being able to judge foods for quality and palatability and also having learning skills that would allow the recognition of "good" and "bad" foods (good foods being those of nutritional benefit and bad foods providing negative consequences such as poisoning or malnutrition). Judgement of food by P. americana concerns the external perceptive abilities including chemo- and mechano-receptors.

The first correlation between dietary preference and specific compounds in plants was demonstrated in caterpillars by Verschaffelt (1910). Studies of discriminatory ability lead to measurements of the

sensitivity of olfactory and gustatory receptors (McIndoo 1919, Dethier 1937, 1941). Some insects have been shown to elicit specific responses to single compounds suggesting that there is a coding mechanism that relies on specialized receptor types (Kaissling 1971, Selzer 1981). Sass (1976) has demonstrated the basis of such a coding mechanism by determining the reaction spectra of 7 different antennal receptor cell types in P. americana to various pure substances and complex foodstuffs. He showed that there were receptors specialized to detect key odours and combinations of less specific odour components (Sass 1978). This complex system of stimulus recognition is the key to foraging discrimination.

### III. Feeding motivation

There is some controversy as to what actually stimulates an animal to start feeding. However one of the most likely answers seems to be that recognized food stimuli are combined with internal physiological cues and innate clocks to synthesize a motivational stimulus to begin feeding. Toates (1981) suggested that internal and external cues always act together to initiate or terminate feeding. However, other researchers have found some discrepancy under special circumstances. Internal cues have been shown to act independently, although this may occur only under emergency

situations characterized by severe depletion (Smith et al. 1972). External cues may also initiate feeding independently, as shown by conditioned feeding initiation in satiated rats (Weingarten, 1984). Thus, it seems that feeding initiation may rely on varied factors under specific circumstances, but that normally a combination of both internal and external factors is involved. Various models agree that in the absence of external stimuli feeding motivation does not occur (Sibly 1975, McFarland & Sibly 1975, Bindra 1978, Coons & White 1977) (although the same motivation may drive searching for food). Evidence also exists that even on the most palatable diets there is still some effect of internal stimuli involved with feeding motivation (Mook & Kenney 1977). The combination of factors initiating feeding has been studied by measuring the probabilities of behavioural transitions affected by internal and external factors such as previous meal size, light, food-stimuli, recent defecation and short-term rhythms (Simpson & Ludlow 1986). Sibly (1975) and McFarland & Sibly (1975) suggested that feeding was induced by the product of the incentive value of available food rewards and the degree of food deficit. Of course the stimulus presented by any food may be either negative or positive, where a negative value would represent a deterrent and a positive

value a reinforcing stimulus (Bernays & Simpson 1982).

The above arguments have described the method of decision making when an animal encounters food. However, the actual drive to seek out food was not explained. This drive is not clearly defined in the literature. It seems that there are two ways in which animals find food. First, they might seek out food. Motivation may drive the search for food, after which tradeoffs are made to decide whether to eat the food. Alternatively, animals may accidentally discover food while engaged in mobile tasks exclusive from foraging, and immediate cues may reinforce feeding motivation. Both mechanisms probably operate.

#### IV. Self-selection of diet

When factors influencing feeding motivation are combined with learning and perception, it might be expected that animals can control food consumption and choose balanced diets that will be most beneficial at any time in their life cycle. Such behaviour has been called "self-selection" (Richter et al. 1938), "optimization of diet mix" (Westoby 1974) and "diet mixing" (Greenstone 1979). The term "self-selection" will be used exclusively here. Self-selection has been tested using numerous methodologies (Overmann 1976). There are two main approaches: either

healthy animals are presented directly with dietary choices or some method of inducing a dietary requirement is invoked before offering food choices. Following this protocol the animals are offered a total self-selection regime where either purified or natural foods are offered or there are limited choice situations where the animals must select from two or three key nutrients (Overmann 1976). Using these approaches animals have been tested for capacities such as compensation after deprivation (e.g. Richter et al. 1938, Rozin & Kalat 1971, Simpson & Abisgold 1985), maintenance of essential nutrient levels (e.g. Waldbauer et al. 1984, Dicke & Groenefeld 1986), responses to gradients of food concentration (e.g. Jakobsen & Johnsen 1987) and social learning that affects food selection (e.g. Galef & Beck 1985, Galef 1989)(see also review by Scriber & Slansky 1981). These experiments have provided a vast basis for continued research in self-selection.

#### V. Control of foraging

It has been argued that the basis of a behaviour must be understood before ultimate goals for that behaviour can be proposed (Lester 1984 a,b). In this study the experiments involving self-selection were used as the basis to understanding the mechanisms underlying feeding control and homeostasis, the ultimate goal being a model of the

nutritional ecology of Periplaneta americana. Various kinds of overall behavioural controls have been suggested in past research on foraging systems. Some of these include coarse behaviour rules (Bookstaber & Langsam 1985), short- and ultrashort-term feeding regulation (Novin & Van der Weele 1977) and on-off versus proportional controls (Hainsworth & Wolf 1983). The foraging model emerging in the present study is a novel synthesis of existing models with extensions based on my results and previous observations from this laboratory (see: Geissler & Rollo 1987, Gunderman 1989). Control involves both short and long term efforts by the animals to maintain physiological homeostasis. The two control systems interact to maintain or re-establish the internal nutritional state of the individual.

Factors influencing ingestion over numerous days were considered long-term features. Where reserves (e.g. fat body stores) were severely depleted or in emergency situations of imbalance, compensatory feeding responses could persist for weeks. Presumably the fat body and its associated reserves are monitored and deficits accounted for. With severe imbalance, the quality of what is eaten became less critical whereas quantity consumed was increased enormously. Thus the fat body can be considered central to long-term homeostasis (Downer 1981) and can induce relatively coarse, and

substantial changes in daily feeding.

Emergency nutritional imbalances were induced in the laboratory by deprivation of either all food or specific nutrients. It was hypothesized that when extreme starvation occurs, fine tuned balancing of nutrients would become less important than simply filling the crop with food. However, there may be a preferred nutrient according to the immediate nutritional requirement of the animal such as growth or reproductive requirements.

Short term controls were considered to be fine-tuning actions regulating the balance of nutrients having an effect on the fitness of the individual. Fine-tuning would occur only to make minor adjustments to reserve balance when reserves are all relatively full and physiological demands are relatively normal. Thus, fine-tuning was hypothesized to occur during feeding by animals with good nutrition and adequate reserves.

The distinction between long and short term controls might be best defined by their final effects. These effects are respectively macro- or micro-adjustments to internal physiological conditions based on the consequences of ingestion. Although coarse and fine tuning can only be identified relative to one another as opposite poles of a continuum, this was a useful paradigm for understanding the

overall control system. The criteria used to define extremes were as follows:

1. Coarse responses show relatively large adjustments in quantitative consumption compared to fine controls.
2. Malnutrition corrected by coarse responses requires many days for completion, whereas nutrient balancing by fine controls occur within one or a few days.
3. Coarse responses involve long term proportional shifts in consumption of specific nutrients (e.g. carbohydrates and proteins), where fine controls involve subtle switches between resource types with minor overshoot/undershoot reactions.
4. Coarse responses usually follow a malnutritive situation, whereas fine controls occur when the animal is nutritionally healthy as a response to internally altered nutritional requirements.

The immediate internal conditions affected include body hydration, blood sugars and fat body reserves. If these factors are influenced by foraging controls then there should be some ability to monitor their state. These physiological components have been shown to influence foraging through feedback mechanisms (Gunderman 1989). Body hydration and osmotic effects have been shown to influence feeding by affecting acuteness of sensory ability in



Locusta migratoria (Bernays & Chapman 1972a,b) and by directly affecting neural feeding correlates of terrestrial slugs (Kerkut & Taylor 1956, Deaux & Kakolewski 1971, Prior 1983, Phifer & Prior 1985). The fat body has been shown to be important in regulation of homeostasis. It is a dynamic tissue responding to prevailing physiological conditions (Downer 1981). Along with storing fats, glycogen, salts, protein and uric acid, the fat body is involved in intermediary metabolism such as liberating and converting amino acids, sugars and fatty acids (Wigglesworth 1974). Thus the fat body is not simply a dumping ground used for storage, there must be a delicate control of its physiology by balanced nutrient input. The hypothesized control is fine-tuning or long term regulation as described above.

In the present study short- and long-term controls were empirically identified by changes in consumption and the timing of these changes with respect to experimental manipulation. In order to hypothesize the simplest case of foraging regulation a second factor affecting nutrient utilization had to be eliminated as a solution to the question of controlling factors. This factor was assimilation efficiency. It is possible that a combination of controlled consumption rates and assimilation efficiencies were responsible for nutrient regulation.

However, Rollo (1984) showed no change in assimilation efficiency due to starvation or compensatory responses. Thus, the only factor considered to be a possible factor in nutrient control was regulation of consumption.

## MATERIALS AND METHODS

### I. Animals

Feeding choice experiments were conducted with male Periplaneta americana because this species is large and easily monitored. Female cockroaches were not usually employed for food choice experiments because their reproductive cycles effect their feeding (Sutherland 1982, Rollo & Gunderman 1984). In addition male cockroaches have smaller fat reserves than females (Roth 1981, Rollo 1984) and thus can be made nutritionally deficient more quickly. Experiments where the nutritional impact of a diet on productivity was of interest were performed with females. Reproductive effort was monitored using females because the oothecae were easily collected and weighed. Cockroaches were obtained from cultures reared on a diet of sucrose, ground Purina Dog Chow<sup>®</sup> (21% crude protein, 8% crude fat, 4.5% fibre) and water. Experimental diets were created from the recipes given below.

Considerable research is available on the nutrition of generalist insect herbivores (e.g., Gordon 1972, House 1974a, Slansky & Scriber 1985). Artificial diets were employed because their composition can be quantitatively altered to test the influence of nutritional, gustatory and

olfactory constituents. A high quality diet was synthesized from diets described by various authorities (House 1949, O'Dell & Rollinson 1966, Bignell 1978, Horie & Watanabe 1983, Simpson & Abisgold 1985) (Appendix 1). For each diet, all ingredients except those that were heat-labile were mixed with 25% of the water. Agar was stirred into 70% of the water and cooked at 100 °C for 5 minutes. This mixture was cooled to 50 °C and combined with the remaining heat-labile ingredients which were mixed with the remaining water. The final product was allowed to congeal at 2 °C. Samples of each artificial diet were offered in the form of pellets made by taking a core out of the congealed food with a stainless steel tube of diameter 12 mm and slicing the core into pellets approximately 5 mm thick. Various substances have been shown to have stimulatory effects on the activities of cockroaches (e.g. lemon oil, Selzer 1981; bay leaf, Verma & Meloan 1981; cucumbers, Scriven & Meloan 1984 a,b; lemon & kirsch, Geissler and Rollo 1987). Two aromatic substances that provided a strong baseline for attractant and repellent phagostimulants were used. The first, kirsch concentrated aroma, is a commonly used baking ingredient that is low in nutrients and has even consistency. Previous experiments showed that kirsch was an attractant phagostimulant for P. americana (Geissler & Rollo

1987). The second, bay leaf, is recorded as being repellent to cockroaches (Verma & Meloan 1981). Bay Leaf extract was made by boiling 4 g of ground bay leaves in 100 ml of distilled water and filtering the product.

Since food pellets were offered in a moist state, dry food consumption was estimated by determining the water content of ten sample pellets and using this information to convert original wet weights to dry weights. Sample pellets were taken each time that food was offered to eliminate error due to changes in the water content of the food during storage.

## II. Habitat

Preference experiments were conducted in a transparent maze having four acrylic tubes protruding from an acrylic cube measuring 13 cm cubed. The arm that acted as a shelter was made of black opaque acrylic. The tubes measured 12 cm in length and 7 cm in diameter. Food was accessed at the ends of the tubes through an 8 mm hole which allowed the head but not the body of the cockroach to pass. One food choice was offered per tube. The baffle that separated the resource from the cockroach ensured that only feeding activity triggered a response. Water was supplied ad libitum at the midpoint between the arms. Feeding stations were continuously monitored by infrared photocells

interfaced to a computer such that a signal was recorded every time the beam was broken by the insect's head (Fig. 2).

Periplaneta americana has a strong circadian rhythm that is entrained by light cycles (Sutherland 1982, Rollo 1984). A photoperiod of L:D = 16:8 h entrained the cockroaches so they rested during the photophase and fed during the scotophase. Food was offered at the beginning of the scotophase. All experiments were carried out at 22 °C and a relative humidity of 55%.

### III. Experimental Protocol

#### A. Compensatory Responses to Diluting Nutrients Over Time

This experiment tested the feeding and reproductive responses of female cockroaches to decreasing amounts of either carbohydrate or protein in the diet. The intention was to detect how depletion of a particular reserve might influence food choices and ingestion rates. Thirty animals were starved for two weeks prior to being tested. All animals were housed individually in clear plastic containers measuring 90 X 90 X 70 mm. A substrate of fine sand (5 mm deep) was provided as an ovipositional medium. Fecal material was removed from the substrate to prevent coprophagy. Ten control animals were given constant protein and carbohydrate diets for sixty days (Appendix 1). Twenty

others were given varying diets. Carbohydrate and protein diets were offered in separate containers in every case. Fresh food was provided daily. Ten experimental animals were given a constant protein diet and a diet of carbohydrate that decreased to 50% of the original concentration on day 22 and to 25% on day 42. The remaining 10 animals were given a constant carbohydrate supply and a protein supply that decreased according to the same protocol as above. Daily consumption was monitored until day 60 when food was no longer offered. Deposited oothecae were collected daily for 90 days and their dry mass was measured.

#### B. Preference for Sucrose Concentration

This experiment investigated the ability of P. americana to discriminate and choose different concentrations of a key nutrient. Five males were offered a variety of five food choices differing only in their concentration of digestible carbohydrate. Food ingredients included water (125 ml), agar (4 g) and sucrose (0.37, 1.10, 3.30, 10.0 or 30.0 g). Preparation of the food was the same as the method described above.

Twenty samples of each food type were placed in a 10 X 10 randomized grid pattern (total 100 feeding locations)

on the floor of a covered feeding arena measuring 0.60 X 0.60 X 0.15 m. Food samples were made by putting 0.45 g (three drops) of uncongealed food mixture on the top of a 1 dram vial stopper and letting the food congeal. These stoppers fit into holes drilled in the floor of the feeding arena. The closest distance between food samples was equal to the average body length of P. americana (38  $\pm$  2 mm, n=10). Water was supplied ad libitum in all corners of the feeding arena. Individual cockroaches were released in the feeding arena at the beginning of the scotophase. Feeding behaviour was monitored by time-lapse video-recording for four hours. The floor of the feeding arena was wiped with 95% ethanol after each trial to remove any trails left by previous subjects.

### C. Reactions to Gustatory/Olfactory and Nutrient Cues

To ensure that all individuals were hungry, they were starved for one week prior to testing. Water was supplied ad libitum in all stages of the experiment. To determine whether there were tradeoffs between sensory stimuli and actual nutritional value of a food, the foods were first ranked according to preference. Preference rank was assumed to be proportional to the amount eaten or time spent feeding. Six animals were tested in each preference



test. Each test was run for five days to eliminate compensatory responses to food ingredients. Ingredients for each diet are listed in appendix 1.

The following comparisons were made:

1. Equal<sup>®</sup> versus Sugar Twin<sup>®</sup> versus Blank I.
2. Sucrose versus Equal<sup>®</sup> versus Blank I.
3. Kirsch versus Bay Leaf versus Blank I.
4. Bay Leaf & Sucrose versus Kirsch & Equal<sup>®</sup> versus Blank I.
5. Amino acid mix without flavouring versus Amino acid mix with kirsch versus Blank I.

Equal<sup>®</sup> and Sugar Twin<sup>®</sup> are commercial low calorie sugar substitutes (containing 360 and 255 calories per 100g respectively as compared to sucrose with 690 calories per 100g). Equal<sup>®</sup> is composed of dextrose (86%), aspartame (0.035%) and silicon dioxide (10.5%). Sugar Twin<sup>®</sup> is composed of dextrose (62.5%), sodium cyclamate (37%) and silicon dioxide (0.5%). The point was to find a diet with high phagostimulant value but low energy content.

The fourth comparison was made on the basis of the results from the previous three comparisons. Here, kirsch and bay leaf scents were added as a known scent/taste preferability dimension for comparison with the nutritional preferability dimensions between sucrose and Equal. The

more preferable scent (kirsch) was combined with the energetically poorer food (Equal) and the more aversive scent was combined with the energetically better food (sugar). Time spent eating was monitored for the first half of the scotophase. This determined whether the choice to eat a food was based on scent/taste cues or nutrition.

#### D. Compensatory Responses to Specific Nutrient Starvation

Forty males were starved for two weeks prior to testing to deplete all nutrient reserves. This period was considered adequate since the average male survives only 3-4 weeks when offered only water (Sutherland 1982). Each animal was housed individually to prevent cannibalism. The containers were cleaned daily to avoid coprophagy. Water was supplied ad libitum from a wet sponge held in a plastic 35 mm film canister. Following starvation the males were divided into four groups (I, II, III & IV). Each group was then offered one of four diets (Appendix 1) for an initial two days:

- I. Complete diet (PC) - containing protein and carbohydrate.
- II. Protein diet (P) - containing only protein.
- III. Carbohydrate diet (C) - containing only carbohydrate.
- IV. Blank II diet (B) -containing no protein and no carbohydrate.

Each of the above diets contained the same vitamin and mineral combination so results were unlikely to be biased by micronutrients (Appendix 1). The intention here was to differentially fill a targeted reserve while the other would remain relatively depleted. On the third day all the animals were offered all four diets and consumption was measured. Groups I and IV were used for comparison with groups II and III. Group IV received no protein or carbohydrates, however the blank diet did contain approximately the same amount of bulk, vitamins and minerals per unit mass as the carbohydrate and protein diets. Bulk weight was maintained by replacing deleted ingredients with an equal amount of cellulose. Vitamins and minerals were added to the blank diet as controlled substances. The first ingredient, agar, is not digested by most organisms (Wallace et al. 1981). The second ingredient, cellulose, is usually considered a non-nutritive material used to dilute artificial diets of omnivorous insects (Bignell 1978), although a small amount of nutrient may have been derived from the activity of gut flora (Martin 1983). Regardless, the nutritive value of cellulose is substantially less than that available in the full carbohydrate diet (C). Kajura (unpublished) recently confirmed that the blank diet does not sustain growth or survival of P. americana. Despite this, agar and cellulose

are both readily ingested by P. americana (Martin 1983, Rollo and Gunderman 1984). This was confirmed in the present study (see experiment C).

## RESULTS

The variables measured for the various experiments were feeding duration, amount of food consumed (dry mass) and oothecal production (daily dry mass of oothecae). Food choice was recorded for all preference situations. Results were interpreted relative to controls or relative to baseline choices in the preference experiments. The data are represented as averages over the number of subjects for each experiment.

### A. Compensatory Responses to Diluting Nutrients Over Time

Temporal points A, B and C (figs. 13-18) represent times when the diets were altered by nutrient dilution (see methods; A = day 22, B = day 42, C = day 60). In all of the nutrient dilution experiments there were large initial peaks in consumption occurring from approximately day 1 to day 15. This was because the animals were starved previous to the testing days. Similar increased feeding following complete deprivation has been shown by other researchers (Gordon 1968, van Herrewege 1971, Rollo 1984). For this reason, regression analyses of either raw data or data generated from moving average analyses were performed beginning at day 16. Although regression analysis revealed trends in

consumption, the correlation coefficient may have been artificially low because of fluctuations introduced by cyclical feeding and egg production. Ideally, time series analysis would be employed, but this requires a very long series of observations. The period of cycles (the average time between major peaks) was determined by exploratory analysis with moving averages. A three day moving average effectively smoothed minor cycles and allowed easier interpretation of experimental results.

#### i. Controls

Regression analysis of the control carbohydrate consumption showed a negative slope of  $-4.69 \times 10^{-5}$  g/day (Fig. 3). This indicated that over the experimental period the animals did not stabilize at a constant consumption level (i.e. there was still some compensation carrying over from the initial starvation). A comparable slope was also found for the amount of protein consumed (Fig. 4: slope =  $-4.08 \times 10^{-5}$  g/day). Carbohydrate consumption was cyclic with a period of approximately  $6.7 \pm .70$  days (Fig. 5) and protein consumption was cyclic with a period of  $6.2 \pm .58$  days (Fig. 6). When daily carbohydrate and protein consumption were totalled, regression analysis gave a slope of  $-8.64 \times 10^{-5}$  g/day. The period of the cycle of total

consumption was  $5.8 \pm .46$  (Fig. 7). Total daily oothecal production of the control animals was measured (Fig. 8). A period of  $6.2 \pm .43$  days was shown. Regression analysis indicated a positive slope of .05 mg/day of oothecal production (Fig. 10).

Since the components of the experimental diet (carbohydrate pellets and protein pellets) were offered in separate containers it was possible to determine the proportions of each food chosen by the cockroaches (Fig. 11). Controls showed a relatively constant proportion of carbohydrate to protein over the sixty-day experimental period with carbohydrate at 59% and protein at 41%. When first order regression was performed on the daily proportions of carbohydrate and protein slopes of  $-0.046$  and  $+0.046$  %/day were obtained. These are so close to zero that they indicate that, as expected, the proportions did not change over the course of observations. Since the regression lines did not cross, there was also no switching indicated.

#### ii. Carbohydrate Diluted Diet

As the carbohydrate diet was diluted, the animals showed a rapid decline in carbohydrate consumption compared to controls. Regression analysis showed a negative slope of  $-1.31 \times 10^{-4}$  g/day (Fig. 12). A period of  $6.7 \pm .75$  days

(Fig. 13) was shown, the same as the controls. As carbohydrate was diluted, the animals increased their protein consumption (Fig. 14). Regression analysis indicated a positive slope of  $1.34 \times 10^{-4}$  g/day, much greater than the response shown by controls. There was a period of  $6.0 \pm .68$  days in the protein consumption data (Fig. 15). When daily carbohydrate and protein consumption were totalled, regression analysis obtained a slope of  $1.76 \times 10^{-4}$  g/day (Fig. 16) indicating a substantial increase in total intake. Total daily oothecal production was recorded (Fig. 17). When moving averages were calculated the data showed a period of  $7.4 \pm .51$  days (Fig. 18). Regression analysis on the average daily oothecal production showed a positive slope of .03 mg/day (Fig. 19). These positive slopes probably indicate that reproduction gradually increases as reserves are re-filled.

Proportions of carbohydrate and protein chosen by the cockroaches were also calculated and regression analyses were carried out on these data (Fig. 20). First order regression revealed slopes of  $-1.19$  and  $+1.19$  %/day. The lines crossed indicating a switch in feeding preferences from carbohydrate to protein. Third order regression (Fig. 21) indicated that the rate of change of the proportions varied through the different stages of the experiment. As



the carbohydrate component was diluted the cockroaches decreased carbohydrate consumption and increased protein consumption.

### iii. Protein Diluted Diet

In this treatment carbohydrate consumption decreased more slowly than the controls (Fig. 22). Regression analysis indicated a negative slope of  $-8.69 \times 10^{-6}$  g/day. When moving averages were calculated a period of  $7.7 \pm .64$  days was shown (Fig. 23). When regression analysis was performed on the absolute protein consumption the slope was similar to controls (Fig. 24: slope =  $-4.01 \times 10^{-5}$  g/day). Moving average analysis indicated a period of  $6.6 \pm .46$  days (Fig. 25). When daily carbohydrate and protein consumption were totalled, regression analysis showed a slope of  $-4.96 \times 10^{-5}$  g/day (Fig. 26). Thus, as protein was diluted, total consumption decreased overall for both types of food. Total daily oothecal production was measured (Fig. 27). Moving average analysis showed a period of  $6.1 \pm .33$  days (Fig. 28). Regression analysis of the average daily oothecal production showed a slope of  $+0.04$  mg/day (Fig 29).

Dietary proportions of carbohydrate and protein were calculated. Regression analysis revealed that in this treatment the animals chose the opposite balance of

carbohydrate and protein components compared to controls (Fig. 30), that is, protein was preferred over carbohydrate on a proportional basis. Third order regression analysis suggested that a switch occurred early in the experiment so that protein was preferred over carbohydrate despite overall decreases in combined intake (Fig. 31).

Average consumption was determined for both carbohydrate and protein diets (Fig. 32-33). The consumption data was divided into the three temporal segments A, B and C (as above). Independent averages were calculated for each period. Generally, average carbohydrate consumption decreased as the experiments progressed (Fig. 32). This supports the overall regression analyses mentioned above. Protein consumption also decreased in the control and protein diluted situations. The only absolute increase in protein consumption was shown by the cockroaches fed the diluted carbohydrate diet (Fig. 33). This indicated a compensatory response to the diluted carbohydrate by increasing protein consumption.

In the protein diluted experiment carbohydrate consumption decreased faster than the controls (fig. 32). However, protein consumption decreased less than the controls (fig. 33) and less than the carbohydrate consumption (compare fig. 32 & 33). Thus, in relative terms,

there was compensatory feeding on protein. Increased protein consumption mirrored decreased carbohydrate consumption thereby showing relative compensation on protein.

Similar time-spanned averages were calculated for daily oothecal production data (Fig. 34). Similar results to those of the regression analyses performed above were found. The group fed the carbohydrate diluted diet demonstrated an increase in oothecal production from day 1 to day 60. After this period the animals were denied all food. After day 60, the carbohydrate diluted group decreased their oothecal production. It appeared that the increased oothecal production occurred in synchrony with the increased protein consumption between days 42 to 60 (compare Figs. 33 & 34). The group given diluted protein diet decreased their oothecal output at the first dilution but maintained the same output after the next dilution. After all food was removed (day 60) oothecal production was decreased again. Controls demonstrated an approximately constant increase in oothecal output over the 90 day experimental period.

#### B. Preference For Sugar Concentration

Time spent feeding was recorded for each food type. Mean time spent feeding on each food type was calculated (Fig. 35). As food quality (concentration of sugar) increased, the amount of time spent at each food type also

increased. With the exception of food type one, increases in time spent feeding were approximately proportional to the increases in sugar concentration in the food pellets. More time was spent feeding on food type one than on food type two. One possible explanation for this was that the sugar concentration of food type one was very low. Possibly this food was used as a water source, since all the foods contained large quantities of water. Water was available in the corners of the feeding arena, however food type one may have been a more convenient source of water.

### C. Reactions to Gustatory/Olfactory and Nutrient Cues

All preferences were measured in terms of time spent feeding on a particular food type. Data were analyzed as means for the number of individuals tested (n=6 for each treatment). In the first treatment cockroaches were given a choice of food with Equal, Sugar Twin or no flavour added (Blank) (Fig. 36). Approximately 20 times longer was spent feeding on the Equal-flavoured food than Sugar Twin or Blank. In the second treatment it was shown that 10 times more time was spent eating sucrose-flavoured food than Equal-flavoured (Fig. 37). Approximately 10 times more time was spent feeding on Equal-flavoured food than the Blank. When standard errors were considered in the third treatment

almost the same amount of time was spent feeding on Kirsch-flavoured food and the blank food (Fig. 38). Approximately 20 times longer was spent feeding on Kirsch-flavoured food or the blank than on Bay leaf-flavoured food.

Treatments 1 through 3 were used to establish baseline preferences exhibited by the cockroaches. These results were used to design the next treatment. When aversive and attractant cues were combined with nutrient cues in the fourth treatment approximately 35 times more time was spent on the combination of Bay leaf and sugar than on the blank food and 8 times more time was spent on Bay leaf and sugar than on the Kirsch and Equal combination (Fig. 39). This indicated that in this case the actual nutrient elicited a stronger response than the artificial scent/taste cues, even when aversive cues were combined with preferable nutrient stimuli. In the last treatment the blank food was preferred by 2 times over the amino acid mix even if this was combined with a preferred scent/taste cue (Kirsch) (Fig. 40). Amino acids with Kirsch, however, were preferred 20 times more than the same amino acid mix with no scent/taste cues. This showed that when nutrients are constant, scent/taste cues can independently determine diet choice.

To establish a relative rank of preferences for all the foods tested a preference index was established (Fig. 41). The most preferred food (sugar) was assigned an index value of 100 and all the other foods were ranked proportionately. Results showed that foods did not have a fixed preference level. For example, in treatment one, Equal had a preference index of 50. This index value changed to 10 when the combination of foods offered with Equal was changed in treatment two. Also the blank food was not altered in any of the treatments but the index value for the blank food ranged from 1.4 to 38 depending on the available foods offered. Apparently food preferences were relative to the spectrum of stimuli present when a choice was made. Moreover, the results indicated that a food item may be chosen based on either scent/taste cues or nutritional cues.

#### D. Compensatory Responses to Specific Nutritional Deficiencies.

Food consumption was measured for cockroaches acclimated to four different food types: combined protein and carbohydrate (PC), carbohydrate (C), protein (P) and blank (B) (Fig. 42 - 45). Animals that were acclimated to PC and B diets were used as comparisons for the C and P groups. The PC acclimated group was considered to have a

nutritionally complete diet. When these animals were offered a combination of all the food types (day 3) diet PC was the most preferable (Fig. 42). Average consumption of diet PC was  $.0170 \pm .0024$  g. Diet C was almost as palatable as diet PC ( $.0135 \pm .0039$  g). Diet P and diet B were of comparable palatability ( $.0061 \pm .0023$  g and  $.0071 \pm .0033$  g). However these were approximately one half as palatable as diet PC and diet C. Cockroaches acclimated to diet C showed strong preference for diet PC ( $.0309 \pm .0069$  g) (twice control consumption, compare with fig. 42) when all the food types were offered on day 3 (Fig. 44). This preference was followed by diet P ( $.0114 \pm .0043$  g) (twice controls), diet C ( $.0063 \pm .0027$  g) (half of controls) and diet B ( $.0001 \pm .0001$ ) (essentially ignored). Thus there was a strong compensatory response to replenish protein reserves. Cockroaches that were acclimated to diet P also found diet PC most palatable on day 3 ( $.0305 \pm .0067$  g) (twice controls) (Fig. 43). The carbohydrate diet (C) was second most palatable ( $.0195 \pm .0037$  g) (1.5 times controls). This was followed by the blank diet (B) ( $.0058 \pm .0026$  g). The least palatable was the protein diet (P) ( $.0038 \pm .0008$  g) (half of controls). This indicated a preferential response to replace carbohydrate reserves. Cockroaches acclimated to diet B showed a great aversion to the diet B on day 3 ( $.0006$

$\pm .0003$  g) (Fig. 45). Palatability for the other three diets was approximately equal (PC:  $.0274 \pm .0055$  g (twice controls), P:  $.0195 \pm .0066$  g (3 times controls), C:  $.0228 \pm .0052$  g (twice controls)). Thus, feeding on a poor diet elicits compensatory intake of both carbohydrate and protein.

Total daily consumption was determined for cockroaches acclimated to each food type (Fig. 46). Food consumption of cockroaches fed diets P and PC on days one and two decreased from day one to day two. On day three mean consumption increased for both groups. Individuals that were fed diet C on days one and two showed no change in total daily consumption over all three days. The animals that were fed diet B on days one and two consumed equal amounts on these days. On day three their consumption increased by three times. When the four different treatments were compared the animals acclimated to diet B consumed the least amount on days one and two and they consumed the greatest amount on day three.



## DISCUSSION

There are two key problems connected with foraging. The first concerns the internal motivation that drives foraging and initiates feeding. The second concerns the decision of what to eat given choices. The original formulation of optimal foraging theory postulated that optimally foraging animals should maximize caloric intake or minimize foraging/feeding time (Emlen 1966). However, foods with the greatest caloric value may not lead to greatest fitness since energy is not the only requirement for balanced nutrition. Optimal foraging theory was expanded to include requirements for other nutrients as well (Pulliam 1974). This was rationalized by changing the rules outlined in the optimal foraging model. If only energy is maximized then foragers should specialize, eating only those items with the highest energy yield. However, if a forager maximizes nutrient intake, extra food items may be eaten so that partial preferences result. The problem is that maximization models are mathematically constrained to solve for only one criterion. If it is energy, then somehow other nutrients must be converted to this currency or added on merely as constraints. Organisms do not sympathize with our mathematical limitations. They optimize multiple criteria using the equivalent of numerical methods - natural

selection. Thus, attempts to extend optimal foraging theory to nutritional ecology are resting on a totally inadequate analytical foundation.

If the forager consumes more than one food to acquire nutrients and energy, then there must be some method of balancing amounts of various ingested food types. The present study was concerned with behavioural efforts by Periplaneta americana to balance nutrients and energy intake. Since all of the individuals tested were adults, carbohydrates and proteins would be used for immediate energy, maintenance and reproductive purposes but not for growth. Thus the elicited behaviours reflect the maintenance of physiological homeostasis.

Another way of considering optimization in foraging is the selection of optimal diet mixes by animals (Waldbauer & Bhattacharya 1973). Optimization of diet mixes implies that the entire regimen of required nutrients is optimized rather than just one nutrient. Most foraging models only show optimization of single nutrients and treat others as constraints on the selected criterion (energy). To optimize dietary mixes an animal must have an ability that was not included in original optimization theory. This is the ability to balance a diet by selecting foods chosen from an array of possibilities. This has been termed "self-

selection". Self-selection has been demonstrated in both healthy animals (MacFarlane & Thorsteinson 1980) and for those compensating for diluted (Cohen et al 1987), or missing nutrients (Simpson et al 1988). This concept is different from optimal foraging theory since the mode of achieving maximum fitness is different. If an animal is balancing holistic nutrition, then it may neither maximize energy intake or minimize time spent, although these may still be important goals. There may also be suboptimality because of tradeoffs with other activities (Booth et al. 1974). The results found in this study support the general hypothesis that foraging in P. americana is regulated to achieve holistic set points rather than maximization of any particular nutritional criterion. In fact, maximization of feeding would only make sense if growth rates and/or reproductive rates had no upper limits. Given an evolutionarily selected "best" growth rate, a set point feeding rate to meet this objective must follow. If this perspective is true, then the basic paradigm of maximized feeding is inappropriate.

### A. Compensatory responses to diluting nutrients

Over approximately the first 15 days all animals showed initially large peaks in consumption that gradually diminished (Figs 3-7, 12-16, 22-26). This reflected compensatory feeding in response to the two week pre-experimental starvation (see Rollo 1984). Varying the amount of consumption is one form of compensation commonly elicited by starvation or deficiency (Simpson and Abisgold 1985). As per the criteria defined earlier, this seemed to be a more coarsely controlled compensation compared to more subtle tuning shown later in the experimental period. When insect foragers are starved, decreased selectivity commonly results (Bernays and Simpson 1982, Geissler and Rollo 1987, Schoonhoven et al. 1987). This initial response may be a quick method of filling depleted reserves when uncertainty of the next meal is high. Coarse behaviour has been proposed as an insensitive response to infrequent surprise events such as those created in a laboratory environment (Bookstaber and Langsam 1985). It helps to average out short term fluctuations that are not too important by not responding to them but rather by responding to the long term trends. For an omnivorous forager such as P. americana coarse responses would be an adaptive tactic for deprivation like the two-week starvation period imposed here. That is,

when a long-term trend creates a large anomaly, the response mechanism may be different than day to day fine-tuned balancing.

After the initial 15 day compensation period there appeared to be a change in foraging control (Figs 3-7, 12-16, 22-26). Consumption decreased by at least 50% following which the amounts of carbohydrate and protein consumed by the controls became relatively stable (Fig. 3 & 4). It appeared that after the cockroaches had repleted their basic energy and protein reserves, foraging became more finely controlled. Given that the cockroaches were no longer deprived, there was no longer any need for emergency coarse control (Fig. 7). The proportions of carbohydrates and proteins consumed were not altered substantially throughout the experiment (Fig. 11). This suggests that there was a particular balance of nutrients consumed for homeostasis. The proportion of carbohydrate was greater than the proportion of protein eaten by the controls. This was probably because carbohydrates are not only needed for general energy needs, they are also required for protein metabolism (Stryer 1981). Thus, carbohydrates are probably in greater general demand, since they would be depleted faster during starvation and thus should be replenished with greater priority. Protein metabolism is probably altered by

the availability of carbohydrate-derived energy. The importance of carbohydrate compensation was shown by Gordon (1968) who showed that compensatory sugar consumption by Blatella germanica exactly matched the amounts lost during deprivation. Following compensation, consumption of carbohydrates returned to stable, low levels, as was also shown in the present study.

When considering the stability of consumption it is important to note that this does not necessarily mean constant consumption rates. As seen in all of the plots of consumption versus time, feeding was highly cyclical. This was in large part related to the reproductive cycles of the animals (see discussion below). However, another factor leading to the cyclic feeding may have been overshoot-undershoot dynamics in the feedback control system used in compensatory feeding. Evidence for this was provided by Gunderman (1989) who found feeding cycles in males, even though they have no reproductive cycle. Such oscillations are commonly observed in feedback systems where the responses are non-linear. Given these phenomena, the feeding regulation used by P. americana does not follow the maximization model. The fact that animals decrease consumption (undershoot) following high level intake does

not conform to a maximization paradigm, but agrees with dynamic regulation to a homeostatic set point.

When the cockroaches were given a constant protein source but carbohydrates were diluted sequentially, a fine-tuned response was evoked. Consumption of carbohydrate containing food remained similar to the controls (Fig. 12). However, protein consumption showed the opposite trend as the controls. Mean protein consumption approximately doubled from day 15 to day 60 (Fig. 14), whereas in controls it was relatively stable. Switching to alternate resources of nutrient is a type of response shown for changes in dietary nutrients (Simpson & Abisgold 1985). This response was considered fine-tuned because it did not result from a situation of uncertainty (e.g. food deprivation). Nutritious food was available, but as one food was diluted, consumption had to be altered to maintain balance. Evidently, the cockroaches compensated for the diluted energy source by increasing protein consumption. Protein can be catabolized in biochemical energy pathways (Stryer 1981) and was probably being substituted as an energy base. The increase in protein consumption caused total consumption to gradually increase as the carbohydrate component of the diet was diluted, probably because protein is less effective as an

energy source and also would incur water balance and excretory costs (Fig. 16).

Increased consumption has been shown in other insects as a form of compensation (Gordon 1968, Sinoir 1968, McLean & Kinsey 1969, Belzer 1970, van Herrewege 1971). The change in amounts of food consumed was accompanied by a change in relative proportions of the diets (Fig. 20 & 21). Such a change indicates that consumption is not simply an effort to maximize intake but it is a controlled effort to balance nutrients. Although animals have been shown to compensate for deprivation from foods, the combination of coarse and fine tuning controls for compensation of food in general and of specific diet contents has not been previously made clear.

In the complementary experiment where carbohydrate was constant and proteins were diluted, it was not possible to compensate for the biochemical value of the protein by substituting carbohydrate. The decreased consumption of both carbohydrates (Fig. 22) and protein (Fig. 24) (see also Fig. 26) showed that even feeding on energy rich substances may be reduced if the metabolism is limited by other specific nutrients. This result indicates that even where two nutritional criteria can be translated into a mutual currency (i.e. energy) they may not be symmetrically



interchangeable. Moreover, the value of one material to overall fitness will vary with the availability of others (e.g. too much carbohydrate lowers reproduction). The optimality paradigm does not consider the idea that the value of a currency may fluctuate or interact with others.

This finding was similar to the findings of Simpson et al. (1988). They found continued lack of protein in the diets of Locusta migratoria and Spodoptera littoralis resulted in overall decreased consumption even when carbohydrates were present ad libitum. In the present study, even though consumption of both carbohydrates and proteins decreased, this occurred at different rates. As a result, the proportions in the chosen diet mix changed (Fig. 30 & 31) compared to the controls. This is evidence again that there is a fine control of nutrient balancing and that control systems integrate the needs of various reserves.

When average consumption for each dilution period was compared, evidence for both coarse and fine tuning was evident (Fig. 32 & 33). Coarse tuning was shown by the large amounts eaten in the first time period as a result of the previous deprivation period. Fine tuning was shown by the fact that the animals attempted to compensate for specifically diluted nutrients in their diets.

Nutritional compensation has been shown to be qualitatively correct, but is commonly quantitatively incomplete meaning that the missing nutrients are correctly replaced but not necessarily in amounts proportional to the deficiency (Louveaux 1977, Mattson 1980, Simpson & Abisgold 1985). These studies explain qualitative correctness as increased consumption of the diluted nutrient. The present study demonstrated that diluted carbohydrates were compensated by increased protein consumption, so compensation may not involve the particular material that is missing. Previous studies may have overlooked this possibility since they examined only short term compensation as compared to the present investigation. In addition, in situations where no choice is possible, animals would be forced to offset dilution by increased processing of the only available food.

When studying nutritional ecology it is important to show that the diets tested play a significant role in the functioning of that animal. To demonstrate the significance of the foraging control as described in this study, reproductive responses correlated with the changes in foraging strategy were investigated. Since there presumably is a reason for controlling foraging it was hypothesized that there should be a close link between nutrition and

fitness criteria such as reproduction. Thus, oothecal production for each treatment was monitored (Figs. 8, 17, 27). Analysis showed that feeding and reproductive cycles were synchronous. This was done by comparing the average time between peaks in the moving average analyses performed on both consumption and oothecal production data for the controls (compare Figs. 5,6 & 9 ), the carbohydrate diluted treatment (compare Figs. 13, 15 & 18) and the protein diluted treatment (compare Figs. 23, 25 & 28). Regression analysis showed that average daily oothecal production increased over the 90 day experimental period for each treatment (Figs. 10, 19, 29). This could have been explained by the generally improved nourishment of all the animals following the deprivation period. Also, the large increase in total consumption by the carbohydrate diluted group at day 40 (Fig. 16) was reflected as an increase in total daily oothecal production in the same time interval. The fact that reproductive effort increased as energy consumption decreased is totally at odds with optimality theory since reproductive effort is linked to a function other than energy maximization in this case.

Given that *P. americana* responds to long-term food deprivation and dilution by tactical compensatory responses, the next two experiments were designed to demonstrate the

ability to recognize food quality and preferences. Quality and palatability of food may be useful in determining which foods to incorporate in a compensatory response since short-term motivation to feed is affected by both quality and palatability. However, the predominant cues of specific foods may not correspond exactly to the actual nutritional content of the diet. This is why motivation must be the result of a number of factors such as the food cues, internal cues and learning associated with that particular food. A complex motivational stimulus provides safe guards against the risks of malnutrition or poisoning.

#### B. Preference for sucrose concentration

The fact that the animals tested spent more time eating higher quality sucrose samples (Fig. 35) indicated that they were able to select foods that would supply more energy for the amount of effort spent. Selection for food quality has been shown for various animals (Richter et al. 1938, House 1967a, 1970, Waldbauer & Bhattacharya 1973, Greenstone 1979, Waldbauer et al. 1984, Simpson & Abisgold 1985, Cohen et al. 1987, Simpson et al. 1988). The majority of these studies use the "cafeteria" analogy of food selection to show that animals can choose the most nutritious food or diet mix from an array of foods presented

to them. This approach is meant to mimic the natural situations of the various animals. In the present investigation the cockroaches chose from multiple samples of five different sucrose qualities arranged on a random grid. This arrangement was meant to increase the probability of each individual to experience every food type equally.

### C. Reactions to Gustatory/Olfactory and Nutrient Cues

In experiment B, P. americana was shown to be able to select for nutrient quality. The nutrient tested was sucrose. However, as mentioned above food cues may not always directly indicate nutritive value of the food. Thus quality and palatability can be considered as independent food type variables. When a hungry animal comes in contact with a food it must decide whether or not this food should be eaten. This choice is aided by recognition which is the result of either past experience or innate programming (Rozin & Kalat 1971). The ability to use gustatory, olfactory and nutritional cues as stimuli which elicit preference or aversion is an adaptive response in terms of risk taking (Rozin & Kalat 1971). Such risks can be measured on two levels; in terms of poisons and energy gains. Thus,

there may be two reaction types: aversions to poisonous foods or preferences to foods having positive consequences.

In the present study, preferences and aversions to various nutritional and gustatory/olfactory cues were determined first (Figs. 36-38). Then these cue types were combined in contrasting pairs and the overriding cue type was determined (Fig. 39). It appeared that sucrose, which was a positive nutritional cue, had greater effect than bay leaf extract, an aversive olfactory/gustatory cue, when these were mixed together. Note, that bay leaf had previously been shown to be aversive in the absence of sugar. This does not mean, however, that the tested gustatory/olfactory cues have no effect on food choice.

It seems that unless there is a specific hunger or an innate preference, food cues become ranked relative to each other, and this varies with the particular combination of cues and with the nutritional state of the animal. For this reason a palatability index (Fig. 41) was derived for the various preference tests. This was done by giving the most palatable food of all the choice tests a value of 100 and scaling all other choices accordingly.

The first example of relative palatability ranking was found in the consumption of the blank diet. The range of the palatability index for the blank food ranged from

approximately 3 to 40 index units (Fig. 41) depending on the combination of foods offered. The second example was the change in preference for Equal<sup>®</sup>. The palatability index for Equal<sup>®</sup> decreased five times when it was offered in conjunction with sucrose instead of Sugar Twin<sup>®</sup> (Fig. 41). The third example was found in the change of preference between an amino acid mix and the same mix with an added aroma. The amino acid mix containing kirsch aroma was 200 times more palatable than without the aroma (Fig. 40). Similar results concerning changes in palatability have been shown. For example, Harris *et al.* (1933) conducted various experiments showing that vitamin B deficient rats could recognize foods containing vitamin B. They found that added flavouring enhanced correct choices, and that an array of variously flavoured foods complicated the choice. Thus, the palatability of any one substance is not absolute. The palatability index of a food can be changed relative to a number of other variables. Such complexity is not addressed by optimal foraging theory.

This type of adjustment is a fine-tuned control of foraging. The probability of having preprogrammed palatability for a particular food type would be very low (Rozin & Kalat 1971) unless the material is extremely critical or it can be detected by a relatively "cheap"

receptor (e.g. salt, sugar, water etc.). The ability to adjust consumption on the basis of palatability allows for balancing of nutrient intake and maintenance of physiological homeostasis. Thus, it seems more likely that there would be preprogrammed guidelines that would allow for adaptive responses in constantly changing situations (Geissler & Rollo 1987). Also, such a flexible system of scaling might be very adaptive for omnivores since required nutrients may be available in a wide variety of food types. Exactly how foods are ranked along the palatability index is not clear.

The magnitude of incentive values is one possible factor affecting the variable palatability index of foods, where incentive is the value of the expected nutritional consequence as indicated to the animal by either olfactory or gustatory stimuli. This value may be either positive or negative depending on whether the effect of the food is beneficial or not. The incentive value of a particular food may change in the presence of different food combinations based on tradeoffs between such factors as urgency of specific nutrient requirements and handling time of the foods.

Incentive is a variable considered to be influential in feeding initiation and continuation (see review by Toates



1981). Food preferences can result from either anticipated positive consequences or from acquired taste preferences for specific stimulatory cues (Rozin & Fallon 1981). However, only humans and select mammals have been shown to develop taste preferences specifically for stimulatory cues that are not linked to nutritive value (Rozin and Kennel 1983). Since internal factors such as innate palatability and learned taste preferences seem to be less likely explanations in an adaptive sense, then possibly palatability is influenced by an external factor such as incentive. Incentive is influenced by both excitatory value and the current nutritional state of the animal (Booth 1980). The various combinations should lead to the ranking of foods by palatability.

Another result found in this experiment that strongly contradicts optimal foraging theory was the fact that the blank diet was consumed in large quantities. The consumption of the blank diet represented more than just sampling. It was included as a definite food item. Since consumption of a non-nutritive substance could not maximize any part of the animal's foraging success, this evidence contradicts maximization theory. Possible reasons for the consumption of the blank diet are: 1. As a source of roughage. 2. Because there was a positively associated conditioned response to

agar based food media. 3. As a form of gut volume maintenance even though there was no nutritional value. 4. The animals' behaviour is so poorly adapted that they will eat any material that has the consistency of food. Optimality theory would not allow such explanations which may be entirely possible.

#### D. Compensatory Responses to Specific Nutrient Starvation

Experiment A showed that *P. americana* was able to compensate for total deprivation and specifically for diluted nutrients. The following experiments (B & C) showed the abilities to differentiate food quality and to fine-tune a diet based on palatability. Given this information, the final experiment (D) was designed to test whether *P. americana* could compensate on the short term for the correct nutrient after deprivation from a specific food group. Compensation for deprivation of both carbohydrates (C) and proteins (P) did occur (Figs. 44 & 43). This was evidenced by greater consumption of the missing nutrient when all nutrients were offered to the cockroaches. Food C was slightly more palatable than P for cockroaches acclimated on both complete (PC) food and the blank food (O) (Figs 42 & 45). However, the animals preferred the premixed protein/carbohydrate (PC) food to foods P and C in all treatments. This preference may be an adaptive response in

the case of omnivores with risky nutrients. Even if the nutrient balance is not correct, it would be better to select a food containing some of all the essential materials, than to risk missing an essential nutrient all together by seeking various complementary foods. The choice to do this would be affected by whether the animal is coarse or fine tuning its diet. Thus, optimality may be abandoned if a safely sufficient food was readily available. The need to balance an extremely complex mix of nutritional requirements might actually make the idea of optimal diet selection intractable not only for our analysis, but for the animals themselves.

Various investigations have shown similar results. Rats have been most commonly tested for specific hungers and self-selection of nutrients (Overmann 1976). They regulate a number of nutrients such as sodium (Nachman 1962, Stricker & Wilson 1970) and thiamine (Richter et al. 1938, Rozin et al. 1964). Recently, insects have been added to the list of animals self-selecting diets. Simpson et al. (1988) found that Locusta migratoria and Spodoptera littoralis selected nutrients missing from a conditioning diet when offered a choice of various foods. These nutrients were found in artificial protein and carbohydrate mixes similar to the ones used in the present study. The experimental protocol

were also similar. The conditioning period used by Simpson *et al.* (1988) was 4, 8 or 12 hours and the animals were monitored directly after the new choices were offered.

Self-selection for missing nutrients may also involve aversions to low quality foods or food types not complementing the nutrient deficiency. This was best demonstrated by the animals conditioned on the blank diet (O) (Fig. 45). On the conditioning days of the experiment these animals consumed the blank diet in amounts only slightly lower than the more nutritive foods (Fig. 46). On the trial day the blank diet was almost completely excluded from the chosen mix of foods (Fig. 45). Thus both preferences and aversions were entailed in fine-tuning a balanced diet.

Coarse control of compensation was also shown by the animals conditioned on O diet. There are two reasons for considering that this response was coarser than the other groups. First, the discrimination between PC, P and C foods was less than that displayed by cockroaches conditioned on PC, P or C foods (compare Fig. 45 with 44 & 43). As mentioned in the discussion of experiment A, selectivity decreases with coarser responses. Second, on the third feeding day the total amount of food consumed increased by a factor greater than any of the other conditioned cockroaches

(Fig. 46). This increased consumption response was similar to the one shown in experiment A. As proposed there, increased consumption may be a coarse response prompted by uncertainty experienced in the environment such as the artificial situations created in a laboratory. The situation here was unusual for the animals because they were filling their crops but not obtaining nutrient value from the ingested food.

## SUMMARY

An important point to remember when considering a behaviour as flexible as foraging is that the conclusions drawn from observations in either manipulative experiments or in the field are all relative to the inherent properties of the animals tested and to the protocol of the experiments.

One of the conclusions based on the observations made in this study was that optimality theory does not provide a satisfactory model for omnivores such as Periplaneta americana. Foraging did not appear to be an all or none decision, which was one of the assumptions of optimality theory. The animals did not decide that a food was suitable and proceed to consume the maximal amount in a minimal time. Thus the maximization concept is also not a general rule, although it may be implemented in an appropriate situation.

The proposed alternative model of foraging was one of foraging regulated to fulfil a homeostatic physiology. The regulators were hypothesized to be innately programmed preferences or general rules that directly or indirectly guide the animals to correct choices concerning quality and quantity of food. The two hypothesized types of control were accepted. Foraging may be coarsely controlled by generalized rules used to respond to circumstances of uncertainty or

where resources are unreliable. In this case risk taking increases as preferences become less specific and a greater variety of food types and qualities becomes acceptable. In both cases storage reserves and physiological demands determine the state of the dynamic system. It is notable that few papers based on optimal foraging theory consider the role of reserves or long-term regulation at all.

When the environment presents less uncertainty foraging becomes more finely controlled. Fine tuning of the diet must involve either innate controls such as specific hungers or generalized rules which increase discrimination of foods. Judgement of food quality and palatability becomes more specific.

The adaptive value of integrated fine and coarse foraging control can be measured in terms of the consequential value of risk taking. Basically, if an animal is malnourished or if its resources are insecure, it should assume greater risks than when well nourished. A genetic program which allows for such flexible alternative responses is a definite advantage to a ubiquitous omnivore such as P. americana.

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Figure 1. Arrangement of randomly located food samples in the feeding arena. Twenty samples each of five food types (Total of 100 food samples).

3.1	4.1	1.1	4.2	1.2	4.3	3.2	4.4	4.5	3.3
3.4	1.3	3.5	1.4	2.1	5.1	2.2	3.6	3.7	3.8
2.3	4.6	1.5	5.2	2.4	4.7	3.9	3.10	4.8	4.9
1.6	4.10	2.5	2.6	5.3	4.11	4.12	5.4	2.7	5.5
2.8	4.13	1.7	2.9	2.10	3.11	3.12	1.8	5.6	3.13
1.9	5.7	1.10	4.14	1.11	2.11	3.14	5.8	2.12	5.9
5.10	1.12	5.11	5.12	5.13	1.13	2.13	1.14	2.14	4.15
3.15	4.16	2.15	1.15	2.16	4.17	5.14	5.15	3.16	1.16
4.18	2.17	3.17	2.18	1.17	5.16	1.18	2.19	1.19	5.17
1.20	5.18	2.20	5.19	4.19	5.20	3.18	3.19	4.20	3.20

—replicate number

—food type

Figure 2. Experimental apparatus and computer monitoring system. Arms lead to shelter, water or food choices (X).  
PET - computer and monitor  
PIA - computer interface between computer and infra-red station sensors.

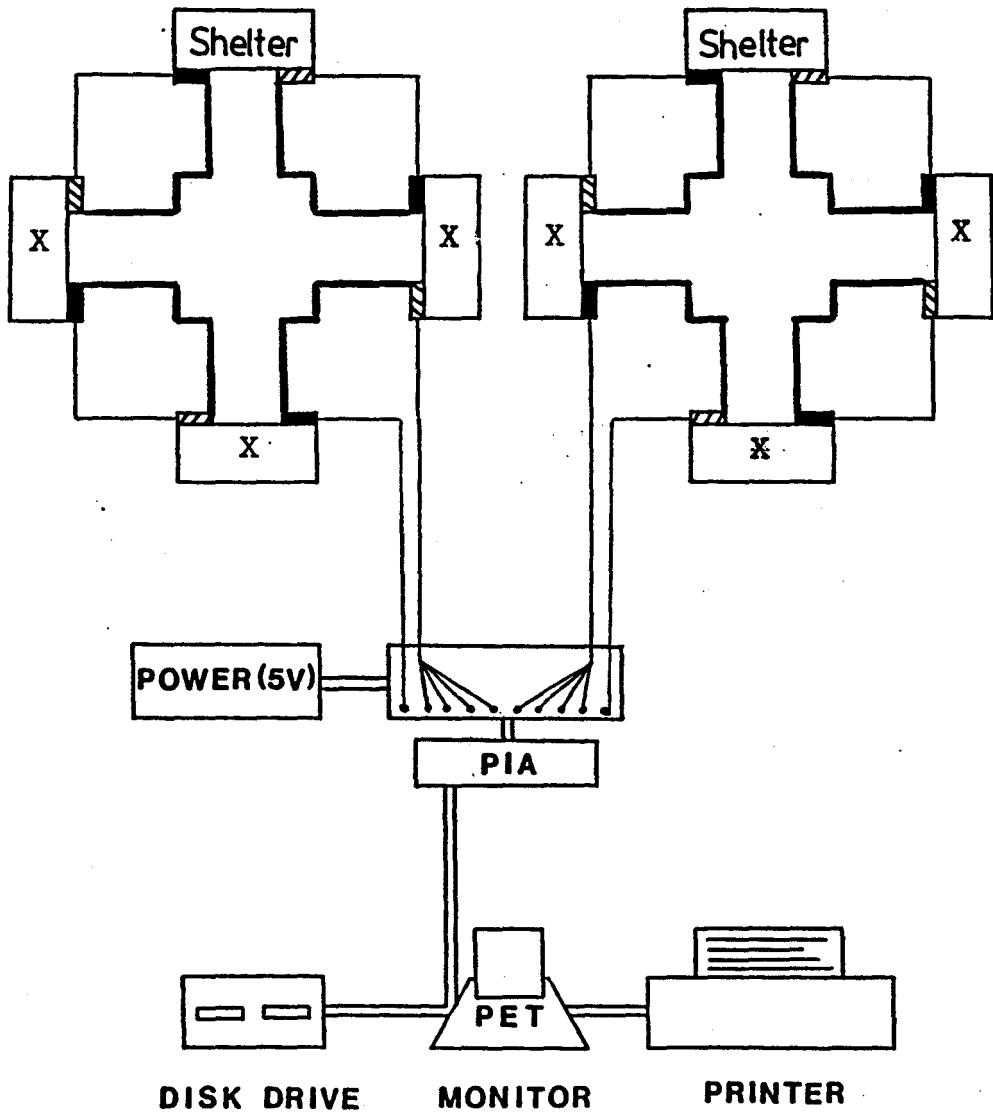


Figure 3. Control treatment, n = 10.  
Individuals fed equal amounts of carbohydrate  
and protein pellets. Daily carbohydrate  
consumption showing first order regression  
( $r=.5071$ ,  $p<0.10$ ).

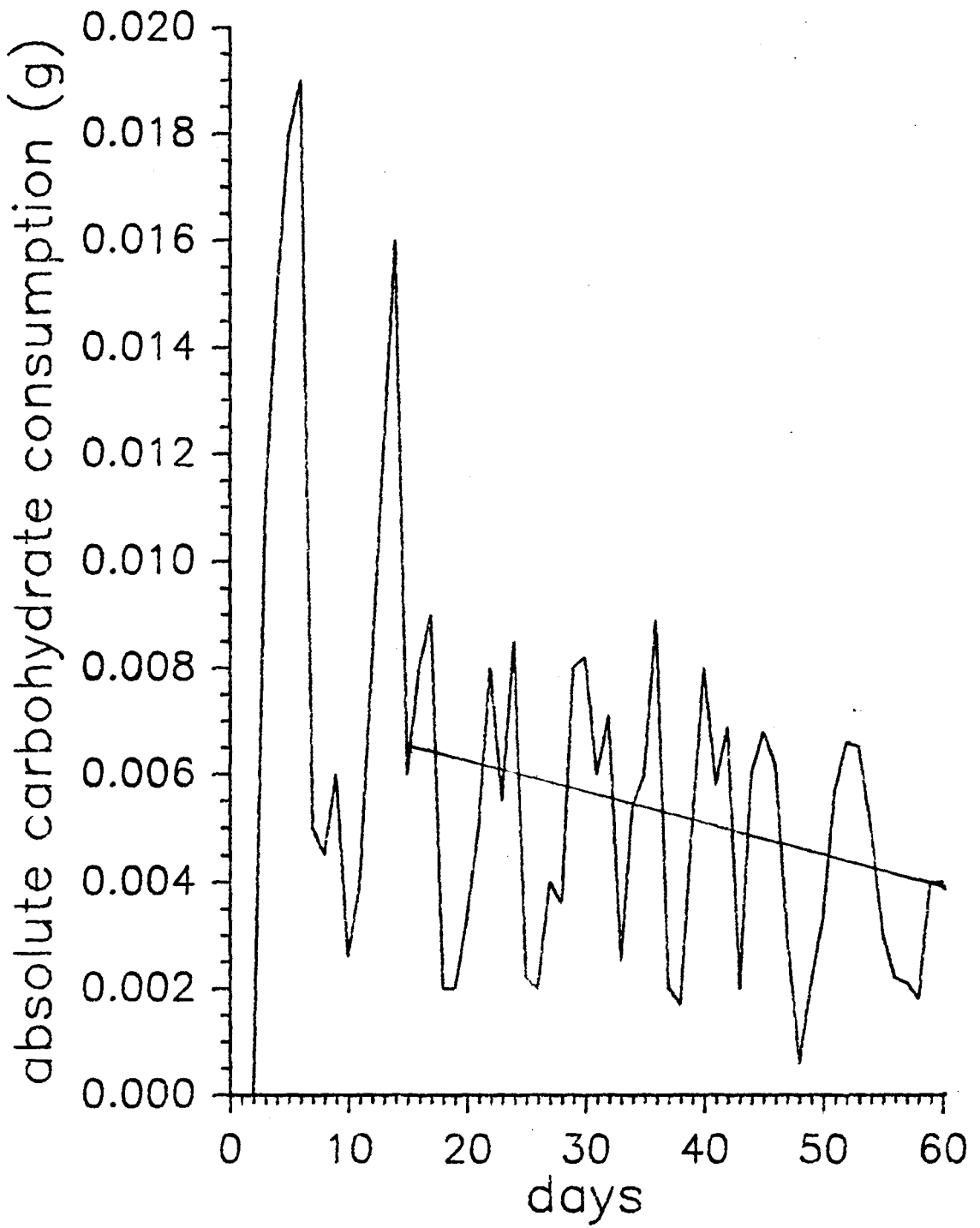


Figure 4. Control treatment, n = 10.  
Daily protein consumption showing first  
order regression ( $r=0.5919$ ,  $p<0.10$ ).



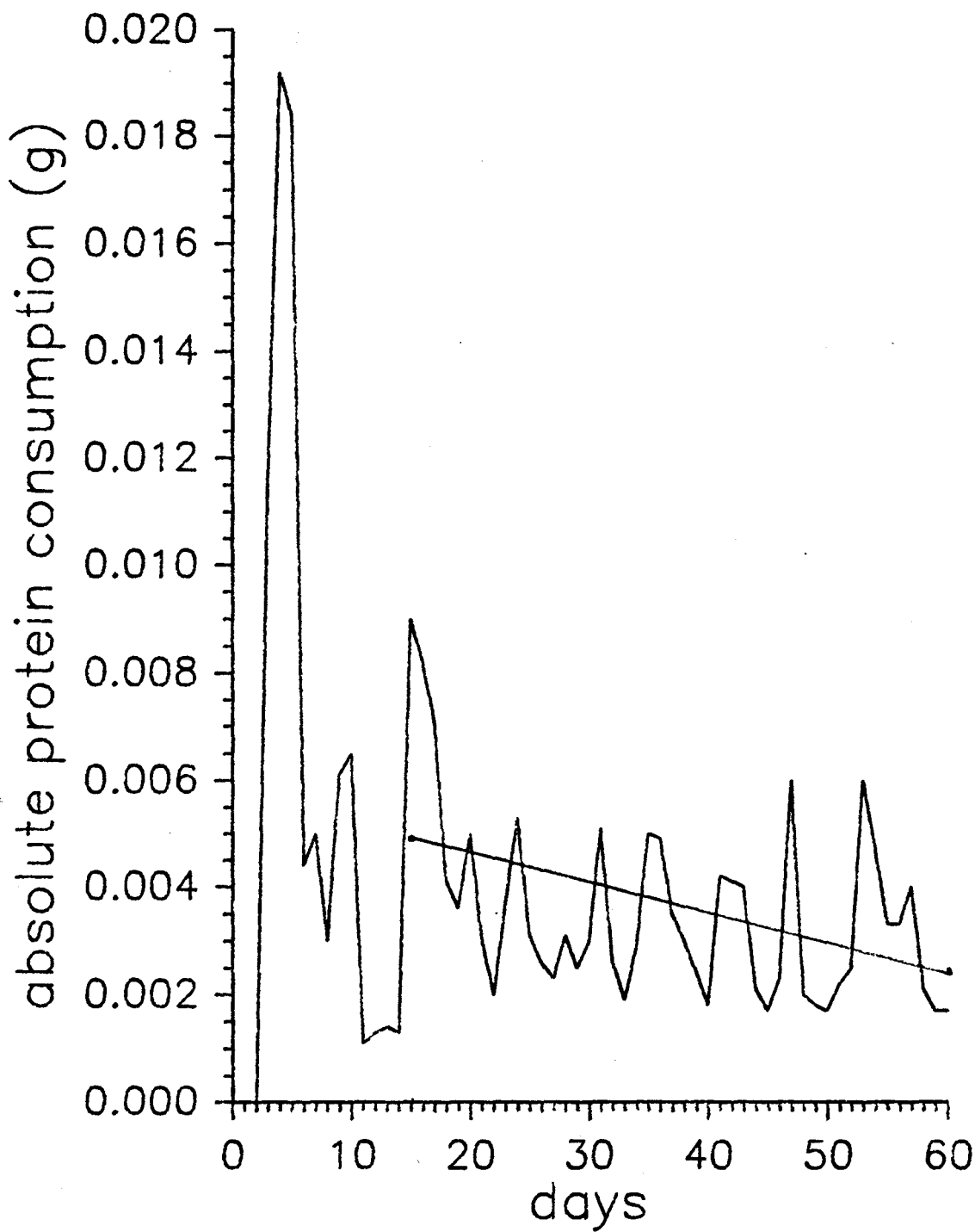


Figure 5. Control treatment, n = 10.  
Three day moving average analysis of daily  
carbohydrate consumption ( $r=0.5186$ ,  $p<0.10$ ).

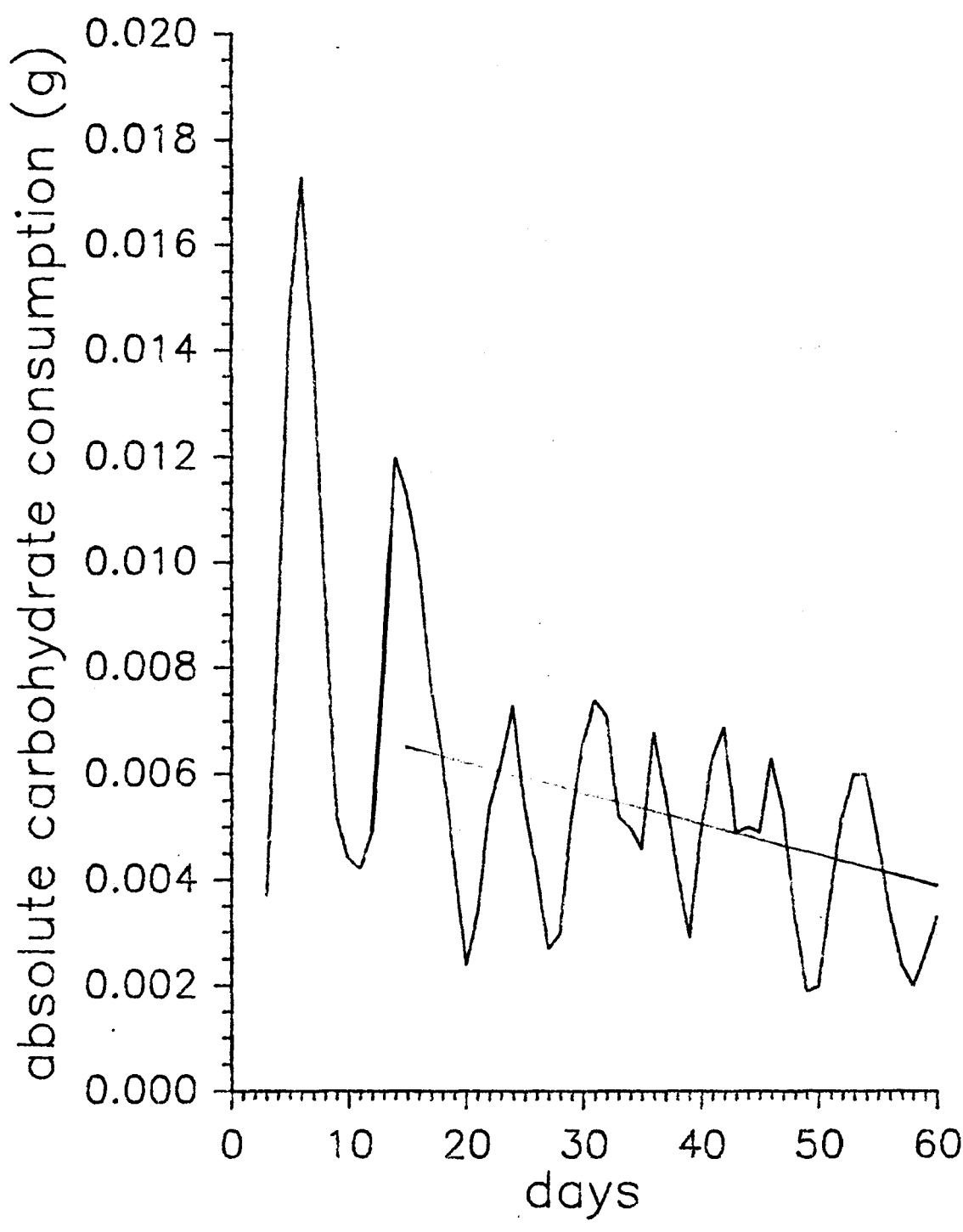


Figure 6. Control treatment, n = 10.  
Three day moving average analysis of daily  
protein consumption. First order regression  
shown ( $r=0.6155$ ,  $p<0.10$ ).

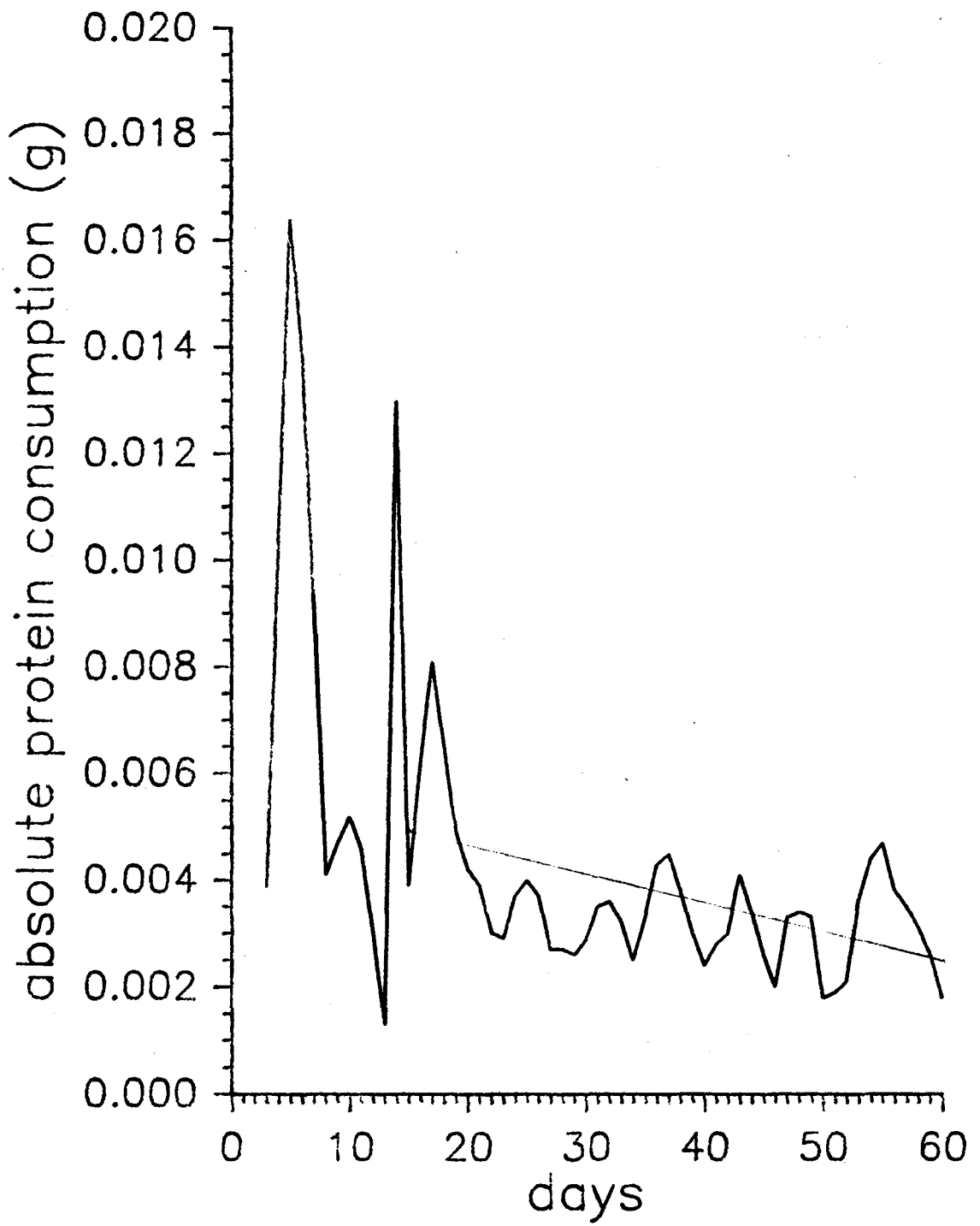


Figure 7. Control treatment, n = 10.  
Daily total carbohydrate and protein  
consumption showing first order regression  
( $r=0.6081$ ,  $p<0.10$ ).

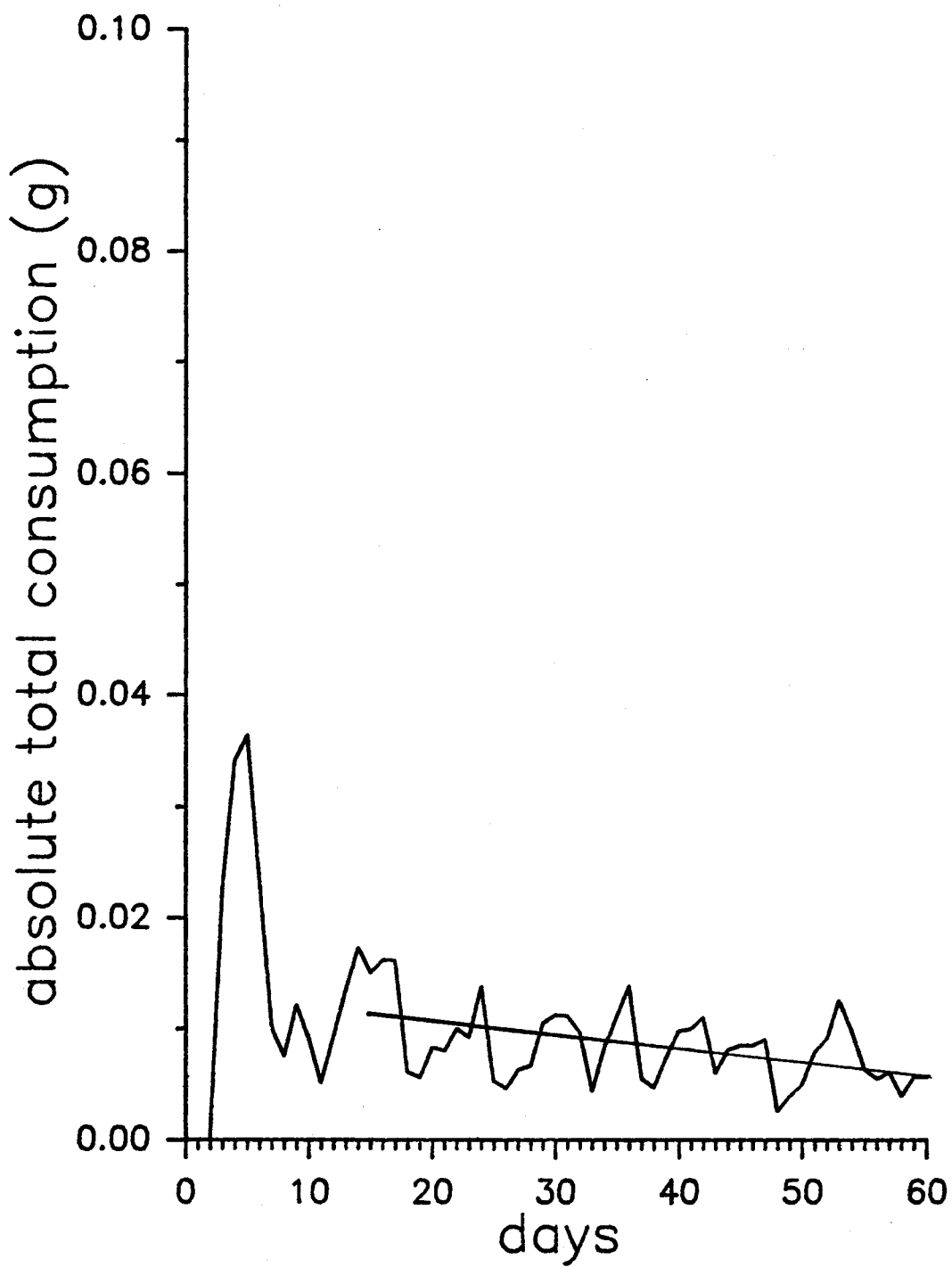


Figure 8. Control treatment, n = 10.  
Total daily oothecal production.



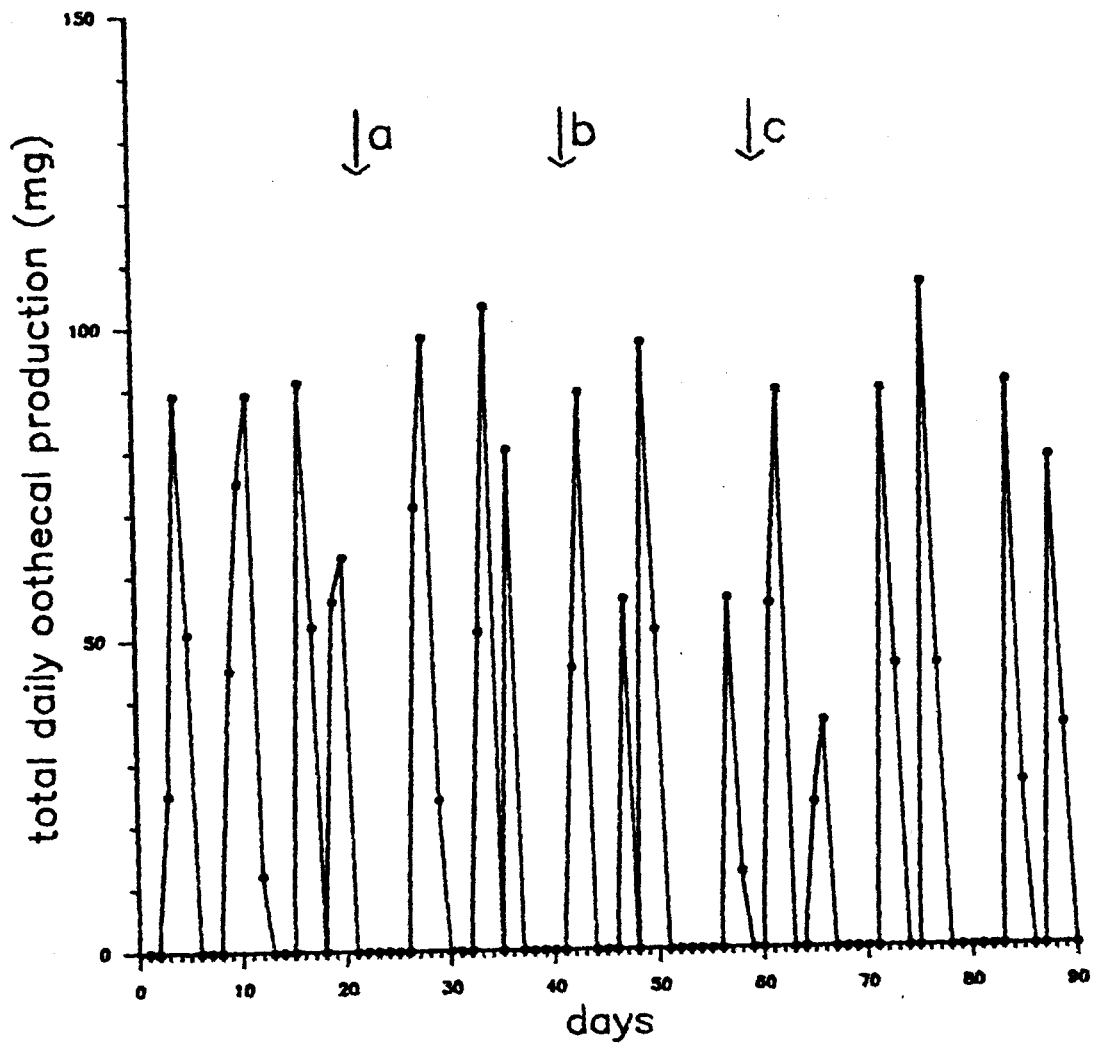


Figure 9. Control treatment, n = 10.  
Three day moving average analysis of total  
daily oothecal production.

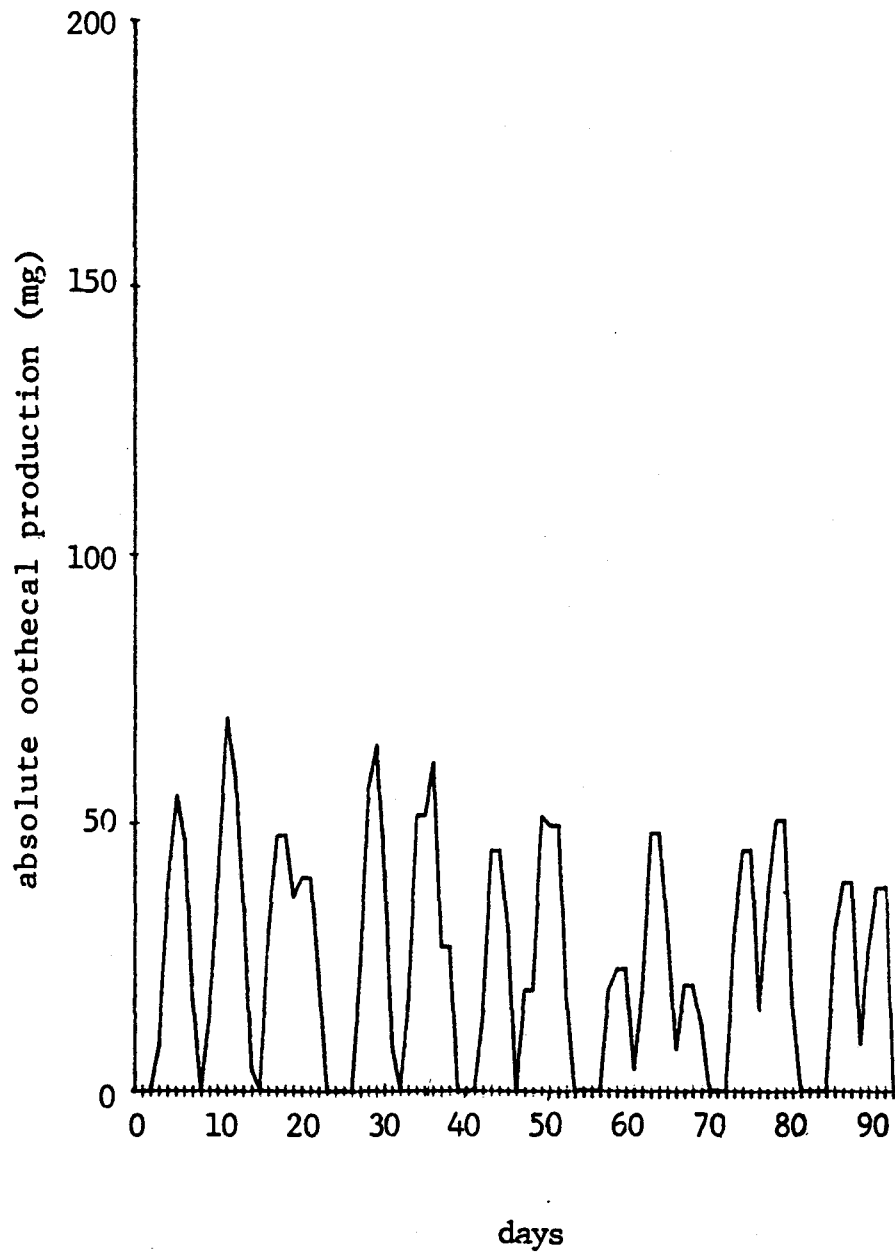


Figure 10. Control treatment, n = 10.  
Average daily oothecal production showing  
first order regression ( $r=0.5896$ ,  $p<0.10$ ).

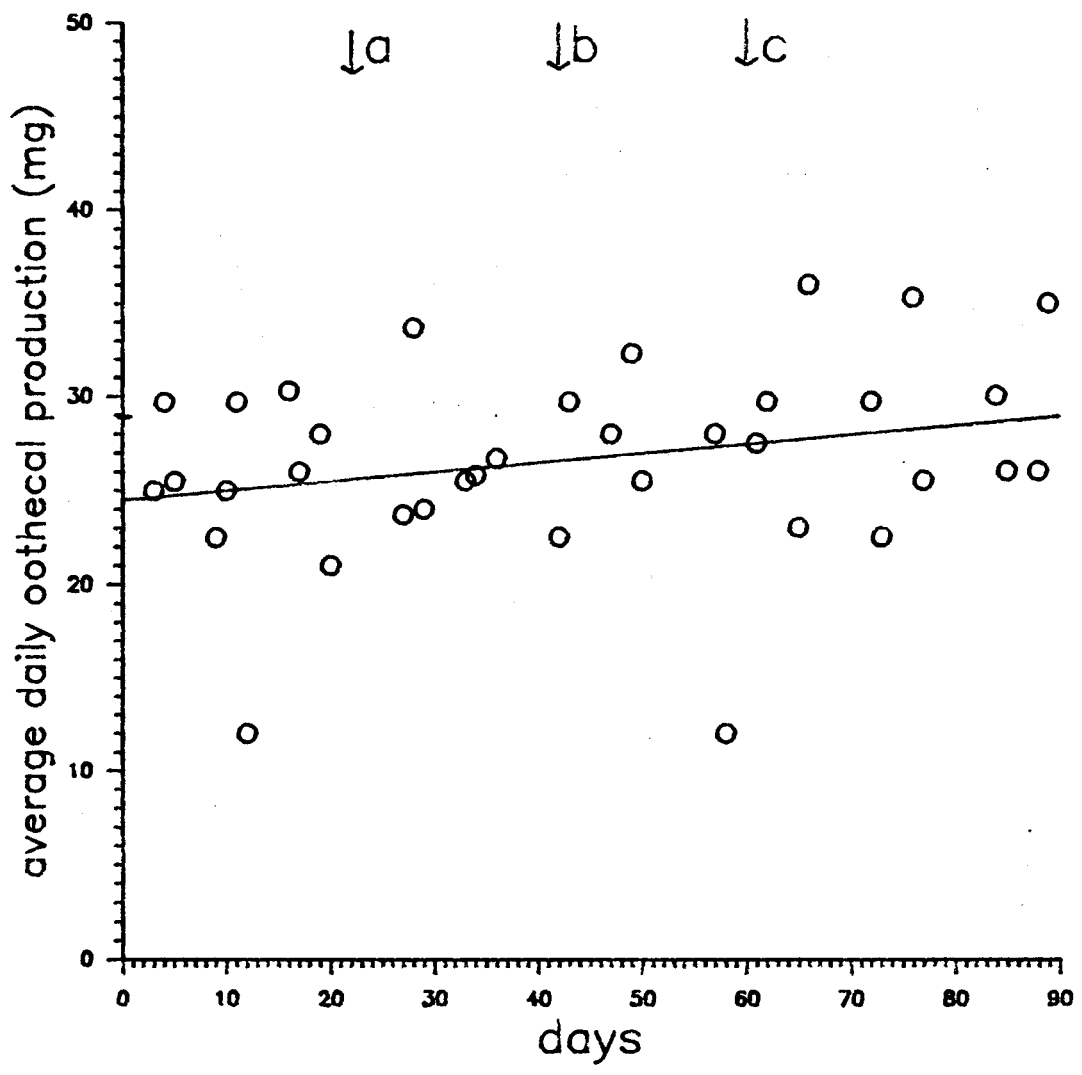


Figure 11. Control treatment,  $n = 10$ .  
Proportionate representation of carbohydrate  
and protein consumption. First order  
regressions are shown ( $r_{\text{carbohydrate}}=0.5139$ ,  
 $p_{\text{carbohydrate}} < 0.10$ ,  $r_{\text{protein}}=0.5139$ ,  $p_{\text{protein}} < 0.10$ ).

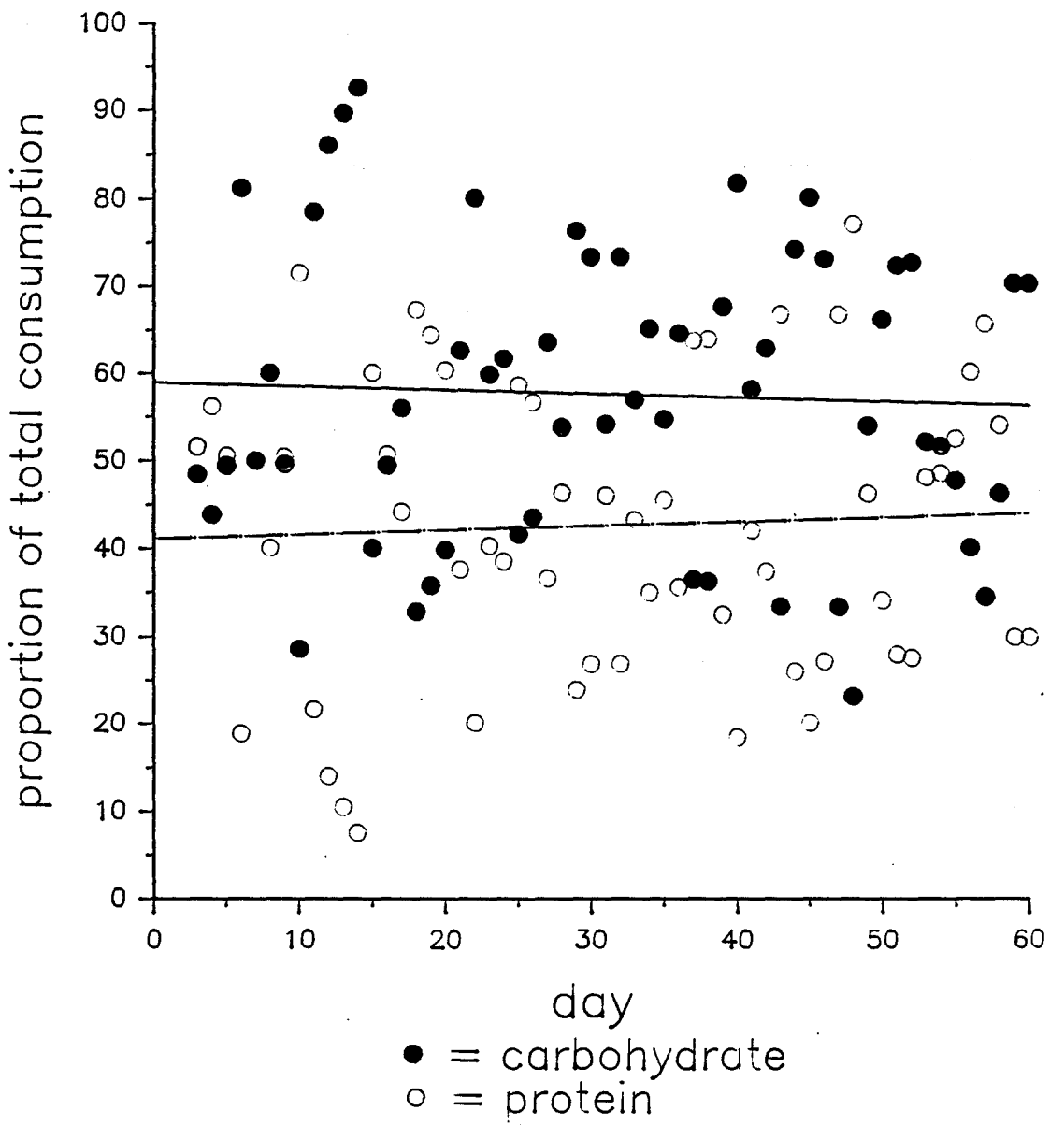


Figure 12. Cockroaches given diluted carbohydrate diet, n=10. Daily carbohydrate consumption showing first order regression ( $r=0.6025, p<0.10$ ).



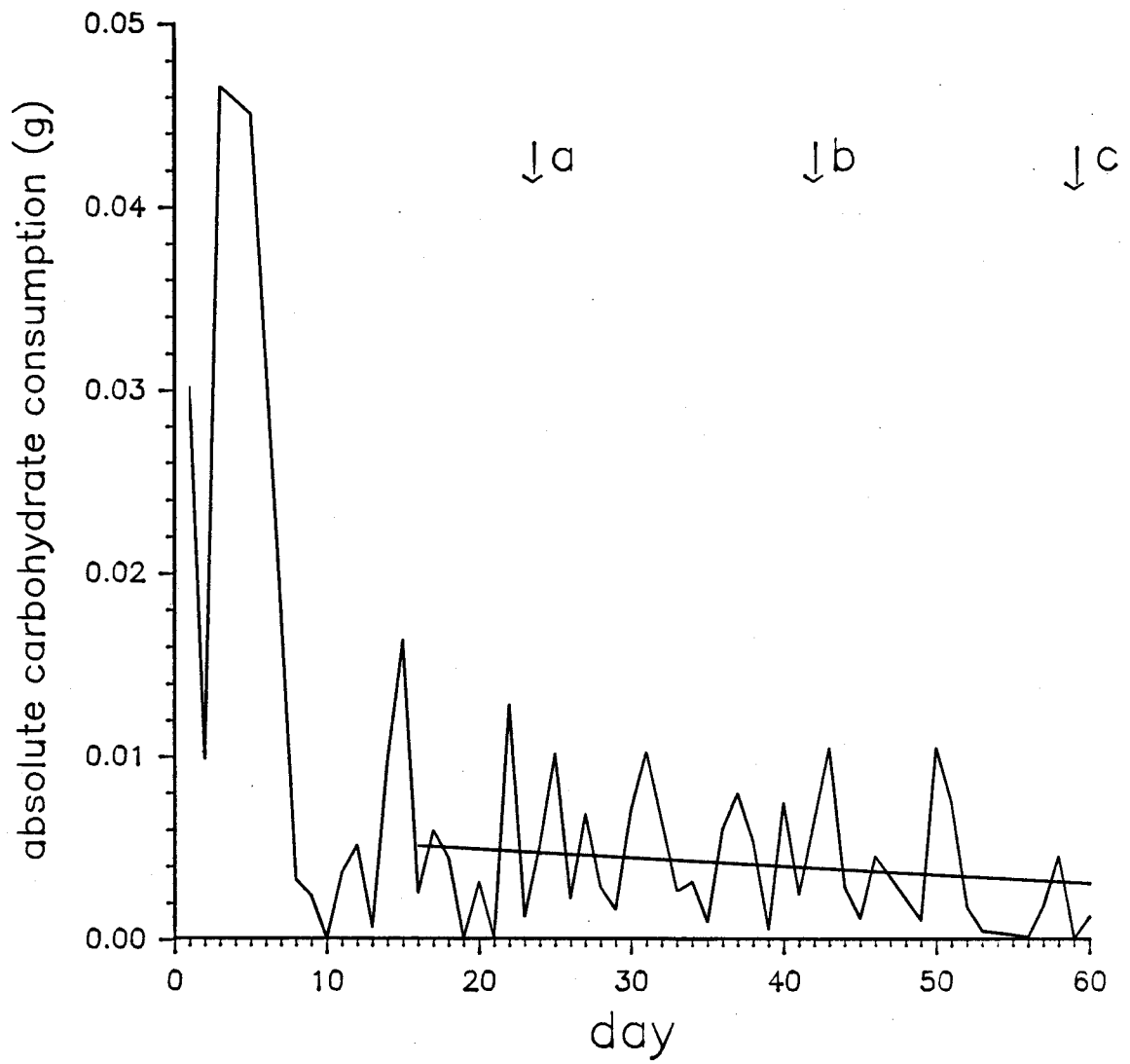


Figure 13. Cockroaches given diluted carbohydrate diet, n=10. Three day moving average analysis of daily carbohydrate consumption. First order regression shown ( $r=0.6039$ ,  $p<0.10$ ).

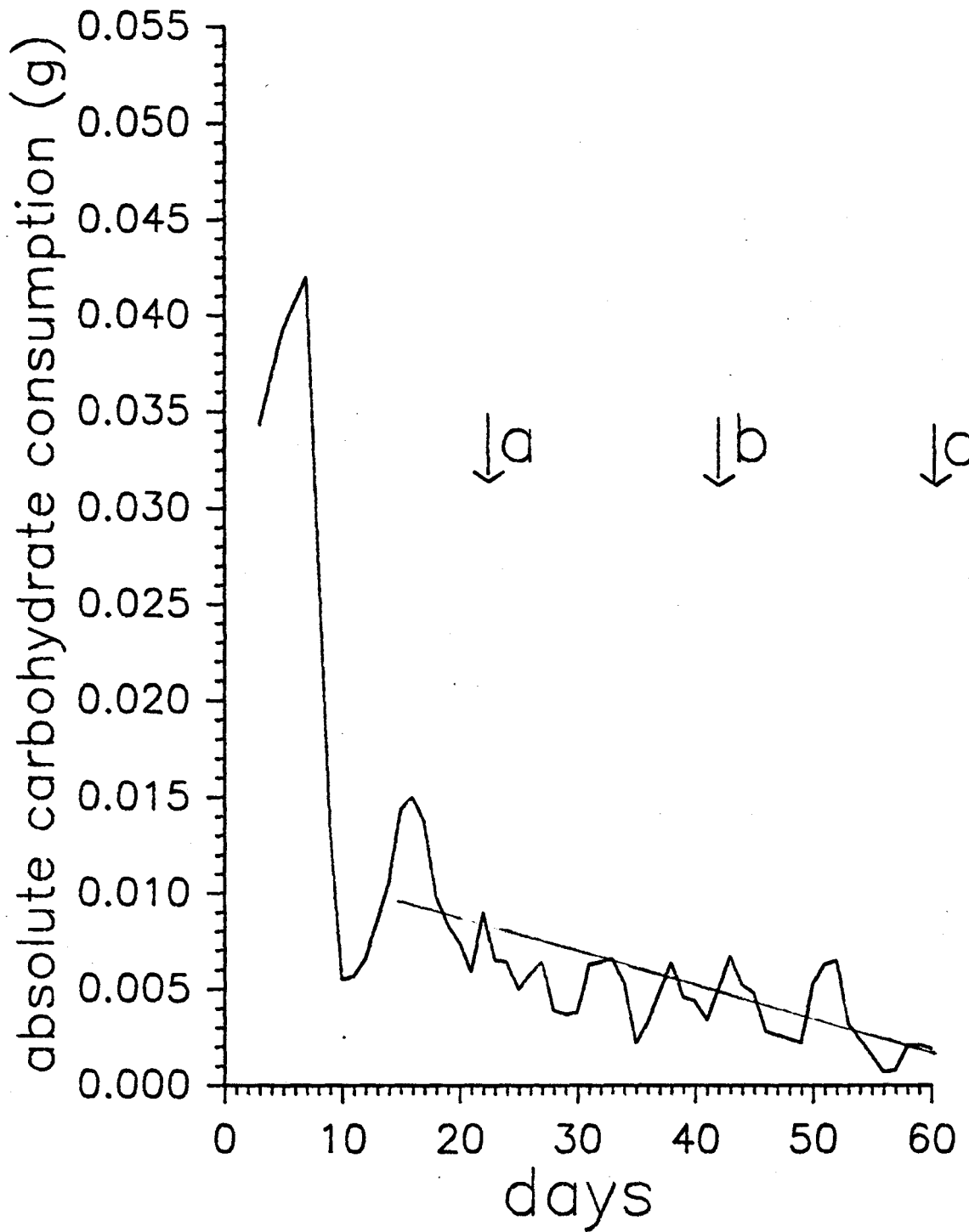


Figure 14. Cockroaches given diluted carbohydrate diet, n=10. Daily protein consumption showing first order regression ( $r=0.5292$ ,  $p<0.10$ ).

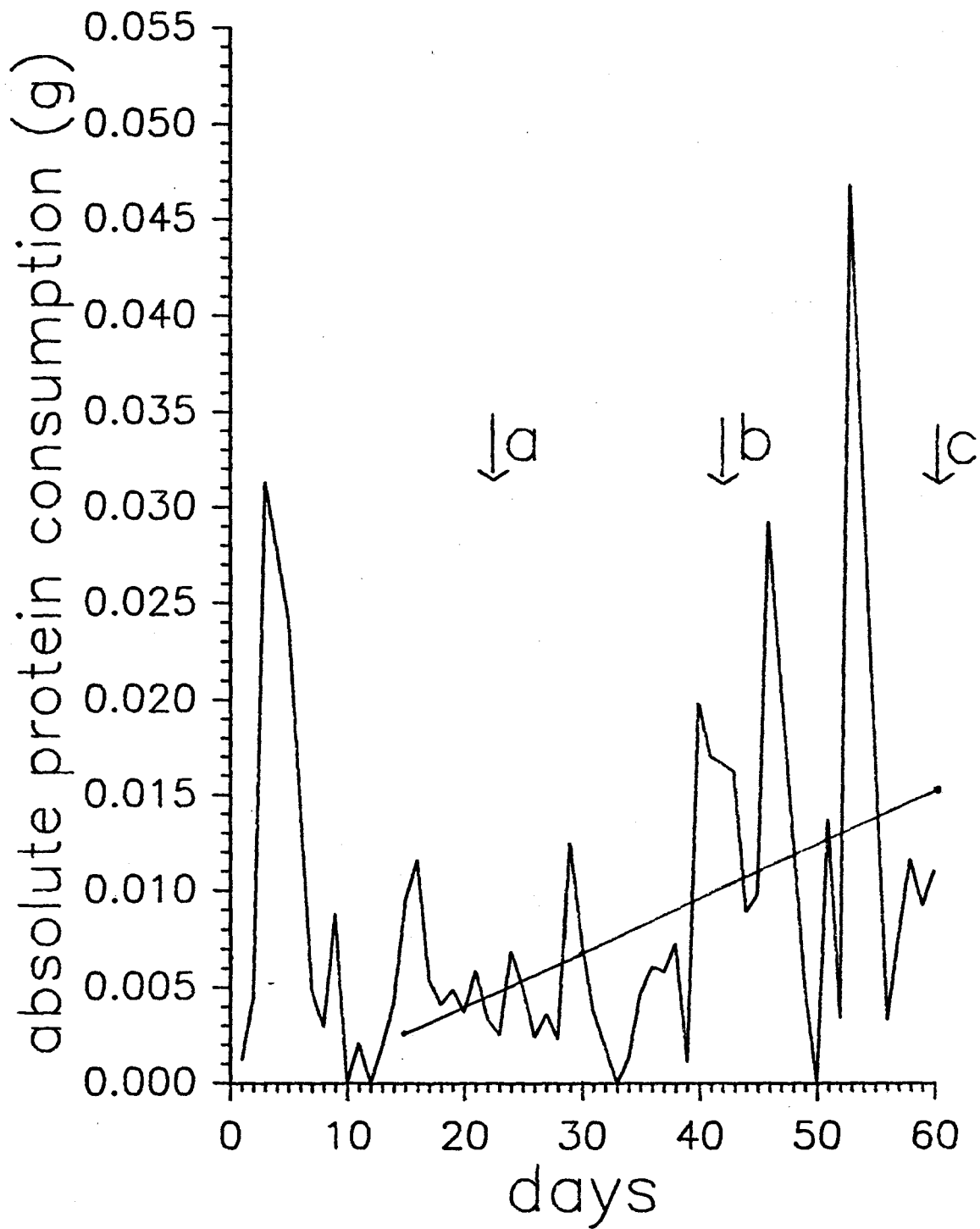


Figure 15. Cockroaches given diluted carbohydrate diet, n=10. Three day moving average analysis of daily protein consumption ( $r=0.5392$ ,  $p<0.10$ ).

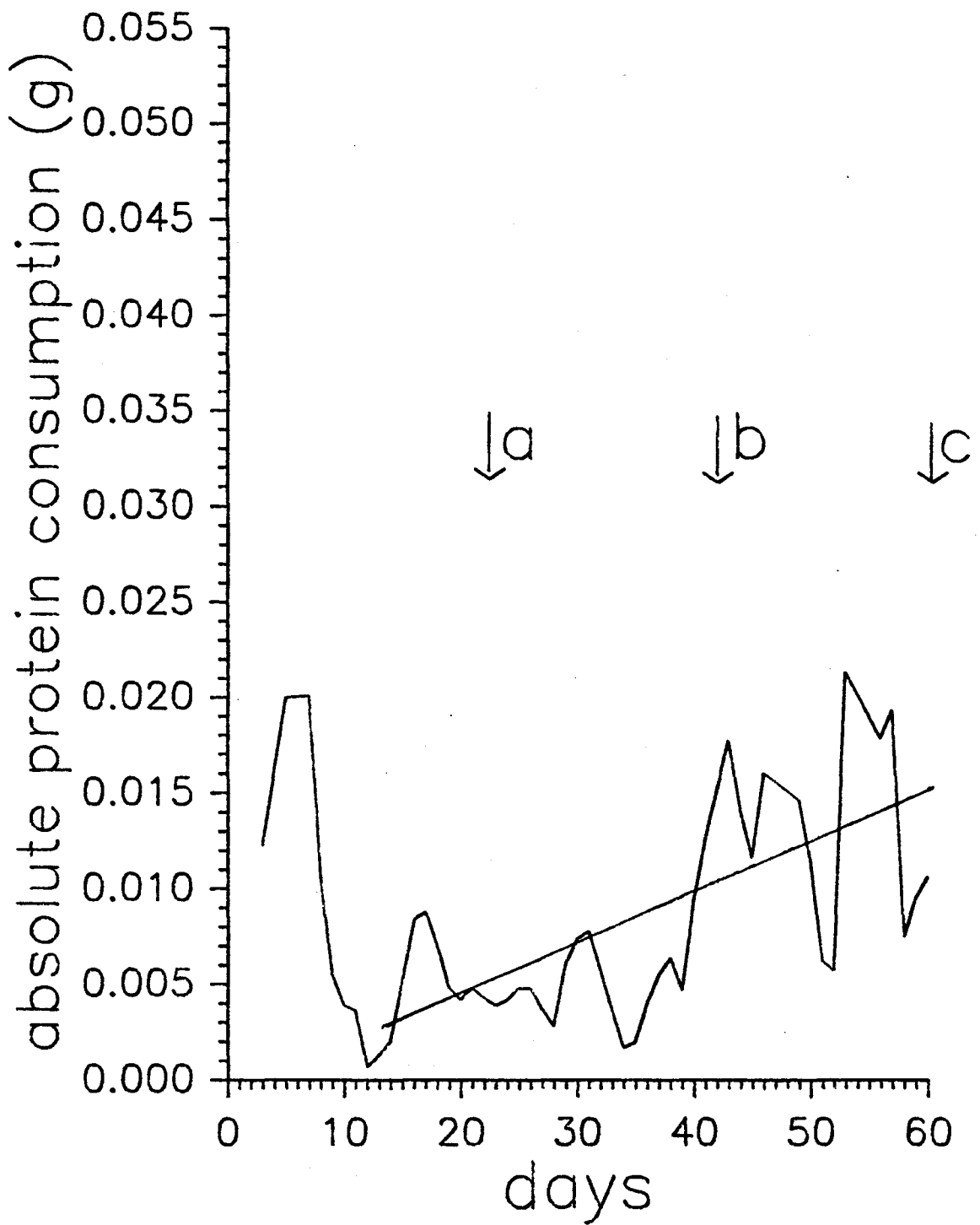


Figure 16. Cockroaches given diluted carbohydrate diet, n=10. Total daily consumption of carbohydrate and protein showing first order regression ( $r=0.5342$ ,  $p<0.10$ ).



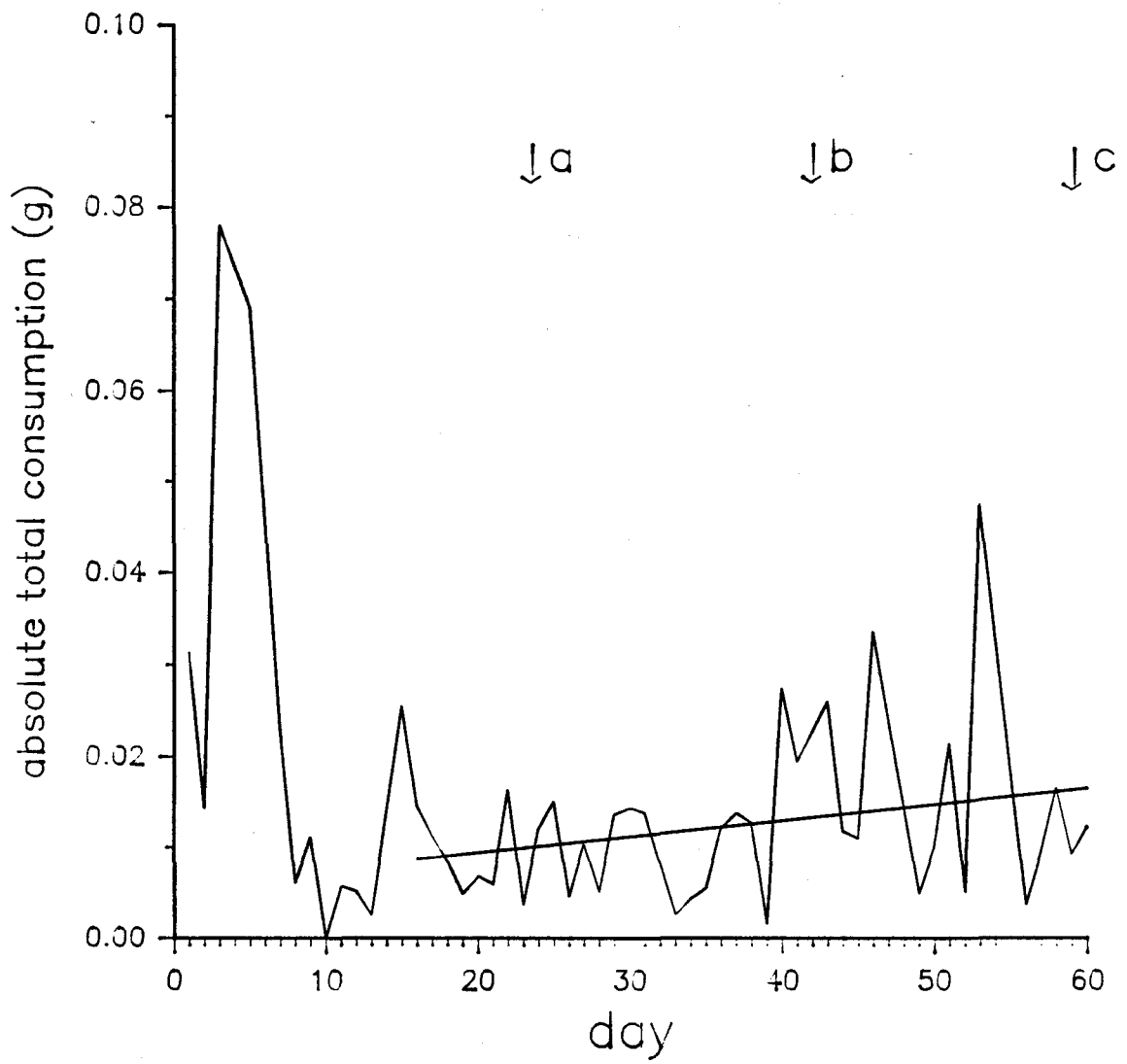


Figure 17. Cockroaches given diluted carbohydrate diet, n=10. Total daily oothecal production.

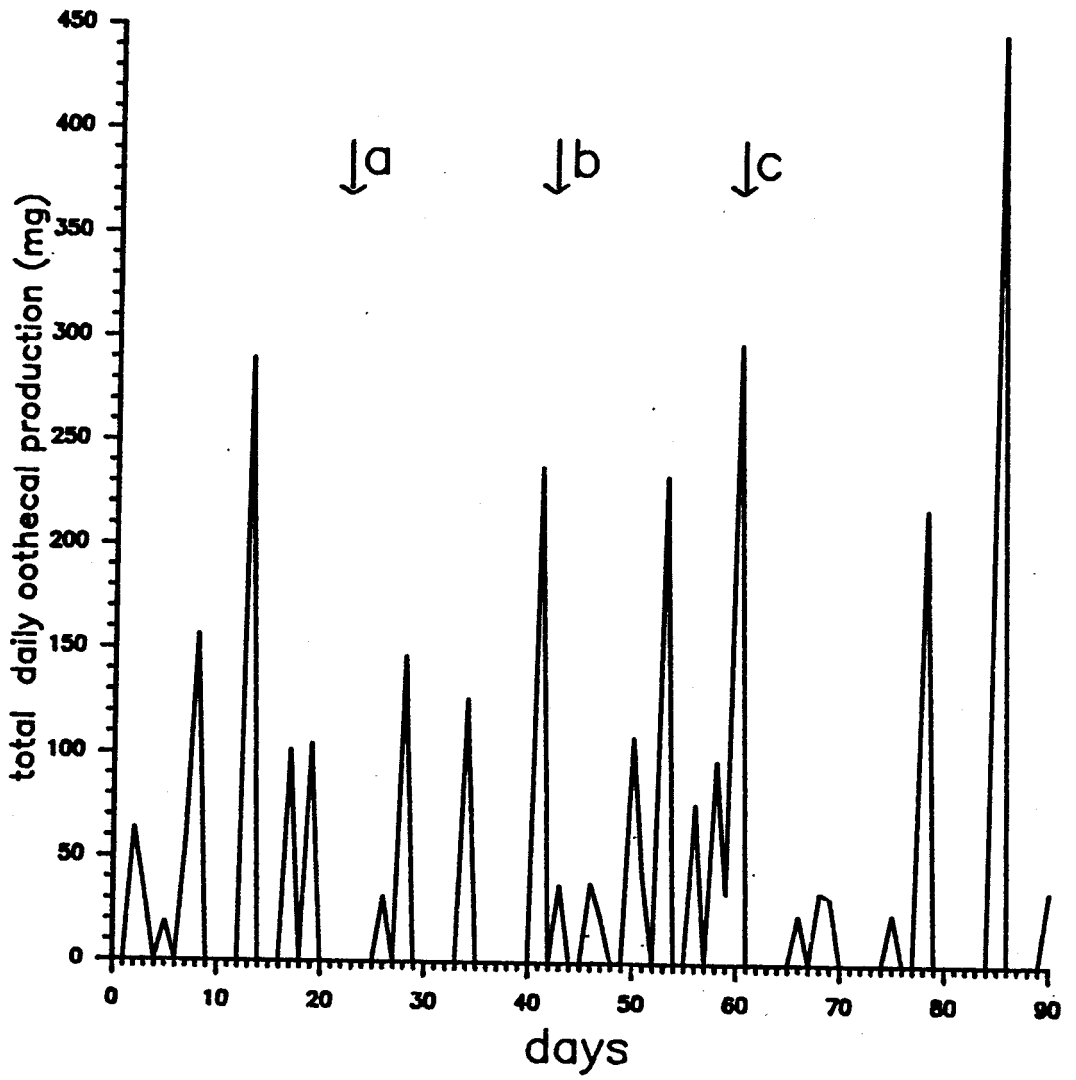


Figure 18. Cockroaches given diluted carbohydrate diet, n=10. Three day moving average analysis of total daily oothecal production.

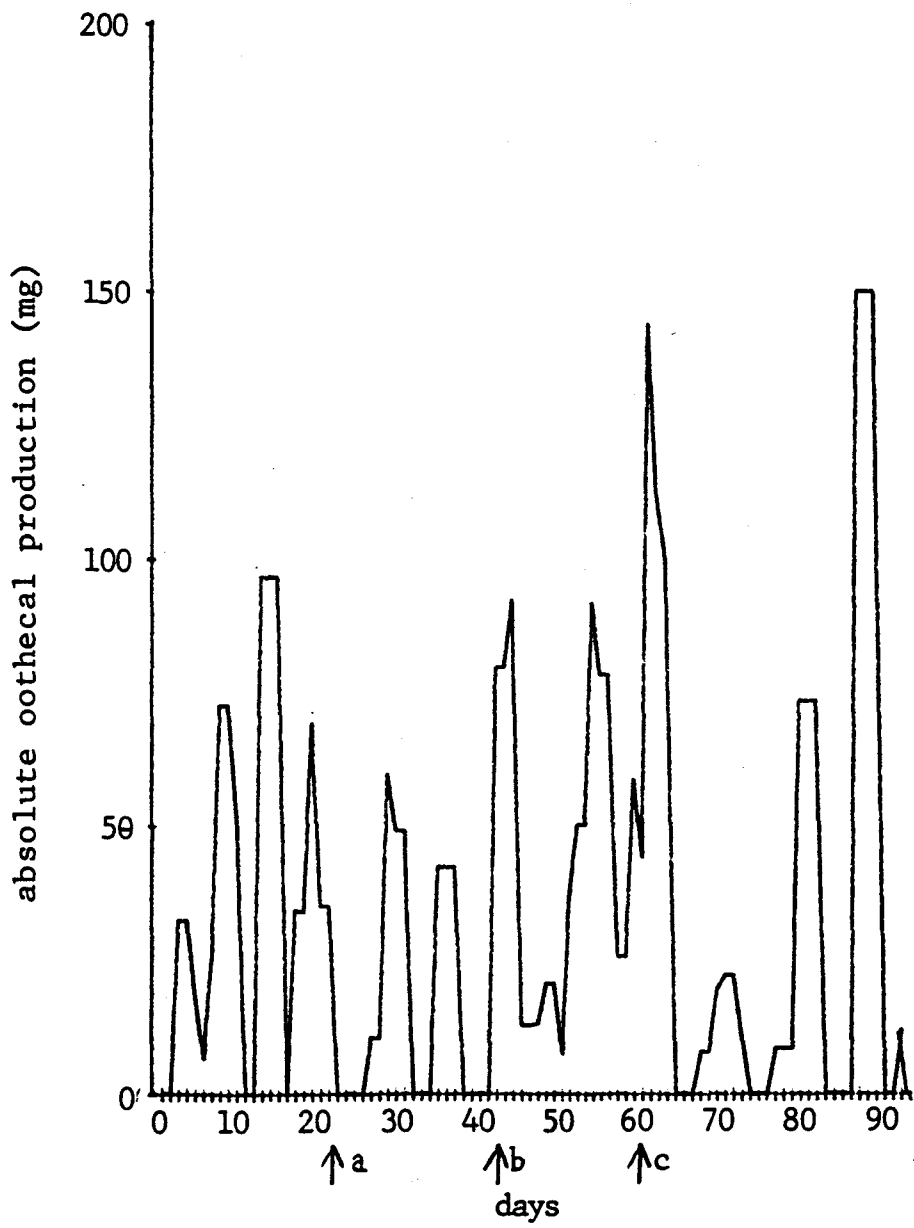


Figure 19. Cockroaches given diluted carbohydrate diet, n=10. Average daily oothecal production showing first order regression ( $r=0.6734$ ,  $p<0.05$ ).

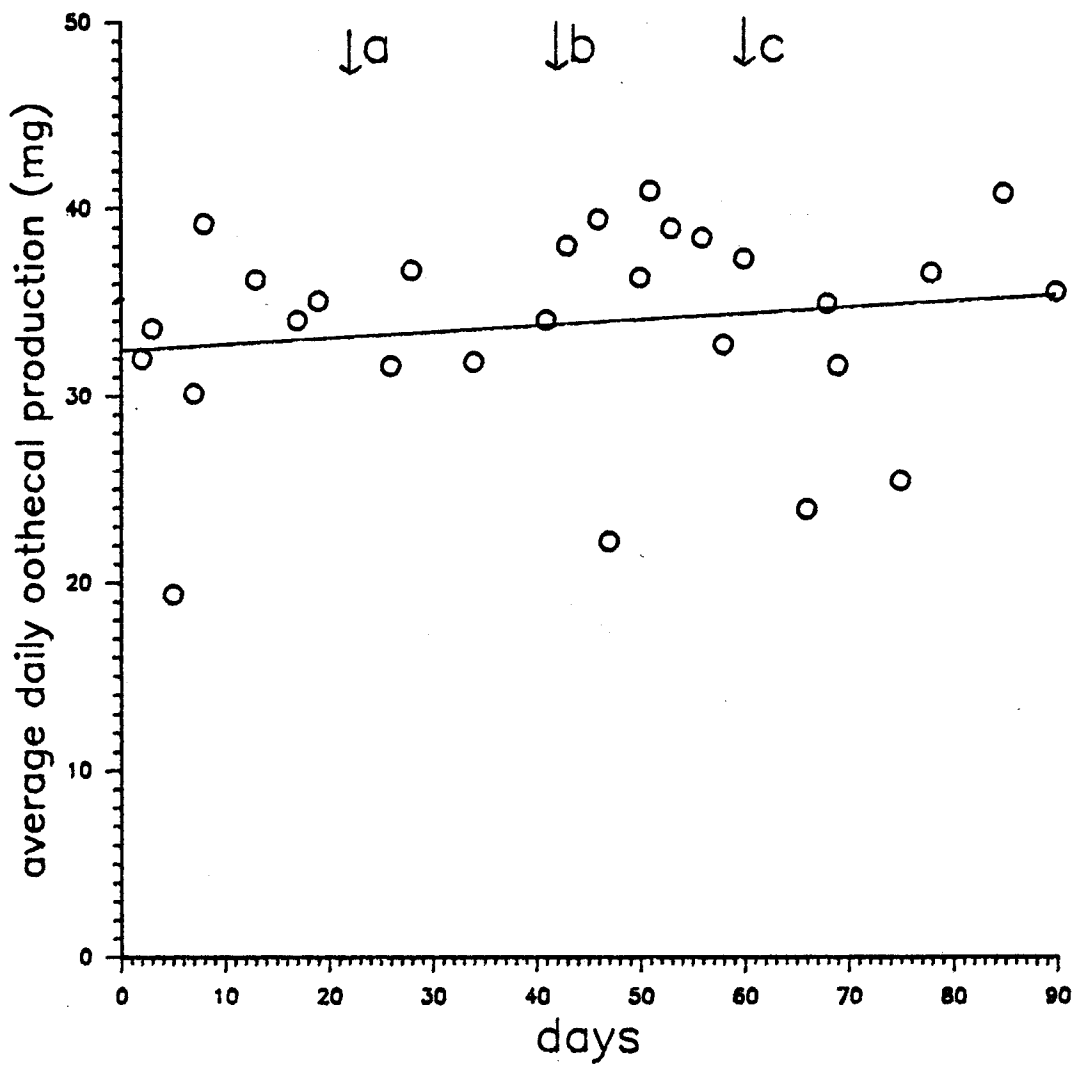


Figure 20. Cockroaches given diluted carbohydrate diet, n=10. Proportionate representation of total daily carbohydrate and protein consumption showing first order regression ( $r=0.7025$ ,  $p<0.05$ ).



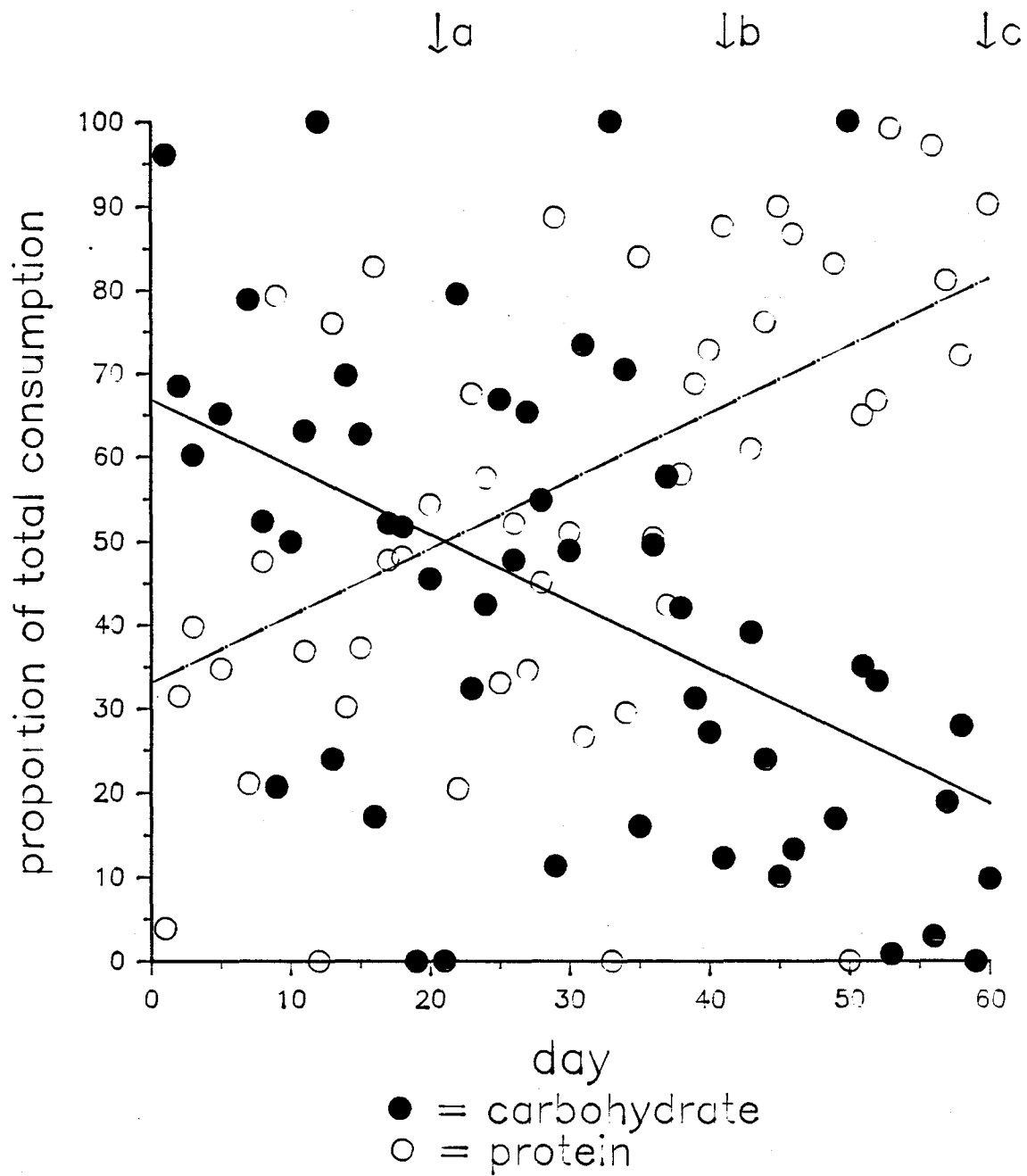


Figure 21. Cockroaches given diluted carbohydrate diet, n=10. Proportionate representation of total daily carbohydrate and protein consumption showing third order regression ( $r=0.7931$ ,  $p<0.05$ ).

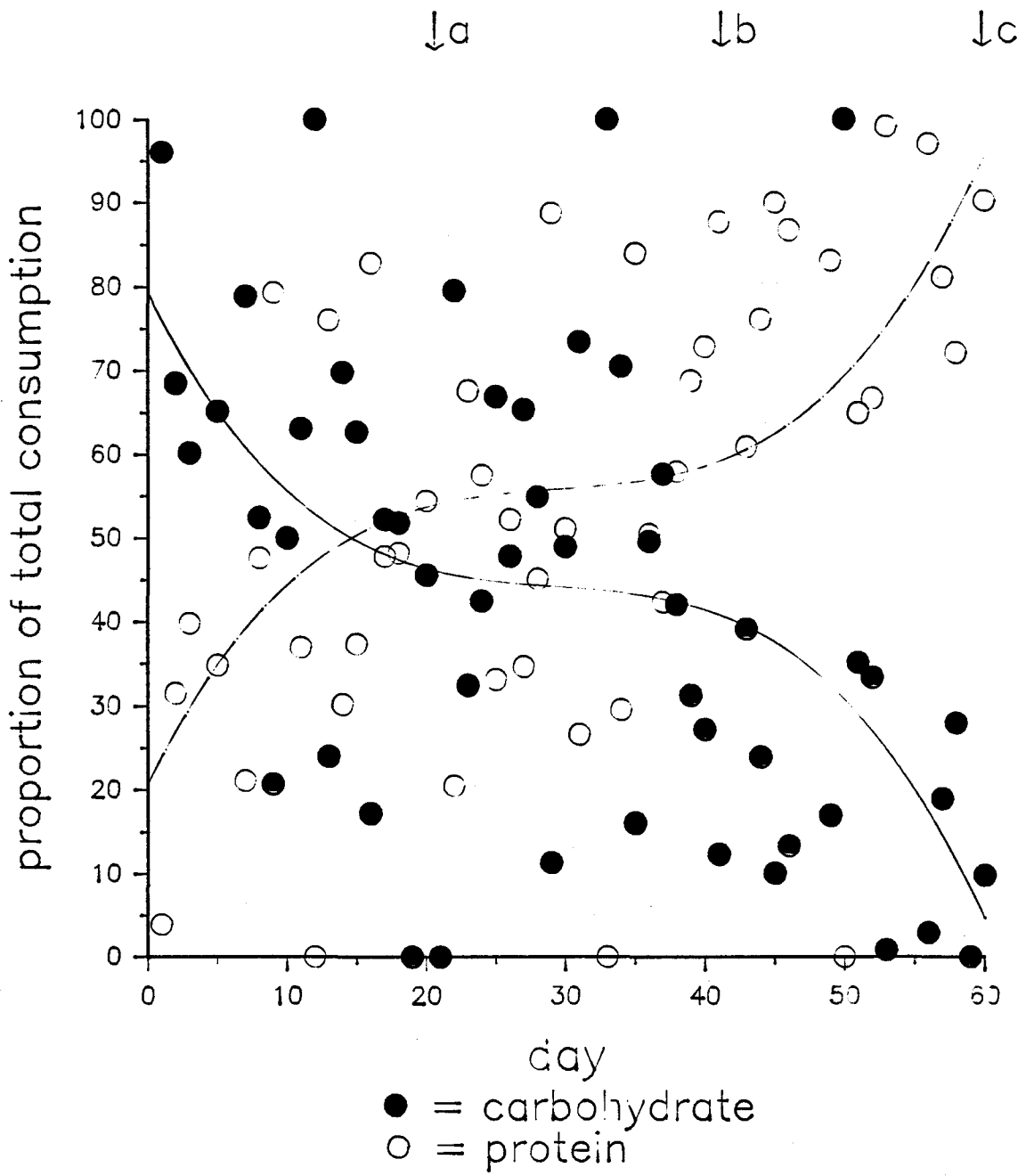


Figure 22. Cockroaches given diluted protein diet,  $n = 10$ . Daily carbohydrate consumption showing first order regression ( $r=0.5323$ ,  $p<0.10$ ).

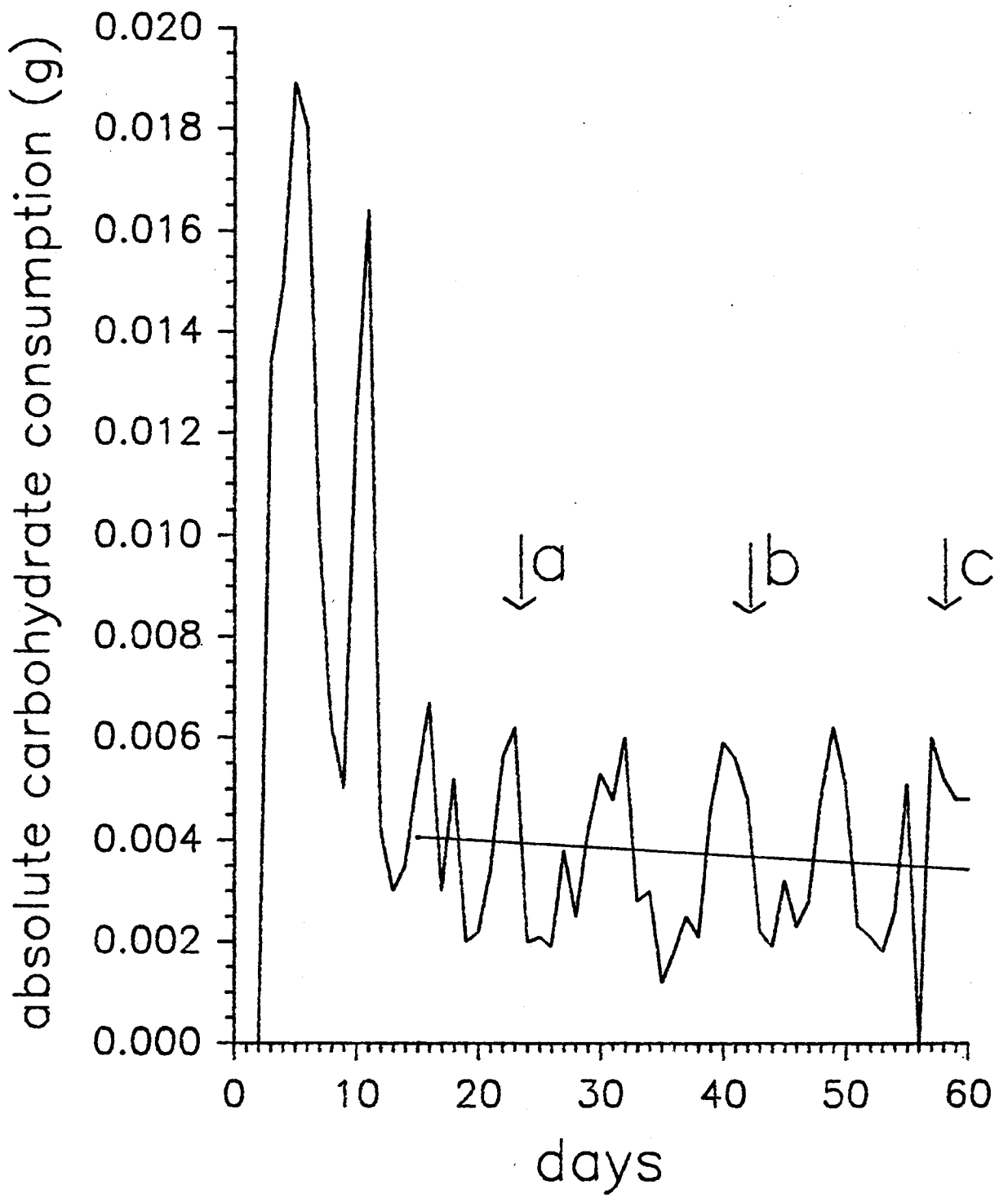


Figure 23. Cockroaches given diluted protein diet, n=10. Three day moving average analysis of daily carbohydrate consumption. First order regression shown ( $r=0.5493$ ,  $p<0.10$ ).

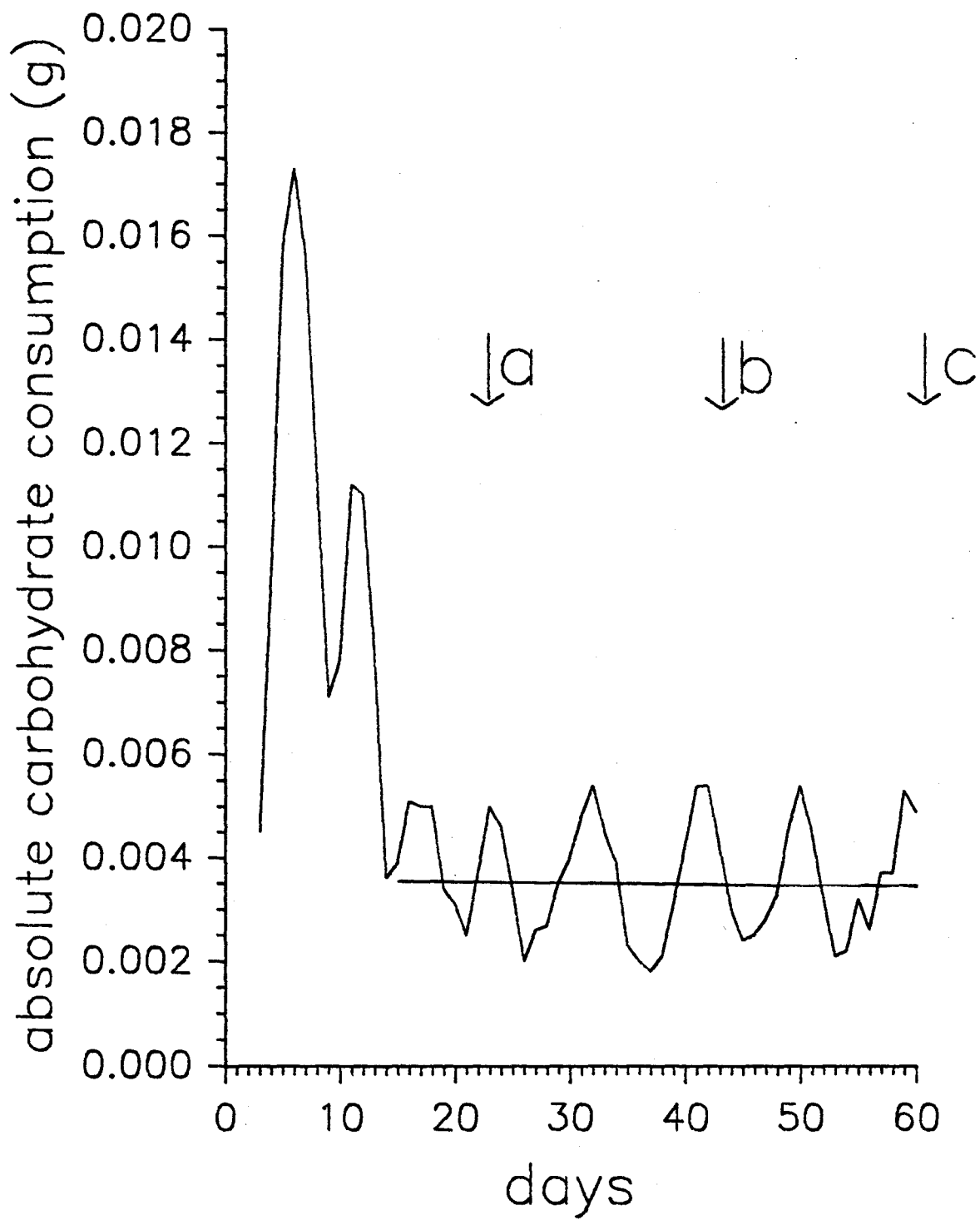


Figure 24. Cockroaches given diluted protein diet,  $n = 10$ . Daily protein consumption showing first order regression ( $r=0.5236$ ,  $p<0.10$ ).



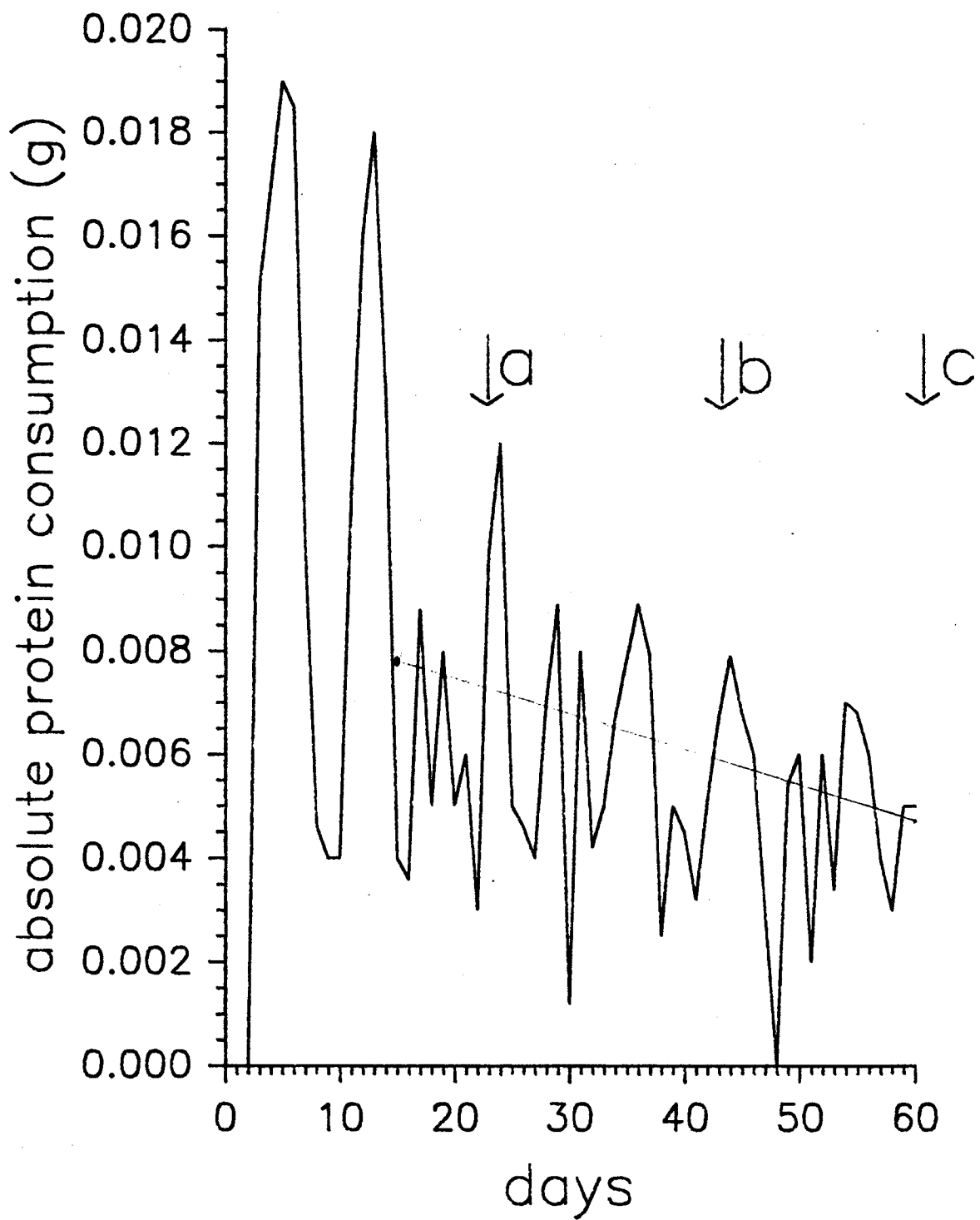


Figure 25. Cockroaches given diluted protein diet, n = 10. Three day moving average analysis of daily protein consumption. First order regression shown ( $r=0.5349$ ,  $p<0.10$ ).

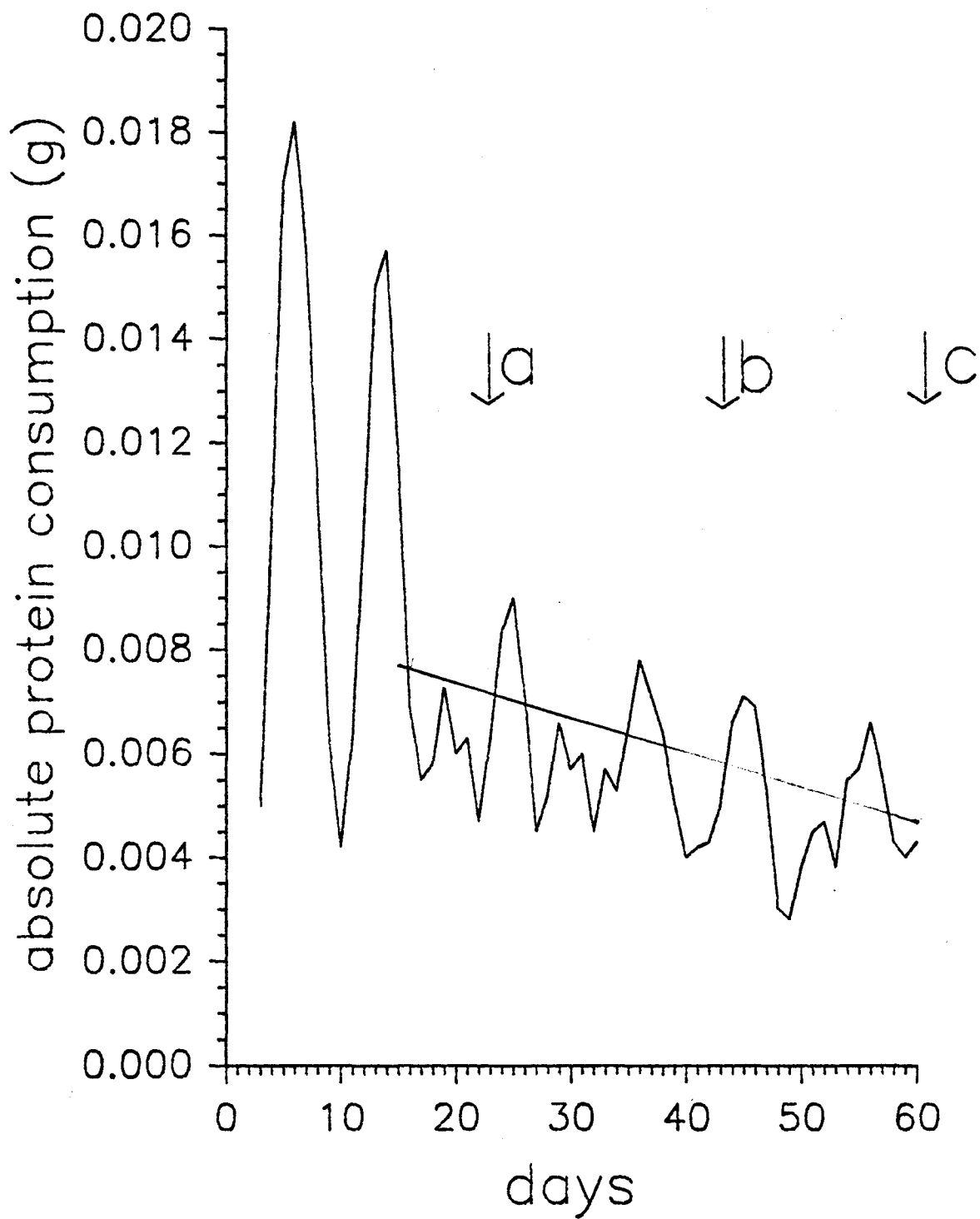


Figure 26. Cockroaches given diluted protein diet,  $n = 10$ . Total daily consumption of carbohydrate and protein showing first order regression ( $r=0.6110$ ,  $p<0.10$ ).

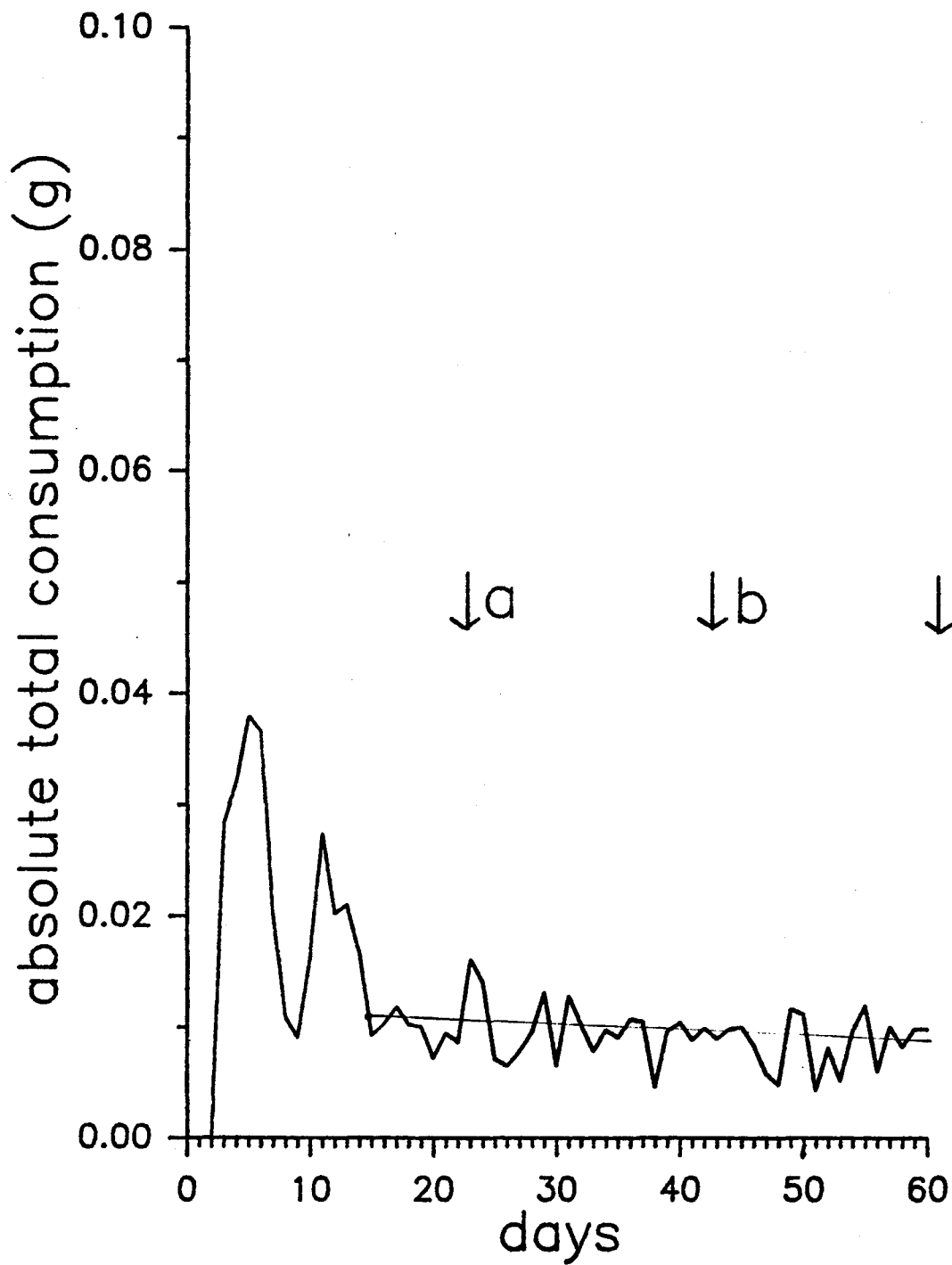


Figure 27. Cockroaches given diluted protein diet, n = 10. Total daily oothecal production.

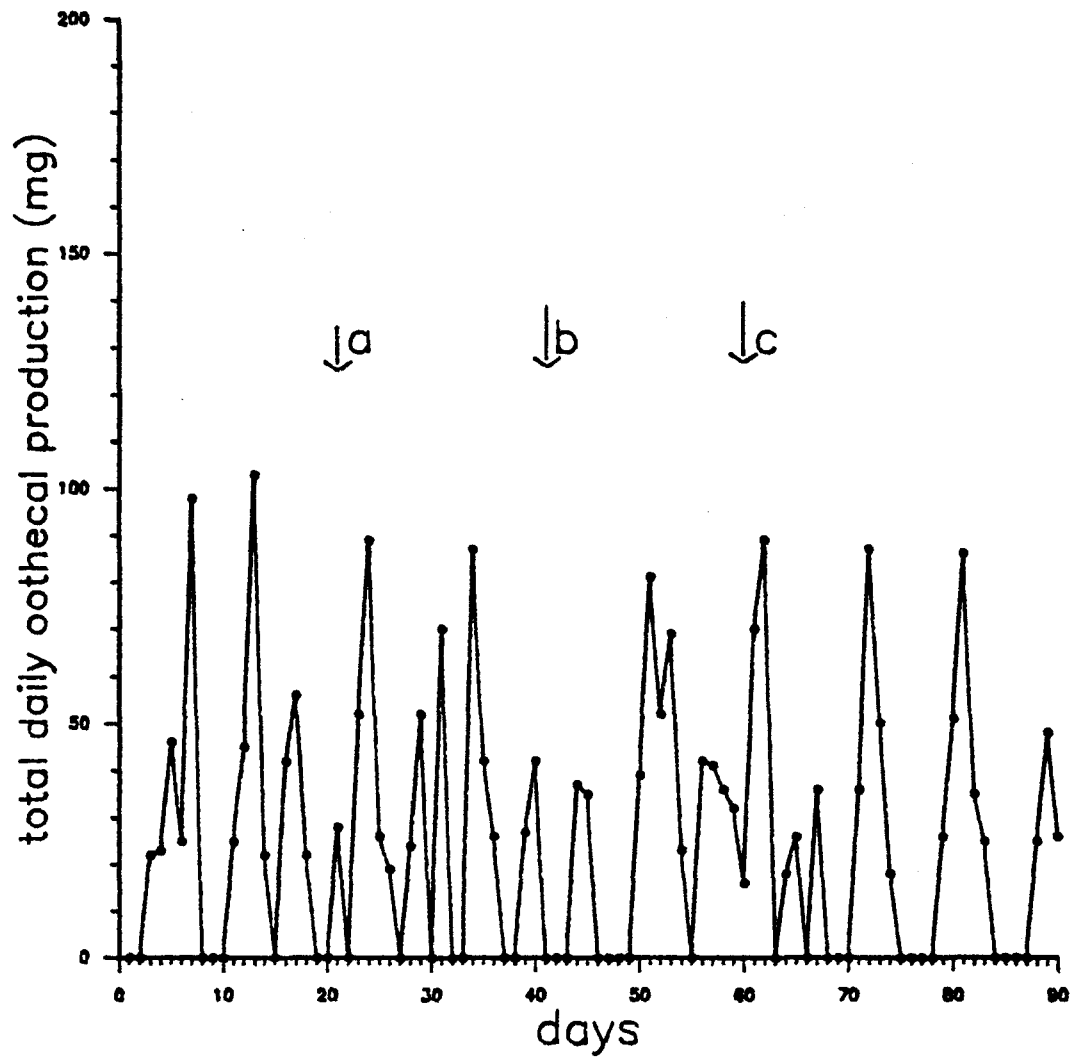


Figure 28. Cockroaches given diluted protein diet, n =10. Three day moving average analysis of total daily oothecal production.



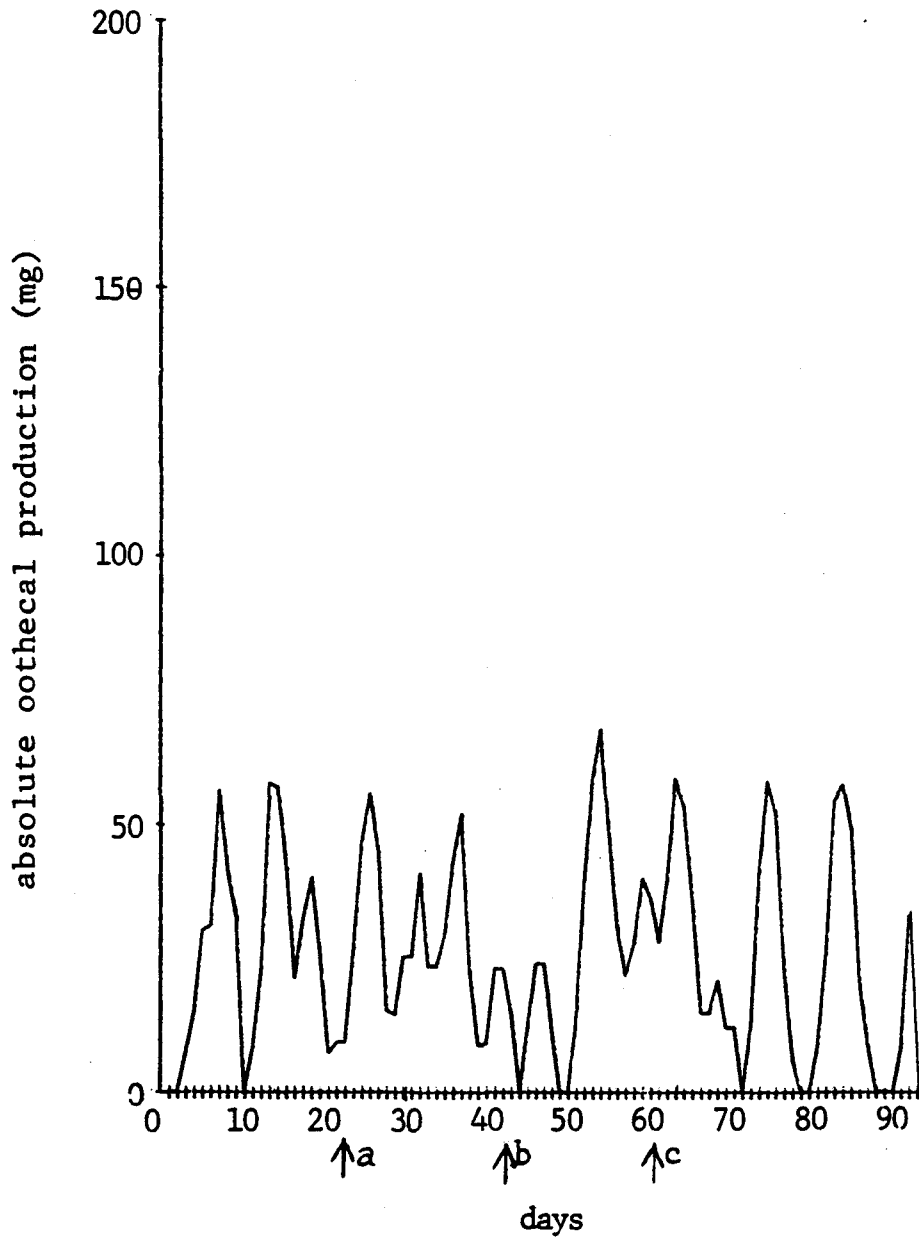


Figure 29. Cockroaches given diluted protein diet, n = 10. Average daily oothecal production showing first order regression ( $r=0.6091$ ,  $p<0.10$ ).

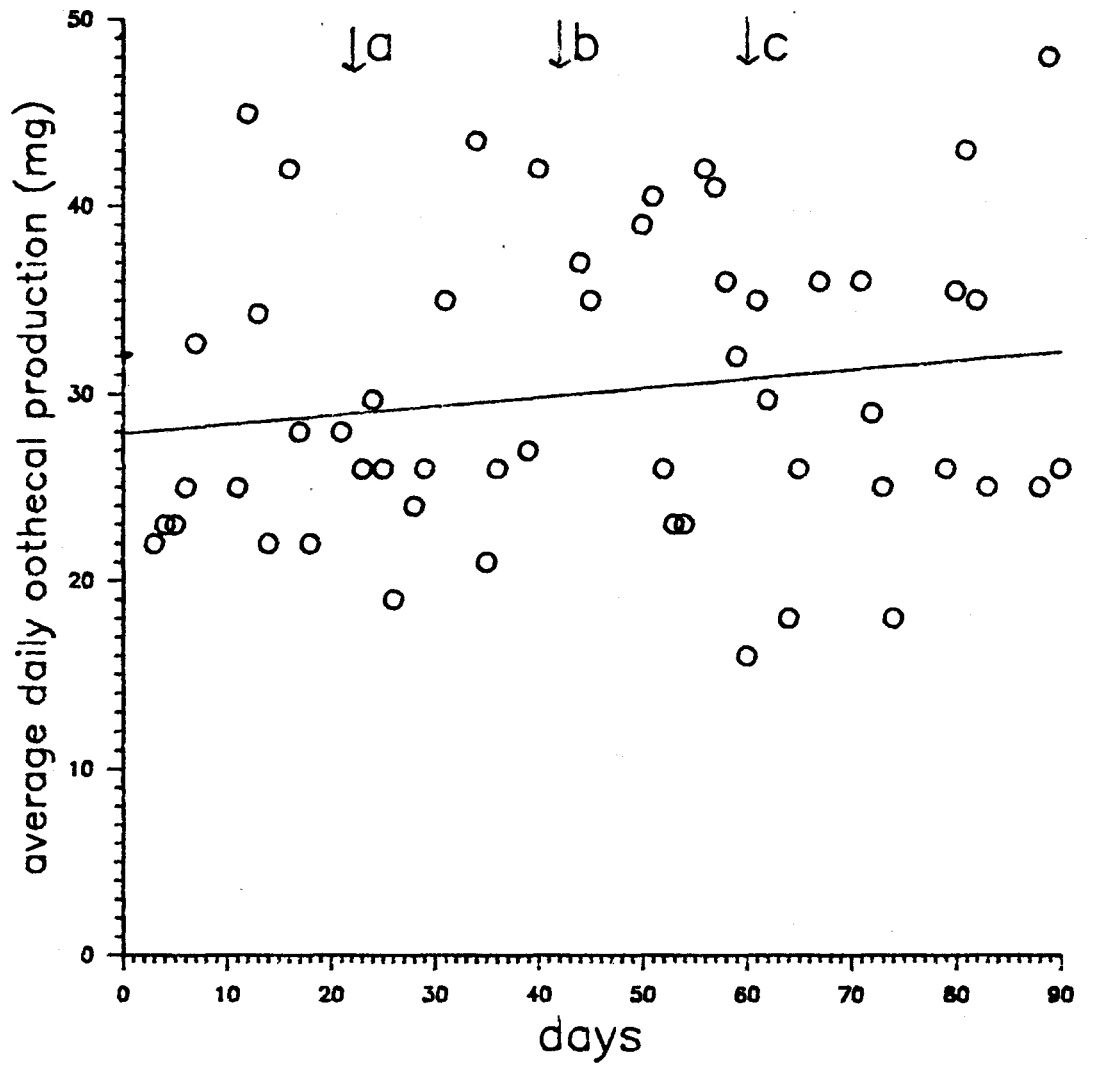


Figure 30. Cockroaches given diluted protein diet,  $n = 10$ . Proportionate representation of daily carbohydrate and protein consumption showing first order regression ( $r=0.4129$ ,  $p<0.20$ ).

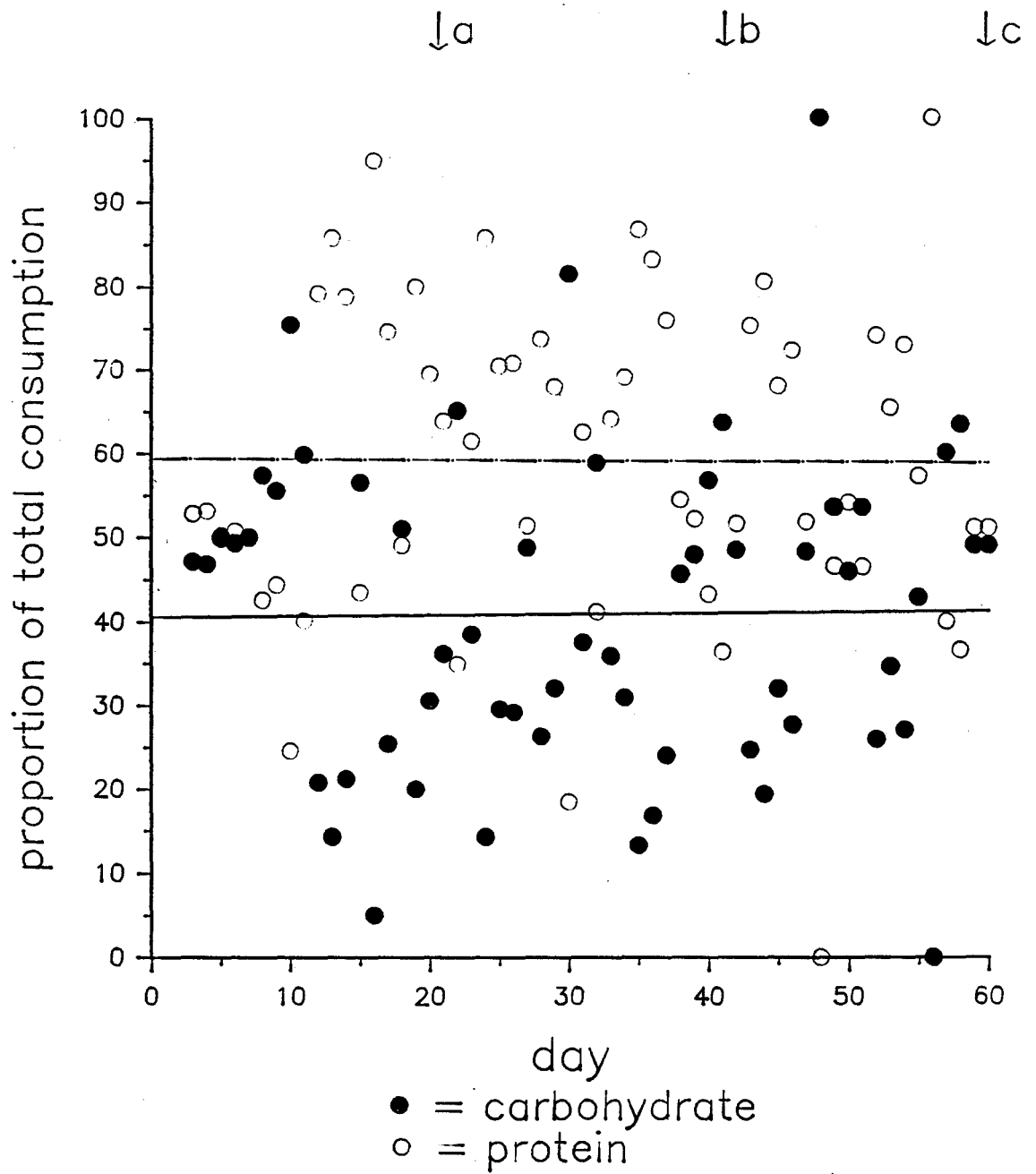


Figure 31. Cockroaches given diluted protein diet,  $n = 10$ . Proportionate representation of daily carbohydrate and protein consumption showing third order regression ( $r=0.5023$ ,  $p<0.10$ ).

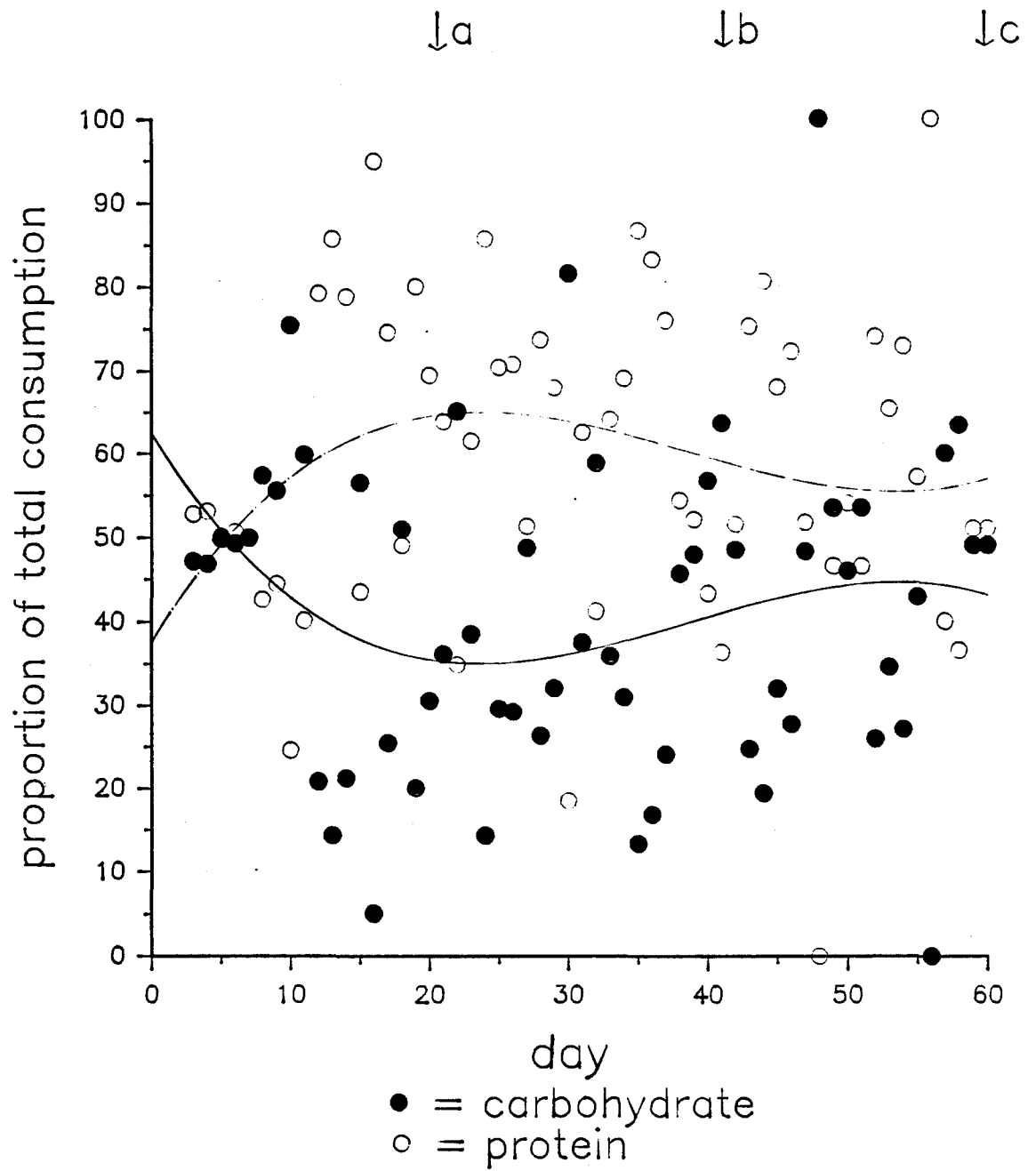


Figure 32. Comparison of average carbohydrate consumption for three treatments. Data were divided temporally according to the dilution bouts (A, B and C). Standard error indicated.



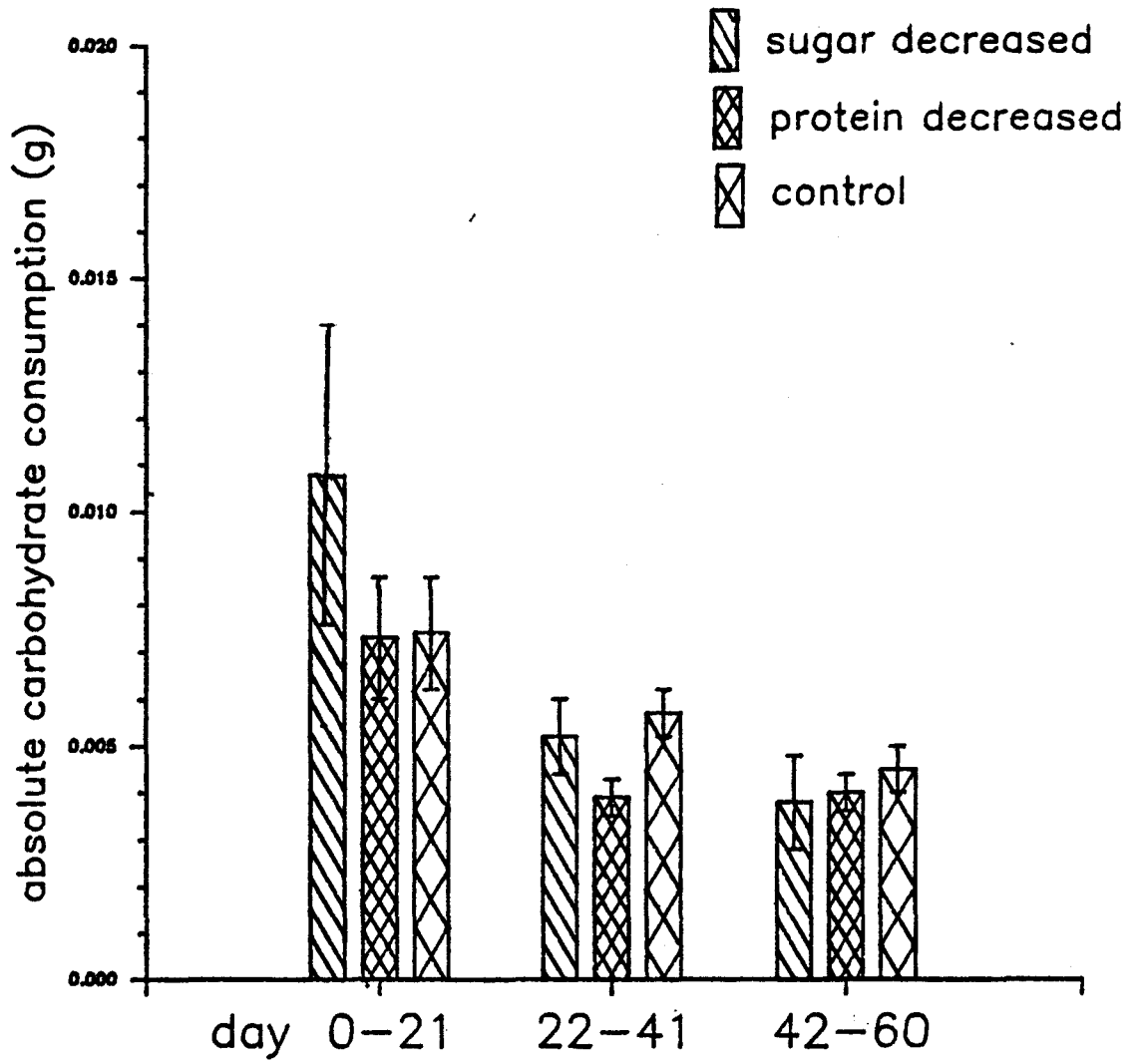


Figure 33. Comparison of average protein consumption for three treatments. Data were divided temporally according to the dilution bouts (A, B and C). Standard error indicated.

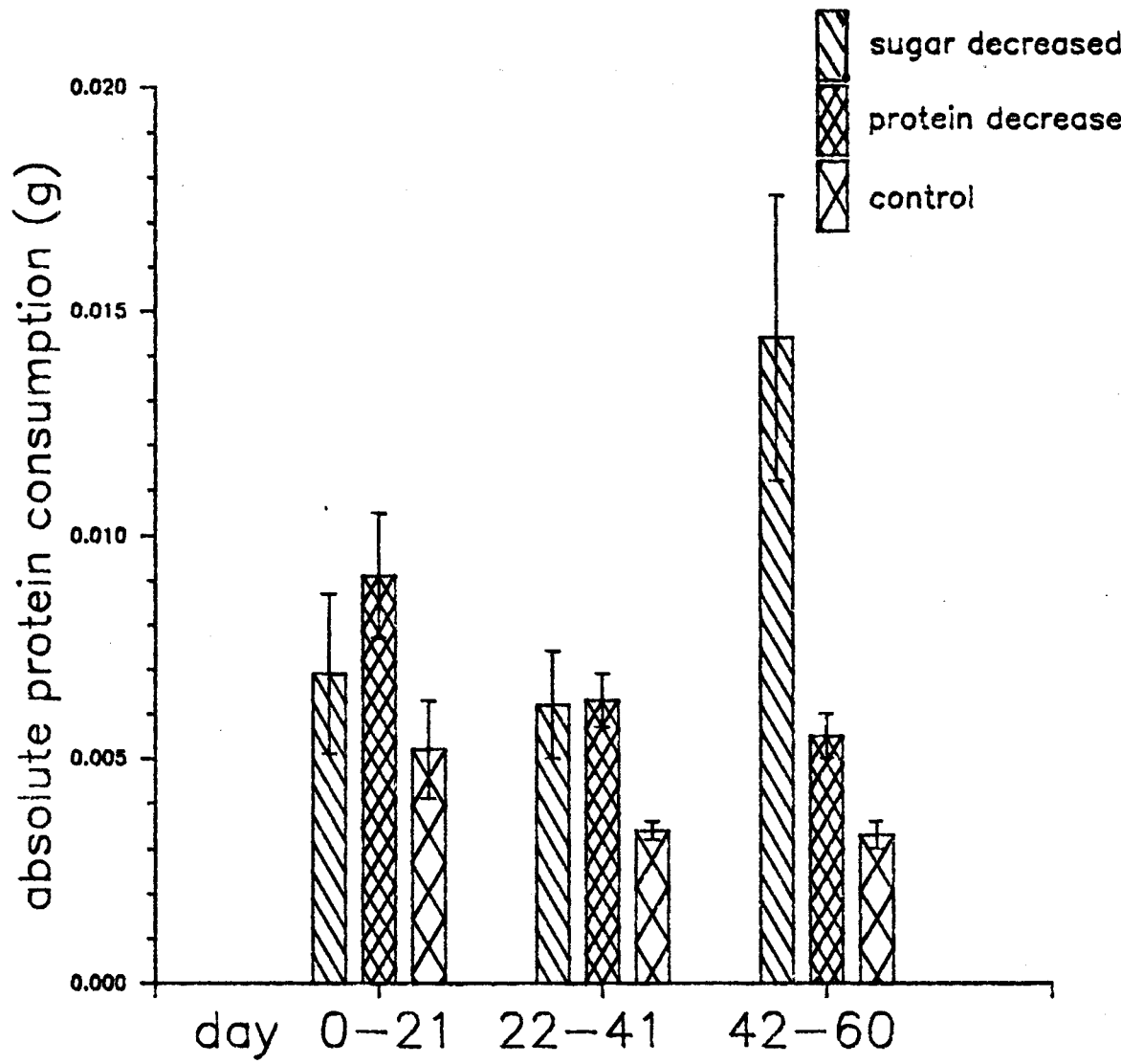


Figure 34. Comparison of average oothecal production for three treatments. Data were divided temporally according to the dilution bouts (A, B and C). Standard error indicated.

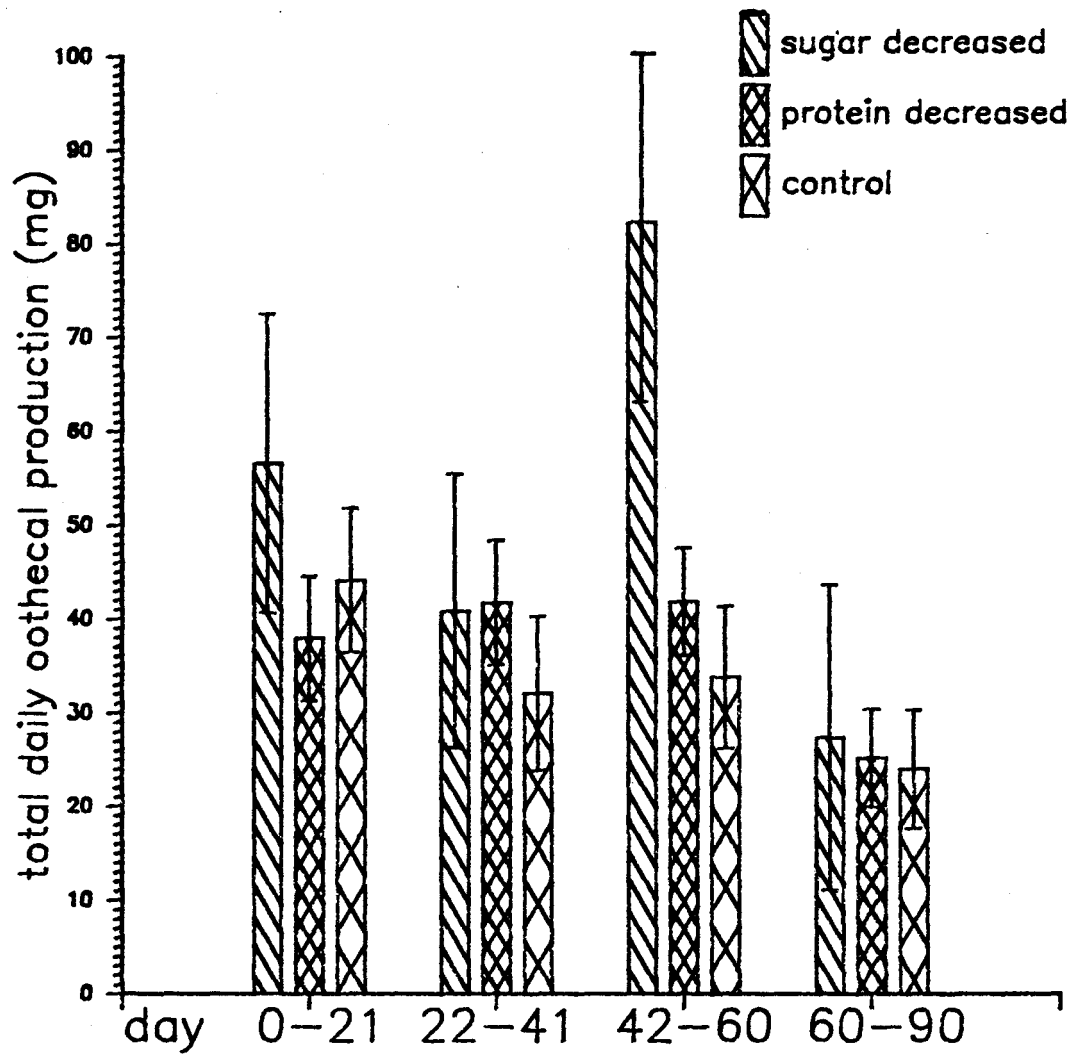


Figure 35. Mean time spent feeding according to food type. Food quality increased from food type one to five. ( $n = 5$ ). Standard error indicated.

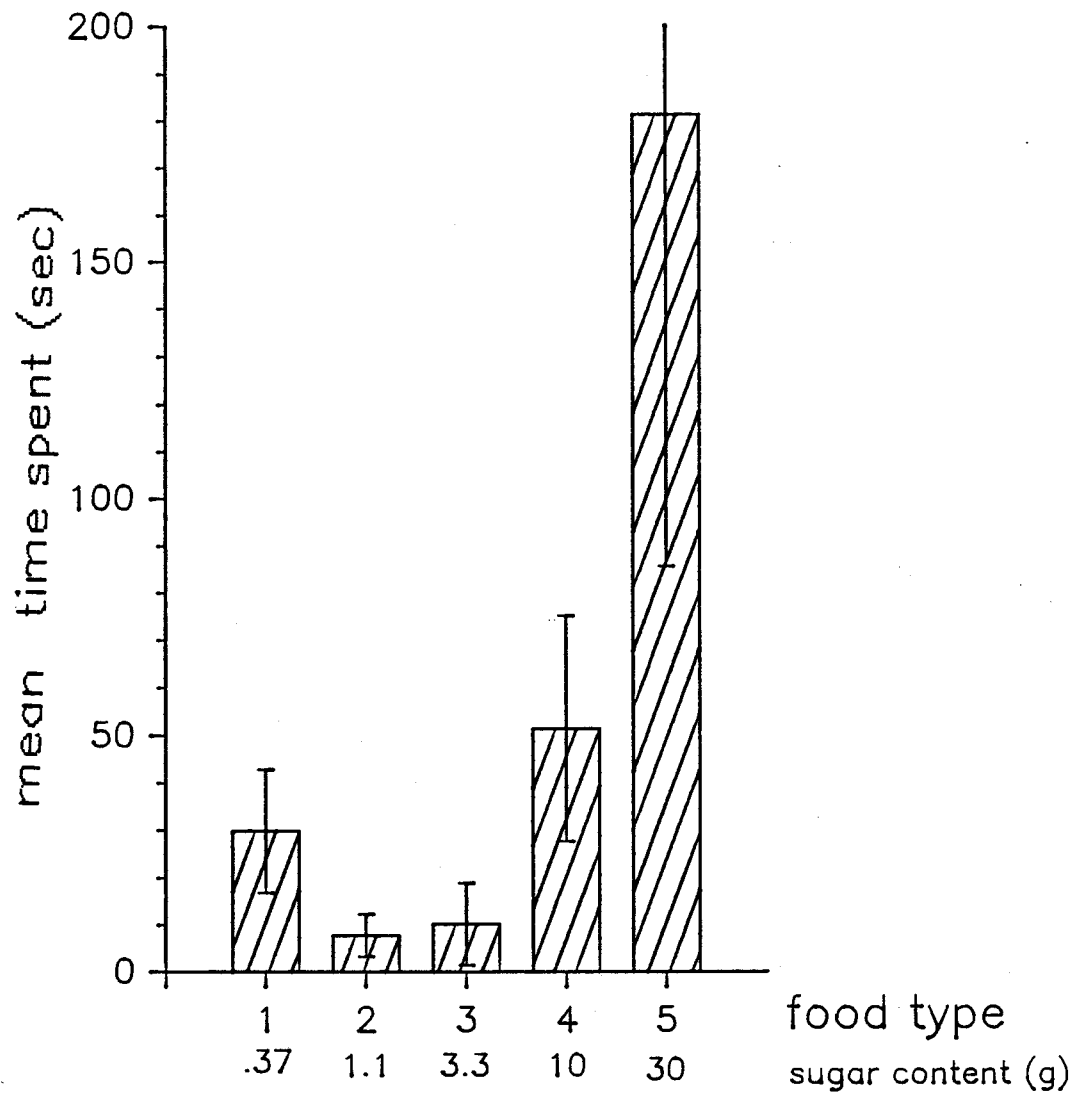


Figure 36. Time spent feeding on alternate foods: Equal, Sugar Twin or blank (n = 6). Standard error indicated.



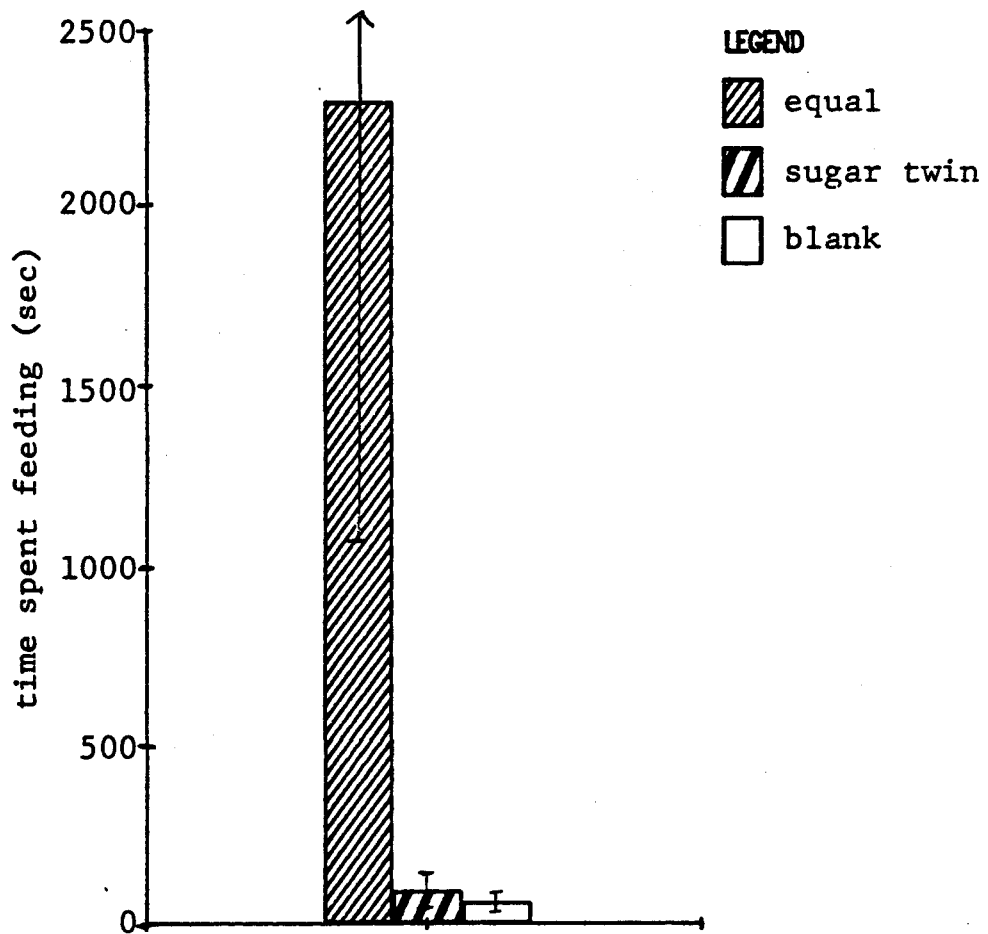


Figure 37. Time spent feeding on alternate foods:  
Equal, sugar or blank (n = 6). Standard  
error indicated.

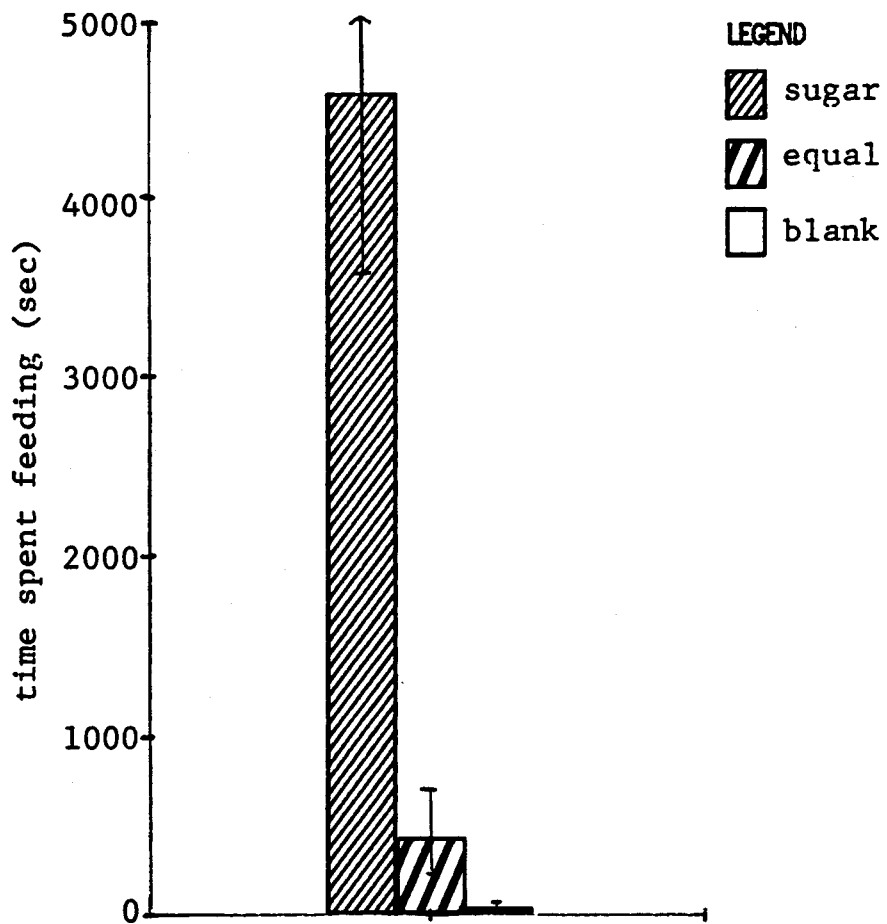


Figure 38. Time spent feeding on alternate foods: Kirsch, Bay Leaf or blank (n = 6). Standard error indicated.

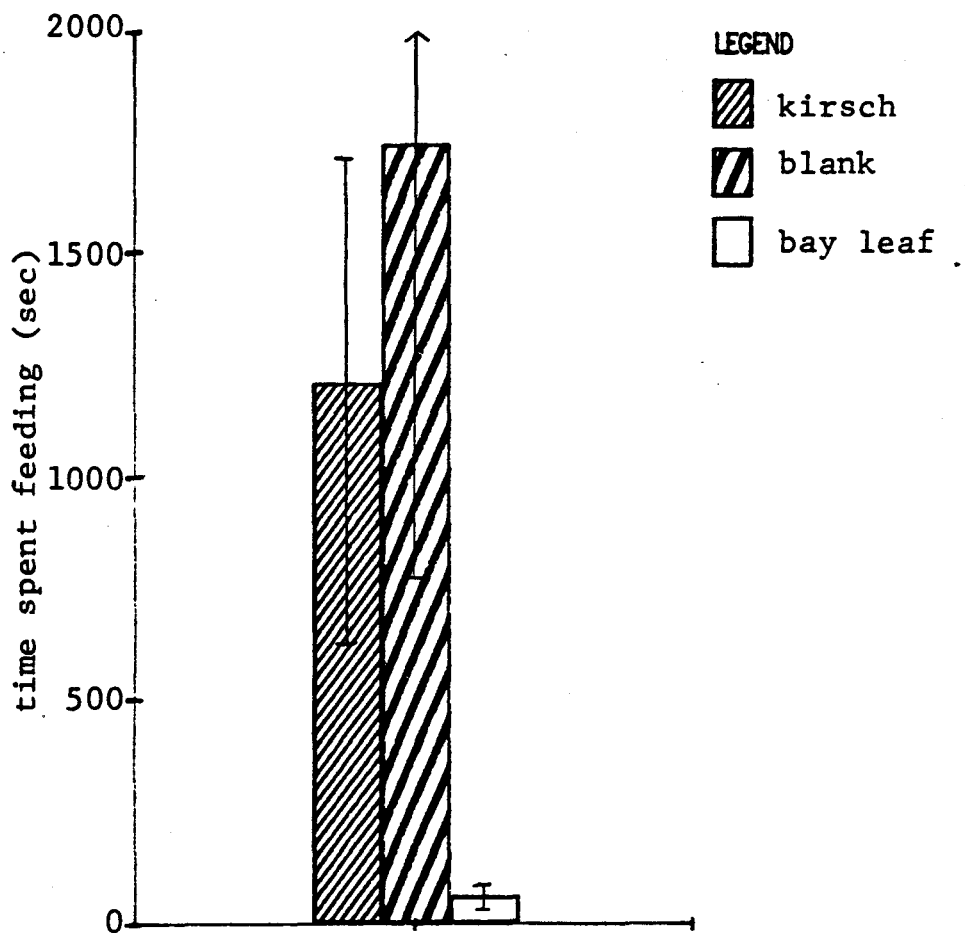


Figure 39. Time spent feeding on alternate foods: Kirsch and Equal, Bay Leaf and sugar or blank (n = 6). Standard error indicated.

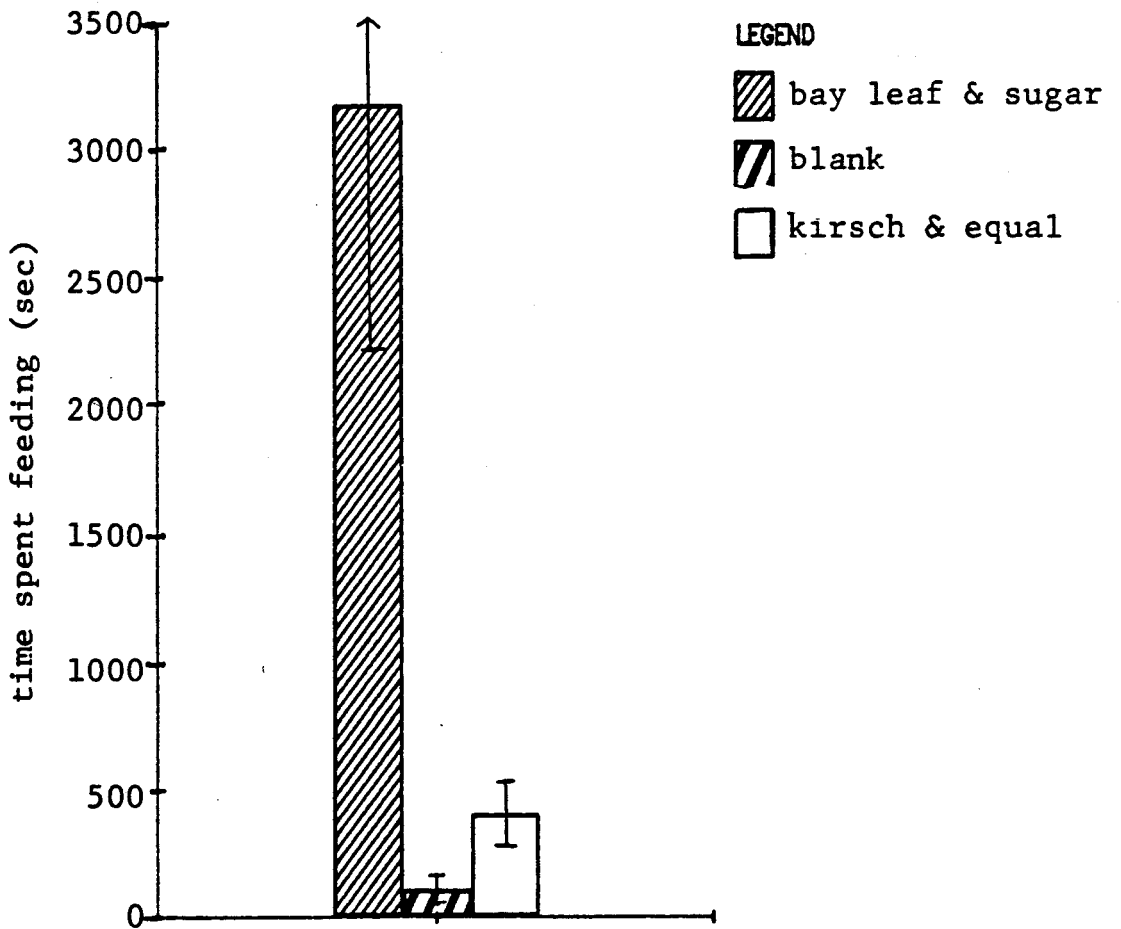


Figure 40. Time spent feeding on alternate foods: Amino acid mix with no scent/taste cues, amino acid mix with kirsch or blank (n = 6). Standard error indicated.



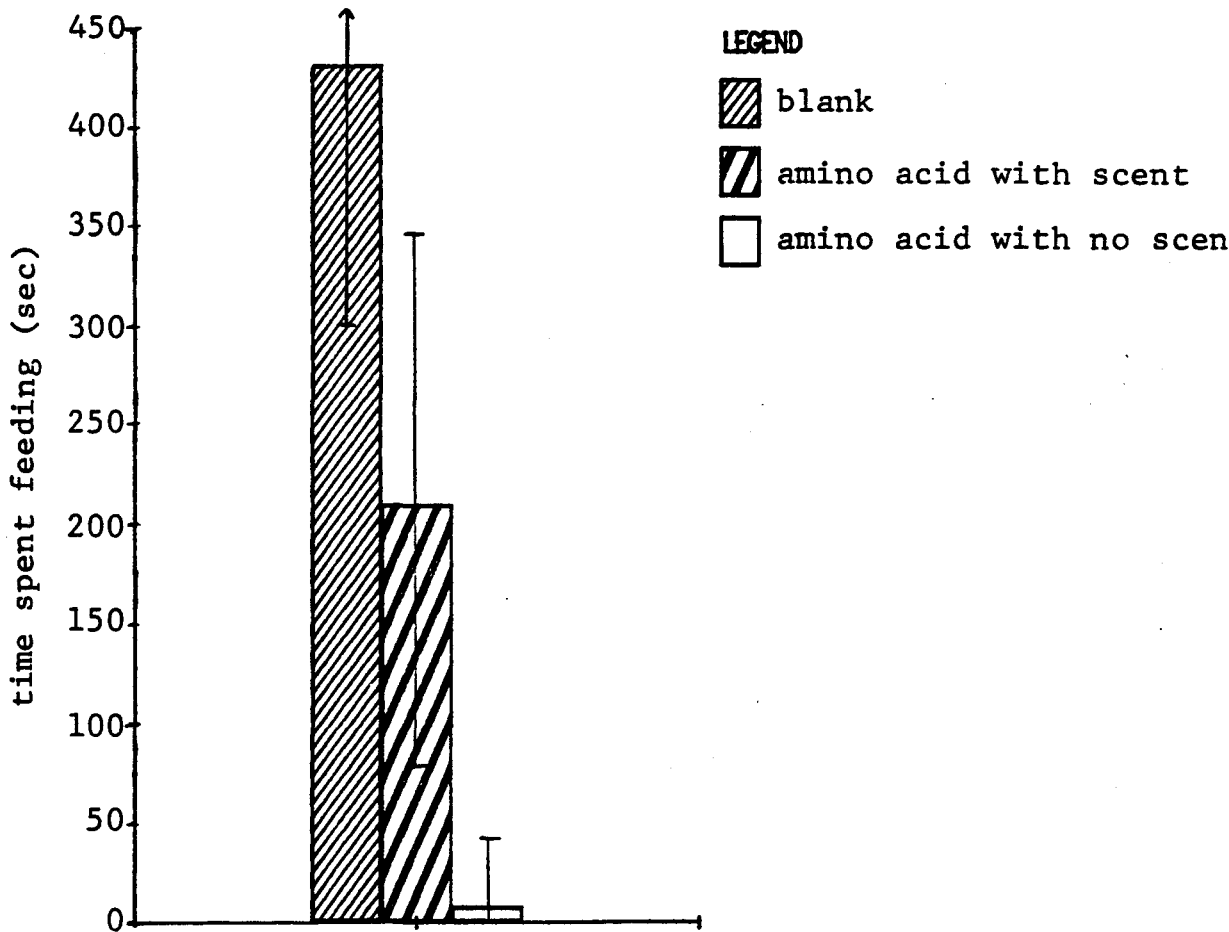


Figure 41. Palatability index of all foods tested in scent/taste/nutrient experiment. Food types are represented in the triplets as they were offered.

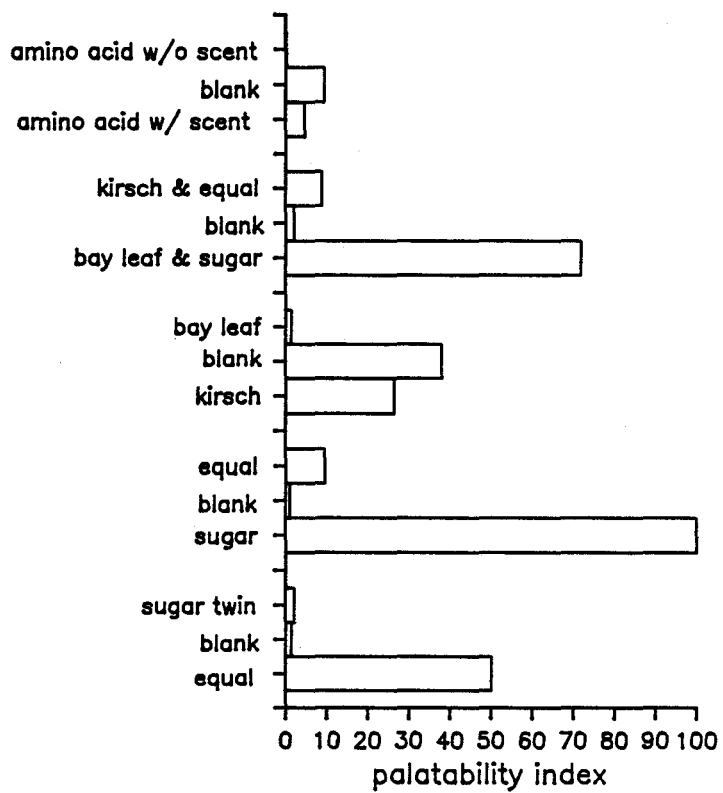


Figure 42. Food consumption of cockroaches (n = 10) acclimated to a fully balanced diet (PC). Standard error indicated.

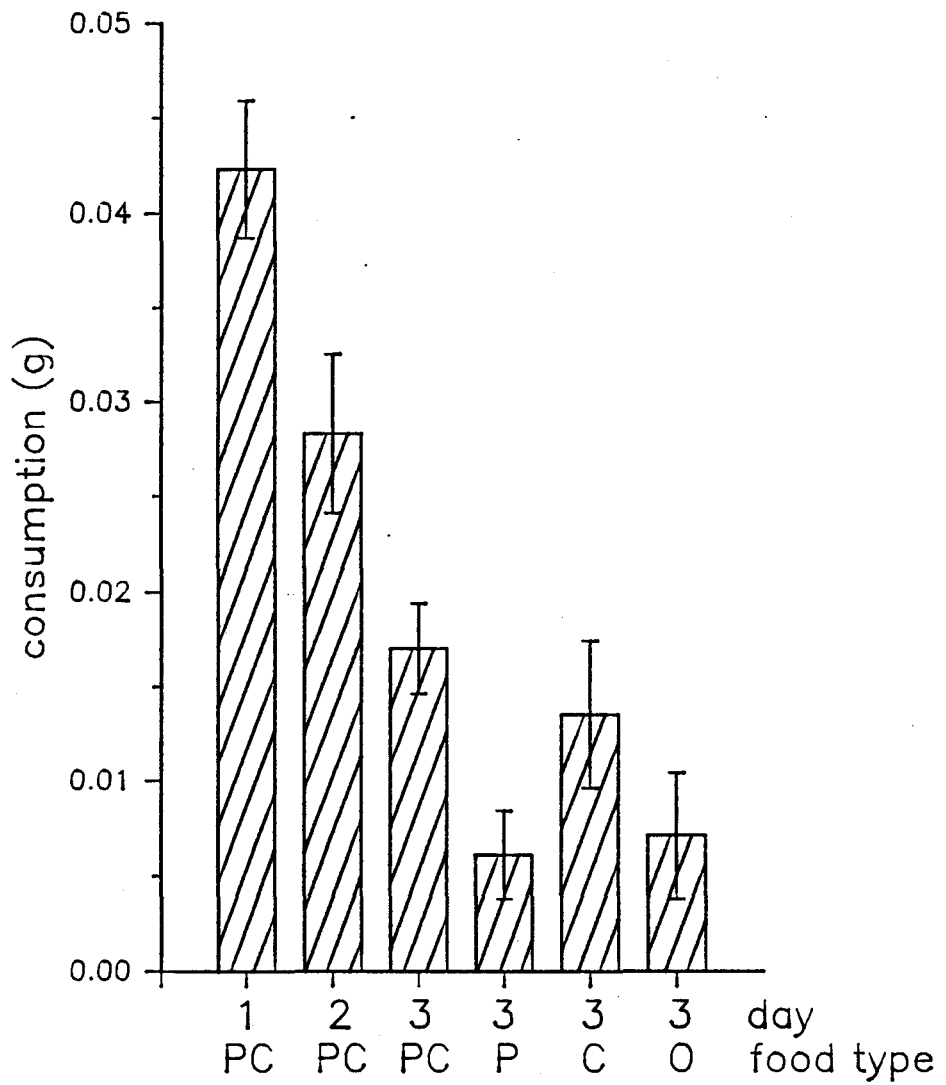


Figure 43. Food consumption of cockroaches (n = 10) acclimated to a carbohydrate deficient diet (P). Standard error indicated.

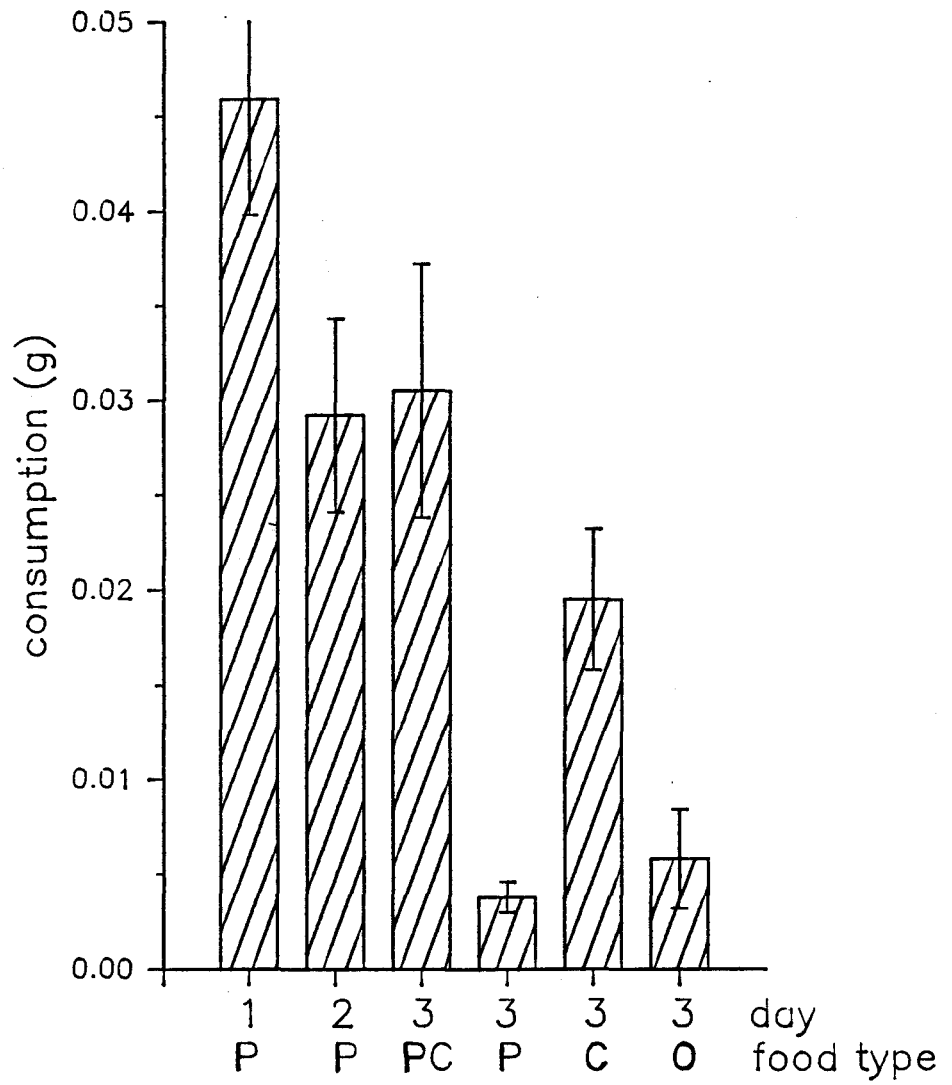


Figure 44. Food consumption of cockroaches (n = 10) acclimated to a protein deficient diet (C). Standard error indicated.



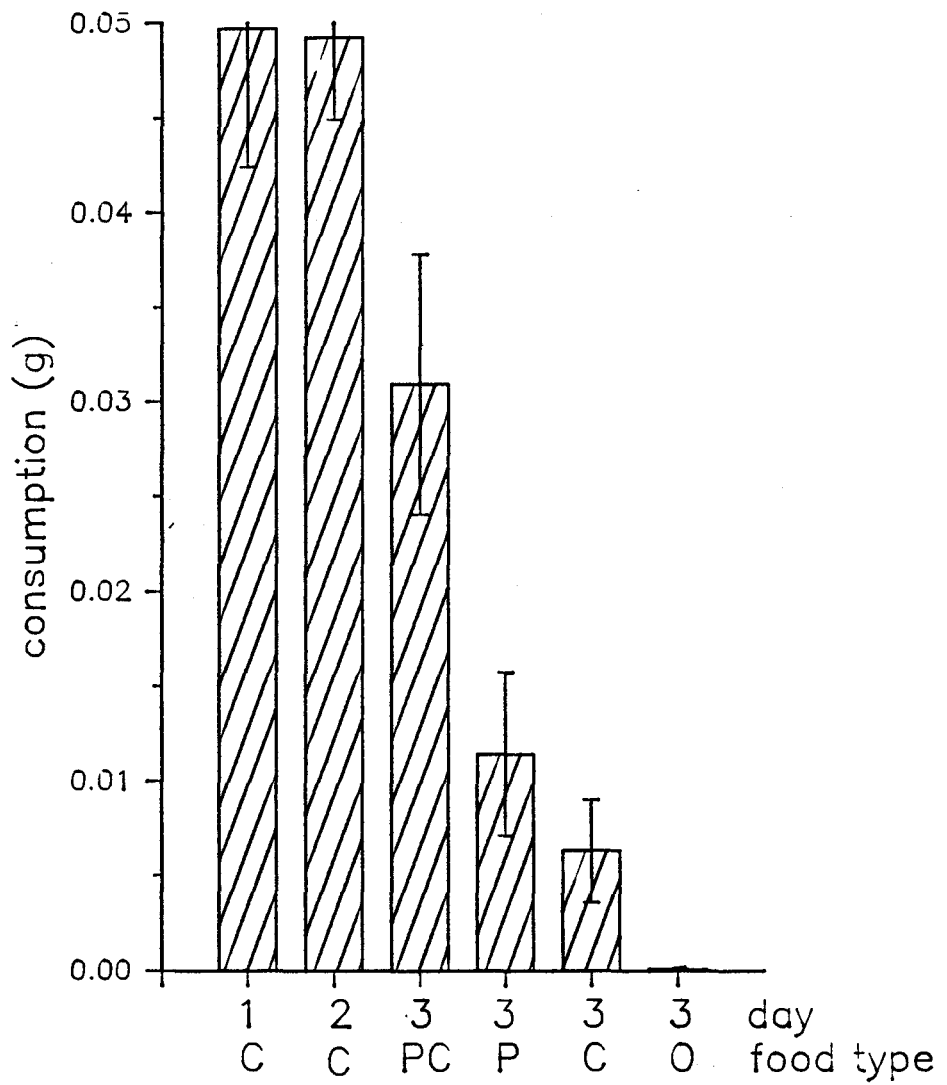


Figure 45. Food consumption of cockroaches (n = 10) acclimated to a diet deficient of carbohydrates and protein (O). Standard error indicated.

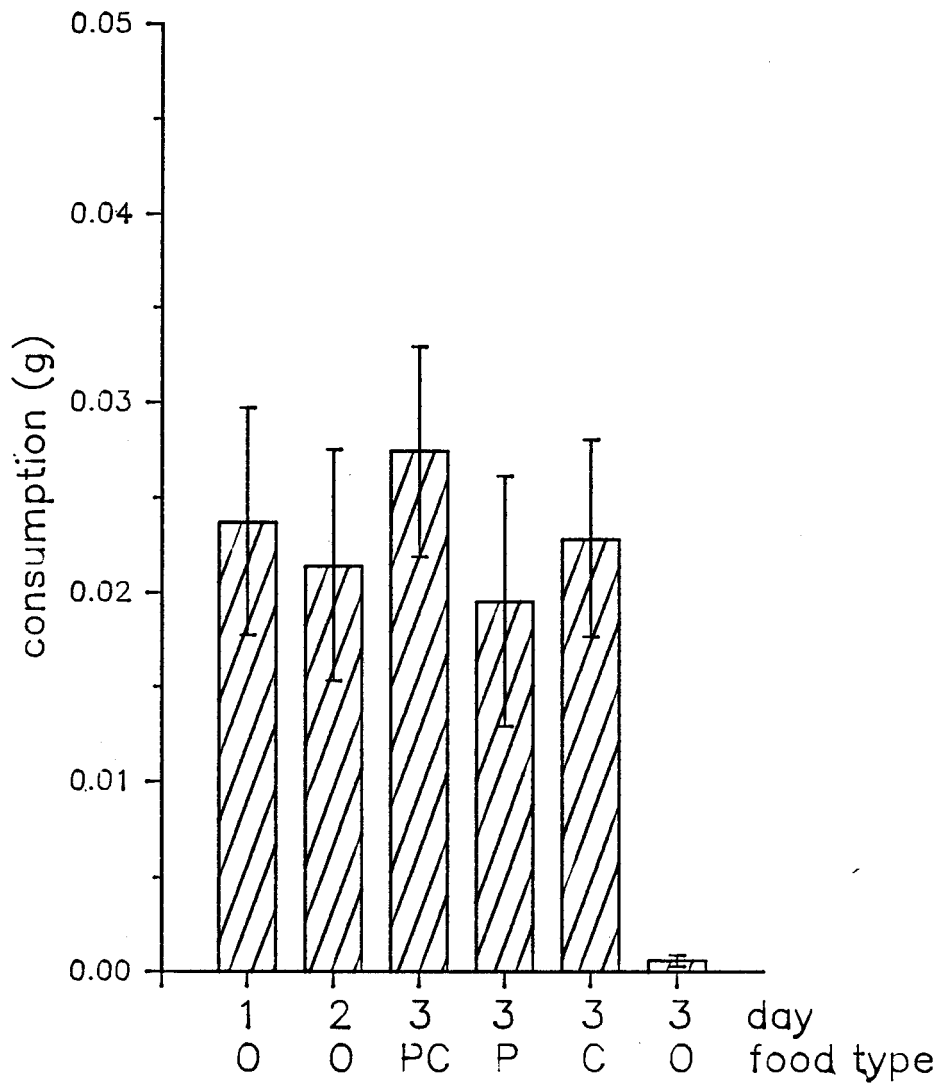
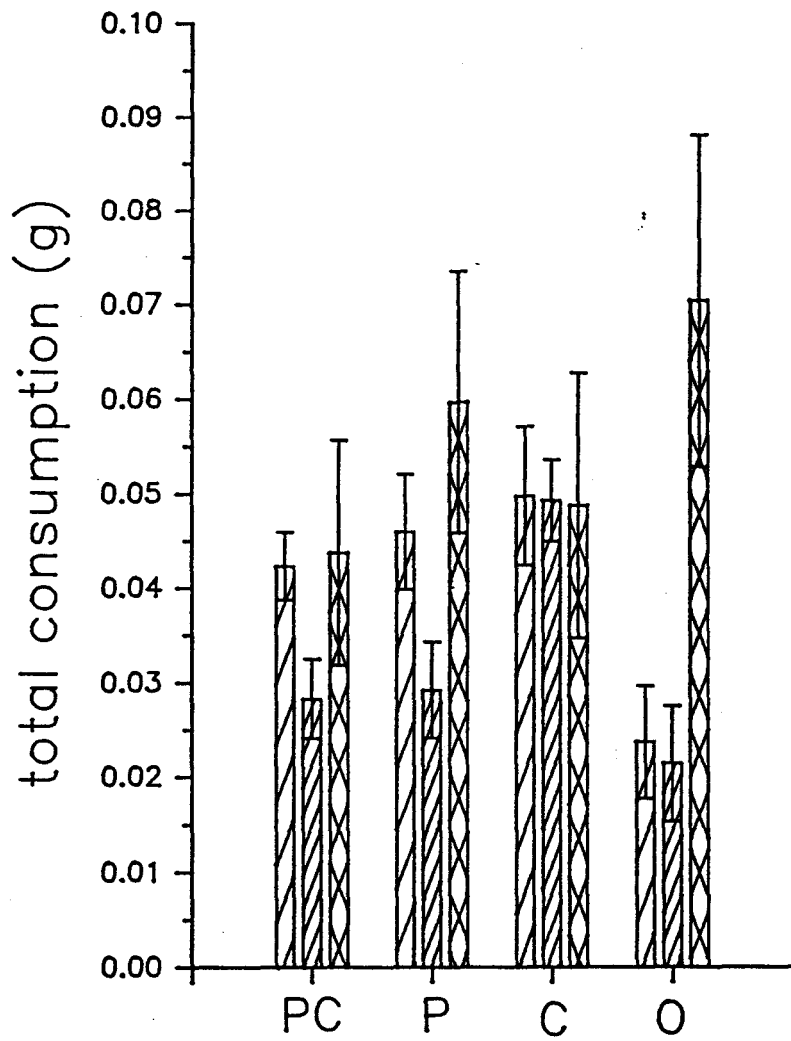





Figure 46. Total daily consumption of cockroaches (n = 10) acclimated to different food types. Standard error indicated.



 = day 1  
 = day 2  
 = day 3

Appendix 1. Diet recipes (all masses in grams).

Ingredient	Diet Name					
	Complete	Blank I	Blank II	Protein	Carbohydrate	Vitamin Mix
Cellulose Powder	22.6	82.6	82.6	52.6	52.6	82.6
Agar	11.7	11.7	11.7	11.7	11.7	11.7
Wesson Salt Mix	3.5	0	3.5	3.5	3.5	0
Tegosept Solution	*	*	*	*	*	*
Citric Acid	0.4	0	0.4	0.4	0.4	0.4
Sorbic Acid	0.2	0	0.2	0.2	0.2	0.2
Ascorbic Acid	1.6	0	1.6	1.6	1.6	1.6
Vitamin B-Complex	0.04	0	0.04	0.04	0.04	0.04
Casein	15	0	0	15	0	0
Soy Oil	5	0	0	5	0	0
Soy Meal	10	0	0	10	0	0
Sucrose	20	0	0	0	20	0
Corn Starch	10	0	0	0	10	0
Water	&	&	&	&	&	&
Other Additives	-	-	-	-	-	-

\* 5 drops / 100g in all diets

&amp; 3 mL / 100 g in all diets

## Appendix 1 (continued)

Ingredients	Diet Name					
	Equal	Sugar Twin	Sugar	Bay Leaf	Kirsch	Amino Acids
Cellulose Powder	82.6	82.6	82.6	82.6	82.6	82.6
Agar	11.7	11.7	11.7	11.7	11.7	11.7
Wesson Salt Mix	0	0	0	0	0	0
Tegosept Solution	*	*	*	*	*	*
Citric Acid	0	0	0	0	0	0
Sorbic Acid	0	0	0	0	0	0
Ascorbic Acid	0	0	0	0	0	0
Vitamin B-Complex	0	0	0	0	0	0
Casein	0	0	0	0	0	0
Soy Oil	0	0	0	0	0	0
Soy Meal	0	0	0	0	0	0
Sucrose	0	0	0	0	0	0
Corn Starch	0	0	0	0	0	0
Water	&	&	&	&	&	&
Other Additives	10 g Equal	10 g Sugar Twin	-	4 g ground bay leaf	10 drops Kirsch Conc.	Amino Acid Mix @

\* 5 drops / 100 g in all diets

& 3 mL / 100 g in all diets

@ Amino Acid Mix Ingredients: (grams per gram of diet)

arginine 0.0174, lysine 0.0146, leucine 0.0262, histidine 0.0079, glutamic acid 0.1997, tyrosine 0.0087, phenylalanine 0.0197